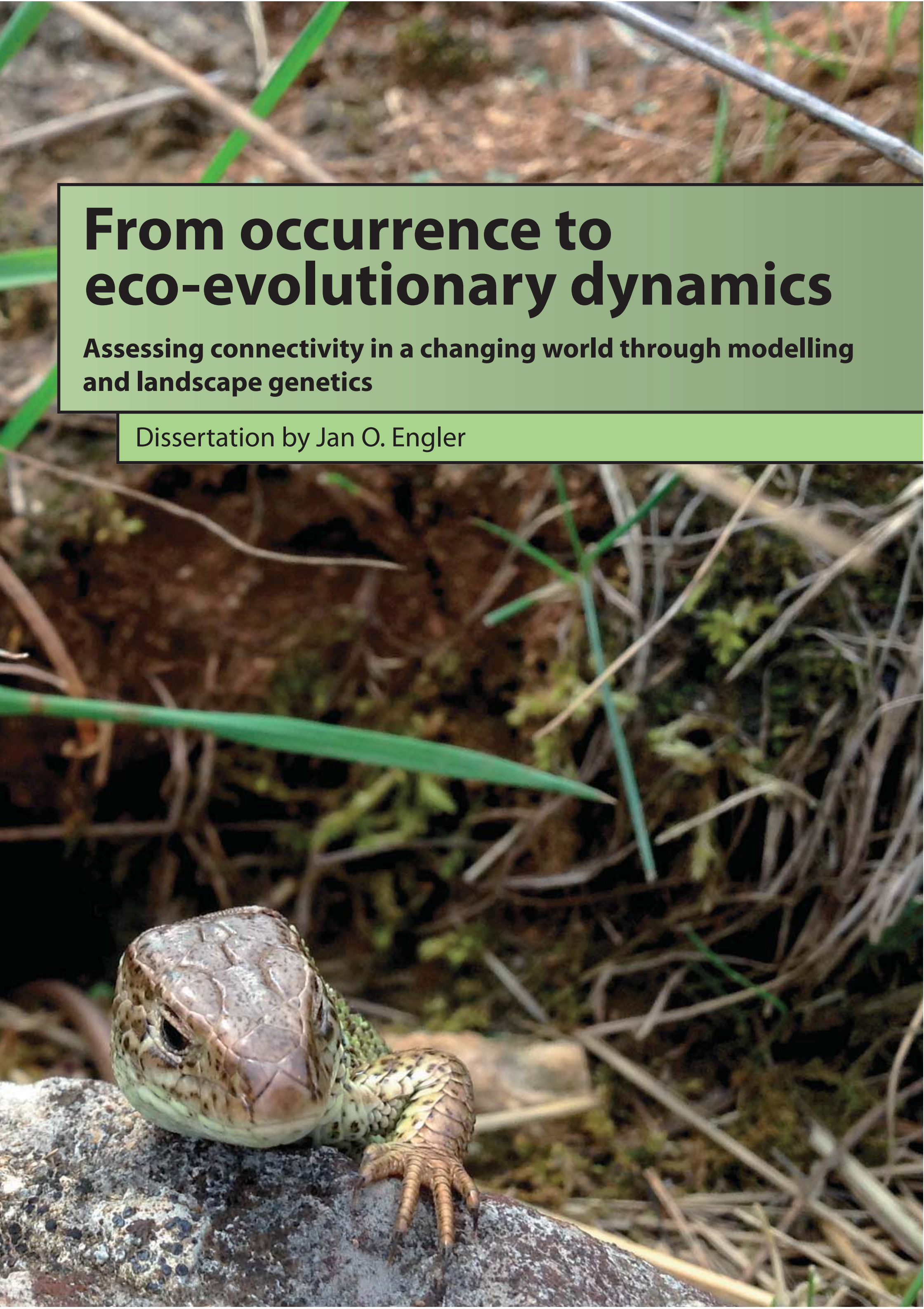

From occurrence to eco-evolutionary dynamics

Assessing connectivity in a changing world through modelling and landscape genetics

Dissertation by Jan O. Engler

FROM OCCURRENCE TO ECO-EVOLUTIONARY DYNAMICS: ASSESSING CONNECTIVITY IN A CHANGING WORLD THROUGH MODELING AND LANDSCAPE GENETICS

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Bonn, den 18.11.2015

Jan O. Engler

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With references, with summaries in Englisch and German

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AIMS & SCOPE

"A journey of a thousand miles begins with a single step. Dissertations begin with a single word."

— ALESHIA TAYLOR HAYES AS MODIFIED FROM LAOZI

Aims & Scope

Climate change and the intensification of human landuse are generally accepted as leading factors for global biodiversity loss (Bellard et al. 2012; Devictor et al. 2012). However, considering both factors in synergy, the effect of species loss could be even higher (Travis 2003; Hof et al. 2011) and go way beyond what we expected from climate change alone (Parmesan & Yohe 2003; Thomas et al. 2004).

Habitat loss and fragmentation can hamper the exchange among populations or even prevent it. This can lead to negative demographic and genetic effects for the affected populations (Templeton et al. 1990; Keyghobadi 2007). These effects, imprinted in genes, range from a decrease of genetic diversity (e.g., Habel & Schmitt 2012) and inbreeding (Andersen et al. 2004; Zachos et al. 2007), up to the extinction of affected populations (Petterson 1985).

To counteract these effects, and to develop more efficient conservation efforts, knowledge on population connectivity is mandatory. This thesis aims to contribute to this knowledge by linking tools from different disciplines for their application in conservation planning and spatial ecology. Known as *potential connectivity models* (PCMs), they will cover two main parts of the thesis:

Part A: Generating additional information about fine-scale and spatially explicit exchanges in matrix-sensitive species for conservation management and environmental planning.

Part B: Quantifying landscape elements responsible for the genetic exchange among populations across spatial scales using contemporary genetic information.

The methodological concept behind PCMs is identical for both parts, but makes additional use of genetic information for the quantification of connectivity in Part B.

A central part of PCMs are predictive niche models (also known as species distribution models—SDMs—or environmental niche models—ENMs). Thanks to the increasing availability of digital spatial data, SDMs became a central tool in the analysis of species distributions over the past decade (Franklin 2009). SDMs were used in a lot of ecological and evolutionary disciplines, covering a broad range of spatial and temporal scales and have been central to a lot of conservation-related aspects such as reserve design and species action plans (GUISAN et al. 2013).

Aside from all the opportunities that SDMs can offer to the scientific community, there are a lot of conceptual and methodological challenges to face. Methodological and technical errors can result in poor models and their predictions could lead to wrong implications e.g. for conservation management. Based on this, potential error sources such as the choice of environmental predictors, the most suitable algorithm, or the impact of gaps in species occurrence information, are part of an ongoing discussion in the scientific community (e.g., GUISAN & ZIMMERMANN 2000; HERNANDEZ et al. 2006; WISZ et al. 2008; VAN GILS et al. 2014). One core problem is that the available methods to estimate model fit are dependent on the contrast between the environmental conditions at the occurrence location by those from a chosen background area (or true absence records). This way of evaluation, however, is prone to systematic errors due to over-parameterization when using predictors that are too heterogeneous, or too many predictors at all (e.g., GUISAN & ZIMMERMAN 2000; DORMANN et al. 2007). Detected contrasts are then no longer biological signals, but statistical artifacts. From this, a general question is derived: how much biological relevance is covered in a statistically *good* SDM? What can such a model tell us about the biological requirements for a species to persist within its populations and successfully exchange among them? An independent measure of high biological relevance could shed light into these issues. In this regard, the third part of this thesis is:

Part C: How can contemporary genetic information inform SDMs to generate better predictions for current and future ranges in a changing world?

In this section, the framework from Part A & B is not used to gain ecological insight about the functional connectivity of a species. Instead, ecological principles (e.g., functional connectivity) that can be assessed using genetic information (e.g., gene-flow) are used here to inform SDMs and evaluate their fit from a biological perspective.

The three thesis sections are covered by a number of single chapters from which some have been published, are submitted to, or in preparation for international journals:

Chapter	**Published, submitted, or in prep.**	**status**
3	**ENGLER JO**, CORD AF, DIECKER P, WÄGELE WJ, RÖDDER D 2014: Accounting for the 'network' in the Natura 2000 network: A response to Hochkirch et al. 2013. arXiv:1408.7076.	Published
4	FILZ KJ, **ENGLER JO**, WENZEL M, SCHMITT T 2013: Missing the target? A critical view on butterfly conservation efforts on calcareous grasslands in south-western Germany. *Biodiversity & Conservation* 22:2223-2241.	Published
5	RÖDDER D, CORD AF, NEKUM S, **ENGLER JO**: Coupling satellite data with species distribution and connectivity models as a tool for environmental management and planning in matrix-sensitive species. submitted to *Environmental Management.*	Submitted
6	**ENGLER JO**, BALKENHOL N, FILZ KJ, HABEL JC, RÖDDER D 2014: Comparative landscape genetics of three closely related sympatric Hesperid butterflies with diverging ecological traits. *PLoS one* 9: e106526.	Published
7	**ENGLER JO**, BALKENHOL N: A statistical learning approach to improve ecological inferences in landscape genetics by accounting for spatial nonstationarity of genetic differentiation.	In prep.
8	**ENGLER JO**, BALKENHOL N, GRAHAM CH: Genes to the niche! How contemporary DNA can help to refine niche theory for predicting range dynamics in the Anthropocene.	In prep.

CHAPTER 1

General Introduction

> *"When we try to pick out anything by itself, we find it hitched to everything else in the Universe."*
>
> — JOHN MUIR

What is connectivity?

Ever since the term *connectivity* spread within the field of biology and applied biological conservation, questions arose about what it is exactly and how one can characterize or quantify it. In a very broad sense, connectivity is the degree of exchange of organisms or processes (CROOKS & SANJAYAN 2006)—the more exchange, the more connectivity.

Up to this point, the idea of connectivity is rather reasonable. The problem starts if we want to narrow down the definition with further detail. It then becomes obvious that connectivity depends on the spatial and temporal scale, the study system, and even the scientific background of the researcher. When it comes to applications, a universal definition of connectivity is therefore impossible.

Depending on the landscape and the focal study organism, there are two broad types of connectivity: (1) structural connectivity, which focuses on the spatial arrangement of landscape elements no matter the demands of the species or its mobility; and (2) functional connectivity, which focuses on the realized use of the landscape matrix by a species. In contrast to structural connectivity, a functional perspective always needs information about the species' specific habitat use (BENNETT 1999; TISCHENDORF & FAHRIG 2000; TAYLOR et al. 2006).

The differences between structural and functional connectivity can be rather large or very similar (Fig. 1.1). If, for instance, a species is strongly dependent on certain landscape elements and its movement decisions are defined by the landscape (e.g., lizards), then we call it a matrix-sensitive species (IMS 1995). In this case, the structural connectivity is identical to the functional connectivity—or at least rather similar. In contrast, mobile species (e.g., birds) are able to cross areas that are uninhabitable for them. For these species, the differences between structural and functional connectivity can be large.

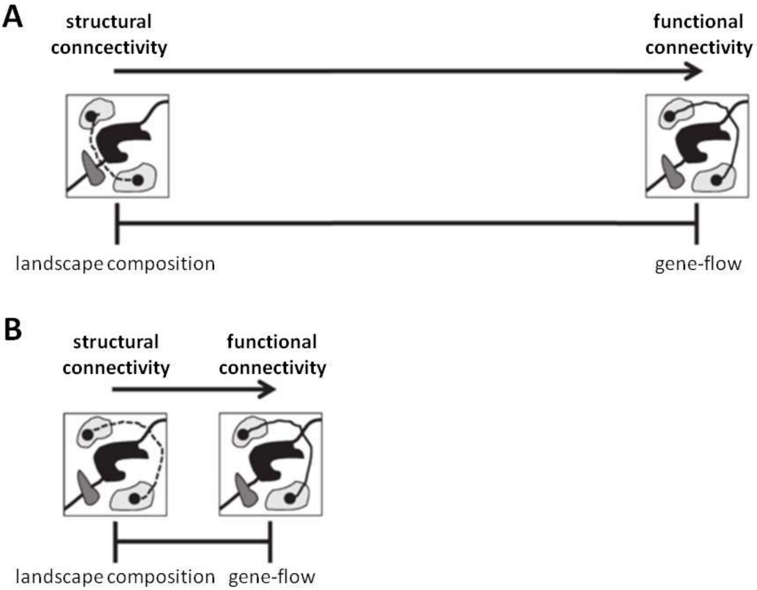

Figure 1.1: Illustration of the differences between structural connectivity (landscape matrix) and functional connectivity (here quantified by gene-flow) for mobile species (A) and matrix-sensitive species (B; modified from Spear et al. 2010).

In addition to this broad distinction, functional connectivity can be distinguished in two further categories, depending on the available mobility information. These are potential and realized connectivity (Fagan & Calabrese 2006). Potential connectivity can be calculated if indirect information about the dispersal capacity of the species is available. Realized connectivity uses, in addition to this capacity, active tracking information, which can be obtained from GPS devices, for example.

Even if the structural connectivity is easy to estimate, a more detailed sub-division of functional connectivity shows that, depending on the available data sources, the functional aspect of connectivity is far from unification. Connectivity is highly species-specific and structurally well-connected landscapes could be functionally important for some species but not for others. Some species might even suffer from structurally well-connected landscapes, which can serve as pathways for pathogens, predators or competitors. However, to achieve some degree of comparability, it is important to provide methods that are easy to handle and tools that are freely available so that their use is not restricted to just a few experts, but open to stakeholders and managers, as well.

Connectivity in Conservation and Environmental Planning

In 1992, the European Union set its first directive for nature conservation. The goal of the habitat directive (92/43/EEC) was to stop biodiversity loss within its communal borders. The directive was the legal basis for the EU-wide reserve network, Natura 2000, and obliges member states to conserve species and habitats listed in Annexes II, IV and V. In addition, Art. 10 of the habitat directive calls for the need to achieve '*ecological coherence*' (i.e. connectivity conservation) among Natura 2000 sites (KETTUNEN et al. 2007).

In Germany, the Federal Nature Conservation Act (BNatSchG) is responsible for the national implementation of the habitat directive. Here, Art. 21 of the BNatSchG regulates the presets from the Art. 10 habitat directive, setting the scene for a legal, country-wide network of habitats. Since its revision in 2006, the BNatSchG became more restrictive, making Art 44(1) especially central here. In the following, Art. 44(1) is printed in its original (translated) form (from http://www.bmub.bund.de/fileadmin/Daten_BMU/Download_PDF/Naturschutz/bnatschg_en_bf.pdf, accessed at 18/08/2015):

> *Article 44 Provisions for specially protected fauna and flora species and other certain fauna and flora species*
>
> *(1) It is prohibited:*
>
> *1. to pursue, capture, injure or kill wild animals of specially protected species, or to take from the wild, damage or destroy their developmental stages,*
>
> *2. to significantly disturb wild animals of strictly protected species and of European bird species during their breeding, rearing, molting, hibernation and migration periods; a disturbance shall be deemed significant if it causes the conservation status of the local population of a species to worsen,*

3. to take from the wild, damage or destroy breeding or resting sites of wild animals,

4. to take from the wild, wild plants of specially protected species, or their developmental stages, or to damage or destroy them or their sites.

From this, it is clearly visible that the legal conditions for conducting environmental impact assessments, which are the formal procedure in environmental planning, focus mainly on the protection of source populations. In other words, even if the habitat quality of an area is good for a focal species, it does not mean that such a site would also be protected under Art. 44(1), unless it were known that the species is actually present there (i.e., records on the species' presence in that area are available). Further, by following this law strictly, habitats that are important for connectivity (i.e., areas of small metapopulations, through which individuals may pass but not necessarily remain) are more likely to disappear than areas used for reproduction (i.e., source populations with a higher density of individuals); Art. 44(1) finds no conflict here, and thus there is no legal barrier to stop development in such habitats.

One major problem is defining a local population, which is by no means an easy task (see WEMDZIO 2011 and references therein). Habitats of poor quality for reproduction in matrix-sensitive species could especially be mandatory to maintain connectivity in neighboring populations where habitat quality is better, thereby building up a local population. The most often flawed distinction of a local population in environmental planning can therefore lead to a stronger fragmentation of populations of species with a special protection status. This is a dilemma, because in such a situation, Art. 44(1) is not immediately conflicted. However, it could cause a time-lagged decline of the species of interest due to a loss of connectivity. This will indeed stand in conflict with Art. 44(1), but only well after a development has been realized. Therefore, it is mandatory to quantify potential connectivity in these species in an objective way as an additional source of information to characterize local populations.

Connectivity in Landscape Genetics

To quantify effective exchanges among populations, genetic information is very useful, as this kind of information also considers successful reproduction via the heredity of the immigrant's genetic material. This is a big advantage over the sole analysis of movement, which normally lacks information about reproduction. The degree to which genetic differentiation among populations draws inferences about the mobility, or, rate of exchange, of a species reaches from very high (no differentiation, or, panmictic; i.e., random mating) to sedentary (high differentiation, or, isolation). The area in between these extremes is characterized by a dependency of increasing genetic differentiation to increasing geographic distance among populations. This positive relationship has been described by Sewall WRIGHT in 1943 and is known as *isolation by distance* (IBD; WRIGHT 1943). Since then, tests of IBD have become a standard analysis in population genetic studies.

With growing computer power and the increasing availability of digital geographic information, new tools have arisen. One of the first ones were *least cost path* (LCP) analyses (SINGLETON et al. 2002; ADRIAENSEN et al. 2003). An LCP is a vector that follows the path of least landscape resistance to connect to sites in the landscape. The main advantage of LCP over classical IBD is the better estimate of effective distances to gene-flow and has been used to quantify movement rates and dispersal pathways (SUTCLIFFE et al. 2003; WANG et al. 2009). However, except from linear habitat structures such as river systems, LCPs are limited in their biological interpretation as one major assumption, which is that there is just one *best* route and that this route is *a priori* known by the organism. In particular, this drawback becomes prominent if distances among sampled populations are so long that they cannot be connected by direct exchange (e.g., DRIEZEN et al. 2007). In addition, there are also problems with the definition of *costs*, which could have a high impact on the position of LCPs; this could lead to wrong implications for conservation management (SAWYER et al. 2011). Based on these disadvantages, model frameworks that incorporate the whole study area in the analysis are better suited to quantify the connectivity of species across landscapes (MCRAE & BEIER 2007).

For more than ten years now, this field has developed rapidly, which led to its own discipline, called *landscape genetics* (MANEL et al. 2003; MANEL & HOLDEREGGER 2013). Landscape genetics is located at the intersection of population genetics, landscape ecology and spatial statistics (STORFER et al. 2007), although some authors argue that this field has yet to fulfill the requirements for being called interdisciplinary (DYER 2015a). The central goal of landscape genetics is to understand which landscape elements are responsible for gene-flow or its restriction. For this, analyses need to go beyond IBD and LCPs. One core concept in this regard is the quantification of genetic differentiation by estimating spatial resistances. Adapted from IBD-theory, genetic differentiation increases with increasing spatial resistances. In its simplest form, this spatial resistance is IBD, but it can also be restricted by functional barriers of certain landscape elements. This concept was introduced as *isolation-by-resistance* (IBR; MCRAE 2006), and plenty of different methods use it to calculate species-specific resistance surfaces and correlate these in a separate step with genetic differentiation (e.g., MCRAE & BEIER 2007; BRAUNISCH et al. 2010; SHIRK et al. 2010; VAN ETTEN 2011).

The parameterization of resistance surfaces is crucial for investigating IBR, but it is far from being standardized yet. SPEAR et al. (2010) highlighted several challenges to be faced in the coming years to reach a comparable and standardized framework for resistance surface parameterization. Three major points are (1) the type of parameterization, (2) the range of resistance values of the surface and (3) the objectivity of parameterization that should turn from expert knowledge to directly inferred biological information (SPEAR et al. 2010). Most often, resistance surfaces are modified depending on expert opinion to improve the functional relationship between genetic and environmental information. Ideally, future methods should use the available biological information on genetic structure and species-environment relationships, process them objectively and optimize parameters without the need of using subjective expert opinion.

SDMs could be a possible way to meet these challenges as they objectively process ecologically-relevant information about the distribution of a species into a probability surface of potential occurrence. The inverse probability surface could then be used as a resistance surface for landscape genetic studies. Several studies followed this logic and used SDMs to parameterize resistance surfaces (e.g., WANG et al. 2008; ROW et al. 2010).

Because of their high potential, SDMs are the core of the PCM framework, as shown in this thesis. In the following chapter, I will to provide detailed information on the methodological background of the conceptual framework of PCMs, the role of the implemented SDMs, and the data needed for analysis.

CHAPTER 2

Conception of Potential Connectivity Models

“Ecology is the art of proving the obvious with increasingly sophisticated statistics.”

— KEVIN RICE

The PCM presented here is a combination of two existing pieces of software: one that models the potential species distribution (the SDM) and one that estimates effective distances over the whole study area's extent, using resistance surfaces delivered by the SDM. To model this it is mandatory to have access to species occurrence records and digital environmental information. In the following, I will focus on the single components that build a PCM (Fig. 2.1).

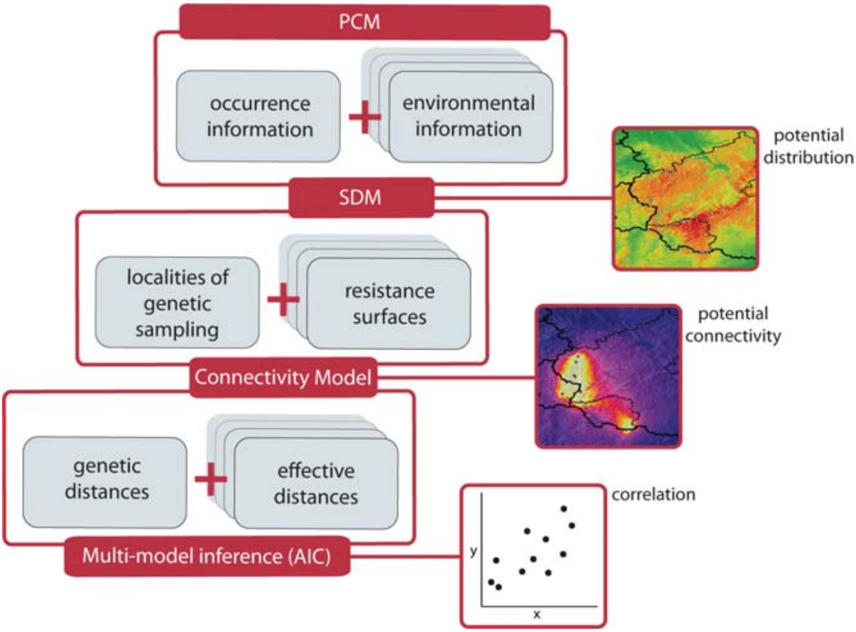

Figure 2.1: The potential connectivity model (PCM) framework—from the data input until the resulting end products.

Environmental Information

Data on environmental conditions of the geographic area of interest are essential for SDMs (Fig. 2.1), and are available as digital layers. Thanks to the massive research efforts to understand climate change, as well as the expanded earth observations from space, more and more data sources become digitally available. For PCMs, the spatial resolution of these data sources depends on the study question, the spatial scale of interest, the study extent and, of course, the data availability. Most SDM applications that focus on the macro-scale to work on biogeographic research questions use interpolated climate information that are globally available in different spatial resolutions ranging from 10 arc minutes down to 30 arc seconds (HIJMANS et al. 2005). These climate data are available as monthly averages over the past 50 years, which can be used to calculate biologically relevant (i.e., bioclimatic) variables. They also cover possible future (following IPCC climate change scenarios) and past scenarios, covering for instance the mid-Holocene climate optimum, the last glacial maximum and the last interglacial period.

Next to climatic information, there are datasets available that globally cover topography and land use. Topographic information is available in resolutions as fine as 30 meters (SRTM Shuttle Mission), while processed data on land cover classes are available at 300 meter resolution (PFEIFER et al. 2012). Some studies show that the use of landscape parameters derived from remote sensing can improve SDM predictions, as opposed to using bioclimatic information alone (CORD & RÖDDER 2011).

In the past few years, more and more fine-scale remote sensing data become available for large parts of the world. This would even allow for the spatially explicit modeling of habitat suitability for locally restricted areas. The resolution here is at 30 meters or below and can be as fine as one meter for some data products. This allows for the analysis of entirely new study questions, such as the characterization of potential distribution or habitat suitability, or the assessment of demographic processes like abundance (VANDERWAL 2009) or reproductive success (BRAMBILLA & FICETOLA 2012)—all especially useful in the environmental management sector. My own preliminary study revealed that the prediction of butterfly abundance is impossible to make by using coarse-scaled climatic information alone (FILZ et al. 2013b); fine-scale environmental information is therefore mandatory to allow for the inference and prediction of such processes.

Depending on the question of interest, I use very different spatial layers for PCMs in my thesis. While applications for environmental planning need fine-scaled environmental information, it is more practical to use coarse-scaled environmental predictors in landscape genetic studies that cover large extents.

Occurrence Informaton

For the computation of an SDM, occurrence records from the focal species are needed (Fig. 2.1). The spatial scale (or, resolution) of these occurrence records (defined as grain; FRANKLIN 2009), would need to at least be as fine as the respective environmental layer. If, for instance, occurrences recorded at a large grain (e.g., records resulting from a 100 m wide transect) were modeled against environmental layers of a finer resolution (e.g. grids of 25 m), then they could be falsely linked to a neighboring grid cell with different environmental conditions (MEYER & THUILLER 2006; GUISAN et al. 2007). Consequently, these inaccurate occurrences could yield an erroneous model output, as the forecasted habitat suitability would get blurred by wrongly assigned environmental conditions that are actually unsuitable for the species. This effect, however, decreases with decreasing resolution of the environmental layers and is less important for coarse-scaled environmental layers (THOMAS et al. 2002; GUISAN et al. 2007).

The SDM

Species distribution models, habitat suitability models or environmental niche models all follow the same principle: they link spatially explicit information about the presence (or, absence) of a species to the environmental conditions in geographic space with a predictive model (FRANKLIN 2009). The value ranges of these environmental predictors (or, variables) at the presence locations are compared with the environmental conditions found at absence locations or a defined set of random locations (i.e., the background or pseudo-absences). Depending on the algorithm, the model will be calculated and projected to a defined geographic area, together with an estimate of variable importance.

In the last couple of years, this framework has become widely applied in different fields of ecology and evolution (FRANKLIN 2009; PETERSON et al. 2011), such as in conservation biology (e.g., ARAÚJO et al. 2004; GUISAN & THUILLER 2005; KREMEN et al. 2006; RÖDDER et al. 2010), invasion biology (e.g., PETERSON & VIEGLAIS 2001; FICETOLA et al. 2007; STIELS et al. 2011) climate change biology (e.g., IHLOW et al. 2012), evolutionary biology (e.g., KOZAK et al. 2008; KOZAK & WIENS 2007, SMITH & DONOGHUE 2010; ENGLER et al. 2013), biodiversity research (e.g., CARNAVAL & MORITZ

2008; SCHIDELKO et al. 2011) and as an additional tool in phylogenetic reconstruction (e.g., KOZAK & WIENS 2007; CHAN ET AL. 2011; RÖDDER et al. 2013). The number of algorithms is as diverse as their fields of application. In this thesis, I focus on the software MAXENT (PHILLIPS et al. 2004; PHILLIPS et al. 2006; PHILLIPS & DUDÍK 2008). MAXENT is a machine-learning algorithm derived from the field of artificial intelligence and follows the principle of maximum entropy (JAYNES 1957; ELITH et al. 2011). Among the many competing methods, MAXENT always ranked among the top performing approaches (e.g., ELITH et al. 2006; HEIKKINNEN 2006; HERNANDEZ et al. 2006; POULOS et al. 2012)—even under limited species occurrence information (e.g. WISZ et al. 2008)—and is known to be tolerant against multicollinearity, as long as model results are not projected (e.g., PHILLIPS et al. 2006; BRAUNISCH et al. 2013). Detailed model specifications follow in the respective chapters. MAXENT's resulting map highlights the occurrence probability of the study area, which can be used to identify regions that are potentially suitable or unsuitable. These probability values are logistically distributed and cover a range between 0 (no predicted occurrence) and 1 (highest probability for occurrence).

Thresholds applied to this distribution of values can cut off low values that can be seen as noise and do not contribute to potential distribution. These thresholds should be dynamic and not fixed (LIU et al. 2005). This is because the data settings are different for each model and depend on the number and position of occurrence records, the extent and position of the study area, and the number of environmental predictors used for modeling. Since thresholds follow fixed deterministic rules, they remain comparable in their validity. A conservative threshold, for instance, would be based on the lowest estimated occurrence probability measured at a given set of occurrences used for model training (i.e., *minimum training presence*). In contrast, a more sensitive threshold would set this limit higher by omitting the lowest 10% of the occurrence probability measured at the respective set of presence records (i.e., *10th percentile training presence*).

For the PCM, these thresholds can optionally be used as fragmentation thresholds (ANDRÉN 1994; METZGER & DÉCAMPS 1997) that highlight absolute barriers to structural connectivity. From this, the modeled map of potential suitability will turn into a resistance surface of the study area, which can be fragmented when such thresholds are applied.

The Connectivity Model

The prepared resistance surface can now be used in a connectivity model to estimate effective distances among sample sites (Fig. 2.1). Here, I use the software CIRCUITSCAPE, which is based on electric circuit theory and follows the principles of Ohm's law (MCRAE & BEIER, 2007; MCRAE et al. 2008). CIRCUITSCAPE allows the assessment of multiple connections in the study area, and thus is not restricted to the limits of the least cost path framework and as consequence outcompetes LCP models (MCRAE & BEIER 2007). The estimated effective distances can be used either for comparisons with genetic distances (see below) estimated from individuals sampled at the same locations, or for visualizing the potential connectivity among the considered locations across the study area for management purposes.

Linking genetic information with PCMs

Information about the genetic differentiation (i.e. the genetic distance) of a focal species in a study area can be correlated to the estimated effective distances measured by the PCM (Fig. 2.1). Genetic distances can be measured with different metrics, such as F_{ST} (WRIGHT 1965) or D_{est} (JOST 2009). To understand the relative importance of certain landscape elements, multiple resistance surfaces can be modeled and subsequently compared to genetic distances. For the correlation of genetic distances with effective distances, many different methods exist (BALKENHOL et al. 2009). Here, I used a multi-model inference approach, based on linear regressions, which compares effective distances from competing resistance surfaces and finds the set of landscape elements with the highest information content. Model importance is not tested here by using classic null hypothesis significance testing, but instead through maximum likelihood methods based on information theory, the Akaike information criterion (AIC; BURNHAM & ANDERSON 2002; JOHNSON & OMLAND 2004). AIC evaluates different models given their explained information content and ranks them according to their importance. Differences between AIC values among the models inform about their importance. A general rule is that a model is considered best if the difference between the AIC in the highest ranked model and the next largest AIC value (delta or Δ) is >2. If there are one or more models of $\Delta < 2$, then they need to be considered together with the highest ranked model (BURNHAM &

ANDERSON 2002). The main advantage of this method is that the non-independent data structure of pairwise comparisons—a classical error in statistics—is the same for each model. Hence, the non-independence error cannot influence the relative ranking of the candidate set of models used in the comparison.

Taken together different tools and information into a single framework as outlined above, offers new opportunities to quantify connectivity for environmental planning, to find limiting environmental conditions for genetic exchange, and to widen our understanding of species distribution as a whole. In the following chapters I will discuss the need for such a holistic perspective and exemplify how PCMs can contribute to different aspects, when fed with real data.

PART A
PCM'S IN CONSERVATION & ENVIRONMENTAL PLANNING

CHAPTER 3

Accounting for the 'network' in the Natura 2000 network: A response to Hochkirch et al. 2013

> *"The more "connected" we become, non-human life with which we share this planet becomes increasingly disconnected."*
>
> — KEVIN R. CROOKS & M SANJAYAN

This chapter has been published on the ArXiv preprint server: arXiv:1408.7076

The work was conducted in collaboration with ANNA F. CORD from the Helmholtz Centre for Environmental Research, PETRA DIECKER from the Institute of Ecology at the Leuphana University Lüneburg, as well as WOLFGANG J. WÄGELE and DENNIS RÖDDER from the Zoological Researchmuseum Koenig.

Commentary

Worldwide, we are experiencing an unprecedented, accelerated loss of biodiversity triggered by a bundle of anthropogenic threats such as habitat destruction, environmental pollution and climate change (BUTCHART et al. 2010). Despite all efforts of the European biodiversity conservation policy – initiated 20 years ago by the Habitats Directive (EU 1992) that provided the legal basis for establishing the Natura 2000 network – the goal to halt the decline of biodiversity in Europe by 2010 has been missed (EEA 2010). HOCHKIRCH et al. (2013) identified four major shortcomings of the current implementation of the directive concerning prioritization of the annexes, conservation plans, survey systems and financial resources. They hence proposed respective adaption strategies for a new Natura 2020 network to reach the Aichi Biodiversity Targets.

Despite the significance of these four aspects, HOCHKIRCH et al. (2013) did not account for the intended 'network' character of the Natura 2000 sites, an aspect of highest relevance. Per definition, a network requires connective elements (i.e. corridors) between its nodes. From an ecological perspective, the Natura 2000 network must guarantee that the species of concern are able to exchange between habitat patches (above all for maintaining/fostering gene flow; e.g., STORFER et al. 2007). Several studies have shown that reserves fail to protect the species they were designed for due to their isolated character in an anthropogenically degraded landscape matrix (e.g., SEIFERLING et al. 2012), even though they are well managed (FILZ et al. 2013a). In turn, habitat connectivity greatly enhances the movement of species within fragmented landscapes (GILBERT-NORTON et al. 2010). Both Habitats (Art. 10) and Birds Directive (Art. 3) explicitly mention the importance of elements providing functional connectivity ('ecological coherence') outside the designated Special Areas of Conservation (SACs) for species of Community interest. However, since the member states are responsible for the designation of SACs, their selection often represents a consensus of various political, economic and ecological considerations. This weakness is well acknowledged in a guidance document from the Institute for European Environmental Policy (KETTUNEN et al. 2007). The authors formulated a framework for assessing, planning and implementing ecological connectivity measures in a way that is legally binding and standardized across borders. Additionally, they presented measures increasing habitat connectivity and future research needed on this topic. Besides the strategies proposed by HOCHKIRCH et al. (2013), there is hence an urgent need to investigate the inter-reserve connectivity in the Natura 2000 network as a whole and specifically for the priority species for which SACs have been designated. Recent software developments and the increasing availability of high-resolution environmental data in combination with extensive fieldwork will help to meet these research requirements. Finally, the results derived from such research must be implemented into a binding EU-legislation as well as a standardized planning policy across national borders to reach scientific consensus on corridor design, which often lacked in the past (BENNETT et al. 2006). This might ultimately ensure an ecological coherence between SACs, which is the prerequisite, over any other strategies, ensuring a Natura 2020 network being worth its name.

CHAPTER 4

Missing the target? A critical view on butterfly conservation efforts on calcareous grasslands in south-western Germany

“Like the resource it seeks to protect, wildlife conservation must be dynamic, changing as conditions change, seeking always to become more effective.”

— RACHEL CARSON

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Introduction

Europe is undergoing a continuous period of invertebrate decline (VAN SWAAY et al. 2011). In particular, the loss of typical habitats like semi-natural grasslands due to intensive agriculture and urban development has been particularly dramatic for butterfly species (BOURN & THOMAS 2002; VAN SWAAY 2002; WENZEL et al. 2006). In this aspect, calcareous grasslands of south-western Europe are considered to be one of the most important habitat types for insect conservation (VAN SWAAY 2002; WALLISDEVRIES et al. 2002). These habitats contain a renowned biological diversity including a variety of species listed under the habitat directive of the Bern Convention (VAN HELSDINGEN et al. 1996). 274 (i.e., 48%) of the 576 butterfly species reported as native in Europe occur on calcareous grasslands. Moreover, from the 71 species considered threatened in the same area, 37 (i.e., 52%) can be found in theses habitats (VAN SWAAY 2002). Consequently, many calcareous grasslands are protected as nature reserves and are integrated in the Natura 2000 program of the European Union (VAN SWAAY et al. 2011). However, even such legally protected sites continue to be lost or are still losing species despite protection. As a result, many specialized and rare species are now threatened or already extinct (WARREN 1997; WENZEL et al. 2006).

Many European countries are experiencing similar population declines. The Netherlands have lost over 24% of its butterfly fauna (WYNHOFF & VAN SWAAY 1995) and 30% of the indigenous species became extinct in Flanders during the 20th century (MAES & VAN DYCK 2001). In Britain, nearly nine percent of the resident butterfly species have gone extinct (WARREN 1997) and in Moravia (Czech Republic) BENES & KURAS (1998) recorded a 60% loss of butterflies during the same time period. The decline of butterflies has caused an increasing concern in Western Europe and the subsequent implementation of conservation activities for Lepidoptera and other wildlife (THOMAS 1995; VAN SWAAY & WARREN 2006; VAN SWAAY et al. 2011).

The prevalent conservation strategy has been to designate threatened habitat types as nature reserves. The habitat types most deserving protection have been identified by the conservation value of the habitat itself and/or by the presence of a great number of rare and endangered species. Until today, such biodiversity assessments have been the major tool in conservation planning and implementation. However, this strategy has had the negative effect of frequently creating small habitat patches isolated by unsuitable, unprotected landscape, which prevents the inter-patch exchange of species. Moreover, small habitat patches may lack the possibility to buffer large-and meso-scale environmental effects (for a discussion see HOF et al. 2011). Habitats are lost due to diverse land-use changes, which do not necessarily stop at the margin of protected areas, but also changes subtly the characteristics of semi-natural grasslands (DOVER & SETTELE 2009). The negative impacts of nutrient and pesticide loads as well as climatic changes influence the habitat structure as well as microclimatic conditions (PARMESAN 2006; BARTHOLMESS et al. 2011). Frequently, a loss of plant diversity and changes in plant communities is followed by butterfly declines, and especially species with high specialization on particular food plants might be affected (e.g., WARREN et al. 2001; POLUS et al. 2007).

Besides the impacts of agricultural improvements on adjacent patches, abandonment is considered to be one major threat to semi-natural habitats (VAN SWAAY 2002). As many butterfly species depend on the preservation of habitats created by extensive human land-use activities, habitat management is considered to play a crucial role for the practical conservation of threatened species (WARREN 1993a,b). Many species are restricted in their local distribution to these often small and fragmented remnants making them susceptible for any change in habitat quality (DOVER & SETTELE 2009). As a consequence, today species conservation is more than ever a question of protecting habitats in a changing environment, but also to retain species diversity within small and fragmented habitats.

However, the lack of habitat quality and habitat connectivity have led to decreasing numbers of butterfly species not only in legally protected semi-natural habitats, but even more severely in unprotected agricultural areas (DOVER & SETTELE 2009). In the latter, remnants of pre-industrial human land-use (e.g. as fallow grounds) are today considered to belong to the most species rich habitats in these areas (SCHMITT & RÁKOSY 2007). These fallows act as retreats as well as stepping stones for many specialized taxa, consequently turning into habitats with high conservation value (WEIBULL 2000; SCHMITT & RÁKOSY 2007; SCHMITT et al. 2008; LIZÉE et al. 2011). Agricultural areas adjacent to fallow grounds affect population dynamics and community structures within these habitats. Additionally, the ongoing loss of stepping stones reduces overall habitat area and landscape connectivity. Hence, patch size and isolation, as well as missing management activities often favor the vulnerability of this habitat type to environmental effects. Consequently, the decline of butterfly species should proceed even faster in cultivated landscapes than in protected areas.

In this study, we aim to identify the mechanisms responsible for the vulnerability of butterfly species and their habitats using the examples of calcareous grasslands and fallow grounds. We intensively re-investigated butterfly communities after a 40-year time period within a defined region of south-western Germany in both managed and legally protected as well as unmanaged grasslands. Regarding the location, geographical integration and management activities of the different grasslands, we evaluate the connectivity of specific habitat types in the landscape and discuss the possible impacts of recent land-use changes and local global warming on the stability of functional trait diversity in butterfly communities. In particular, we assess whether and how butterfly species richness and community composition in managed versus unmanaged grasslands have changed over the last decades and discuss the appropriateness of conservation strategies for nature reserves.

Material and methods

Study sites

Our study area is located at the south-western boarder of Germany (Fig. 4.1a). The vicinity of Trier is characterized by a long tradition of human settlement. Anthropogenic land-use created a manifold mosaic of habitat types ranging from vineyards, agricultural fields, fallows, flower rich meadows, woodlands, rivers and floodplains to several semi-natural habitats like calcareous grasslands. Today, traditional farming systems and semi-natural habitats, which ensured the survival of a diversity of species for thousands of years, are replaced by intensive cultivated agricultural areas. Since the middle of the 20th century, land-use changes have caused serious consequences for the conservation of these traditional habitats as their quality and quantity have declined. Habitats are being lost due to, intensive agricultural usage, anthropogenic loads of nutrients and the failure of extensive management, which lead to advanced succession and final loss of these habitats (BURGGRAAFF & KLEEFELD 1998).

Calcareous grasslands

For our study, we selected six calcareous grasslands. During the last 40 years, the patches remained as grassland and five of them are preserved as nature reserves. Calcareous grasslands rank among the most species-rich habitats in Europe (VAN SWAAY 2002) and are classified as highly endangered in the Red List of endangered habitat types in Rhineland-Palatinate. A strong decline of these habitats has already been observed during the last decades in our study area (BIELEFELD 1985; WENZEL et al. 2006; M. WEITZEL own observations.) and even legally protected sites continue to decline (WENZEL et al. 2006).

The phytocoenosis of the study sites can be described as Mesobromion errecti dominated by flowering herbs and grasses (e.g., *Bromus errectus*, many Orchidaceae), interspersed with single stands of shrubs (e.g., *Crataegus monogyna*, *Prunus spinosa*) or small trees. Vegetation varied in height throughout the year, but in general was corresponding to the dominating plant species less than 30 cm high. In four reserves, structural characteristics were preserved by tending strategies (mowing and clearing). Like most semi-natural habitats, the patches were highly fragmented and under external pressure from agricultural intensification and changing land-use. The degree of isolation, calculated using the formula of POWER (1972), varied between 78.8% (Echternacherbrück) and 99.9% (Kelsen). The isolation of the investigated habitats can be explained by natural limiting factors like the geological condition, microclimatic factors or by anthropogenic fragmentation.

In total the study sites extended over 136 ha, which represent a considerable proportion of the 752 ha of calcareous grasslands known in Rhineland-Palatinate (KLEIN et al. 2001). The minimum geographic distance between patches was 3 km between Igel and Wasserliesch. In the other cases, distances exceeded 10 km. Spatial autocorrelation among sites could be excluded.

Patch size varies considerably from 1.5 ha (Kelsen) to 68 ha (Echternacherbrück). Depending on the total size of the reserve, one to four transects per patch (transect length 40-385 m) were established in 1972. All transects were re-established and re-investigated in 2011 in cooperation with the initial observer (M. WEITZEL).

Vineyard Fallows

Eight xerothermic vineyard fallows were selected for field surveys. Theses patches were structurally young fallows in 1973 and have been abandoned from agricultural use for at least fifty years. Old fallows are considered to hold a significantly higher species richness and heterogeneity and host more Red List species than earlier stages (BALMER & ERHARDT 2000). Vegetation height varied throughout the year, but on average did not exceed 80 cm. The vegetation was dominated by perennial bunch grasses, a variety of thermophilic flowering herbs as *Onobrychis vicifolia*, *Daucus carota*, *Centaurea* ssp., *Medicago* ssp., *Vicia* spp, *Rumex* ssp. and few interspersed hedge structures composed of *Rosa* ssp., *Rubus* ssp., *Cytisus scoparius* and *Crataegus monogyna*. Geological conditions and microclimatic factors prevent the vegetation of converting into secondary forests. Moreover, structural characteristics have been maintained by occasional extensive sheep pasturing. All patches suffer from a high degree of fragmentation as well as external pressure from adjacent intensively cultivated farmland (mostly vineyards), hay meadows and housing areas. Minimum distance between patches was 200 m (Brettenbach I; Brettenbach II). In the other cases, geographic distances were on average 1.6 km. A spatial autocorrelation among patches could be excluded. Patch size varied between 2.7 ha (Kernscheid) and 5.8 ha (Brettenbach I). In total, the studied vineyard fallows extended over 34.5 ha. In 1973, one transect of varying length (432-1430 m) was established per patch. The transects were re-established and re-investigated in 2010 in cooperation with the initial observer (M. WEITZEL).

Field sampling design

In both grassland types, data were taken from standardized transect counts along fixed transects. The structure of this monitoring was similar to that described by POLLARD & YATES (1993). Each butterfly seen within an observation radius of 5 m ahead and 2.5 m on each side of the observer was counted. Individuals were either identified and counted by sight or captured with a butterfly net for closer determination to species level. If possible, each transect was visited every ten days from April to October for a time period appropriate to their length. The observations were conducted randomly between 10:00 am and 5:00 pm if weather conditions permitted (POLLARD & YATES 1993; SETTELE et al. 1999), i.e., temperature above 17°C, wind less than six Beaufort and no rain (VAN SWAAY et al. 2008). Variations due to weather and time of day were counterbalanced by randomizing the visits. Records were kept along with descriptions of weather conditions and recent management activities. In total, 105 transect walks were performed in 2011 and a similar amount in 1972 on calcareous grasslands. 136 transect walks were conducted in 1973 and 109 in 2010 on vineyard fallows. To obtain unbiased data, observations were conducted throughout the same time period each year using identical transects as well as field methods.

Classification of butterfly species

We categorized all butterfly species regarding their national conservation status and classified them into functional groups defined by habitat requirements, dispersal behaviour, larval food plant specialisation and global distribution.

We used the classification of BINK (1992) for the analysis of dispersal abilities. For increasing the statistical power, the nine dispersal classes were condensed to three: sedentary species (class 1-3), mobile species (class 4-6) and migrants (class 7-9). We used the classification of REINHARDT & THUST (1988) for general habitat requirements to distinguish between ubiquitous, mesophilic, hygrophilic and xerothermophilic species. Caterpillars were classified, respective to their food plant use, as monophagous, oligophagous and polyphagous (EBERT & RENNWALD 1991). Global distribution data were obtained from KUDRNA (2002). We classified butterfly species as Mediterranean if their distribution area includes southern Iberia, southern Italy or Greece, i.e. ensuring their survival in Mediterranean glacial refugia during the LGM. The distribution areas of continental species usually exclude these regions and do not reach the lowland areas along the coast of the Atlantic or the British Isles. These species usually survived in the last glacial period in extra-Mediterranean and/ or more eastern refugia. Species were classified as a Mediterranean-continental species if their distribution area includes at least one of the areas typical for the Mediterranean species, but also extends to the continental parts of Eurasia. The classification of each species is given in Table 4.1.

Table 4.1: Presence-absence data of all butterfly species recorded on six calcareous grasslands and on eight vineyard fallows with the number of study sites with the species being present in 1972/73 and 2010/11 including their species specific functional traits (D1: sedentary, D2: medium, D3: migrant; P1: monophagous, P2: oligophagous, P3: polyphagous; H1: xerothermophilic, H2: mesophilic, H3: hygrophilic, H4: ubiquitous; A1: Mediterranean, A2: continental, A3: continental-Mediterranean, A4: migrant)

	Calcareous grasslands		**Vineyard fallows**		
	1972	**2011**	**1973**	**2010**	**Traits**
Hesperidae					
Erynnis tages (L., 1758)	6	4	7	0	D1 P2 H1 A1
Carcharodus alceae (Esp., 1780)	1	0	7	0	D2 P2 H1 A1
Spialia sertorius (Hoff., 1804)	6	3	6	0	D1 P1 H1 A1
Pyrgus malvae (L., 1758)	6	5	8	5	D1 P2 H2 A1
Pyrgus serratulae (Ram., 1839)	1	0	0	0	D1 P1 H1 A3
Carterocephalus palaemon (Pal., 1771)	4	0	3	0	D1 P2 H2 A2
Thymelicus lineola (O., 1808)	6	6	8	6	D2 P2 H2 A2
Thymelicus sylvestris (Poda, 1761)	6	6	5	6	D1 P2 H2 A1
Thymelicus acteon (Rott., 1775)	3	0	0	0	D1 P2 H1 A1
Hesperia comma (L., 1758)	1	1	0	0	D1 P2 H2 A3
Ochlodes sylvanus (Esp., 1778)	6	3	8	4	D2 P3 H4 A1
Papilionidae					
Papilio machaon (L., 1758)	6	5	8	6	D2 P3 H2 A1
Pieridae					
Leptidea sinapis (L., 1758)/ *reali* (Reiss, 1989)	6	6	8	8	D2 P2 H2 A1
Anthocharis cardamines (L., 1758)	6	5	8	8	D2 P2 H2 A3
Aporia crataegi (L., 1758)	5	3	6	5	D2 P2 H2 A1
Pieris brassicae (L., 1758)	6	6	8	3	D3 P3 H4 A1
Pieris rapae (L., 1758)	6	6	8	8	D2 P3 H4 A1
Pieris napi (L., 1758)	6	6	8	6	D2 P3 H4 A1
Pontia daplidice (L., 1758)	1	0	0	0	D2 P3 H1 A1
Colias croceus (Fourc, 1785)	3	0	2	0	D3 P2 H4 A4
Colias hyale (L., 1758)	6	4	8	6	D2 P2 H2 A2
Colias alfacariensis (Rib., 1905)	5	1	0	0	D2 P2 H1 A1
Gonepteryx rhamni (L., 1758)	6	6	8	7	D2 P2 H2 A1
Lycaenidae					
Hamearis lucina (L., 1758)	5	0	5	0	D1 P1 H2 A2
Lycaena phlaeas (L., 1761)	6	4	8	6	D2 P1 H2 A1
Lycaena dispar (Haw., 1803)	0	0	0	1	D2 P1 H3 A2
Lycaena tityrus (Poda, 1761)	6	2	8	3	D1 P1 H2 A3
Lycaena hippothoe (L., 1761)	0	0	1	0	D1 P1 H3 A2
Thecla betulae (L., 1758)	6	2	8	1	D1 P1 H2 A2
Neozephyrus quercus (L., 1758)	4	0	3	0	D1 P1 H1 A3
Satyrium ilicis (Esp., 1779)	4	0	0	0	D1 P1 H1 A3
Callophrys rubi (L., 1758)	6	6	8	5	D2 P3 H2 A1
Satyrium w-album (Knoch, 1782)	0	0	3	0	D1 P1 H2 A2
Satyrium pruni (L., 1758)	6	3	8	0	D1 P1 H1 A2
Satyrium acaciae (Fab., 1787)	3	0	0	0	D1 P1 H1 A3
Cupido minimus (Fues., 1775)	6	6	4	0	D1 P1 H1 A3
Cupido argiades (Pallas, 1771)	0	0	0	2	D2 P2 H1 A2
Celastrina argiolus (L., 1758)	6	3	8	1	D2 P3 H2 A3
Maculinea arion (L., 1758)	3	0	0	0	D1 P2 H1 A3
Aricia agestis (Den.&Schiff., 1775)	6	6	0	7	D2 P3 H1 A1
Polyommatus semiargus (Rott., 1775)	6	6	7	7	D2 P1 H2 A1
Polyommatus icarus (Rott., 1775)	6	6	8	7	D2 P2 H4 A1
Polyommatus coridon (Poda, 1761)	6	5	4	0	D2 P1 H1 A1

Polyommatus bellargus (Rott., 1775)	1	0	0	0	D1 P2 H1 A1
Nymphalidae					
Argynnis paphia (L., 1758)	6	4	8	1	D2 P1 H2 A3
Argynnis aglaja (L., 1758)	6	5	7	3	D1 P1 H2 A1
Issoria lathonia (L., 1758)	6	5	4	6	D2 P1 H2 A1
Brentis ino (Rott., 1775)	0	0	2	0	D1 P2 H3 A2
Boloria selene (Den.&Schiff., 1775)	6	1	8	0	D1 P1 H3 A2
Boloria euphrosyne (L., 1758)	4	0	0	0	D1 P1 H2 A3
Boloria dia (L., 1767)	0	4	0	0	D2 P1 H1 A2
Vanessa atalanta (L., 1758)	6	3	8	5	D3 P1 H4 A4
Vanessa cardui (L., 1758)	6	1	8	0	D3 P3 H4 A4
Inachis io (L., 1758)	6	4	8	8	D2 P3 H4 A3
Aglais urticae (L., 1758)	6	6	8	7	D2 P1 H4 A1
Polygonia c-album (L., 1758)	6	3	8	4	D2 P3 H2 A1
Araschnia levana (L., 1758)	6	3	8	5	D2 P1 H2 A2
Nymphalis polychloros (L., 1758)	4	0	3	0	D2 P3 H2 A3
Euphydryas aurinia (Rott., 1775)	0	1	0	0	D1 P2 H3 A3
Melitea cinxia (L., 1758)	6	0	3	1	D1 P1 H2 A3
Melitea diamina (Lang, 1789)	2	0	6	0	D1 P1 H3 A2
Melitea athalia (Rott., 1775)	6	3	7	2	D1 P3 H2 A3
*Melitea aurelia (*Nick., 1850)	2	1	0	0	D1 P3 H1 A2
Limentis populi (L., 1758)	1	0	2	0	D1 P1 H2 A2
Limentis camilla (L., 1764)	5	0	6	0	D1 P1 H2 A2
Apatura iris (L., 1764)	5	1	1	0	D1 P1 H2 A2
Pararge aegeria (L., 1758)	6	4	8	1	D2 P2 H2 A1
Lasiommata megera (L., 1767)	6	5	7	3	D2 P2 H2 A1
Lasiommata maera (L., 1758)	1	1	0	0	D1 P2 H1 A3
Coenonympha arcania (L., 1761)	4	6	8	5	D1 P3 H2 A3
Coenonympha pamphilus (L., 1758)	6	6	8	7	D1 P3 H2 A1
Pyronia tithonus (L., 1771)	6	6	8	8	D1 P2 H1 A3
Aphantopus hyperantus (L., 1758)	6	6	8	7	D1 P3 H2 A2
Maniola jurtina (L., 1758)	6	6	8	8	D2 P3 H4 A1
Erebia medusa (Den.&Schiff., 1775)	4	0	7	0	D1 P3 H2 A2
Hipparchia semele (L., 1758)	2	0	0	0	D2 P3 H1 A1
Melanargia galathea (L., 1758)	6	6	8	8	D1 P2 H2 A1
Species number	70	52	59	41	

The categorisation of endangerment was taken from the respective Red Data Book for Rhineland-Palatinate (SCHMIDT 2010) and the national law of wildlife conservation (BArtSchV §1). Due to taxonomic revisions within the investigated time period, *Leptidea sinapis* and *L. reali* were treated as a sibling species complex in this study. The nomenclature of butterflies follows GAEDIKE & HEINICKE (1999).

Statistical analysis

For each study patch, we constructed a data matrix containing the presence-absence data of all recorded butterflies. Species estimate accuracy was calculated computing expected species accumulation curves (sample-based rarefaction curves) and incidence-based richness estimators (Chao1, Chao2, ICE, first-order jackknife, Michaelis-Menten) using ESTIMATES WIN 8.00.

Differences in species composition between the study years were evaluated for each study patch. Tests among study sites and observation years were done by Wilcoxon tests, Cochran Q tests and χ^2 tests for heterogeneity in SPSS 15.0. We also performed separate statistical calculations for each functional group using Cochran-Q-tests to analyse community shifts between the observation years.

Turn-over rates were estimated for both grassland types to identify the changes of the faunas between the two observation years in MICROSOFT EXCEL 2003. It was calculated as the number of species recorded in only one of the observation years divided by the total number of species observed during both observation years. Comparisons of the similarity of the community structures were made using the Sørensen similarity index. It was calculated on the basis of presence/absence data as the number of shared species divided by the number of species in the two samples, respectively.

Independently from changes in absolute species composition, we evaluated changes in relative functional trait diversity by using PCA in combination with linear discriminant analysis (LDA) in SPSS. We calculated relative proportions for the functional trait classes separately for each site and time slice. In consequence, each trait (Dispersal: 3 classes; Foodplant use: 3 classes; Habitat: 4 classes, Distribution 4 classes) was summed to 1 on each side. This information was thereafter transformed via PCA into a multivariate scenopoetic trait space by taking principal components that exceeds the value of one after conducting a varimax rotation. Group discrimination (i.e. taking year as grouping variable) was tested thereafter using cross-validated LDA.

To test for differences in parallelism of the community shifts between calcareous grasslands and the vineyard fallows, we performed a circular ANOVA using the circular package in R (JAMMALAMADAKA & SENGUPTA 2001; R DEVELOPMENT CORE

TEAM 2010), where the directions of each vector connecting the two observation years in the PCA-space were used as dependent factor.

Resistance surface modeling

To infer patterns of habitat fragmentation in both habitat types, we combine an environmental niche model with a habitat connectivity model using fine-scale environmental GIS-layers as predictors for model building. The environmental layers comprise four different vegetation indices based on multispectral ASTER (Advanced Space Borne Thermal Emission and Reflection Radiometer) data in 30 m resolution (NDVI, NDWI, soil-brightness, vegetation-greenness) as well as topography information derived from the ASTER global digital elevation map of the same resolution (altitude, slope, aspect). Further, we used categorical CORINE landcover data of 2006 (available through: eea.europe.com) with a resolution of 100 m. The Normalized Different Vegetation Index (NDVI), developed by ROUSE et al. (1974), is a simple vegetation index for remotely sensed data that quantifies the density of plant growth on earth, and so provides information about vegetation biomass (JENSEN 2007). The calculation of the Normalized Difference Water Index (NDWI), introduced by GAO (1996), provides information about the vegetation water content and allows assessments to be made of changes in plant biomass and water stress of vegetation.

Suitable satellite data for the purpose of a study like this need to have a sufficient spectral resolution to ensure a spectral discrimination of different land cover types. Furthermore, a high spatial resolution is required to accurately depict small landscape structures. The ASTER multispectral imager onboard NASA’s Terra satellite is largely compliant with these requirements. ASTER has three separate imaging subsystems which cover the visible and near infrared (VNIR), the shortwave infrared (SWIR) and the thermal infrared (TIR) spectral ranges with 3, 6 and 5 spectral bands with spatial resolutions of 15 m, 30 m and 90 m (YAMAGUCHI et al. 1999; ABRAMS 2000). In this study, one ASTER scene (acquisition date: June 26, 2001), covering the northern and central parts of Rhineland-Palatinate was selected for analysis.

ASTER spectral bands 1-4, primarily designed for assessing vegetation properties, were selected. From the especially narrow band in the 2-2.5 µm range, conceptualized mainly for the purpose of surface soil and mineral mapping (YAMAGUSHI et al. 1998), a single broad bandwidth channel centered at 2.2 µm was synthesized by averaging channel 5-7, thereby prioritizing improved signal-to-noise ratio versus spectral resolution considered less important for the study purpose. No Thermal bands were used in this study.

Since remote sensing data with medium spatial resolution has only been of limited use for the identification of species compositions (WULDER 1998), the reduced spatial resolution of the ASTER channels in the SWIR Range (i.e. 4 and the synthesized channel 5) has been adjusted to match the 15-m pixel size of the visible and near-infrared bands (1-3). The data fusion was performed with a local correlation approach that preserves the spectral characteristics of the low resolution input and transfers the textural properties of the high resolution reference to the ASTER-SWIR channels (HILL et al. 1999).

The ASTER-scene was calibrated by converting the original digital numbers to absolute reflectance values for each pixel based on ASTER calibration functions (YAMAGUCHI et al. 1999; ARAI & TONOOKA 2005) and full radiative transfer modeling (ATCPRO©; HILL & STURM 1991; HILL & MEHL 2003) based on the 5S Code by TANRÉ et al. (1990). As the terrain of the study area is very mountainous, the removal of topographic effects is important prior to the analysis of landscape structures. On basis of the ATCPRO© model, terms describing illumination can be approximated by the integration of a digital elevation model and finally compensated for each raster cell of the dataset. In addition to the radiometric correction, the data preprocessing comprised a precise georectification. The resulting ortho-projected datasets were referenced to the national Gauss-Krüger coordinate system with sub-pixel accuracy and later projected onto the classical WGS reference system using ARCGIS 9.3, thereby fulfilling all requirements for an efficient integration of external geodata.

The Tasseled Cap Transformation (KAUTH & THOMAS 1976) could be described as a guided and scaled linear transformation, which transforms the input satellite data into three (or four) bands of known characteristics. A Tasseled Cap Transformation was applied to the ASTER scene, and three thematic bands representing: soil-brightness, vegetation-greenness and soil- and vegetation-wetness were derived.

Within the study extend (Fig. 4.1a), georeferenced locations of the respective habitat type were set by visual inspection of aerophotos (using Google Earth) and during several field surveys resulting in 12 and 34 locations for either habitat type, respectively.

Environmental niche models were computed using MAXENT 3.3.3k, a machine learning algorithm based on the principles of maximum entropy (PHILLIPS et al. 2006; PHILLIPS et al. 2008; ELITH et al. 2011). MAXENT has frequently outperformed other approaches, especially when the number of georeferenced locations is scarce (e.g. HERNANDEZ et al. 2006; ELITH et al. 2006; WISZ et al. 2008). Thus, this algorithm became the method of choice. We used the standard settings, randomly splitting the dataset into a 70% training and a 30% testing subset and using a bootstrap approach between 100 different replicate runs to average model output. Variable importance was assessed by jackknifing the training datasets. The output was scaled in a logistic format. Despite recent criticisms (LOBO et al. 2008; JIMÉNEZ-VALVERDE 2011), but in lack of other alternatives (e.g. BALDWIN 2009), AUC statistics (SWETS 1988; FIELDING & BELL 1997) were used, as implemented in MAXENT, to validate model performance. As threshold for identifying areas of low suitability probability, we used the non-fixed equal training sensitivity and specificity threshold as previously recommended (LIU et al. 2005). Connectivity between study sites in either habitat was assessed depending on habitat specific suitability maps within a connectivity model.

Here, we used the program CIRCUITSCAPE V. 3.4.1 (MCRAE & BEIER 2007; MCRAE et al. 2008), which calculates pairwise resistance values between a defined set of locations (here: habitat specific study sites). CIRCUITSCAPE is based on circuit theory recently adapted from electrical engineering for the solution of landscape ecological problems (MCRAE et al. 2008). By incorporating multiple pathways, CIRCUITSCAPE reproduces connectivity between sites more accurate and with higher biological relevance than more classical approaches like isolation-by-distance models or least cost path models (MCRAE & BEIER 2007).

Prior to analysis, habitat suitability maps as derived from MAXENT models were retransformed by multiplication of each probability by 10000 and again saved as integer value, to reduce calculation time derived from long decimals, but without loss of information (B. MCRAE pers. comm.). Further, values below the previously defined absence threshold were set to the defined positive minimum integer value (i.e., setting to a value of 1) indicating highest resistance in those areas. Generally, the habitat suitability map acts as conductance surface for the connectivity model. This means that the higher the resistance, the lower the value is. Circuitscape was run in four-node mode to safe computing time. For comparison of resistance values, we used the site location used to build the resistance surfaces because they cover the entire study extent. Depending on the difference of absolute location numbers, we get 561 pairwise comparisons for fallow grounds and 66 pairwise comparisons for calcareous grasslands.

To obviate misleading conclusions by comparing an unbalanced study design (i.e., 561 vs. 66 records), we resample the higher number of fallow ground comparisons in a bootstrap approach with 1000 iterations. For each iteration, we selected just as many records randomly as records were available for the smaller group (i.e., 66 records). Using this subset of fallow ground records, we subtracted the resistances of the fallow grounds by those from the calcareous grasslands. Repeating this procedure for each iteration, we get a distribution of the mean difference between both groups. According to NAKAGAWA & CUTHILL (2007), this effect size is superior for comparing groups outside of a classical null-hypothesis-significance-testing approach. A significant difference is unlikely, if the 95% confidence interval of the distribution of this effect size includes zero.

Results

Species decline

During the field surveys in the 1970s and 2010/11, significantly different numbers of species (Cochran-Q-Test, all $p<0.001$) were observed on calcareous grasslands as well as on vineyard fallows. In both habitat types, a remarkable loss of species and changes in community structures were detected. However, neither the absolute number nor the proportion of species loss was considerably different between managed and semi-natural grasslands. After 40 years, 18 species have disappeared in vineyard fallows, i.e., 31%. Similarly, 17 species, i.e., 25%, were not redetected on calcareous grasslands after the same time period. 53% of the species lost were identical in both grassland types. Turnover rates were high on all study patches indicating a shift in community composition over time. No major difference in the average species turnover rates was detected between semi-natural grasslands (i.e., 26%) and fallow grounds (i.e., 35%). Moreover, Sørensen similarity index demonstrates community composition changes over time, on averaging 74% on calcareous grasslands and 63% on vineyard fallows. The proportion of species recorded newly was low and no major differences in the absolute number or proportion of such species were detected between the two grassland types. In all cases, the amount of newly appearing species did not balance the recorded species losses. The number of observed species for each transect in 2010/11 ranged from 80% to 97% of the species numbers predicted by species richness estimators. Presence-absence data for all species are given in Table 4.1.

Degradation of functional groups

Analyses of changes in community composition regarding the observed functional groups produced comparable results for vineyard fallows and semi-natural grasslands. In both habitat types, all functional groups were re-detected in 2010/11, with the exception of hygrophilic species. The latter had disappeared from a similar amount of semi-natural grasslands and fallows in 2010/11. Moreover, species declines accompanied by significant changes within the composition of each functional group were recorded in both habitat types (Cochran-Q-test, $p<0.01$). Losses of species numbers with similar traits were also comparable. In this aspect, butterfly species with high functional specialization showed the strongest negative impacts. In 2010/11, community composition exhibited a significantly higher proportion of generalist species in both habitat types (Cochran-Q-test, $p<0.01$).

Regarding specific species traits, the strongest decline was apparent in sedentary species, independently from the habitat type. Butterflies with poor dispersal abilities showed a highly significant decline of 60% (Cochran-Q-test, $p<0.01$) in vineyard fallows and 37% (Cochran-Q-test, $p<0.01$) on calcareous grasslands, respectively. Medium and good dispersers declined considerably less. Besides, monophagous species showed a significant decline in both habitat types (Cochran-Q-test, $p<0.05$) exceeding those of oligo- and polyphagous species. Xerothermophilic and mesophilic species exhibited high decrease rates. In combination, both groups had a comparable amount of decline on both grassland types. However, considerably different species decrease rates were calculated for each single trait: xerothermophilic species decreased slightly more on fallows, whereas mesophilic taxa decreased remarkably more on calcareous grasslands. In a similar way, species declines were documented for all distribution categories, with highest decrease rates of Mediterranean species on calcareous grasslands and of continental species on vineyard fallows.

Concerning the conservation state of the observed butterfly species, following the German national law of wildlife conservation (Bundesartenschutzverordnung §1), species listed as "highly protected" declined significantly and species listed as "strictly protected" were lost completely on calcareous grasslands. Only slightly higher losses were recorded for the protected species in vineyard fallows. Taking into account the categories of the Red Data Book of Rhineland-Palatinate, especially those categories, indicating the highest conservation demand, shrank significantly by 70 to 75% on calcareous grasslands (Cochran-Q-test, $p<0.01$). On vineyard fallows, the number of species also declined in all categories of the Red Data Book, but less severe compared to the declines on calcareous grasslands. However, the overall number of endangered and/or protected species was lower on vineyard fallows than on calcareous grasslands in the early 1970s.

Changes in relative trait diversity

The first three principal components of the PCA explained 86.2% of the entire variance (Table 4.2). The obtained factor loadings strongly support the above described rearrangements of the assignments to the different species traits. The first two components, separated in a calcareous grassland and the vineyard fallow part in Figure 4.2, support a stronger shift and a more stochastic change of community compositions on the vineyard fallows. However, this result could not be assured statistically as between group differences in the circular ANOVA becomes non-significant ($F = 0.038$, $df = 1$, $p = 0.8487$). LDA using the time frame as grouping variable leads into a complete differentiation between the groups.

Table 4.2: Factor loadings as well as Eigenvalues and cumulative explained variance (in %) for each of the three Principal components (PC) extracted. Bold values indicate most significant correlations for a single PC. Underlined values highlight highest loadings without a clear significant contribution to a single PC (D1: sedentary, D2: medium, D3: migrant; P1: monophagous, P2: oligophagous, P3: polyphagous; H1: xerothermophilic, H2: mesophilic, H3: hygrophilic, H4: ubiquitous; A1: mediterranean, A2: continental, A3: continental-mediterranean, A4: migrant).

	PC1	PC2	PC3
D1	**0.85**	0.31	-0.24
D2	**-0.75**	-0.53	0.26
D3	-0.06	**0.93**	-0.17
P1	**0.70**	0.62	-0.15
P2	-0.28	**-0.87**	0.21
P3	**-0.88**	-0.11	0.03
H1	0.57	-0.21	**-0.77**
H2	0.02	-0.17	**0.86**
H3	0.57	0.57	0.33
H4	**-0.96**	0.13	0.07
A1	-0.54	**-0.79**	0.06
A2	**0.72**	0.50	0.27
A3	0.02	0.58	-0.62
A4	0.15	**0.93**	0.05
Eigenvalue	5.03	4.90	2.13
Cum %	35.93	70.94	86.16

Connectivity modelling

Environmental niche models provide good to excellent results depending on AUC inference (AUC: 0.893 +- 0.037 on calcareous grasslands, Fig. 4.1b; 0.977 +- 0.006 on vineyard fallows, Fig. 4.1c). CORINE Landcover information was by far the most delimiting factor for model construction for both habitat types followed by topographical and multispectral information (Table 4.3). The threshold that cuts areas with low habitat suitability was 0.3969 for calcareous grasslands and 0.185 for vineyard fallows. Consequently, mean connectivity (Fig. 4.1d/e) differs significantly between both habitat types indicating a generally better connectivity between vineyard fallows than between calcareous grasslands (mean difference: -0.172, 95% CI = -0.319 - -0.034, p = 0.004).

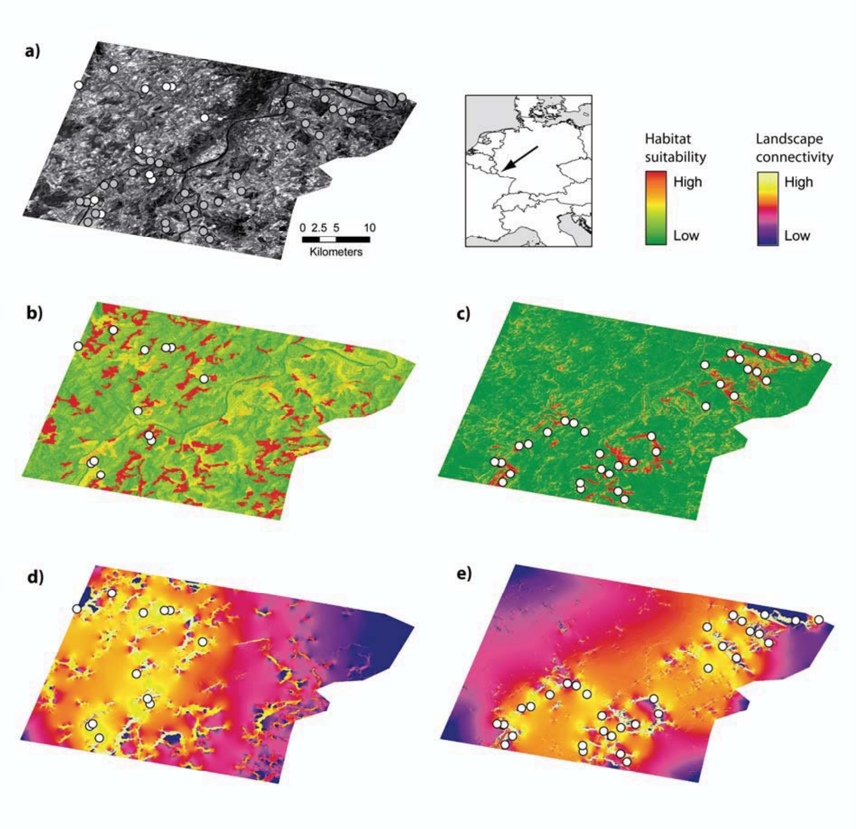


Figure 4.1: Location of the study area near Trier in south-western Germany (a) as well as habitat suitability and potential connectivity maps from the same region. Blank circles indicate locations of selected calcareous grasslands and grey circles represent vineyard fallows used for connectivity modelling respectively. Habitat suitability maps based on the locations of both habitat types were generated (b: calcareous grasslands; c: vineyard fallows) and used for connectivity models (d: calcareous grasslands; e: vineyard fallows).

Discussion

Butterflies have declined remarkably in the region of Trier, both on unmanaged vineyard fallows, but also on managed calcareous grasslands. However, the latter showed considerably higher numbers of species (including rare species) than the vineyard fallows in the 1970s. Nevertheless, the observed species decline was stronger on the fallows than on the calcareous grasslands, and also the turn-over rates were higher on the former. Furthermore, the evolution of the butterfly communities was much more at random than at the calcareous grasslands, which showed more directed changes of their communities.

These results underline that the applied management strategies on the observed calcareous grasslands (mowing, sheep pasturing, cutting of shrubs and little trees) had, at least some, success in preserving the previously existing diverse butterfly communities as well as rare and habitat specific species (cf., BALMER & ERHARDT 2000). This goes in line with results obtained from Carinthia (Austria), demonstrating the direct positive effects of calcareous grassland management measures on the population development of several habitat specific butterfly species (RÁKOSY & SCHMITT 2011).

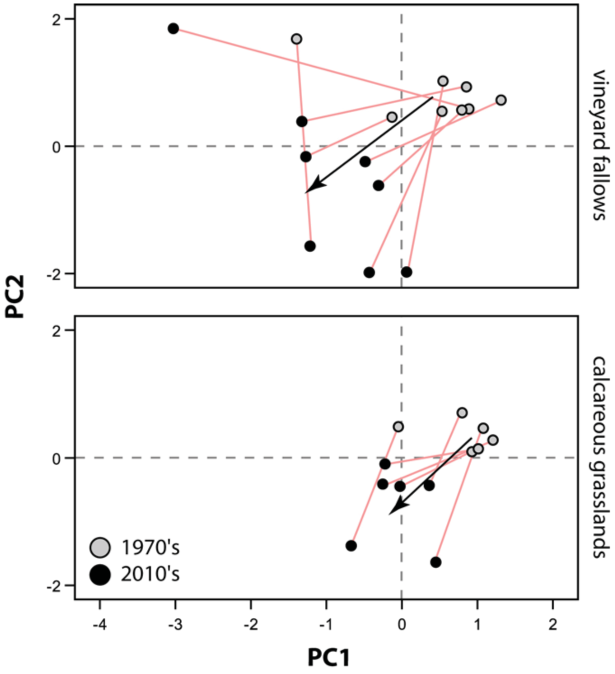


Figure 4.2: Trait space spanned by the first two principal components for either vineyard fallows (upper panel) and calcareous grasslands (lower panel), respectively. Grey circles represent sites from the first surveys in the 1970s, black circles from the second surveys in 2010/11. Arrows indicate mean change within trait space.

Nevertheless, the conservation success is not as high as desired: A considerable number of target species (e.g. *Glaucopsyche alexis*, *Maculinea arion*, *Hipparchia semele*) disappeared from all study sites, and the rate of species loss at calcareous grasslands was, in general, only gradually lower than at the unmanaged vineyard fallows. Thus, the applied management strategies were not able to preserve the status quo of the 1970s on the calcareous grasslands, but simply prevented natural succession in a mostly similar way. Therefore, these measures only archived that community shifts on these sites were somewhat less severe and more in parallel than on vineyard fallows, which showed much more arbitrary and stochastic community shifts. Consequently, the management concepts applied at these calcareous grasslands were not able to outweigh the complex external impacts affecting these habitats (e.g. influences from adjacent areas, nutrient loads, changing climate), but had the capability to buffer these negative influences to some extent.

In contrast, the community shifts at the studied vineyard fallows were much more dynamic, reflecting habitat characteristics and the unbuffered effects resulting from large and meso-scale environmental changes over the last few decades. Turn-over rates were considerably higher at the vineyard fallows fostering their stochasticity in community evolution. The higher habitat connectivity of the vineyard fallows compared to the highly isolated calcareous grasslands might reinforce these turn-over dynamics. Consequently, the missing connectivity among calcareous grassland makes that arbitrary losses of species cannot be compensated by immigration within short time. Furthermore, gene flow among these isolated populations will be strongly hampered or even completely blocked so that populations might also disappear due to the degradation of their gene pools (cf. HABEL & SCHMITT 2012).

In spite of the notable differences between the managed calcareous grasslands and the unmanaged vineyard fallows, both habitat types show remarkable colinearities in the ecological traits of the species being lost (Fig. 4.2). These colinearities are unlikely to be influenced by the differences in management and connectivity, but apparently are triggered by large-scale environmental factor complexes provoking destructive impacts on butterfly communities in general, independently from habitat type. As a result, these impacts cause a similar evolutionary trend towards species poor and generalist-dominated communities, and thus represent a more holistic problem for the conservation of biodiversity (e.g., MCKINNEY & LOCKWOOD 1999; WARREN et al. 2001; POLUS et al. 2007).

Table 4.3: Percentage of the importance of predictor variables used for constructing environmental niche models of calcareous grasslands and vineyard fallows respectively. The higher the value, the larger is the importance of the respective environmental variable for the model construction.

	calcareous grasslands	vineyard fallows
altitude	2.0	1.6
aspect	9.7	17.2
brightness	9.9	1.3
landuse	72.2	40.3
greenness	1.1	2.3
NDVI	2.5	6.4
NDWI	0.2	5.2
slope	2.4	25.7

Interpreting the observed functional rearrangements of the community structures reflected by strong modifications in the proportional assignments to the different species traits analyzed, two major fields of impacts might have predominant influence on the observed calcareous grasslands and vineyard fallows. Eutrophication and monotonization of the landscape might mostly explain the strong decline of monophagous, sedentary and xerothermophilic species whereas climate change might mostly impact hygrophilic, mesophilic and continental species. However, the combined influence of both factors might enhance their single effects.

While it is obvious that rising global temperatures should harm hygrophilic, mesophilic and continental species not adapted to such a warmer environment, they also should, on the other hand, favour heat-loving species. However, eutrophication of habitats is strongly enhancing growth capacities of plants, hereby remarkably deteriorating the microclimatic conditions close to the ground. This microclimatic cooling still is not compensated by the global increase of temperatures and is particularly affecting the successful development of pre-imaginal stages of xerothermophilic species. These climatic changes are even aggravated by the missing connectivity of the landscape not allowing species to shift their habitats for compensating negative climatic effects (cf. HOF et al. 2011). All these aspects together foster communities dominated by common generalist species and the successive and unrecoverable loss of specialists (cf. BOURN & THOMAS 2002; WENZEL et al. 2006). Therefore, island-like nature reserves have shown to be able to preserve habitat structures, but they have not been capable to conserve the functional characteristics of an interconnected system of habitats necessary to preserve their complex biological diversity. Without adjustments in nature conservation strategies and considerably enhanced efforts in enlarging and connecting high quality habitats, the future perspectives cannot be seen more optimistic.

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

This chapter has been submitted to *Environmental Management*

The work was conducted in collaboration with ANNA F. CORD from the Helmholtz Centre for Environmental Research, as well as SWEN NEKUM and DENNIS RÖDDER from the Zoological Researchmuseum Koenig.

Introduction

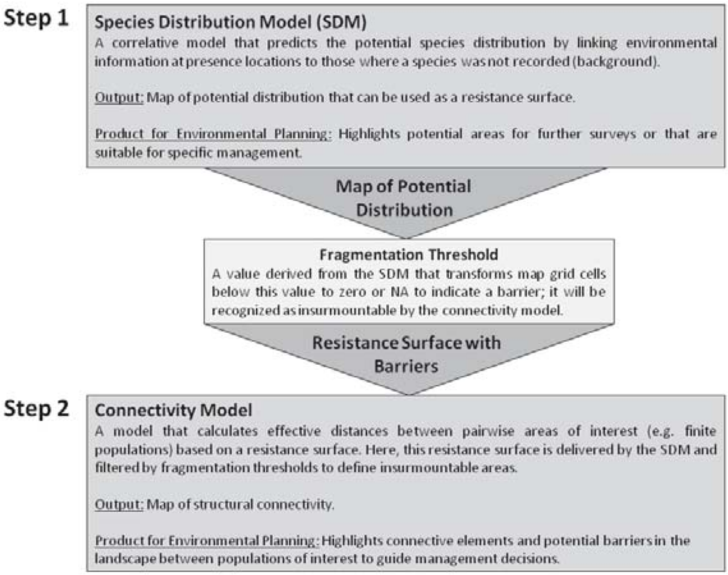
Climate change and continuing habitat loss through human land-use are currently considered as major threats for global biodiversity (Bellard et al. 2012; Devictor et al. 2012). Although not fully understood, some authors (e.g., Hof et al. 2011) assume synergistic effects between both processes could 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).



Species Distribution Model (SDM)
A correlative model that predicts the potential species distribution by linking environmental information at presence locations to those where a species was not recorded (background).

Output: Map of potential distribution that can be used as a resistance surface.

Product for Environmental Planning: Highlights potential areas for further surveys or that are suitable for specific management.

Fragmentation Threshold
A value derived from the SDM that transforms map grid cells below this value to zero or NA to indicate a barrier; it will be recognized as insurmountable by the connectivity model.

Connectivity Model
A model that calculates effective distances between pairwise areas of interest (e.g. finite populations) based on a resistance surface. Here, this resistance surface is delivered by the SDM and filtered by fragmentation thresholds to define insurmountable areas.

Output: Map of structural connectivity.

Product for Environmental Planning: Highlights connective elements and potential barriers in the landscape between populations of interest to guide management decisions.

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	Tasseled Cap Transformation, involving bands 1-5 & 7	comparable to a principal component analysis to transform correlated bands into orthogonal axes			
brightness					
wetness					

$_a$ 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.

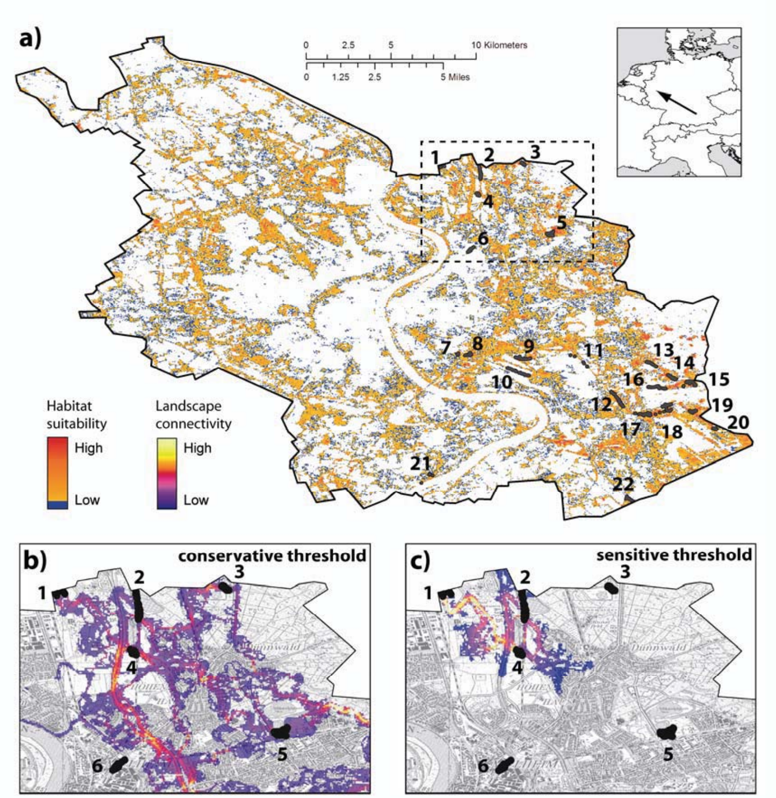


Figure 5.2: Potential distribution (a) and connectivity (b & c) of the sand lizard (*Lacerta agilis*) in the city of Cologne. The upper panel shows the predicted habitat suitability, where blue color highlights the value range between the two fragmentation thresholds used in this study. Non-colored regions 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.

PART B
PCM'S IN LANDSCAPE GENETICS

CHAPTER 6

Comparative landscape genetics of three closely related sympatric Hesperid butterflies with diverging ecological traits

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"Doing science, particularly the synthesis of disparate ideas, is not as arcane as it is often made out to be. Discipline and taste play a vital role, but the activity is familiar to anyone who has made some effort to be creative"

— JOHN HENRY HOLLAND

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The work was conducted in collaboration with NIKO BALKENHOL from the Wildlife Science Department, University of Göttingen, KATHARINA J FILZ from the Biogeography Department, University of Trier, JAN C HABEL from the Department of Ecology and Ecosystemmanagement at the TU Munich and DENNIS RÖDDER from the Zoological Researchmuseum Koenig.

Introduction

In the theory of island biogeography, MCARTHUR & WILSON (1967) predicted the evolution of biodiversity on islands based on two key factors: habitat size and isolation. Later, this island based model was adopted to explain population structure of organisms in mainland ecosystems consisting of habitat patches surrounded by a semi- or non-permeable matrix. This mainland transformation of the theory of island biogeography inspired the fundamental paradigm of the metapopulation concept (LEVINS 1969; HANSKI 1999) and also of the neutral theory in both macroecology and population genetics (HU et al. 2006; LOMOLINO & BROWN 2009). Ultimately, island biogeography theory revolutionizes our thinking on habitat fragmentation and conservation biology (summarized in LAURANCE 2009). Apart from habitat size and isolation, spatial biodiversity patterns are also influenced by additional factors such as habitat quality (DENNIS & EALES 1997), intrinsic characteristics of species-specific dispersal behaviour (CONRADT et al. 2001; VAN DYCK & BAGUETTE 2005) and ecological tolerance (HABEL et al. 2009a) of species. Importantly, population responses are highly species-specific, when the quality of the landscape matrix in between suitable habitat patches is reduced (GOODWIN 2003). This would also have consequences for global biodiversity (FAHRIG 2003; HOF et al. 2011) and large scale conservation efforts (SEIFERLING et al. 2012).

Understanding the effects of the landscape matrix on realized dispersal and functional population connectivity is also a major focus of landscape genetics (HOLDEREGGER & WAGNER 2008; STORFER et al. 2010; MANEL & HOLDEREGGER 2013). Incorporating spatial landscape information with population genetic data goes far beyond the classical analysis of isolation-by-distance (IBD; WRIGHT 1943). Species respond differently to the landscape, in terms of their dispersal, which ultimately affects the rates of gene flow among local populations (GOLDBERG & WAITS 2010; RICHARDSON 2012). While the classical isolation-by-distance approach introduced by WRIGHT (1943) accounts for the geographic (Euclidean) distance between sampled populations only, other approaches such as the recently proposed isolation-by-resistance (IBR) concept (MCRAE 2006) accounts for these species-specific responses to different landscape components that impede or favor gene-flow across a given landscape matrix.

Many studies assess landscape effects on gene flow in only a single species. However, to understand how landscape effects on gene flow differ between species, and to take effective conservation actions, it is important to analyze multiple species in the same landscape using identical methods (SCHWENK & DONOVAN 2011). However, past studies comparing different species mostly focused on species that inhabited comparable habitats, but were taxonomically independent (GOLDBERG & WAITS 2010; RICHARDSON 2012; POELCHAU & HAMRICK 2012). A different comparative approach is to analyze landscape genetic relationships in closely related taxa inhabiting the same landscape. Such a focus on taxonomically related sympatric species (i.e., congeneric species which have the same or overlapping geographic ranges, regardless of whether or not they co-occur at the same locality) allows the assessment of traits that gradually change between the congeners independently from confounding effects that may arise in relation to different evolutionary histories or environments, respectively (STEELE et al. 2009; DAWSON 2012). Next to dispersal propensity, niche breadth (i.e. the degree of specialization on specific habitat traits) is a very important trait in this respect, as it is directly associated with the available habitat within a landscape.

Generalist species can be found in a broader variety of ecosystems, showing higher abundances and broader spatial distributions. In contrast, specialist species demanding certain habitat conditions are often geographically restricted to specific habitats and usually occur in lower local abundances (HABEL et al. 2013). Apart from ecological demands, connectivity among local populations is further influenced by the dispersal propensity of species. Typically, sedentary species are mostly characterized by rather limited individual exchange compared to species with strong dispersal behavior. These ecological and behavioral traits also affect the genetic structure of generalist versus specialist species (HABEL et al. 2009a; 2013; HABEL & SCHMITT 2012). Organisms with specific habitat demands and restricted dispersal behavior should generally be characterized by low gene flow resulting in strong genetic differentiation. In contrast, species with weaker habitat specificity and higher dispersal propensity should show increased levels of gene flow, leading to a lack of genetic differentiation. Importantly, landscape influences on gene flow and resulting genetic patterns could also differ between generalist and specialist species inhabiting the same landscape.

In this study, we present a comparative landscape genetic analysis involving three closely-related butterfly species, to assess the impact of landscape parameters (i.e., land use, topography and climatic conditions) on the genetic structure of sympatric species with different ecological traits. We re-analyzed a molecular dataset taken from a previous study (LOUY et al. 2007), where landscape effects were previously ignored, involving three congeneric, but ecologically divergent skipper species of the genus *Thymelicus* (HUBNER 1890). The three species include the generalist *T. lineola*, which occurs in high abundances and shows strong dispersal propensity; the specialist *T. acteon* which is sedentary and occurs restricted to specific habitats; and *T. sylvestris,* which lies in between these two extremes in terms of habitat specificity and dispersal abilities. Using these three species, we (i) investigate the impact of ecological traits on species-specific functional landscape connectivity and (ii) determine the overall relevance of landscape characteristics for connectivity in each species, as well as the individual importance of topography, climatic conditions and land-use parameters. We hypothesized that species-specific landscape effects on gene flow should follow the cline of specialization in the three Hesperid butterflies, with strongest landscape effects on genetic differentiation in the most specialized *T. acteon* and weakest landscape effects in the generalist *T. lineola*.

Material and Methods

Ethics statement

The research was conducted under permission, to collect butterflies and to work in several protected areas, by the local authorities of Saarbrücken (Germany, Saarland), Koblenz (Germany, Rhineland-Palatinate), Luxembourg, and Metz (Loraine, France). Imagoes of the respective species were stored in liquid nitrogen until genetic analysis.

Study area and species

Our study area is located in the south-west of Germany and includes adjacent parts of France and Luxembourg (Fig. 6.1, Table 6.S1). The sampling sites covered an area of approximately 120 km in north-south direction and 100 km in east-west direction. The landscape is characterised by a mosaic of residential areas, agricultural land, meadows, forests and semi-natural calcareous grasslands. Especially grasslands, but also some meadows and forest skirts provide suitable habitats for the three selected *Thymelicus* species, acting as valuable retreats and stepping stones (WENZEL et al. 2006).

The three selected model species *T. sylvestris*, *T. lineola* and *T. acteon* are closely related to each other with *T. lineola* and *T. acteon* being most distant related and where *T. sylvestris* clusters to a monophylum with *T. acteon* (Supporting information, Material 6.S1). The three species show different habitat demands, even if they are co-occurring at suitable grassland patches: *T. lineola* occupies a broad ecological niche (ASHER et al. 2001) and exhibits strong dispersal behaviour (BINK 1992). This combination of wide occurrence and strong dispersal behaviour results in a wide-spread, spatially continuous distribution. In contrast, *T. acteon* demands specific habitat characteristics like xerothermic climatic conditions and consequently occurs only in highly restricted, geographically disjunct calcareous grasslands. The third, intermediate species, *T. sylvestris* stands in-between both extremes, showing a broad ecological tolerance (ASHER et al. 2001), similar to the generalist *T. lineola*, but shows a rather restricted dispersal behaviour (Bink 1992).

Molecular data and genetic cluster analysis

For our comparisons, we used a population genetic dataset based on 15 polymorphic allozymes published previously by (LOUY et al. 2007) who did not account for landscape effects. Several studies have shown that the implications as drawn from allozymes and, where available, microsatellites loci were highly congruent in butterflies (MEGLÉCZ et al. 1998; HABEL et al. 2009b; HABEL et al. 2011). Here, the use of allozymes instead of other marker systems such as microsatellites has two advantages. 1) In Lepidopterans, locus-specific microsatellites are difficult to find and suitable polymorphic loci are consequently rare (MEGLÉCZ & SOLINAC 1998; MEGLÉCZ et al. 2004; HABEL et al. 2008; FINGER et al. 2008). This is most likely due to almost identical flanking regions in the Lepidopteran microsatellite DNA (MEGLÉCZ et al. 2004; ZANG 2004). However, specificity of these regions is a crucial prerequisite for successful primer annealing (ZANG 2004). 2) From a landscape genetic perspective, the use of potentially adaptive marker systems might be beneficial in the detection of spatial genetic differentiation in contrast to neutral marker systems, because spatial signals in markers under selection would appear more rapidly (LANDGUTH & BALKENHOL 2012).

The data set comprised in total 1,063 individuals (417 *T. sylvestris*, 380 *T. lineola*, 160 *T. acteon*) sampled at 12 locations which were distributed across the same study area. Sample sizes ranged from 17 to 44 individuals per species and location. *Thymelicus sylvestris* and *T. lineola* were sampled at identical locations, while *T. acteon* was not found at four of the sampled locations and the data set was supplemented by one additional location (Fig. 6.1). The 15 enzyme systems provide the following 18 loci: MDH (2 loci), G6PDH, ACON, MPI, AAT (2 loci), FUM, PGI, ME, HBDH, APK, PGM, 6PGDH, IDH (2 loci), GPDH and $\text{PEP}_{\text{Phe-Pro}}$. Most of these enzymes showed polymorphisms, except enzyme ME in *T. lineola* and GPDH in *T. sylvestris*. Details about the analytical procedure and the specific running conditions are given in (LOUY et al. 2007). We used the resulting dataset to estimate pairwise F_{ST} and D_{est} for each species in programmes ARLEQUIN 3.1 (EXCOFFIER et al. 2005) and SMOGD (CRAWFORD 2009), respectively. The use of these two different measures of inter-population differentiation was recently recommended (LENG & ZHANG 2011), because of the different underlying assumptions of either measure so that their combination might provide a more detailed impression into the underlying evolutionary processes of differentiation (see LENG & ZHANG 2011 and discussion in this study for further details). Tests for Hardy-Weinberg equilibrium and summary statistics for genetic diversity and differentiation were also calculated in ARLEQUIN 3.1.

Prior to inferring landscape effects on genetic differentiation, the number of genetic groups (*K*) as well as their spatial delineation was evaluated for each species separately using the genetic clustering method implemented in the software GENELAND (GUILLOT & SANTOS 2009). This was necessary because (*i*) genetic differences can occur without any obvious landscape pattern (e.g. along secondary contact zones after postglacial expansion from distinct refugia or through anthropogenic introductions from another source population), which in turn would lead to (*ii*) erroneous conclusions on isolation-by-distance IBD/isolation-by-resistance IBR analyses on spatially independent structured data. GENELAND assigns geo-referenced individuals to genetics clusters (*K*) that maximize Hardy-Weinberg- and Linkage-Equilibrium. *K* was treated as unknown to allow GENELAND to vary *K* within a given range between 1 and the maximum number of populations depending on the species (i.e. 7 in *T. acteon* and 11 in both *T. sylvestris* and *T. lineola*). Markov Chains were run for 3,000,000 generations and sampled every 1000th generation, after an initial burn-in of 300 samples after thinning (10 %). Markov Chains with these settings were run 10 times independently and the iteration with the highest log posterior probability was chosen for inferring the most likely *K* and individual assignments.

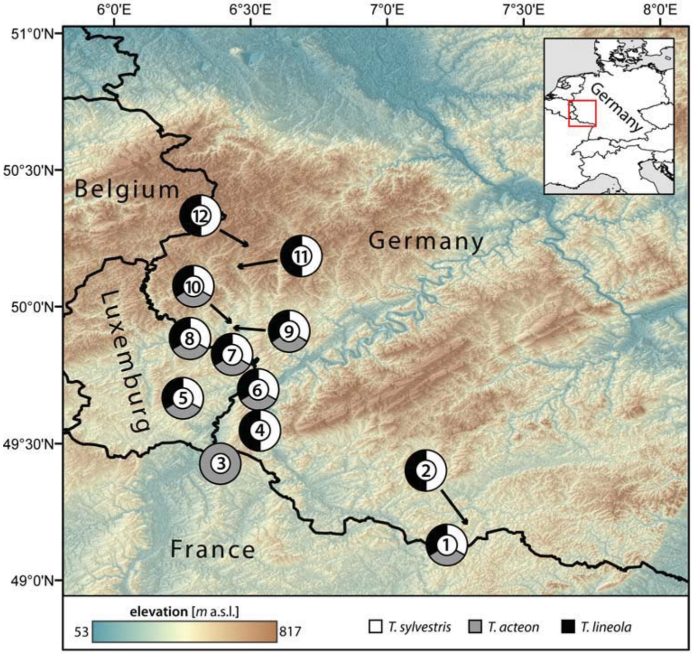


Figure 6.1: Locations of populations studied for all three *Thymelicus* species in southwestern Germany and adjoining areas in France and Luxemburg.

Modelling landscape effects on genetic differentiation

To test for landscape influences on genetic differentiation in each species, we modeled multiple species distribution models (SDM) incorporating topographic, bioclimatic and/or land use features. We then used resulting SDMs as resistance surfaces to derive inter-population connectivity estimates based on electrical circuit theory, and statistically compared these connectivity estimates to actual genetic differentiation. SDMs are increasingly applied for resistance surface parameterization in landscape genetic studies (POELCHAU & HAMRICK 2012, ORTEGO et al. 2012) even under longer evolutionary time scales (BELL et al. 2009, DEVITT et al. 2013), since they avoid the subjective parameterization of resistance surfaces which was criticized in the past (SPEAR et al. 2010).

Species records

To model SDMs for the three *Thymelicus* species in the study area, presence data were taken from personal observations of JCH, D. LOUY and T. SCHMITT (Germany) covering the years 2003-2012. Further presence data were added from high resolution records downloaded from the GBIF database (www.gbif.org). The final datasets comprised 67 records for *T. sylvestris*, 62 for *T. lineola* and 28 records for *T. acteon*. Given their specific habitat demands and the sampling effort that was performed across the study area for either species (Fig. 6.1), we are confident to have compiled a representative sample that covered the realized distribution of the species in our study area.

Environmental layers

For construction of the SDMs, we used freely available GIS based environmental layers. Bioclimatic data based on monthly averaged temperature and precipitation data with 30 arc seconds spatial resolution was obtained from the Worldclim Database (Vers. 1.4; www.worldclim.org; HIJMANS et al. 2005). The comprehensive set of 19 bioclimatic variables are thought to be highly relevant for shaping species' Grinnellian (abiotic) niches (BEAUMONT et al. 2005). In order to minimize the degree of inter-correlation among the variables (i.e. to keep pair-wise Pearson´s $R^2 < 0.75$), we selected a subset of variables (bio3, 7, 8, 9, 10, 11, 12, 15, 18, see Table 6.3 / Appendix 6.S3 for definitions) which were assumed to be most relevant for the study species. Topography-related data were derived from the SRTM Shuttle mission in 90 meters resolution (available through USGS seamless server; Table 6.S2). Based on the altitude layers, we calculated slope and aspect using ARCGIS 9.3 (ESRI Redlands, California, USA). Finally, CORINE land use related data was obtained from the European Environmental Agency (www.eea.europa.eu). We either used CORINE 2006 data to assess current habitat availability as well as CORINE 1990 data for assessing recent land use changes. All environmental layers were re-sampled to uniform grid resolution of 90 m.

Calculating the Potential Connectivity Model

We defined a set of hypotheses based on the available environmental data and generated five variable sets for comparing landscape effects on species-specific gene flow (therein called scenarios, Table 6.S2). These scenarios represent various habitat characteristics (i.e. climate, topography and land use) that were found to be important for butterfly distributions at different spatial scales in previous studies (WEISS et al. 1988; WARREN et al. 2001; PE'ER et al. 2004; 2006; PIN KOH 2007; MARINI et al. 2009; FILZ et al. 2013a). Based on these variable sets and the respective species records, we computed species distribution models (SDMs) with the software MAXENT 3.3.3e (PHILLIPS et al. 2006) to generate maps displaying habitat suitability for each species under a given scenario. As many other presence-pseudoabsence SDM algorithms, MAXENT links environmental conditions at presence records of a given taxon to those environmental conditions available within a specific geographic area (background) to predict spatial patterns of environmental suitability. The SDM output represents the likelihood of species potential occurrence across a geographic area of interest (projection; for a detailed description see ELITH et al. 2011). We used MAXENT instead of other available algorithms because it frequently outperforms other approaches (ELITH et al. 2006; HEIKKINEN et al. 2006), even if the number of presence locations is rather limited (HERNANDEZ et al. 2006; WISZ et al. 2008). We ran MAXENT with the default settings but used a bootstrap approach, which allows random selection of 70% of presence locations for model training and the remaining 30% for model testing. This procedure was repeated for 100 times and an averaged map of suitable habitats was generated across all repetitions. As output we selected the logistic format which ranges linearly from 0 (not suitable) to 1 (fully suitable). For model evaluation, the area under the receiver operating characteristic curve (AUC) was used (SWETS 1988). In particular, the AUC as internally computed in MAXENT is a measure for the ability of the model to distinguish the given presence records from the background data accounting for the proportion of the study area which is predicted to be suitable for the target species (PHILLIPS et al. 2006). The AUC ranges between 0.5 (random prediction) to 1.0 (perfect discrimination between presence and pseudo-absence).

For the land use change scenario, we used land use data from CORINE 2006 as a categorical environmental layer - just as we had done for the land use scenario. However, we subsequently projected the model fit onto the CORINE 1990 layer to assess habitat change in terms of a stability surface. The stability surface is the average of both CORINE layers, with high values indicating suitable habitat patches that remain stable over the 16 years time span, whereas low values represent low habitat suitability, a strong habitat change in time, or both. This approach for calculating stability surfaces is commonly used to estimate land use change and habitat suitability across time (see BELL et al. 2006 and DEVITT et al. 2013 for examples).

The resulting SDMs were used as conductance surfaces (i.e., high values indicate good conductivity between two sites, whereas low values indicate poor conductivity; MCRAE et al. 2008) in CIRCUITSCAPE v.3.4.1 to calculate resistances to movement and gene flow among sampling locations (MCRAE et al. 2008). CIRCUITSCAPE is based on electrical circuit theory, which was recently adapted from electrical engineering for the assessment of landscape ecological questions (MCRAE et al. 2008). In particular, CIRCUITSCAPE defines nodes (grid cells) and associated unit resistors (the resistance value) that connecting two nodes and calculates resistance distances between focal locations based on a nodal analysis algorithm as described in (MCRAE 2006). As the habitat matrix had a very high extent (i.e. ~7.6 Mio. cells), we chose a four-neighbor-connection scheme in order to meet the available computational capacities. It has been previously shown that four and eight-neighbor-connection scheme lead to highly similar outcomes (MCRAE & BEIER 2007).

Comparing connectivity estimates with genetic data

Resulting resistance values among locations were statistically compared to estimates of genetic differentiation (i.e. F_{ST} and D_{est}) using linear regression models as well as multiple regressions on distance matrices (MRDM; LICHSTEIN 2007) in R v.2.14.1 (R DEVELOPMENT CORE TEAM 2012). For the linear regression models, the Akaike Information Criterion corrected for small sample sizes (AICc) was used for model comparisons within each species (BURNHAM & ANDERSON 2002). Despite their sensitivity for non-independence in pair-wise comparisons, multi-model inference based on information theory has been frequently applied in landscape genetic analyses (Goldberg & Waits 2010; Richardson 2012) as the error entering the comparison was assumed to be equal for each model, which did not affects model ranking and thus still allows for assessing the relative model performance. To ascertain results obtained with the AIC model selection, we also estimated significance of MRDM models using 1,000 permutations. For MRDMs, the *ecodist* package for R was used (Goslee & Urban 2007).

Results

Genetic structures

No significant deviation from Hardy-Weinberg equilibrium was detected for any population in the respective species. Genetic diversity was comparatively low in *T. lineola* (mean ± SE; $AR = 1.78 \pm 0.17$ $H_E = 9.6 \pm 2.1$, $H_O = 9.2 \pm 2.1$), while *T. acteon* showed highest genetic diversities ($AR = 1.88 \pm 0.18$, $H_E = 14.9 \pm 2.9$, $H_O = 12.5 \pm 2.6$). *Thymelicus sylvestris* showed an intermediate level of genetic diversity, as compared to its congeners ($AR = 1.80 \pm 0.10$, $H_E = 11.9 \pm 1.5$, $H_O = 11.0 \pm 1.4$). The genetic differentiation was low in *T. lineola* ($F_{ST} = 0.0081$; $D_{est} = 0.0012$; p = n.s.), while we detected highest genetic differentiation for *T. acteon* ($F_{ST} = 0.0718$; $D_{est} = 0.0143$; $p < 0.0001$). Again, *Thymelicus sylvestris* showed an intermediate level of genetic differentiation, with a rather low among-population variance ($F_{ST} = 0.0179$; $D_{est} = 0.0039$; $p < 0.0001$) (Table 6.1).

Table 6.1: Summary statistics for genetic diversity and differentiation for the three *Tymelicus* buttlerflies.

	T. lineola	*T. acteon*	*T. sylvestris*	*source*
AR	1.78 ± 0.17	1.88 ± 0.18	1.80 ± 0.10	Louy *et al.* 2007
H_E	9.6 ± 2.1	14.9 ± 2.9	11.9 ± 1.5	Louy *et al.* 2007
H_O	9.2 ± 2.1	12.5 ± 2.6	11.0 ± 1.4	Louy *et al.* 2007
P_{tot}	52.0 ± 9.7	66.0 ± 9.1	42.9 ± 7.9	Louy *et al.* 2007
P_{95}	36.4 ± 9.4	49.3 ± 13.4	32.3 ± 4.2	Louy *et al.* 2007
F_{ST}	0.0081	0.0755	0.0179	Louy *et al.* 2007
D_{est}	0.0012	0.0143	0.0039	Habel *et al.* 2013

Genetic clustering results

The posterior density and log-likelihood levels of all GENELAND runs stabilized long before the end of the Markov Chains, indicating that convergence was reached (Fig. 6.S1). For each of the species, all 10 replicate MCMC runs converged on K = 1 panmictic cluster (Fig. 6.S1), indicating no absolute barriers affecting IBD or IBR assumptions.

Species Distribution Models

AUC values derived from the SDMs ranged from 'poor' (AUC = 0.66, scenarios 'land use' and 'land use change' in *T. sylvestris*, Table 6.2) to 'good' (AUC = 0.86, scenario 'all' in *T. lineola*, Table 6.2) according to the classification scheme for model quality from (ARAÚJO et al. 2005) adapted from (SWETS 1988). Variable contributions in multi-factorial SDMs (scenarios 'climate', 'topography' and 'all') differed between species (Table 6.3). For the topography scenario, *slope* contributed most to the SDM in all three species, followed by *aspect* and *altitude* (Table 6.3). In *T. acteon* a different set of variables had higher explanative power with respect to the climate scenario. Here, *precipitation of the warmest quarter* (bio18) was most important, followed by a set of temperature related variables (bio3, 7, 8, 9, 11; Table 6.3). In contrast, *Thymelicus lineola* and *T. sylvestris* had very similar variable contributions as a result of the highly similar distribution of occurrence records. In these species, the *mean temperature of the coldest quarter* followed by the *temperature annual range* contributed to more than half of the total model (Table 6.3). Finally, considering the entire predictor set, a combination of *slope* and *land use* contributed most in all species, but where *T. lineola* and *T. sylvestris* had again more similar variable contributions rather than *T. acteon* (Table 6.3). In accordance, *T. lineola* and *T. sylvestris* showed similar potential distributions containing large continuous areas of high suitability, whereas *T. acteon* shows a highly patchy distribution with large unsuitable areas surrounding potential habitat patches (Fig. 6.2).

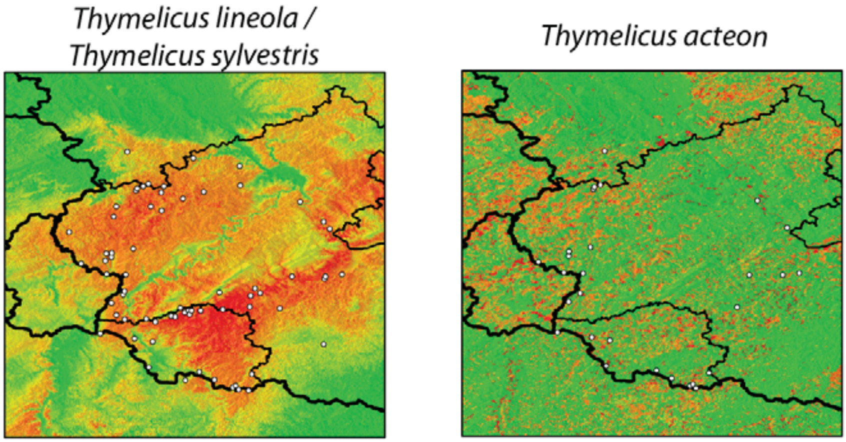


Figure 6.2: SDM output for *Thymelicus lineola* and *T. sylvestris* (left panel) as well as *T. acteon* (right panel) respectively. White circles on SDMs are presence locations used for modeling; Warmer colors (red) indicate higher suitability depending on the best model as presented in Table 2 (climate for *T. sylvestris*; land use change for *T. acteon*; note that *T. lineola* does not have a best model because of its panmictic state. Therefore, also climate is represented here).

Landscape effects of genetic differentiation

Results obtained with the various SDM-based connectivity estimates differed strongly among the three model species (Table 6.2). The generalist species *T. lineola* showed neither IBD nor any form of IBR using F_{ST} (max ΔAICc = 0.86). Using D_{est}, the IBD scenario produced the best model (AICc = -806.68, ω = 0.48) however with a weak relationship ($R^2 = 0.045$, $p = 0.064$). Furthermore, MRDM showed no landscape related signals for either estimate of genetic differentiation in *T. lineola*, suggesting that gene flow in this species is not affected by any spatial or landscape features at this scale. The most specialized species, *T. acteon* showed no significant IBD, but significant IBR for two scenarios (land use & land use change) with both F_{ST} and D_{est} under multi-model inference. These signals become also prominent using MRDM for inference, even though models were slightly insignificant at $p = 0.05$ (land use change F_{ST}: $R^2 = 0.232$, $p = 0.051$ / D_{est}: $R^2 = 0.190$, $p = 0.102$). The combined results from AIC and MRDM suggest that land use and land use change both affect genetic differentiation among *T. acteon* populations. Genetic differentiation in *Thymelicus sylvestris* corresponded most strongly to the connectivity estimates derived from the SDM incorporating all variables (AICc = -271.89, ω = 0.67) using F_{ST}

and the information-theoretic approach. The climate related scenario was also within the most reliable models under AICc (ΔAICc = 1.65, ω = 0.29). However, MRDM suggested that land use and land use change were also important for explaining genetic differentiation in this species. The opposite becomes obvious using D_{est} as differentiation metric. Here, the information theoretic approach reveals climate, land use and land use change as highly informative, with climate being most important (AIC = -723.08, ω = 0.45). Surprisingly, the scenario covering the entire variable set contributed nearly no information (ΔAICc = 4.44, ω = 0.05). In addition, MRDM highlighted only climate as significantly related to genetic differentiation. In summary, the combined results of different differentiation metrics and inference methods suggest that the climatic conditions across the study site deliver the most important and stable relationship for adjusting gene flow in the intermediate species, with additional effects of land use. Classical IBD received less support against IBR models (Table 6.2, Fig. 6.S2) in all species. Interestingly, topography seems to play no role at all for any of the species.

Table 6.2: Comparison of the genetic structure in three *Thymelicus* butterflies with different landscape parameter sets. Genetic differentiation was inferred by F_{ST} (upper half) and D_{est} (lower half) respectively. SDM AUC values for each scenario (excepting classical IBD) showing the model quality are given as well as parameters for both, linear regression models and multiple regression based on distance matrices (MRDM). Bold values highlight models with highest support (ΔAICc < 2 in combination with a significant R^2 in linear regression models; significant R^2 in MRDMs).

	SDM	**Linear regression model**					**MRDM**	
Model F_{ST}	AUC	AICc	ΔAICc	ω	R^2	p	R^2	p
T. lineola								
Fst~distance	-	-321.65		0.21	-0.003	0.359	0.016	0.569
Fst~topography	0.76	-321.44	0.21	0.19	-0.007	0.424	0.012	0.603
Fst~climate	0.81	-321.41	0.23	0.19	-0.007	0.431	0.012	0.602
Fst~all	0.86	-320.87	0.77	0.14	-0.017	0.741	0.002	0.828
Fst~landusechange	0.68	-320.84	0.81	0.14	-0.018	0.795	0.001	0.854
Fst~landuse	0.67	-320.78	0.86	0.14	-0.019	0.893	0.000	0.926
T. acteon								
Fst~landusechange	**0.69**	**-94.70**		**0.56**	**0.202**	**0.009**	0.232	0.051
Fst~landuse	**0.71**	**-93.90**	**0.80**	**0.37**	**0.179**	**0.014**	0.209	0.069
Fst~distance	-	-88.12	6.58	0.02	-0.009	0.393	0.028	0.433
Fst~climate	0.79	-87.87	6.83	0.02	-0.018	0.476	0.020	0.748
Fst~topography	0.79	-87.44	7.26	0.01	-0.034	0.737	0.004	0.821
Fst~all	0.84	-87.41	7.29	0.01	-0.035	0.771	0.003	0.772
T. sylvestris								
Fst~all	**0.85**	**-273.53**		**0.67**	**0.252**	**<0.0001**	**0.266**	**0.002**
Fst~climate	**0.78**	**-271.89**	1.65	**0.29**	**0.229**	**<0.0001**	**0.244**	**0.010**
Fst~land use	0.66	-266.28	7.26	0.02	0.147	0.002	**0.162**	**0.024**
Fst~land use change	0.66	-265.52	8.02	0.01	0.135	0.003	**0.151**	**0.035**
Fst~distance	-	-263.78	9.75	0.01	0.107	0.009	0.123	0.068
Fst~topography	0.78	-262.73	10.81	0.00	0.09	0.015	0.106	0.102

Model D_{est}									
T. lineola									
	Dest~distance	-	**-806.68**		**0.48**	0.045	0.064	0.063	0.176
	Dest~topography	0.76	-803.93	2.75	0.12	-0.004	0.373	0.015	0.559
	Dest~climate	0.81	-804.10	2.58	0.13	-0.001	0.329	0.018	0.535
	Dest~landusechange	0.68	-803.59	3.09	0.10	-0.010	0.493	0.009	0.647
	Dest~all	0.86	-803.31	3.37	0.09	-0.015	0.652	0.004	0.780
	Dest~landuse	0.67	-803.10	3.58	0.08	-0.019	0.951	0.000	0.968
T. acteon									
	Dest~landusechange	**0.69**	**-274.21**		**0.45**	**0.159**	**0.021**	0.190	0.102
	Dest~landuse	**0.71**	**-274.09**	**0.12**	**0.42**	**0.155**	**0.022**	0.186	0.090
	Dest~climate	0.79	-269.81	4.40	0.05	0.015	0.244	0.052	0.608
	Dest~distance	-	-268.92	5.29	0.03	-0.016	0.460	0.021	0.614
	Dest~all	0.84	-268.41	5.79	0.02	-0.035	0.765	0.004	0.784
	Dest~topography	0.79	-268.36	5.85	0.02	-0.037	0.845	0.001	0.893
T. sylvestris									
	Dest~climate	**0.78**	**-723.08**		**0.45**	**0.099**	**0.011**	**0.115**	**0.049**
	Dest~land use	**0.66**	**-721.12**	**1.96**	**0.17**	**0.066**	**0.033**	0.083	0.086
	Dest~land use change	**0.66**	**-721.18**	**1.89**	**0.18**	**0.067**	**0.032**	0.084	0.085
	Dest~distance	-	-720.50	2.57	0.12	0.055	0.046	0.073	0.118
	Dest~all	0.85	-718.64	4.44	0.05	0.023	0.139	0.041	0.259
	Dest~topography	0.78	-717.61	5.47	0.03	0.004	0.272	0.023	0.410

Discussion

Studying taxonomically related species inhabiting the same environment makes it possible to infer how species-specific ecological traits affect population genetic structuring without confounding effects of different landscapes or phylogenetic history (Steele et al. 2009). By conducting a comparative landscape genetic study involving ecologically diverging Hesperid butterflies, we found different impacts of landscape parameters on the genetic structure of the three study species.

The obtained results show strong genetic differentiation and high genetic diversities in the specialist species *T. acteon*, and low genetic differentiation with accompanying low genetic diversities in the generalist species *T. lineola* with *T. sylvestris* standing in-between the two congeners. The amount of genetic diversity is typical for butterflies in this region (reviewed in Habel et al. 2013). Our analyses indicate that climate has a strong impact on the connectivity of *T. sylvestris* but that other variables (such as land use) might have become more influential in the most recent times. Land use as well as changes in land use patterns (i.e. assessed over a 16yr period) influences the connectivity of *T. acteon* populations. In contrast, *T. lineola* populations were panmictic, lacking any landscape related effects on genetic differentiation at this spatial scale.

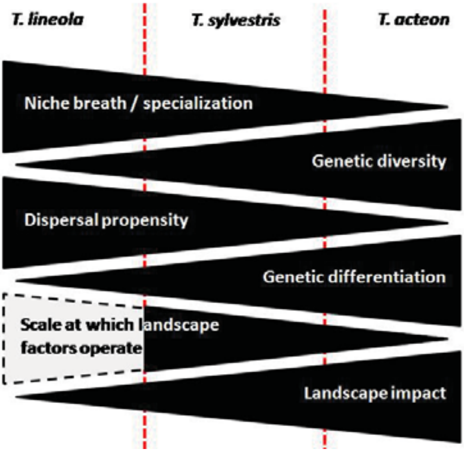


Figure 6.3: Schematic illustration about the gradual effects forcing on the three *Thymelicus* species. Hatched area highlights the hypothesized effect of landscape on gene flow in *T. lineola* on the macro-scale which was not testable in the study area.

Diverging responses to identical landscape conditions

Our data illustrate that closely related species representing a gradient of ecological traits (i.e. from generalist to specialist / from highly mobile to rather philopatric) also show a gradient of changing genetic structures and even more interesting of changing landscape genetic associations (Fig. 6.3). This highlights that ecological traits determine the species-specific resistance of the landscape matrix, so that its effect on population connectivity can differ strongly among closely-related species inhabiting the same landscape.

Table 6.3: Averaged variable contributions for the scenarios 'topography', 'climate' and 'all'. Note that land use dependent scenarios are not shown herein as they contain one single variable.

Scenario	Variable	*T. acteon*	*T. lineola*	*T. sylvestris*
Topograpy	alt	7.1	12.1	10.6
	aspect	21.1	29.7	32.3
	slope	71.8	58.2	57.1
Climate	bio3 (isothermality)	12.0	9.7	8.7
	bio7 (temperature annual range)	10.3	23.8	23.5
	bio8 (mean temperature of wettest quarter)	12.0	3.4	4.0
	bio9 (mean temperature of driest quarter)	11.3	10.1	10.0
	bio10 (mean temperature of warmest quarter)	3.6	4.6	5.7
	bio11 (mean temperature of coldest quarter)	16.1	32.0	31.4
	bio12 (annual precipitation)	5.2	10.0	11.3
	bio15 (precipitation seasonality)	5.4	3.3	3.0
	bio18 (precipitation of warmest quarter)	24.3	3.1	2.4
all	land use	37.7	24.9	23.2
	alt	1.3	8.1	7.7
	aspect	9.3	12.4	14.4
	slope	31.2	24.0	29.7
	bio3 (isothermality)	2.8	3.3	3.3
	bio7 (temperature annual range)	2.3	10.0	8.0
	bio8 (mean temperature of wettest quarter)	4.2	1.9	2.0
	bio9 (mean temperature of driest quarter)	1.0	0.1	0.3
	bio10 (mean temperature of warmest quarter)	0.1	0.7	0.4
	bio11 (mean temperature of coldest quarter)	2.1	6.5	4.7
	bio12 (annual precipitation)	2.1	5.8	4.6
	bio15 (precipitation seasonality)	1.5	1.1	0.8
	bio18 (precipitation of warmest quarter)	4.5	1.2	0.8

The strong genetic differentiation in *T. acteon* is concordant with its patchy occurrence predicted in our SDMs (Fig. 6.2), which were best explained by the land-use parameters derived from the CORINE dataset. Furthermore, land-use related scenarios were the only ones that host an IBR-related signal among all competing scenarios in this species (Table 6.2). Here, the two scenarios 'land-use' and 'land-use-change' fit equally well, irrespective of the genetic differentiation metric or statistical inference method used. Thus, the landscape genetic signal in this specialist species is highly consistent among different analyses, leading to high certainty of inferences.

The slight differences between these two scenarios might be stochastic. However, since there is also consistence about the ranking across all approaches (i.e. land use change steadily explains slightly more variance under each situation than land use), land-use-change might be even more important, when addressing land-use-change over an even larger time period than the 16 years used here. Unfortunately, there is no information available to assess past land-use-changes covering this large geographical extent further into the past. Keeping time-lags between fragmentation and genetic responses accompanying these fragmentations in mind (e.g., as reviewed in KEYGHOBADI 2007) there is some evidence that 16 years are not adequate to detect genetic impacts of altered habitats in this time period in a species with an annual generation time. Changes over this period result just in slightly different resistance surfaces between the scenarios 'land-use' and 'land-use-change'. Nevertheless, *T. acteon* is becoming increasingly vulnerable in large parts of Europe (VAN SWAAY & WARREN 1999) and has likely declined during the past 30 years within the study area due to habitat loss (WENZEL et al. 2006). Thus, the slightly stronger signal of the land-use-change scenario in comparison to the land-use scenario might become even more prominent when extrapolating these changes further decades into the past, highlighting habitat loss as serve danger for this species.

The genetic diversities (such as heterozygosity or mean number of alleles) are highest in *T. acteon* compared to the other two species. This result is somewhat surprising, as the consequence of restricted gene flow and strong geographic restriction of local populations usually leads to rising genetic differentiation and declining genetic diversity, as frequently observed for species demanding specific habitat qualities and/or sedentary dispersal behaviour (HABEL et al. 2009a; KASSEN 2002; PACKER et al. 2005; ZACHOS et al. 2007). However, there are also examples where genetic diversities in rare species exceed those of their common congeners (GITZENDANNER & SOLTIS 2000; ELLIS et al. 2006; KADLEC et al. 2010). This contrasting pattern to neutral genetic theory might be a result from hybridization (RICHARDS & VAN OPPEN 2012; but see ELLIS et al. 2006) or because of time-lags that display the past genetic diversity, when connectivity between populations was much higher than today (KADLEC et al. 2010, SEVERNS et al. 2011). Indeed, genetic differentiation responds to habitat changes quicker than genetic diversity (BALKENHOL et al. 2013; KEYGHOBADI et al. 2005) so that the high genetic diversity observed for *T. aceton* may not yet reflect the negative consequences of on-going habitat alterations for this species.

In contrast to the specialist *T. acteon*, the generalist *T. lineola* represents opposing genetic features: the species shows a broad ecological amplitude and a much higher mobility (HABEL et al. 2009b). This combination led to higher abundance pattern in combination with increased inter-population migration rates. These species traits lead to a rather panmictic genetic structure in our study area that appears to prevent landscape genetic relationships or IBD. This coherence between wide ecological amplitudes, high rates of individual exchanges (e.g., gene flow) and thus low genetic differentiation were frequently observed in other studies (BROUAT et al. 2004; HABEL & SCHMITT 2009). However, it needs to be considered that on a larger study extent, barriers such as oceans, large lakes, mountain ranges might become important for gene flow acting on a macro-scale (LEE-YAW et al. 2009; KEKKONEN et al. 2011). The landscape matrix in our study area did not enable the assessment of such macro-scale effects, since the landscape matrix is rather continuous at this scale and large barriers are lacking, as indicated by the GENELAND results.

Finally, the species standing in-between these two extremes, *T. sylvestris*, has an abundance like *T. lineola* but shows a sedentary dispersal behavior comparable to that of *T. acteon* (BINK 1992). The reduced dispersal propensity of this species coupled with its wide occurrence makes the colonization of a habitat nearby much more likely than of far distant habitats. Consequently, we obtain IBD and IBR signals for many sets of variables in this species (Table 6.2). However, when combining the information from the different assessment methods (F_{ST} vs. D_{est}/multimodel inference vs. MRDM), landscape resistance based on the climate scenario was most important, delivering a consistent strong signal across the different inference methods used

(Table 6.2, see also below). This contrasts to the IBR of *T. acteon*, where climate plays no role at all. In contrast to land-use, climate acts on a meso-scale at our study area (i.e., masking larger areas of the study extent rather than small habitat patches). In *T. sylvestris* the climate related SDM revealed high resistances along river valleys as well as on the higher elevations of the low mountain ranges (Fig. 6.2). These potential barriers act at a much larger scale and extent compared to the small and patchy habitat islands enclosed by more or less unfavourable habitats in *T. acteon.* Consequently, the different landscape features contributing to the IBR signals in these two species highlight the importance of scale and shape of the connective elements (or their respective barriers) in the landscape matrix where methodological shortcomings can be excluded (ENGLER, unpublished). However, the obtained IBR models explain only up to 24 % of the variance in our dataset. That in turn indicates that the remaining variance of our data can only be explained by additional factors such as ecological traits and habitat requirements. These can be even more relevant for butterfly species than habitat size and habitat isolation, e.g. as shown for the Heath butterfly *Coenonympha tullia* (DENNIS & EALES 1997). Nevertheless, the extent of the relationships in our IBD/IBR comparisons are in concert with other studies (GROOT et al. 2011) indicating that gene flow can be interpreted as an important component out of a variety of mechanisms influencing population genetic structure.

Accounting for F_{ST} and D_{est} in landscape genetic studies

Interestingly, in the case of *Thymelicus sylvestris*, the prominent signal under F_{ST} arising from the SDM using all landscape variables becomes completely eliminated when using D_{est} as a differentiation metric. The fact that different metrics can lead to different conclusions is also evident in the ongoing debate about the utility of different genetic differentiation measures (HELLER & SIEGISMUND 2009; RYMAN & LEIMAR 2009; JOST 2009; GERLACH et al. 2010; MEIRMANS & HEDRICK 2011; RAEYMAEKERS et al. 2012). For example, traditional F_{ST}–like metrics are more sensitive to recent demographic changes (which depends e.g. on effective population size) than metrics which are independent of effective population size, such as D_{est} (LENG & ZHANG 2011; RYMAN & LEIMAR 2009; MEIRMANS & HEDRICK 2011; RAEYMAEKERS et al. 2012). This makes F_{ST} more sensible to effects of gene flow or drift in comparison to D_{est}. Thus, from a landscape genetic perspective, using different types of differentiation metrics allows to test for the contribution of landscape effects in contemporary versus past times. If landscape composition change over time (and consequently the amount of gene flow mediated by the landscape), F_{ST} would respond much quicker to those changes while D_{est} remains rather stable over time. In the case of *Thymelicus sylvestris*, this means that D_{est} may highlight the landscape effect (here climate) of highest importance for gene flow in this species in former times, whereas F_{ST} highlights more recent landscape effects on genetic structure that involves also other landscape elements beside climate such as land use and topographical elements.

In contrast to the climate-only scenario, connectivity estimates involving all variables did not give highest importance to climatic factors. In particular, land use and slope contribute almost 54% of the total importance of this scenario, whereas the best performing variables from the climate scenario, bio11 (mean temp of coldest quarter) and bio7 (temp annual range) that contribute together 54.9%, contributing under the full model just 12.7% of the total importance. This might highlight the change of landscape factors important to gene flow in this species. As *T. sylvestris* is indeed common but not very mobile, anthropogenic land transformations of the past decades might now lead to a stronger fragmentation of populations which ultimately lead to changes in the contributions of landscape factors shaping gene flow as shown elsewhere (PAVLACKY et al. 2009). Consequently, this might mean that this species is just at the tipping point of being of conservation concern (*sensu* HABEL & SCHMITT 2012) where population trends swapping from stable to decreasing. Its congeners *T. acteon* and *T. lineola* showing both consistent results across the different metrics underpinning their stable state in terms of their abundance (insentinent and widespread vs. sensible and endangered) and specialization (generalist vs. specialist).

Conclusion

Taxonomically close relatives serve as ideal model systems to study interspecific characteristics in ecological traits without confounding effects derived from different evolutionary histories. Yet, studies investigating the role of landscape on gene flow of closely related taxa inhabiting the same environment are still scarce. Our results reveal that even between sibling species, gene flow is affected by the landscape in very different ways. Thus, it is challenging to predict landscape genetic relationships in one species from a study involving another species, even if the two species are taxonomically closely related. Nevertheless, some generalizations are possible for specialist versus generalist species. In our study, the genetic structure of the generalist species with high dispersal propensities remained unaffected by the current landscape matrix, whereas specialist species were highly sensitive to fine scale habitat features. Changes of these features might therefore affect specialists more readily than generalist species with the negative consequences for their genetic setup. Species with an intermediate degree of specialization (here *T. sylvestris*) also interact with the landscape but at coarser scales in comparison to specialist species (here *T. acteon*). However, in light of global change such species might be on the highest risk due to negative genetic effects such as inbreeding depression, because changes in the habitat matrix can push former meta-population into isolated remnants (HABEL & SCHMITT 2012). This becomes also evident in *T. sylvestris* comparing the genetic structure under either F_{ST} or D_{est}. Further studies focusing on the degree of habitat specialization in addition to dispersal capabilities are needed, ideally conducted with closely related taxa in other areas. Such comparative studies will greatly expand our current understanding of landscape genetic relationships and ultimately lead to more effective conservation and management of biodiversity.

Supplementary material

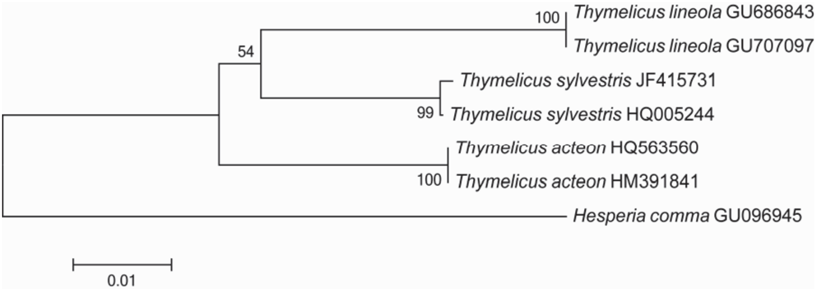
Table 6.S1: Geographic coordinates of the sampling locations. ID numbers correspond to those stated in Fig. 6.1.

Location – ID	lat	lon	*T. sylvestris*	*T. lineola*	*T. acteon*
Niedergailbach – 1	49.128	7.220	x	x	x
Mimbach/Badstube - 2	49.212	7.296	x	x	
Montenach - 3	49.425	6.388			x
Eiderberg/Freudenburg - 4	49.549	6.537	x	x	
Niederanven - 5	49.664	6.252	x	x	x
Wasserliesch - 6	49.696	6.527	x	x	x
Echternacherbrück - 7	49.819	6.428	x	x	x
Ourtal - 8	49.882	6.275	x	x	x
Römersköpfchen - 9	49.921	6.446	x	x	x
Bettingen - 10	49.942	6.427	x	x	x
Schönecken - 11	50.144	6.462	x	x	
Weinsheim/Prüm - 12	50.224	6.488	x	x	

***Material 6.S1.** Evolutionary history of the three Thymelicus butterflies.*

To assess the phylogenetic relationships between the three *Thymelicus* species, we compiled a phylogenetic analysis based on a 658 bp fragment of the mitochondrial COI gene. We conducted a GenBank query under http://www.ncbi.nlm.nih.gov/genbank and selected nucleotide sequences of two specimens for each species as well as choosing one specimen (*Hesperia comma*) as outgroup (Material 6.S1 Table 1; HAUSMANN *et al.* 2011). Sequences were aligned and uncorrected genetic distances (p-distance) between and among species were calculated using the programme MEGA 5.05 (Material 6.S1 Table 2; KUMAR *et al.* 2008; TAMURA *et al.* 2011).

For reconstructing the evolutionary history in *Thymelicus*, a consensus tree based on the Neighbor-Joining method (SAITOU & NEI 1987) was computed in MEGA and inferred using 1000 bootstrap replicates (FELSENSTEIN 1985). The evolutionary distances underlying this consensus tree were computed using the Maximum Composite Likelihood method (TAMURA *et al.* 2004) with transitions, transversions and all three codon-positions included in the analysis (Material 6.S1 Fig. 1).



Material 6.S1 Figure 1: Consensus tree inferred by using the Neighbor-Joining method accounting for the 50% majority-rule. Numbers next to the branches correspond to the bootstrap support (1000 replicates). *Hesperia comma* was used as outgroup taxon.

The generalist *Thymelicus lineola* is most distant related to the specialist species *T. acteon* (5.02 % of substitutions). *Thymelicus sylvestris*, the ecologically intermediary species clusters together with *T. acteon* to a monophylum with a p-distance of 4.3% of substitutions. *Thymelicus lineola* thus represents the paraphylum to the other two species because of a slightly higher genetic distance to *T. sylvestris* (4.5%).

Material 6.S1 Table 1: Species and GenBank accession numbers of the individuals used for estimating genetic distance between species.

Species	GenBank accession no.
Thymelicus lineola	GU686843
Thymelicus lineola	GU707097
Thymelicus sylvestris	JF415731
Thymelicus sylvestris	HQ005244
Thymelicus acteon	HQ563560
Thymelicus acteon	HM391841
Hesperia comma	GU096945

Material 6.S1 Table 2: Uncorrected pairwise genetic distance (average %) of the COI sequences within (diagonal) and between (below diagonal) species of the genus *Thymelicus*.

	T. acteon	*T. lineola*	*T. sylvestris*
Thymelicus acteon (n = 2)	0.00		
Thymelicus lineola (n = 2)	5.02	0.00	
Thymelicus sylvestris (n = 2)	4.30	4.50	0.15

Table 6.S2: Description of the landscape data used for resistance surface building depending on the scenario assumed. Note that the scenarios 'land use' and 'land use change' used the same data source. SDM refers to species distribution model.

Scenario	Description	Data source
Distance	Classical isolation-by-distance measured as straight distance between coordinate pairs.	-
Topography	SDM was computed on three topographical variables: altitude, aspect & slope.	SRTM Shuttle mission available through: http://earthexplorer.usgs.gov
Climate	This SDM incorporates 9 out of 19 bioclimatic variables describing the climatic conditions at each location with respect to species' demands. These are: bio3 (Isothermality), bio7 (Temperature annual range), bio8 (mean temperature of wettest quarter), bio9 (mean temperature of driest quarter), bio10 (mean temperature of warmest quarter), bio11 (mean temperature of coldest quarter), bio12 (annual precipitation), bio15 (precipitation seasonality), bio18 (precipitation of warmest quarter).	Available through: http://worldclim.org
Land use / Land use change	Data for these two SDMs derived from the CORINE Landcover data based on 2006 (land use) and 1990 (projected onto for land use change) landcover.	Available through: http://www.eea.europa.eu
all	Combining topography, climate and land use datasets to assess the impact of all landscape factors in concert.	

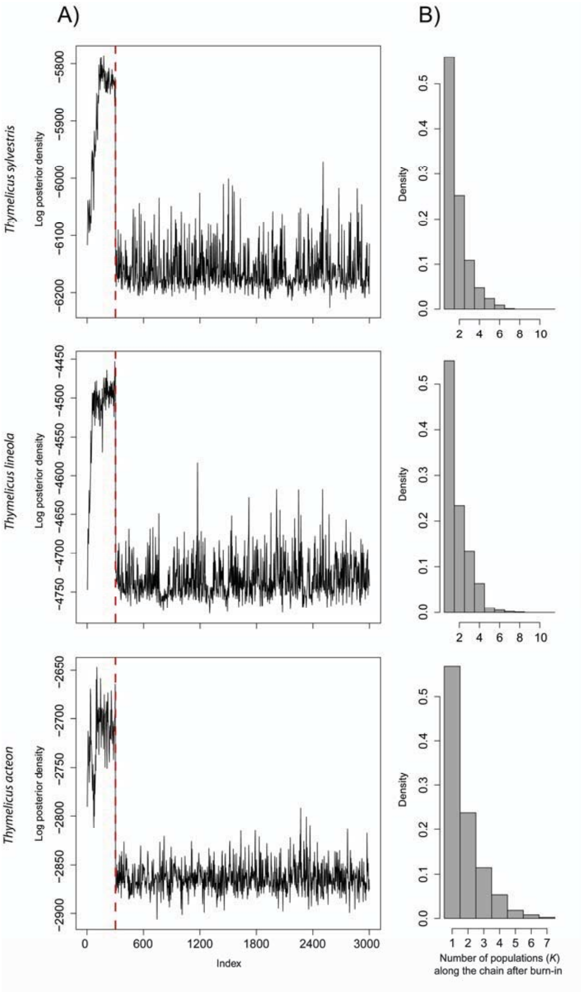


Figure 6.S1: Estimation of the number of panmictic clusters for each species. A) Convergence of the MCMC after thinning (see methods for details). Values prior to burn-in (indicated as red dashed line) were not considered as chain does not reached convergence. B) Frequency of the estimated number of populations along the chain after burn-in.

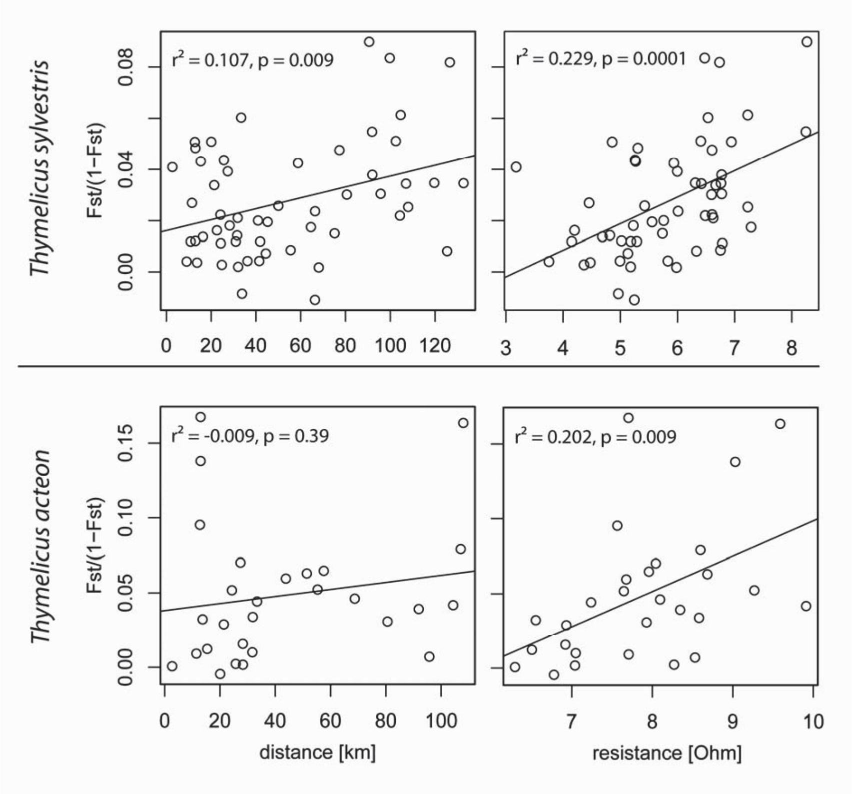


Figure 6.S2: Scatterplots showing the differences of isolation by distance patterns with isolation by resistance patterns in the two species that show a spatial genetic structure (*Thymelicus sylvestris* is shown at the upper half, *T. acteon* at the lower half). Note that just the most prominent isolation by resistance pattern is shown (i.e. climate in *T. sylvestris* and land use change in *T. acteon*).

CHAPTER 7

A statistical learning approach to improve ecological inferences in landscape genetics by accounting for spatial nonstationarity of genetic differentiation

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“In a variable world, averages mostly are just meaningless, unimportant epiphenomena.”

— JEREMY FOX

The work was conducted in collaboration with NIKO BALKENHOL.

Introduction

Landscapes are by definition heterogeneous in space (WU 2012), so that certain landscape elements can be driving ecological processes in some areas while being irrelevant in others. Gene flow is one of these processes, and a central goal of the emerging field of landscape genetics is to understand how and why gene flow is affected by the landscape (MANEL et al. 2003; MANEL & HOLDEREGGER 2013). Therefore, many studies in this field correlate gene flow estimates between sampled locations (i.e., genetic distances) with effective distances, as inferred from the surrounding landscape matrix. Usually, this relationship is unknown, which is why researchers compare genetic distances against a set of different landscape variables to find the strongest correlation (Fig. 7.1). This quantifies the strongest average landscape effect within the study area, yet it largely ignores the heterogeneous and dynamic nature of the landscape itself. In consequence, this approach often leads to a high amount of unexplained variance in gene flow – landscape relationships, which could be caused, in part, by spatial nonstationarity in gene flow patterns (DUFORET-FREBOURG & BLUM 2014).

Spatial nonstationarity refers to the inconsistent relationships of one or many predictor variables to a response variable across space (BRUNSDON et al. 1996). In our case, if gene flow is affected by spatial nonstationarity, it is because migration rates vary across a given study area. For instance, this variation could be masked by demographic discontinuities at local populations across a species' range, or due to landscape effects that directly affect migration rates. In the latter case, exploratory analyses could link different landscape elements to measures of gene flow to test for spatial nonstationarity. One way of doing this is to focus on sampling designs that separate the study area into homogenous parts and restrict comparisons only within these local subsets. However, this strategy has two major drawbacks: first, it would decrease the power of analysis, as comparisons located between these local subsets will consequently get lost; second, most landscapes are complex mosaics of continuously changing elements affected by many interactions in time and space (e.g., disturbance dynamics; TURNER 2010). Therefore, a spatial segregation is hard to realize and is largely impractical—especially when the study extent and/or spatial scale of interest is large.

Here, we propose an alternative approach to assess spatial nonstationarity which is based on statistical learning theory. This theory considers *learning* as the challenge of finding the most appropriate function (f) from empirical data (VAPNIK 2013). In landscape genetics, this learning is mostly supervised, as for each response measurement (i.e., the genetic distance) there are one or more associated predictor measurements available (i.e., the effective distances of different landscape elements).

In a simplified way, this relationship can be expressed as:

$$Y = f(X) + \varepsilon,$$

where the genetic distance is the response variable Y, to one or several predictor variables X, such as effective environmental distances, which are framed in a function f, and supplemented by a random error term ε.

In this general relationship, where Y and X are known, two sources of error exist: the reducible error and the irreducible error. The reducible error is linked to the unknown function f, which represents the systematic information that X provides about Y (JAMES et al. 2013). It can be reduced by learning, which is the most appropriate statistical method to estimate f (JAMES et al. 2013). In landscape genetics, a plethora of statistical methods exist to estimate f, even though there is an ongoing debate about which methods are the most appropriate (e.g., BALKENHOL et al. 2009; JAQUIÉRY et al. 2011; DYER 2015a). The irreducible error is the amount of error that remains after improving f, hence it characterizes variance in Y that cannot be explained by X using f, and is expressed by the random error term ε. This source of error has thus far received little attention in landscape genetics, focusing on limits of measurements of X or Y (e.g., SPEAR 2010; DYER 2015a) but not on the dynamic nature of the landscape itself that could be the cause of spatial nonstationarity patterns in migration rates (DUFORET-FREBOURG & BLUM 2014).

Here, we argue that a large fraction of the irreducible error ε is systemic, because the way landscape patterns are characterized to correlate X with Y across a study area typically ignores the spatial heterogeneity and temporal dynamics of the landscape. To account for this systemic error, we present a framework that improves f by assembling a single solution for X under any situation where $n_X > 1$. This is achieved by choosing the landscape element X_j for a single comparison j with Y_j out of a number of n available landscape elements $X_{j1}, X_{j2}, \ldots X_{jn}$ that minimize the irreducible error ε (Fig. 7.2). In other words, using the information about genetic exchange, we compile a new predictor variable called, *landscape,* from a number of existing predictors covering different but complementary information (such as *climate*, *topography*, or *landuse*) to address spatial nonstationarity . Each single predictor does not account for possible limits of genetic measurements at single comparisons that could be driven by one of the remaining predictors. This can lead to higher amounts of unexplained variance (Fig. 7.1). We exemplify this framework with two empirical datasets of (1) a Central European Hesperid butterfly (Louy et al. 2007; Engler et al. 2014), as well as (2) the wolverine (*Gulo gulo*) across its Nearctic range (Kyle & Strobeck 2001; McRae & Beier 2007). We discuss the results and its implications for study design and inference in landscape genetics.

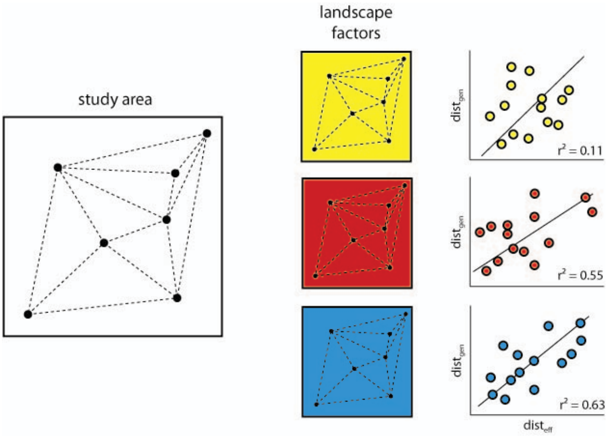

Figure 7.1: A fictive study area that comprises seven localities where genetic information from a species was obtained but where relationships to landscape elements are unknown (left). The goal is to relate the estimated genetic distance (dist_{gen}) to a set of effective distances (dist_{eff}) estimated for each of three landscape elements (yellow, red, and blue). The amount of explained variance increases from the yellow to the blue landscape element (right). All comparisons still lead to a high amount of unexplained variance.

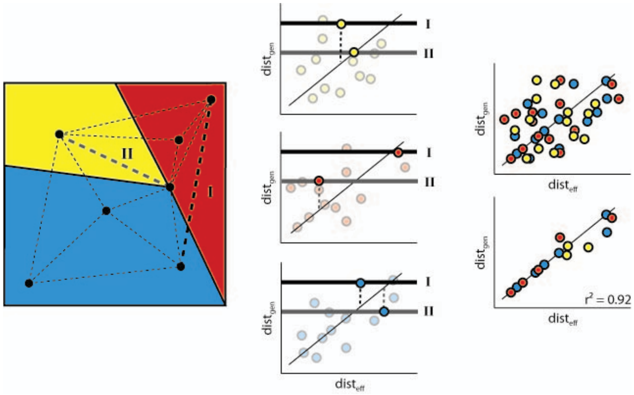

Figure 7.2: Spatial composition of regions where one of the three landscape elements is locally driving gene flow in the study region (left panel). If a dashed line is entirely underlined by a single color, this landscape element is driving the genetic distance (i.e., it is spatially stationary; low unexplained variance ε). In the case where two locations are present in different colors, there will be a change in the landscape factors responsible for explaining gene flow (some ε remains). In example I, the genetic distance measured is largely driven by the red landscape element and to a lesser degree by the blue landscape element, whereas the yellow landscape element does not play any further role. By comparing ε across the three landscape elements (middle panel), ε is smallest in red and much higher for the other two landscape elements. Consequently, the red landscape factor will be seen as the most important for this relationship. In example II, only the yellow landscape element is driving gene flow. The other two play no role at all, which can again be assessed by looking at ε, which is zero in yellow but non-zero in the other two predictors. In applying this learning rule to all comparisons, an optimal solution can be approached after a few iterations. Here, the optimal solution (right panel, bottom) explains a high amount variance, which is a large improvement to the models seen in Fig. 7.1.

Material and methods

The statistical learning approach

The statistical learning approach consists of three main steps: rescaling, optimizing and weighting. These main steps should be applicable to many methods that correlate genetic with effective distances. Here, we exemplify the approach by using simple linear regression models.

Assigning values to resistance surfaces can be a challenging task (Spear et al. 2010). Rescaling effective distances is important to achieve comparability among the different resistance surfaces involved in the statistical learning approach. This is because strong differences in the range of resistance values assigned to the different resistance surfaces lead to very different absolute effective distance values among these surfaces. These absolute values, however, do not contain the information needed; it is their relative distance to each other that relates to the genetic distance. In rescaling absolute values to percentiles, the important information is kept and becomes comparable to effective distances from other resistance surfaces.

The percentiles of the effective distances (i.e. predictors X_1 to X_n) are initially compared against a reference model of isolation-by-distance (IBD) based on percentiles of geographical distance values. From this model, residuals are predicted for each of the predictors. The effective distance with the smallest residual for each comparison can now be selected to calculate a new comparison with the genetic distance. Using linear regressions in our example, this will lead to a reduction of the mean squared error (MSE), hence resulting in a higher r^2. From that model, the residuals for each predictor will be updated and the selection continues for a novel iteration. This process is repeated until r^2 remains constant (i.e., ε is minimized). The optimization procedure returns a vector of the predictor most responsible for each case, as well as a vector of the residual difference to the next closest residual. The latter information can then be used to weight each case in the optimized solution.

We assume that weighting can improve the effect size of driving landscape elements to functional connectivity and thereby the relationship between genetic and effective distances. Comparisons, where a single predictor best explains the genetic distance, show a high difference in residual distances of this predictor to other predictors. In turn, if residual distances are very equal to each other, one predictor could be replaced by another one without having a strong effect on the entire relationship. The weighting itself is also an optimizing process, as there could be instances where weighting does not add to overall model improvement.

These three steps have been compiled in r-code using the *RASTER*, *SCALES* and *VEGAN* packages in R 3.0.2 (WICKHAM 2012; R CORE TEAM 2013; HIJMANS & VAN ETTEN 2012; OKSANEN et al. 2014), and can be found in the supplementary material together with code for plotting using the *SP* package (BIVAND et al. 2013).

Empirical examples

To test the performance of this statistical approach, we used two empirical examples from the literature. Both examples have known relationships between genetic and effective distances, but differ in the study extent and the number of landscape variables.

The first example covers the local distribution of the Hesperid butterfly *Thymelicus sylvestris* in Southwest Germany and adjacent areas in Luxemburg and France (LOUY et al. 2007, ENGLER et al. 2014). It has been shown that the species' genetic differentiation is characterized IBD (LOUY et al. 2007) and even stronger signals of isolation-by-resistance (IBR) of different landscape elements could be found recently (ENGLER et al. 2014). Herein, climate has been identified as the landscape element with the highest information content for explaining gene flow of this species in this region (ENGLER et al. 2014). The landscape across the study area is characterized by a mosaic of different land uses as well as a topographic relief, including distinct mountain ridges and two major river valleys, which also affects local climate. The effective distances used for this study were calculated among eleven sample sites with available genetic information by using three resistance surfaces characterizing climatic, topographic, and land-use information. Calculations were performed in CIRCUITSCAPE (v 3.4.1; MCRAE et al. 2008), and resistance surfaces were parameterized using species distribution models (SDM; see ENGLER et al. 2014 for details).

The second example focuses on the Nearctic distribution of the wolverine (*Gulo gulo*). Across that range, twelve populations were genetically characterized (KYLE & STROBECK 2001) and later tested for IBR patterns based on the species' range shape (MCRAE & BEIER 2007). For our study, we used the species' pairwise genetic differentiation estimates (F_{ST}) from KYLE & STROBECK (2001), range shape information from WILSON (1982), and generated an SDM based on climate condition and occurrence information across continental North America (Supplementary Information). The wolverine strongly depends on the retainment of snow in spring (MAGOUN & COPELAND 1998; AUBRY et al. 2007; COPELAND et al. 2010), which makes climate an inherent factor of its distribution. We calculated effective distances in the pairwise mode of CIRCUITSCAPE by using a focal points table within an eight-neighbor-connection scheme among the genetically sampled sites for the resistance surfaces 'range' and 'climate'.

Results

Both empirical examples increase the amount of explained variance after applying the statistical learning approach, thereby reducing the MSE and thus the irreducible error ε. The r^2 increased in *T. sylvestris* from 0.107 under IBD to 0.574 for the optimized solution after only four iterations. In the wolverine example, the approach also took only four iterations to increase the r^2 from 0.292 under IBD to 0.771 in the optimized solution. The weighted solution further increased the r^2 values to 0.599 in *T. sylvestris* and to 0.774 in the wolverine, respectively.

All of the three assessed landscape elements in *T. sylvestris* showed significant IBR (ENGLER et al. 2014), yet r^2 values varied from 0.09 in topography, to over 0.147 in land use, and 0.229 when taking climatic conditions into account (Fig. 7.3). The weighted and optimized solution shows a high admixture of the three landscape elements involved in the compilation with genetic distances. Here, 23 out of 55 comparisons were assigned to climate, 17 to topography, and 15 to land use. The highest weights (i.e., comparisons where one landscape element outcompetes another) were found in climate, while weights were generally weaker for the other landscape elements (Fig. 7.3). Plotting this information as a network in the study area confirms the strong interplay of the different landscape elements as driving factors for gene flow, but also highlights two sites with a clustering of comparisons with high weights (Fig. 7.4).

In the wolverine example, the two landscape elements *range shape* and *climate* had very high r^2 values of 0.645 and 0.733, respectively (Fig. 7.5). The weighted optimized solution shows a two-fold pattern: in the lower distance percentiles, there is a high admixture between climate and range shape as driving patterns which are characterized by low weights. In contrast, the upper end of genetic as well as effective distances is clearly devoted to climate and high weights (Fig. 7.5). When this weighted network of driving landscape elements was plotted (Fig. 7.6), it was seen that this pattern originated from a single sample site in the southern range of the wolverine (Idaho, USA), where climate seems to be a very important explanatory variable for gene flow. All other comparisons are highly admixed and rather uniform in their weights (Fig. 7.6).

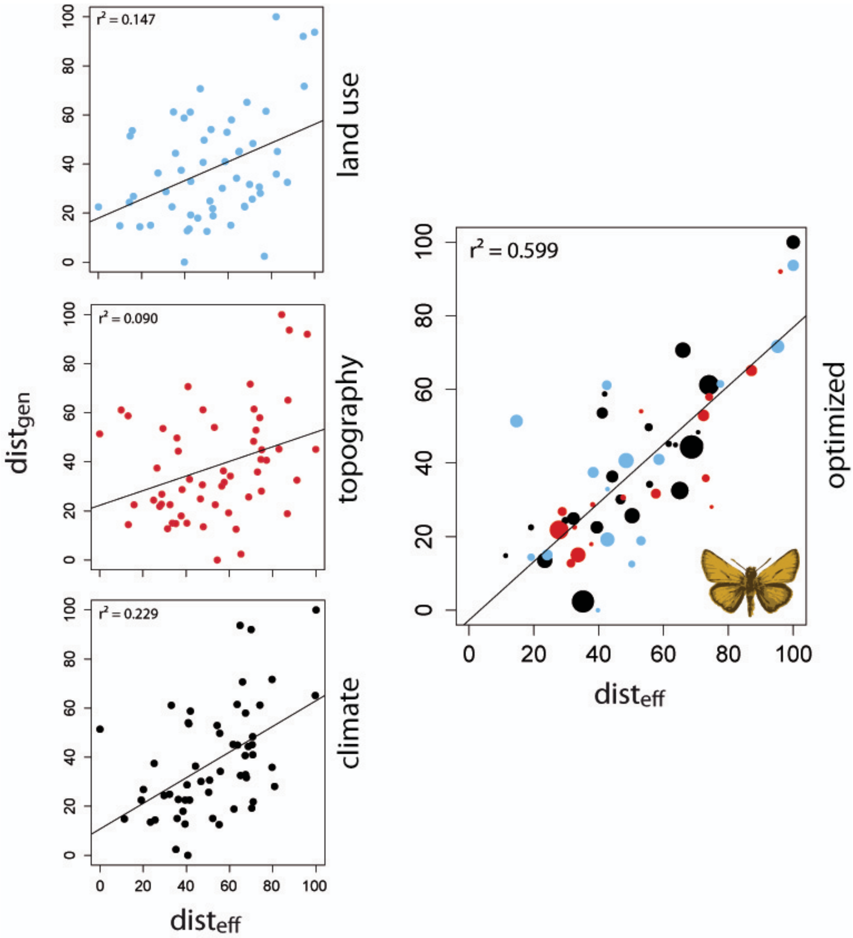

Figure 7.3: Linear relationships between genetic distance with effective distances from land use (blue), topography (red), and climate (black) together with the optimized solution (right panel) for the Hesperid butterfly *Thymelicus sylvestris.*

Discussion

The proposed statistical learning approach is intended as a useful supplemental tool for the exploratory analysis of landscape effects on gene flow. Especially under situations where landscape variables of interest occur together as independent layers, this approach can give insights into where certain variables are more important than others for functional connectivity. Also, in cases where different variables can be easily merged into one layer, this approach offers more detail in the regional driving processes. Focusing on average effects of single predictors underestimates the impact landscape has on gene flow, which makes misleading implications more likely.

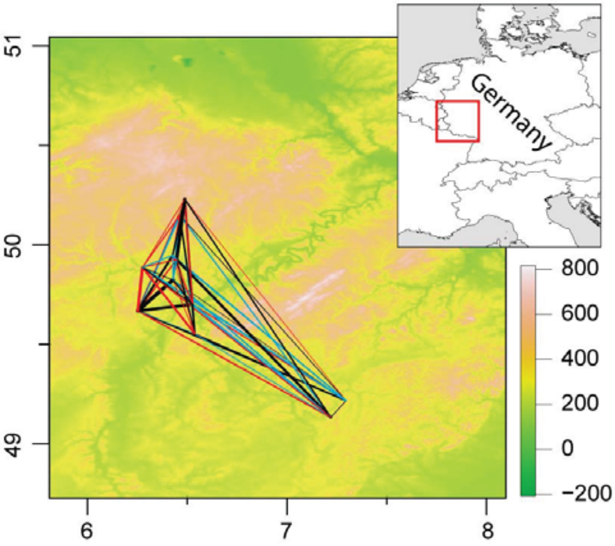

Figure 7.4: The optimized solution plotted as a network of comparisons across the study area from *T. sylvestris.* Line thickness corresponds to the weight given to each comparison (higher weight indicated by thicker lines). Line colors remain the same as in Fig. 7.3. The background correspond to the altitude (in meters a.s.l.).

The landscape genetics in the butterfly *T. sylvestris* turned out to be more complex than previously thought. Despite climate has been, on average, the most important landscape element in the study area, other landscape elements also led to significant but less strong relationships (ENGLER et al. 2014). Our results from using the statistical learning approach confirmed that climate is an important landscape element, both in the number of comparisons assigned and in the weights given to this predictor. However, the appearance of the other two landscape elements, *topography* and *land use*, which together were assigned to more than 58% of the comparisons, show that they also have to be considered. Overall, the result confirms the highly heterogeneous landscape mosaic across the study area, affecting gene flow in this butterfly locally and in various ways.

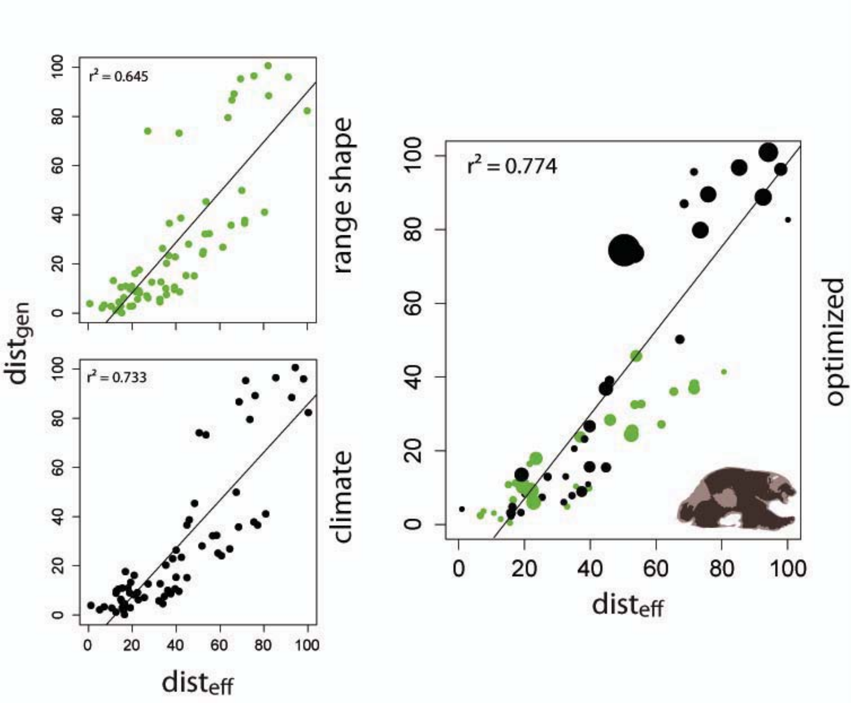

Figure 7.5: Linear relationships between genetic distance with effective distances from range shape (green) and climate (black) together the optimized solution (right panel) for the wolverine.

Our second case study on gene flow patterns across the Nearctic distribution of the wolverine highlights the benefits of our approach at a large spatial scale. Both, range shape and the climatic conditions explain a large amount of the wolverine's genetic differentiation across North America and the effective distances calculated from each of both predictors are highly correlated (Pearson's r = 0.98, p < 0.0001). However, the combination of both predictors in the optimization highlights the climatic isolation of the Idaho population, where the range shape information alone is a bad predictor, as indicated by the high weights assigned to climate in most of the comparisons originating in Idaho. Here, the effect of climatic isolation also becomes evident with comparisons from as far as Alaska. Across the remaining range, the choice of either climatic conditions or range shape is not of high importance, as shown in the low weights assigned and the admixture of both predictors that did not yield any further spatial patterns. These local effects are not obvious when merging both predictors into a single resistance surface (i.e., by masking the climate layer with the range shape information); it will just lead to an increase in explained variation compared to the single variable comparisons, but not to more insights regarding the local effects where these variables are driving gene flow.

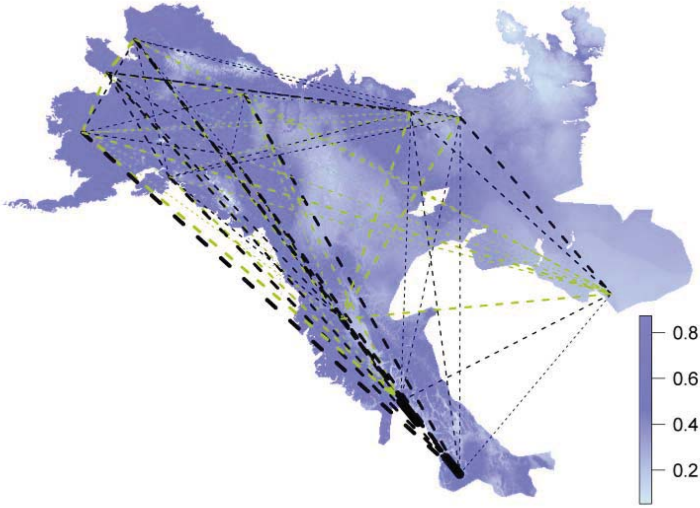

Figure 7.6: The optimized solution plotted as a network of comparisons across the North American range of the wolverine. Line thickness corresponds to the weight given to each comparison (higher weight indicated by thicker lines). Line colors remain the same as in Fig. 7.3. The background corresponds to the wolverine's potential distribution masked by its range shape.

Accounting for the spatial heterogeneity of relationships between variables has been a long endeavor which has led to the development of different approaches (CASETTI 1972; FOSTER & GORR 1986; GOLDSTEIN 1987; AITKEN 1996), among which geographically weighted regression (GWR; BRUNSDON et al. 1996; FOTHERINGHAM et al. 2002) stand out and became a standard tool for this purpose (PÁEZ et al. 2011; CHEN et al. 2012; DINIZ-FILHO & BINI 2012). GWR uses a moving window approach to fit local relationships to a larger dataset (FOTHERINGAM et al. 2002). However, sample size needs to be large to achieve a good fit of local estimates (PÁEZ et al. 2011;

DEVKOTA et al. 2014). In landscape genetics, large sample sizes by means of locations sampled (i.e. n ≈ 160; PÁEZ et al. 2011) are rarely met, even though attempts had been made to use GWR in that way (e.g., SPEAR et al. 2012). As opposed to GWR, our statistical learning approach led to outcomes of local driving and varying landscape patterns—even under sample sizes that are typical in landscape genetics. Our approach therefore allows characterizing the landscape patterns that cause spatial nonstationarity in genetic differentiation under situations, where GWR cannot.

Recently, DUFORET-FREBOURG & BLUM (2014) proposed a method that assesses spatial nonstationarity in IBD patterns using Bayesian kriging and highlight its extension to landscape genetics. In particular, this approach detects genetic discontinuities, where local genetic differentiation is larger (or smaller) than a baseline estimate of genetic differentiation over the entire study area (DUFORET-FREBOURG & BLUM 2014). However, the approach did not correlate these genetic discontinuities to certain landscape elements afterwards, and thus relied entirely on the available methods in landscape genetics to link these outcomes to landscape elements. In consequence, even though spatial nonstationarity of genetic differentiation can be detected, it will be correlated again to approaches that focus on the average effect of single landscape elements instead of linking them directly to the detected discontinuities. Hence, the landscape patterns identified using our optimization technique can offer potential explanations to the genetic discontinuities detected in Bayesian kriging and serve as an important supplemental tool in this regard.

In conclusion, our new approach highlights where specific landscape elements are driving gene flow at a local scale and by this find a solution for each single comparison. This contrasts with most efforts in landscape genetics which focus on the quantification of average effects only. The approach is of particular interest when results are used for management recommendations in conservation and questions the projection of results of landscape genetic studies onto different regions and spatial scales. By this, we recommend its use as an explanatory tool in landscape genetics that can supplement the reliability of average effects and account for spatial nonstationarity in migration rates. To this end, we hope that this approach will be implemented in a wide range of methods that correlate genetic distances with effective distances to fully account for the dynamic nature of the landscape.

Supplementary material

A climate SDM for the wolverine

Species data

We compiled wolverine occurrence information in a query at the Global Biodiversity Information Facility (GBIF, www.gbif.org, retrieved 08/2014), leading to a total of >15,000 records. After removing records without spatial reference, duplicates, or records outside the study area, 500 presence locations remained. These localities were spatially biased towards Alaska (317 records; 63.4% of all records) and Nunavut/Canada (138 records; 27.6% of all records). As spatial sampling bias is well known to negatively affect SDM results due to uneven sampling density (e.g., SYFERT et al. 2013; KRAMER-SCHADT et al. 2013; FOURCADE et al. 2014), we generated a subset of 100 records by using a hierarchical cluster analysis over the geographic space (i.e., by using lat/long coordinates as explanatory variables) and randomly selected one record for each of the predefined solution of 100 clusters. The cluster analysis was performed in SPSS 14.0.

Environmental variables

We used a subset of the 19 bioclimatic variables obtained from the WorldClim database (Vers. 1.4.; HIJMANS et al. 2005) at a spatial resolution of 30 arc seconds. As the wolverine's range is strongly delimited by the retainment of snow in spring (MAGOUN & COPELAND 1998; AUBRY et al. 2007; COPELAND et al. 2010) and to avoid model overparameterization due to the inclusion of too many predictor variables in the species distribution model (HEIKKINEN et al. 2006), we reduced the initial set of 19 predictors to a subset of six predictors that were assumed to be the most biologically relevant to the species (Table 7.S1).

Modeling framework

For the SDM, we used the program MAXENT (vers. 3.3.3k; PHILLIPS et al. 2006), a machine learning algorithm based on the principles of maximum entropy (ELITH et al. 2011). MAXENT frequently outperforms other competing methods and has been shown to be robust under complex scenarios and low numbers of presence records

(HERNANDEZ et al. 2006, ELITH et al. 2006, WISZ et al. 2008). We apply SDMs using auto features and the logistic output format after 100 repetitive runs where we randomly subsampled 30% of the occurrence data for model testing. The resulting suitability maps were reprojected to an equidistant UTM projection at 1km² spatial resolution using the RASTER package in R (HIJMANS & VAN ETTEN 2012).

Table 7.S1: Predictors used for conducting the SDM for the wolverine.

Worldclim code	Meaning
Bio1	Annual mean temperature
Bio4	Temperature seasonality
Bio5	Maximum temperature of warmest month
Bio8	Mean temperature of wettest quarter
Bio12	Annual precipitation
Bio15	Precipitation seasonality

PART C

IMPROVING SDMS USING CONTEMPORARY GENETIC INFORMATION

CHAPTER 8

Genes to the niche! How contemporary DNA can help to refine niche theory for predicting range dynamics in the Anthropocene

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"The north, south, east, and west boundaries of a species' range tell us very little about what is happening inside..."

— ROBERT H. MACARTHUR

The work was conducted in collaboration with NIKO BALKENHOL from the Wildlife Science Department, University of Göttingen and CATHERINE H GRAHAM from the Department of Ecology and Evolution, Stony Brook University.

Niche models, theory, and the recent integration of genetic information

The technological revolution in the past 25 years now allows the analysis of species occurrence information in completely novel ways. Correlative environmental niche models (ENM) that link occurrence information to a set of environmental variables appeared as a central tool in this regard, with applications covering a wide array of disciplines in ecology and evolution (PETERSON & VIEGLAIS 2001; GUISAN & THULLIER 2005; KOZAK et al. 2008; FRANKLIN 2009; PETERSON et al. 2011). These models are based on Hutchinson's niche concept which assumes that species niches are constrained by a combination of environmental tolerances and biotic interactions (BOX 1; SOBERÓN 2007; 2010; 2014; WARREN 2012; 2013). Use of this concept as a basis for ENMs (hereafter referred to as ENM concept), has been criticized (JIMÉNEZ-VALVERDE et al. 2008; MCINERNY & ETIENNE 2013) and recent studies suggest that it should be refined to include more biological detail (e.g., HOLT 2009). To this end, researchers have begun to integrate mechanistic (KEARNEY & PORTER 2009; DORMAN et al. 2012; CABRAL & KREFT 2012) and genetic information into ENMs.

Phylogeographic (CHAN et al. 2011; ALVARADO-SERRANO & KNOWLES 2014), and landscape genetic research (MANEL& HOLDEREGGER 2013; ENGLER et al. 2013) increasingly use ENMs to explore genetic patterns. In addition, the potential of genetic data for improving ENM predictions has been highlighted (HOLT 2009; SCOBLE & LOWE 2010; FORDHAM et al. 2014; GOTELLI & STANTON-GEDDES 2015). However, we currently lack a conceptual framework that integrates population genetic information into the ENM concept. Here, we explore a conceptual framework that demonstrates how genetic information can be used to enhance our understanding of range dynamics and refer, where available, to specific examples from the scientific literature. In particular, we show how integrating genetic information into ENM permits a more holistic view of niche theory and discuss limitations associated with how the ENM concept is currently being used. We assert that in order to address the modeling challenges in the era of the Anthropocene, where habitat fragmentation, biotic invasions, and climate change are major human-caused threats to global biodiversity, use of the ENM concept should be refined. In addition, we provide recommendations for the design of integrated studies using genetic information that will enhance our understanding of species distributions for future range dynamics in a changing world.

Why do we need to consider genetic information in the ENM concept?

Hutchinson's niche concept, as modified by SOBERÓN (2007), simplifies the definition of the realized niche in order to make it suitable for ecological niche modeling (Fig. 8.1). In particular, the ENM concept assumes that $\boldsymbol{A} \cap \boldsymbol{B} \cap \boldsymbol{M}$ (or $\boldsymbol{G_o}$) is the area '*within reach of dispersing individuals*' that has favorable biotic and abiotic conditions (SOBERÓN & NAKAMURA 2009). This means that, in theory, every location within $\mathbf{G_o}$ should have the same probability of being connected with any other location within $\mathbf{G_O}$ (Fig. 8.1a), which would result in weak spatial-genetic structure. However, actual exchange among locations is often limited by distance and depends on the movement capacity of the individuals and their interactions with the landscape (Box 2). For most species this means that range wide connectivity is a multi-generational process, which makes *time* an inherently important aspect in the ENM concept (Fig. 8.1b). Therefore, most species have some degree of genetic structure caused by limited gene flow in relation to genetic drift, local adaptation, or both (Fig. 8.1c). The current ENM concept neither considers differential genetic exchange throughout a species range nor adaptive responses to particular environmental conditions. Therefore, contemporary genetic information offers important insights into how populations are connected, which landscape elements are important for maintaining functional connectivity and how local adaptation and eco-evolutionary dynamics affect the ENM concept and its applications.

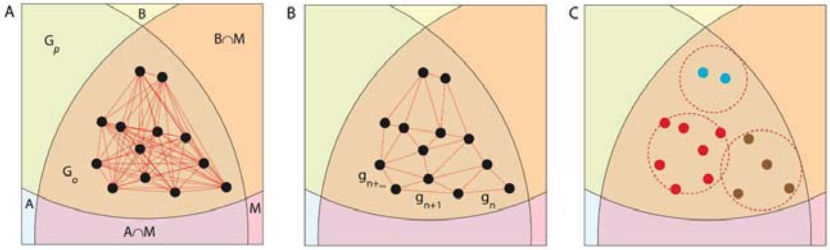

Figure 8.1: The fraction of the BAM plot where species occur (see Box 1 for more information and notation). A) The classic ENM concept assumes all individuals can access all of $\boldsymbol{G_o}$, resulting in weak population differentiation. B) In most real world systems, movement is spatially restricted and

influenced by landscape heterogeneity, which makes the exchange across $\boldsymbol{G_o}$ a multi-generational process (gn, gn+1, gn+…). In consequence, genetic differentiation becomes likely because of restricted gene flow. C) Environmental factors can exert selection pressures that can counteract gene flow, leading to spatial genetic structure.

Integrating genetic information to understand the processes behind range dynamic patterns

To highlight how genetic information can refine niche theory, we focus on five broad aspects: (i) gene flow, (ii) spatial genetic structure, (iii) density blocking, (iv) hybridization, and (v) source-sink dynamics (Fig. 8.B1.1b). While these processes are not fully independent from each other, we focus on each one separately, starting with those directly acting at the level of the occupied realized niche $\boldsymbol{G_o}$**,** followed by processes acting during colonization (expansion of $\boldsymbol{G_o}$) and finally source-sink dynamics acting in the original or expanded $\boldsymbol{G_o}$.

Gene flow and functional connectivity: Exchange within G_o is limited

Gene flow estimates can be used to quantify functional connectivity of landscapes. The ENM concept assumes that all occurrences within $\boldsymbol{G_o}$ '*have been accessible to the species since some arbitrary point in time*' (Soberón 2007: 1120). As such, $\boldsymbol{G_o}$ is treated as a continuous and homogeneous surface which allows exchange among all localities within $\boldsymbol{G_o}$ with the same probability in the long term (Fig. 8.2a). Following this assumption, most EMNs assume that species can disperse to regions where environmental conditions are suitable. This assumption is likely violated because many landscape genetic studies show that environmental heterogeneity can strongly influence dispersal and resulting population connectivity (Manel & Holderegger 2013; Dyer 2015b; Waits et al. 2015). Consequently, ENMs based on climate data may not render spatial occurrence patterns needed for identifying the processes influencing species distributions. However, identifying the processes affecting distributional patterns is needed to mitigate the influence of climate change on populations and species (Box 2). For instance, Engler et al. (2013) showed that ENMs based on climate adequately predicted potential distributions for three congeneric butterflies (Genus: *Thymelicus*). However when related to gene flow, climate was identified as an important predictor for functional connectivity in only one species, while being a poor predictor for the other two (Engler et al. 2013). The current ENM concept does not consider the importance of functional connectivity for range dynamics and how this interplay is affected by increasing habitat fragmentation (e.g., TRAVIS 2003; HOF et al. 2011). This is of particular concern, since habitat loss is assumed to more strongly impact species persistence than climate change (STEFFEN et al. 2015 a;b).

Spatial genetic structure: $\boldsymbol{G_o}$ is more complex and diverse

Species can show spatial genetic structure due to limited gene flow and adaptation to local environmental conditions (Fig. 8.1c). Local adaptation actively counteracts the admixing effect of gene flow and can occur at different spatial scales (RICHARDSON et al. 2014). This can lead to the formation of geographically distinct genetic demes, which remain largely unconsidered in the ENM concept and the definition of $\boldsymbol{G_o}$ (Fig. 8.1c).

Recently, studies have begun to incorporate information on spatially separated genetic demes into EMNs on coarse spatial scales. The consideration of genetic demes yields more accurate predictions of species distributions than the common practice of pooling occurrence records at the species level (PETERSON & HOLT 2003; PEARMAN et al. 2010; VALLADARES et al. 2014). For instance, GONZALEZ et al. (2011) refined their prediction of the potential distribution of old field mice (*Peromyscus polionotus*) after accounting for differences in bioclimatic niche space used by different subspecies. Use of genetic information may be particularly important for generating future projections if unique genetic demes are considered (ONEY et al. 2013). VALLADARES et al. (2014) demonstrated that forecasts incorporating intra-specific variation (due to local adaptations) showed more dramatic declines than when occurrences were pooled at the species level. These examples suggest that incorporating spatial genetic structure can have profound effects on the niche space estimated, potentially reducing the risk of overestimation of $\boldsymbol{G_o}$ (Box 2). Overestimation of the niche might be particularly problematic if the niche delimiting factors are not the same among the genetic demes (e.g., ONEY et al. 2013), or if impacts of environmental heterogeneity on functional connectivity vary across the geographic range of a species (e.g., SHORT BULL et al. 2011; DUDANIEC et al. 2012; LEVY et al. 2013). To accommodate within-species variation in environmental requirements, separate analyses should be conducted with reference to the spatial genetic structure found at finer scales.

Density blocking: Expansion may not be a simple projection of the conditions across the entire native range

Species with spatial genetic structures might behave in very different ways if they colonize new regions. Recently, the term *density blocking* was introduced to summarize interdependent priority effects such as gene/allele-surfing, competitive exclusion, and leading edge colonization (WATERS et al. 2013). These density driven priority effects, imprinted in genetic patterns, are crucial for our understanding of colonization events such as range expansions and biological invasions. Including this information into niche models will result in better forecasts and allow for clearer signals of niche stasis vs. niche evolution (Box 3).

Given that a species range within $\boldsymbol{G_o}$ is often genetically structured and exchange is not equal throughout, density blocking should be considered to better understand and predict expansions of $\boldsymbol{G_o}$. Natural range expansions normally occur into areas in **A** or **B** of the BAM diagram that are adjacent to $\boldsymbol{G_o}$ and become suitable and are thus colonized from source populations along the range edge (i.e., leading edge colonization, HEWITT 1996). In biotic invasions however, expansions are expected to result mostly in the occupation of $\boldsymbol{G_p}$ due to human mediated crossing of macro-scale barriers (i.e., an artificial expansion of **M**). While these two mechanisms likely represent the most common ways in which species expand their range, questions remain as to where within $\boldsymbol{G_o}$ founders come from and what their genetic characteristics are. For instance, leading edge colonization results in density-driven priority effects that favor local genotypes over those that arrive later, and more sporadically, from more distant locations (WATERS et al. 2013). In addition to pure priority effects that dominate leading edge colonization, it is possible that local adaptation may favor immigrants from closer populations more compared to those from distant parts of the range. Under local adaptation, different genetic demes should be detectable in environmental space. In contrast, genetic differentiation due to density blocking does not necessarily coincide with a strong separation in environmental space (Box 3). This information is crucial for interpreting the degree of niche overlap between original ranges and areas of range expansion. If genetic demes are separated in E-space, then comparisons should be made just with the genetic demes involved in the expansion because pooling deems at the species level will lead to lower estimated niche overlap that do not accurately reflect true niche overlap. As a result a false signal of niche evolution could appear where there is a high level of niche stasis.

Hybridization: expansion by accessing new niche space

Hybridization appears above and below the species level and its prevalence often increases during accelerating rates of faunal exchange by human activities (THOMAS 2013). Hybridization between members of different genetic demes can lead to an expansion of realized niche space. Realized niches can be complex in species with spatial genetic structure (BOX 2). If genetic demes come into secondary contact (either by natural range expansions or by human-mediated translocations), their distinct realized niches in E-space might expand due to hybridization and by this enlarge total realized niche space.

Hybridization can lead to an increased adaptive potential, which in turn, can allow the colonization of formerly unsuitable habitat. While hybridization is common in natural populations (ARNOLD 1997; SCHWENK et al. 2008) studying its role in niche expansion can be difficult because hybridization is often an on-going long term process. In contrast, in biological invasions members of different genetic demes are brought into secondary contact providing a short-term perspective on how hybridization might influence species niches. Compared to native populations, a surprisingly high genetic diversity can be found in different populations of invasive species in both plants (LAVERGNE & MOLOFSKY 2007) and animals (KOLBE et al. 2004; 2007; DETWILER & CRISCIONE 2014). Comparative population genetic studies between native and invasive ranges are needed to better understand how niches are altered during biological invasions which might explain invasion success as well as further spread. In particular, such information could contribute to our understanding of whether niche evolution, niche stasis, or niche plasticity influences invasion success (BOX 3).

Source-sink dynamics: beyond classical definitions and implications

Populations are rarely continuous but usually are patchily distributed in geographic space, often as part of a metapopulation network (HARRISON 1991; HANSKI 1999). Depending the landscape heterogeneity, patch size and connectivity, populations can range from large and productive source populations to small sink populations that need immigration from sources to persist. These source-sink dynamics are crucial for landscape ecology and meta-population theory and their implications for niche theory and the ENM concept have long been recognized (PULLIAM 1988; 2000; SOBERÓN 2007).

SOBERÓN (2007) applied the *source-sink area of distribution* as formulated by PULLIAM (2000) to the ENM concept as the area delimited by $\boldsymbol{M}$, where sources were located within $\boldsymbol{G_o}$, and sinks within the remaining area of $\boldsymbol{M}$. However, the integration of source-sink dynamics in classical niche modeling approaches suffers from three main problems. First, information on the source-sink status is lacking for most occurrences. This makes assignment of an occurrence record to either $\boldsymbol{G_o}$ or the remaining $\boldsymbol{M}$ difficult. Second, the source-sink status at a specific location might change over time (JOHNSON 2004). Hence, an occurrence record might be within $\boldsymbol{G_o}$ in some years but outside in others. Finally, depending on the underlying processes behind source-sink dynamics, their impact on model predictions depends on the choice and spatial scale of the environmental predictors used for modeling (DIEZ & GILADI 2009). Thus, whether a location is within $\boldsymbol{G_o}$ depends on the variables considered.

Genetic measures of asymmetrical migration (i.e., gene flow) and effective population sizes (N_e) can be used to characterize source populations as those with high emigration and N_e , while sink populations should show high immigration and low N_e (e.g., HUSEMANN et al. 2015). After this characterization, overlaps in E-space can be calculated and compared against locations assigned to as either sources or sinks. If sources and sinks are distinct in environmental space, sinks should be excluded from ENMs, as they overestimate $\boldsymbol{G_o}$ which has been seen as problematic (HOLT 2009; PAGEL & SCHURR 2012; SCHURR et al. 2012). If, however, no distinction can be made between these two states based on environmental predictors, the categorization as made in SOBERÓN (2007) does not affect ENMs, as the niche space representing $\boldsymbol{G_o}$ would not overestimate these envelopes. Indeed, even sink populations can be within $\boldsymbol{G_o}$, when the demographic processes driving source-sink dynamics act at finer spatial scales or along other environmental dimensions as used in the ENM. For instance, sink populations could be the result of unfavorable climate conditions (e.g., along a range edge), but more likely depend on the availability of resources, disturbances, or predator-prey relationships at the local scale, which are normally unconsidered in ENMs. Further, patterns of connectivity (i.e., a constriction of $\boldsymbol{M}$) allow the existence of sink populations (FURRER & PASINELLI 2015). In particular, sink populations contribute to the persistence of meta-population structures by acting as stepping stones for genetic exchange (GAGGIOTTI 1996), which makes sinks an important part in maintaining functional connectivity of many species and by this $\boldsymbol{G_o}$.

Using genetic data to enhance the ENM concept

Most current applications of ENMs in ecology and evolution are based on information on species occurrence alone. This may be insufficient as local conditions change over time, which usually affects genetic exchange and local adaptation. A genetic perspective can offer additional insights into species-environment relationships with consequences for the current ENM concept. These insights not only offer the opportunity for making better predictions of current distributions and their future forecasts, but also expand our understanding of inter- and intraspecific niche dynamics (Box 2, Box 3). Expanding the conceptional background of ENMs with this genetic perspective thus changes how we study the environmental niche: from the species' distribution (top-down) to the occurrence, spread, and persistence of individual genotypes (bottom-up, Fig. 8.2), or in other words, from a range-to-the-niche to a genes-to-the-niche perspective.

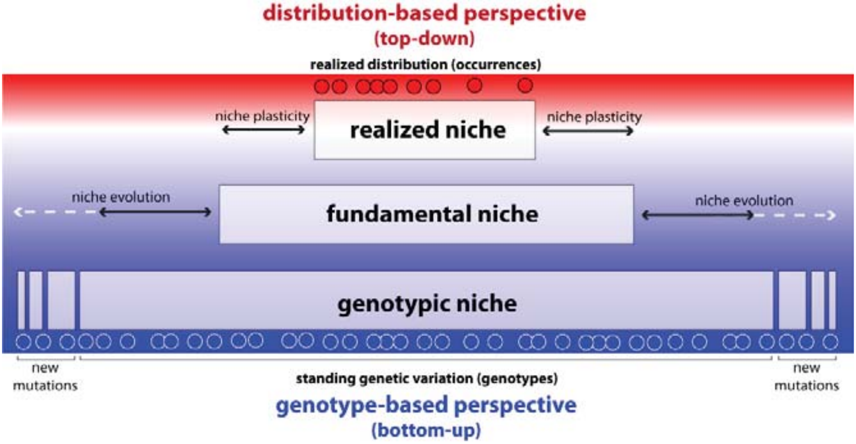

Figure 8.2: Expanding the ENM concept with genetic information. The classical ENM concept is based on a distribution-based perspective using occurrence records to infer the realized niche, as a subset of the fundamental niche. The eco-physiological limits of the fundamental niche are assumed to change slowly via niche evolution, while the realized niche is more plastic in its ability to change within the limits set by the fundamental niche. In contrast the genotype-based perspective uses information on standing genetic variation which frames a genotypic niche that is bound by evolutionary edges. These edges can change over long timescales when novel mutations expand the currently known standing genetic variation and are favored by selection. From this bottom-up perspective, we can assess the realized niche using information on spatial genetic structure and functional connectivity.

The genes-to-the-niche perspective replaces the static fundamental niche by a more dynamic genotypic niche, which allows for a more detailed view of the realized niche and its geographic distribution $\boldsymbol{G_o}$ (Fig. 8.2). Overestimation of $\boldsymbol{G_o}$ may be prevented when taking locally adapted genetic demes and functional connectivity within and among these demes into account. This perspective also allows us to consider how the fundamental niche might change through time to influence species distributions. Characterization of the fundamental niche using a species' eco-physiological limits is one of the cornerstones in the ENM concept (SOBERÓN 2007). Following this perspective, niche evolution is considered to act over long time scales (NOGUÉS-BRAVO 2009). However, this assumption is not always supported with genetic data, indicating that a more dynamic ENM concept may be required to predict range dynamics. Since the interplay of intraspecific local adaptation with environmental conditions (SAVOLAINEN et al. 2013) affects $\boldsymbol{G_o}$ in many ways, the fundamental niche could be expanded to consider standing genetic variation (HENDRY 2013). Experimental studies indicate that species can adapt rapidly to climatic change, even within a few generations (e.g., SKELLY et al. 2007). These adaptations mostly result from standing genetic variation, due to changes of allele frequencies, while new genetic variation from novel mutations are less frequent and take longer to manifest in phenotypes (HENDRY 2013). This makes standing genetic variation a crucial part of eco-evolutionary dynamics, where environmental changes induce evolutionary responses that lead to short-term adaptations. When rapid evolution is considered in the ENM concept, the fundamental niche becomes a dynamic entity that is able to change over very short time scales. By this, standing genetic variation could push the static concept of the fundamental niche towards a dynamic "*genotypic*" niche defined by evolutionary edges that allows some flexibility due to rapid adaption to environmental change (Fig. 8.2).

The dynamic ENM concept we propose here is also important from a conservation perspective. Local adaptation leads to spatial heterogeneity of a species' standing genetic variation. This heterogeneity can be the result of different adaptive strategies to environmental conditions across a species' range (BOTERO et al. 2015). Even though these strategies can be flexible against environmental change, they can cross evolutionary tipping points where one adaptive strategy is replaced by another one (BOTERO et al. 2015). Crossing these tipping points can have profound negative consequences, driving affected populations to extinction if the adaptive strategy they follow is no longer beneficial under the changing conditions (BOTERO et al. 2015). In the context of human made environmental change, populations can be forced towards those tipping points due to increased speed and magnitude of environmental change. In order to facilitate rapid adaptation, not only species but also the genetic variation within these species need to be conserved (MORITZ 1994; CRANDALL et al. 2000; PALSBØLL et al. 2007; SCHWARTZ et al. 2007). Consequently, a dynamic ENM concept based on a genotypic niche can be an important step towards better conservation in the Anthropocene, as it provides an eco-evolutionary complement to the currently prevailing ENM predictions based on eco-physiological limits.

Concluding remarks

Contemporary genetic information can improve niche theory in many ways which will allow generation of better ENMs that link to eco-evolutionary dynamics. The proposed dynamic perspective on the ENM concept accounts for losses of standing genetic variation due to human activities. Applying this ENM concept requires better coverage of genetic information across multiple spatial and taxonomic scales. Given the increasingly (cost) effective techniques for assessing neutral and adaptive genetic variation in non-model organisms, the genes-to-the-niche perspective in a dynamic ENM concept allows to enter new research topics to face the challenges of a rapidly changing world.

Box 1: Integration of niche theory and genetic information

The theoretical basis of ENMs is Hutchinson's niche concept (HUTCHINSON 1957), which was further elaborated for ENM applications by SOBERÓN (2007) in his BAM diagram (Fig. 8.B1.1a). The ENM concept characterizes a species fundamental niche ***A***, a scenopoetic niche space comprising abiotic conditions where the intrinsic growth rate is greater than 1 (i.e. source populations). This fundamental niche is then intersected with biotic interactions ***B***, forming the realized niche $\boldsymbol{G}$ $(\boldsymbol{A} \cap \boldsymbol{B})$. The accessibility ***M*** intersects ***G*** into two parts. The intersection $\boldsymbol{B} \cap \boldsymbol{A} \cap \boldsymbol{M}$ is the occupied area of distribution (GASTON 2003), called $\boldsymbol{G_O}$ (i.e. the part of ***G*** which is accessible by the species). The realized niche that is outside of ***M*** is referred to as $\boldsymbol{G_P}$ (Fig. 8.B1.1a). Various biologically and ecologically relevant aspects, such as source-sink dynamics and limited gene flow, that act in different parts of the BAM-plot (Fig. 8.B1.1b) can be accounted for using genetic information, but are rarely considered in current ENMs.

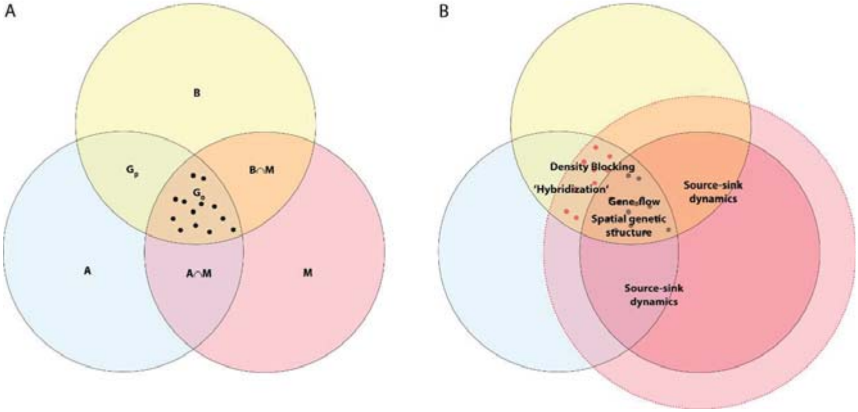

Figure 8.B1.1: a) The BAM diagram (Soberón 2007) as an abstract visualization of the ENM concept in geographic space. b) Biological and ecological aspects that can be quantified with genetic information can be linked to certain compartments of this concept.

Box 2: What can genetic information add to our understanding of the realized niche?

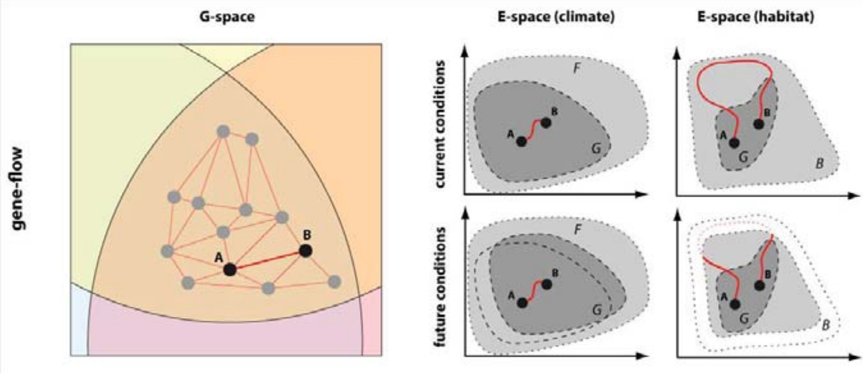

Figure 8.B2.1: Integrating information on contemporary gene flow into niche modeling and theory. Given that the exchange across a species geographic range is a multi-generational process, functional connectivity could be inferred between two locations A and B in geographic (G-)space. The red line represents the environmental conditions faced by individuals moving from A to B. Transferring information about gene flow into environmental (E-)space could lead to very different outcomes depending on the niche delimiting variables considered (right). While the realized niche (G) in the fundamental climate niche space (F) might change under future conditions, effects on gene flow could remain stable. Alternatively, global change might have more profound effects on the environmental niche from the habitat perspective due to increased loss and fragmentation of habitats which are independent from climate change. Herein, the available biotope (B) surrounding suitable habitat patches (i.e., the realized niche G on the habitat scale) might change drastically in consequence and affect functional connectivity between populations A and B (dashed red line outside of B).

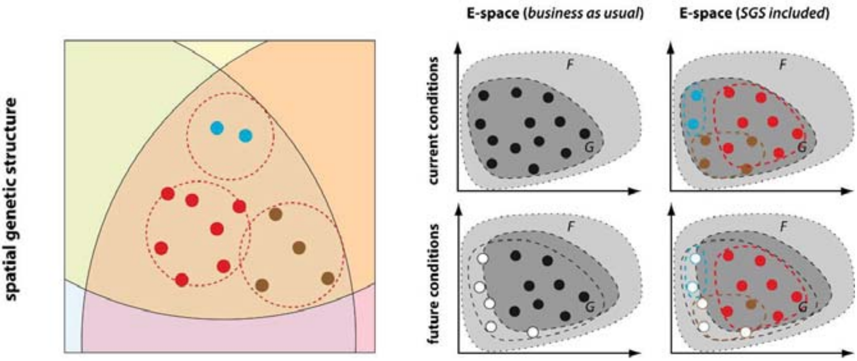

Figure 8.B2.2: Accounting for spatial genetic structure in niche modeling. Environmental selection processes can lead to spatial genetic structure that counteracts the admixing effect of gene flow in geographic (G-)space (left). Changes in environmental conditions over time (e.g., a displacement of the realized niche G through climate change within the species fundamental niche F) can lead to very different model predictions, depending on how spatial genetic structure is dealt with in an ENM. In a business-as-usual scenario that pools all locations at the species level (middle panel) some locations might leave suitable environmental conditions with climate change However, integrating information on spatial genetic structure (SGS), could reveal that some genetically distinct populations (brown and blue locations) are affected more severely than others (red locations) by climate change.

Box 3: What can genetic information add to our understanding of the niche dynamics during colonization?

Colonization occurs either naturally when a species expands its realized range or by anthropogenic translocations. While in either case colonization can be strongly affected by multiple genetic effects, the two main ones are density dependent priority effects (density blocking Fig. 8.B3.1) and hybridization (Fig. 8.B3.2). The following examples on invasive species demonstrate why it is important to consider spatial genetic structure for evaluating invasive niches in the invasive range and comparing between the native and invasive range.

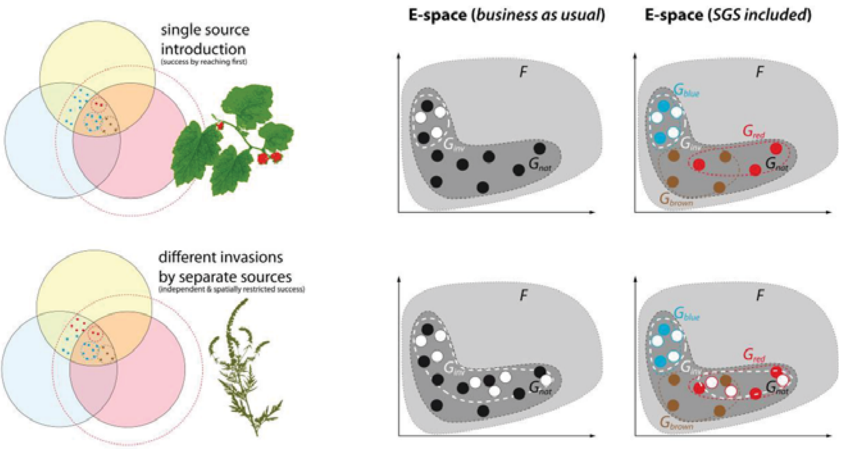

Figure 8.B3.1: Two examples of biological invasions where density blocking may play a key role are *Rubus alceifolius* (top) and *Ambrosia artemisiifolia* (bottom). Shown is the same spatial pattern in geographic space in an idealized BAM scheme (left), and the transformation into environmental (E-) space using a business-as-usual scenario, where genetic information is ignored in the niche modeling process (middle panel, pale circles) and in a scenario where spatial genetic structure is considered (right panel, colored circles). F refers to the fundamental niche in environmental niche space and G refers to the realized niche (either for native (G_{nat}, filled circles), or invasive (G_{inv}, open circles) ranges which are shown for the red (G_{red}), blue (G_{blue}), and brown (G_{brown}) genetic demes.

Example 1: Rubus alceifolius

The giant bramble (*Rubus alceifolius*) is a native plant to Southeast Asia which is invasive in Australia and on several Indian Ocean islands, such as Madagascar and La Reunión (AMSELLEM et al. 2000). AMSELLEM et al. (2000) showed that native populations had a strong genetic structure, whereas invasive populations were genetically very uniform and most probably originated in the Vietnamese region. As illustrated in Fig. 8.B3.1, species with strong spatial genetic structure could also be separated in environmental space. In the case where the genetic deme responsible for the invasion (here G_{blue}) covers just a small fraction within G_{nat}, analyses of niche overlap indicate a low overlap between G_{nat} and G_{inv} but a high niche overlap between G_{blue} and G_{inv}. This is because other genetic demes (here G_{brown} and G_{red}) do not contribute to the invasion. Including just demes that are directly involved in the invasion process in ENMs will result in a reduction or even elimination of over-prediction derived from *business-as-usual* studies.

Example 2: Ambrosia artemisiifolia

The common ragweed (*Ambrosia artemisiifolia*) is native to large parts of North America and is invasive in Europe and East Asia as well as in parts of Australia and South America. Genetic studies showed that individuals introduced to Europe originated from at least two different native regions (GAUDEUL et al. 2011). As with the giant bramble, the identification of genetic demes and comparing these between native and invasive sites (here comparing G_{inv} just with G_{red} and G_{blue}) may lead to a more accurate representation of the niche space covered during the invasion and may help to explain which genetic demes are the most dominant in the invasion process and why.

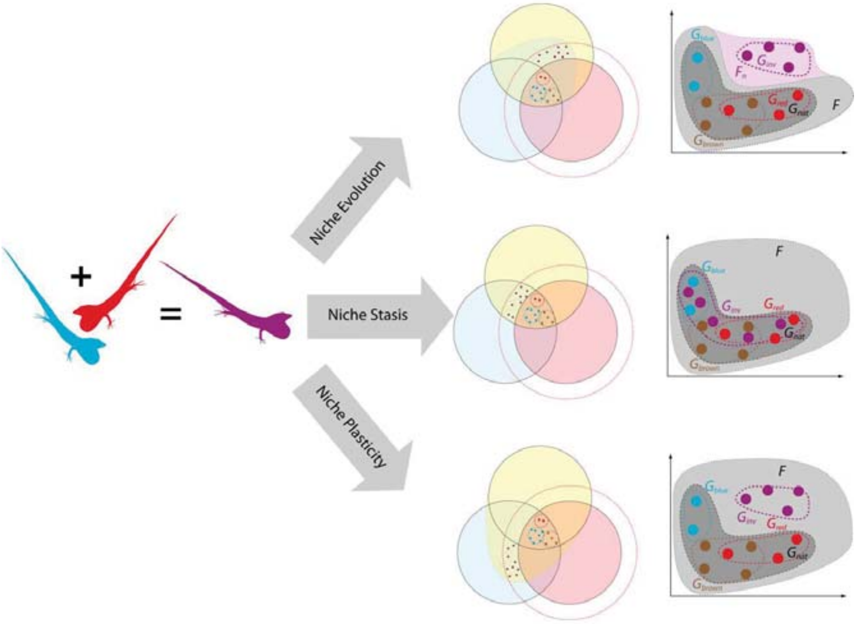

Figure 8.B3.2: Invasion success due to increased adaptive potential following hybridization may result in different niche dynamics (arrows). For example, imagine that hybridization between two locally adapted genetic entities in the brown anole (*Anolis sagrei*, blue & red) result in hybrids (violet). Under niche stasis, no changes in the realized niche (G) of native and invasive ranges (G_{nat}, G_{inv}) will be observed. Expansion of hybrid genotypes in G_{inv} beyond the limits of G_{nat}, could be either due to an expansion of the fundamental niche (F_n) or of G_{inv} within the limits of F. The former case would be referred to as niche evolution, the latter as niche plasticity. Genetic information may provide insight into which of these niche dynamics is the most likely in invasive species derived from hybridization.

Example 3: Anolis sagrei

The brown anole (*Anolis sagrei*) is a Caribbean lizard that has become invasive across large parts of Florida and adjacent areas in the southwestern US (Kolbe et al. 2004; 2008). Kolbe et al (2004) showed that invasive populations across Florida have a higher genetic diversity than expected by typical colonization processes where founder events would lead to a reduction in genetic diversity. They found that invasive genotypes represented an admixture of native populations originating from different Caribbean islands (see also Kolbe et al. 2008). Whether the invasion of the brown anole is accompanied by niche evolution (i.e., an expansion of the fundamental niche) or by niche plasticity (a shift of the realized niche within the constraints of the fundamental niche) is yet unclear. A study comparing environmental niches between native and invasive ranges (ANGETTER et al. 2011) identified niche shifts along some climatic predictors, even though possible local environmental differences among native populations, that could relate to the genetic patterns detected, were not taken into account. Additional genetic and genomic studies focusing on adaptive evolution combined with niche models at finer taxonomic levels would make this species an ideal system to study niche dynamics during invasion.

GENERAL DISCUSSION

“We are approaching a new age of synthesis. Knowledge cannot be merely a degree or a skill… It demands a broader vision, capabilities in critical thinking and logical deduction without which we cannot have constructive progress.”

— LI KA-SHING

The general subject of my thesis was to tie together species distribution models with connectivity models to potential connectivity models (PCMs) to explore spatial exchange among populations in a standardized manner. Without additional genetic information, this synergy of methods is able to assess the potential connectivity of habitats for matrix-sensitive species at very fine spatial scales. These exploratory analyses can be very helpful tools in environmental planning, as they disentangle global trends from local effects and generate easily-legible maps to inform consultants, managers and stakeholders, alike. Furthermore, when combined with genetic information, this approach can fully unfold its potential. Primarily, we can learn how the environment affects a species' functional connectivity to answer different ecological questions. In addition, we can functionally evaluate model settings and their underlying theory, thus improving our understandings and assumptions of species-environment relationships from the conceptual perspective.

The necessity to include standard connectivity assessments in conservation management and policy

Conservation biology is changing its mindset from establishing static and isolated protected areas, to designing dynamic conservation networks. In consequence, connectivity conservation is emerging as a mature sub-discipline to explore the dynamic ways to protect species under changing climatic conditions and anthropogenic pressures (CROOKS & SANJAYAN 2006). Globally, most protected areas are isolated within a highly modified landscape matrix by humans, preventing exchange among sites and making at-site extinctions a lasting state (SEIFERLING et al. 2012). Moreover, when conditions change at the macro scale (e.g., climate), maintaining connectivity at finer scales becomes more important than ever, affecting not only which species to protect, but also the legal status of protected sites (e.g., RÖDDER & SCHULTE 2012). However, as shown and discussed in Part A of my thesis, despite having an exemplary internationally coordinated legal regime for environmental protection, the EU's habitat directive and its accompanied Natura 2000 network of protected sites failed to stop biodiversity loss within the EU borders (EEA 2010). Next to other improvements (HOCHKIRCH et al. 2013), we require an implementation of current knowledge on connectivity conservation to improve the existing infrastructure of Natura 2000 sites (Chapter 3). This includes strategies to effectively compensate for at-site losses due to changing climatic regimes (Chapter 4), and the development and implementation of methodological frameworks as preventive measures in environmental planning (Chapter 5).

The proposed PCM framework can add to our understanding of how connectivity affects the observed patterns of changing distributions and can give spatially-explicit information and guidance; it will provide insight on where future developments will likely affect species. In particular, Chapter 4 has shown that declining trends in specialist species appear in protected and unprotected sites, alike. Even though these changes in butterfly communities were more controlled at protected sites in contrast to more stochastic changes in unmanaged and unprotected fallow grounds, both communities changed from being species-rich to being generalist-dominated. Detected differences in structural connectivity among protected and unprotected sites were not responsible for the observed changes, nor did they lead to contrasting effects in the results. Consequently, this means that environmental factors acting at spatial scales above where connectivity among patches is important are likely to drive species trends at the global to regional level and need to be considered for future management, as well. Integrated studies assessing the effects at different spatial scales—from range shifts due to climate change, to functional connectivity at the habitat level—are therefore mandatory to fully understand and manage declining species. To this end, there is an ongoing debate about the roles of these different compartments in light of biological conservation, and that a focus on connectivity alone cannot solve the problems we currently face (HOGSON et al. 2009; DOERR et al. 2011; HODGSON et al. 2011).

However, the reality of environmental planning—at least in Germany—is at the opposite end of this argument; it largely overlooks estimating connectivity in planning practices, but rather focuses on habitat quality instead. Here, tools such as the proposed PCM framework can help to include connectivity as an additional source of information in the planning process for matrix-sensitive species. As shown in Chapter 5, maps of potential connectivity can be very helpful guides in highlighting areas of well-connected local populations, as well as areas where populations are isolated and might suffer from a higher extinction risk. This way, stakeholders and planners can decide if compensatory measures can be helpful as long-term preventive measures for isolated sites, or if these are simply acceptable to lose. To this end, simulations based on such maps could be used to find out which populations are of particular importance for maintaining the whole network, and which are not (e.g., RUBIO et al. 2015). Using habitat quality as a cornerstone in the evaluation of assessed areas for possible future development contributes—in contrast to its settlement areas—very little in explaining the connectivity of a species. Research has shown that a species' demands on habitat used for dispersal are lower than their demands on habitat where they settle (HADDAD & TEWKSBURY 2005; DOERR et al. 2011). Standard assessment protocols used in environmental planning that focus on habitat quality and abundance of individuals in species of concern therefore neglect the role of connectivity, which increases the danger for more isolated populations in the future. Maps highlighting potential connectivity in matrix-sensitive species can therefore provide a more holistic assessment on the quality of areas under potential future development.

Benefits and caveats of PCMs in landscape genetics

Landscape genetics is a steadily advancing and dynamic field which has led to the development and application of a wide array of approaches during its first decade of existence (MANEL et al. 2003, GUILLOT et al. 2005, MURPHY et al. 2008, BALKENHOL et al. 2009, MANEL & HOLDEREGGER 2013). Our expectations for this field, however, are manifold and strongly depend on the perspective of interest (BALKENHOL et al. 2015a). So was the initial definition of *landscape genetics* by MANEL et al. (2003), focusing on "microevolutionary processes," hence giving a strong emphasis on the genetics, but were rather unspecific about the landscape (BALKENHOL et al. 2015b). Over time, the definition has been extended (HOLDEREGGER & WAGNER 2006; STORFER et al. 2007; BALKENHOL et al. 2015b), up to the point where landscape genetics "[…] *explicitly quantify the effects of landscape composition, configuration, and matrix quality on microevolutionary processes, such as gene flow, drift, and selection, using neutral and adaptive genetic data*" (BALKENHOL et al. 2015b). While the two compartments, "landscape" and "genes," become equally entitled and refined during this process, another issue arose: it heaves the entire field from a descriptive to a quantitative discipline that allows the making of predictions on genetic aspects in the wake of global change (e.g., JAY et al. 2012; WASSERMANN et al. 2012).

In my thesis, I devoted two chapters in Part B to questions related to landscape genetics using PCMs, which supplements the range of available methods and allows the quantification of the impact of landscape elements to gene flow. Yet, both chapters seem to be opposing in their methodological philosophy beyond the use of PCMs. While Chapter 6 compares the average effects of different landscape elements to gene flow in a set of species, Chapter 7 questions this approach and instead goes one step further of what was done in Chapter 6 to improve relationships between landscape and genetic estimates. Nevertheless, both chapters are actually complementary. Chapter 6 focuses on a general ecological question: do landscape effects change with species specialization and mobility? Here, it was most important to compare the average effects of the different landscape compartments among the three species to draw general conclusions. In contrast, Chapter 7 asks how we can incorporate landscape heterogeneity into comparisons between the landscape and gene flow. The butterfly, *Thymelicus sylvestris,* was used in both chapters. Whether the landscape - gene flow relationships focus on average effects of single landscape elements, or on the combined effects of multiple landscape effects, climate remains as the most important landscape variable for the species across the study area. Hence, the general message was that the climatic conditions across the study area are important for this species' persistence. The approach used in Chapter 7, however, added more details beyond the average effect; it showed where climate is driving this correlation the most, and where other landscape elements might be locally more important. This additional information could be very important to understand the local drivers of gene flow and could help guide conservation efforts in species of special concern. It further shows that results made in one area are hardly predictable for other areas, which has been shown in a number of applications so far (SHORT BULL et al. 2011; DUDANIEC et al. 2012; LEVY et al. 2013). The merit of Chapter 7 over those studies is that the presented approach allows for one to visualize the driving factors for each comparison, thereby laying the foundation for further research, asking more precise questions, and establishing more robust sampling designs.

The PCM approach contributes to the development of landscape genetics and accounts for some of the challenges raised by the community (summarized in Balkenhol et al. 2015a), among which the approach as presented in Chapters 6 & 7 contributes to (1) a stronger emphasis on hypothesis testing (STORFER et al. 2007; 2010; CUSHMAN & LANDGUTH 2010; SEGELBACHER et al. 2010; MANEL & HOLDEREGGER 2013); (2) the use and development of predictive models for applications in conservation and management (LANDGUTH & CUSHMAN 2010; MANEL et al. 2010;

SEGELBACHER et al. 2010; BOLLINGER et al. 2014); (3) the selection and understanding of appropriate approaches and their assumptions (BALKENHOL et al. 2009; JAQUIÉRY et al. 2011; WAGNER & FORTIN 2013); and (4) the understanding how scale and the definition of the landscape influence the correlation of landscape effects on genetic variation (CUSHMAN & LANDGUTH 2010; CUSHMAN et al. 2013).

Despite these contributions, there are limitations devoted to PCMs. The main caveat is that the PCM approach does not include dispersal information in the parameterization of the resistance surface. In cases where gene flow is estimated in mobile species at very fine spatial scales, this predictive framework strongly depends on the type and amount of presence records used to model habitat suitability. In the case where these records would entirely represent breeding habitats, areas used for dispersal gets ignored, but these are crucial for studying connectivity (SPEAR et al. 2010). This major critique however invalidates when the grain of environmental predictors decreases and the spatial extent increases, or if occurrence information is also available from dispersal habitats (i.e., from tracked individuals). In the former case (when using climate data, for instance), their grain may exceed that of true dispersal, so that only macro-effects at large spatial scales get quantified. This may prevent a study from drawing implications at finer spatial scales, but it would also depend on the study questions that one is asking. Second, researchers need to keep in mind that dispersal and gene flow may mean completely different things. Genetic exchange is a multi-generational process, and inferences drawn from dispersal studies may not explain genetic variation (SPEAR et al. 2010; BAGUETTE et al. 2014). In the latter case, when occurrence information is available from individuals tracked on a regular basis (e.g., high frequency GPS tracking), more precise PCMs can be parameterized and include the different states of movement, as found in the data. However, for this, there are additional analytical steps required to disentangle occurrence information representing different states which is a complex task on its own (EDELHOFF et al. in prep). But once available, this kind of data could feed into the PCM framework and enable applications in landscape genetics at very fine spatial scales.

From genes to ranges and back: is niche theory ready for the Anthropocene?

One central assumption in niche modeling is that the relevant processes causing range dynamics do not change over time (NOGUÉS-BRAVO 2009). Therefore, many studies use SDMs following the paradigm of 'inferring the past to predict the future' (e.g., ANDERSON et al. 2006; COREDELLIER & PFENNINGER 2009; FICETOLA et al. 2010). This is a fallacy. As humans have become a driving force in changing climate, habitat and global biodiversity, this paradigm no longer stands. The effects are so strong that scientists have even begun to refer to this era as the *Anthropocene* (CORLETT 2014; LEWIS & MASLIN 2015; STEFFEN et al. 2015a;b). This leads to a strong dichotomy in the underlying processes involved for understanding past and future range patterns, with severe consequences to the underlying theories and concepts. Understanding past distributions to make predictions for the future is therefore not easily possible and coupled with high uncertainty.

Time becomes a central element in this dichotomy for two main reasons: the temporal scale and, coupled with human impacts, the directionality between hindcasting and forecasting. The temporal scale usually differs between the hind- and forecasting of SDMs by several orders of magnitude (i.e,. from future decades to past millennia and beyond) and with this, the importance of underlying species-relevant processes also varies. For instance, spatial structure within the realized niche of a species might become less apparent as multi-generational effects turn into stochastic noise over long time scales such as 10k-100ka. Therefore, the ENM concept may be appropriate for a study focused on range dynamics from a historical biogeographic perspective. In contrast, when multi-generational effects become much more important, such as in studies focusing on current or future range dynamics, where the time scale is just in the range of 0.1ka, the classic ENM concept oversimplifies the effects necessary to understand these dynamics. This calls for a refinement of the niche concept for questions related to current and future global change, where climate is no longer the ultimate driving force behind range dynamics. Chapter 8 in Part C shows a possible way to enhance the ENM concept underlying SDMs, using genetic information is able to characterize several ecological aspects.

Including genetic information would also account for the dichotomy regarding the direction of time to where ENMs get projected (i.e., hindcasting vs. forecasting) in relation to the occurrence information used. In hindcasting approaches, potential selective processes (e.g., isolation) have already-influenced populations at their respective locations. In contrast, forecasts lead to the inclusion of occurrence information from populations with potentially negative selection in the future due to human impacts. By this, and outlined in Chapter 8, contemporary genetic information can offer important insights into our understanding of how populations are connected, which landscape elements are important for maintaining functional connectivity, and how local adaptation and eco-evolutionary dynamics affect the precision of ENM predictions and projections. This would allow for working on questions where their answers might help to understand and change the negative impacts the Anthropocene will bring.

Personal outlook

During my thesis, I was able to learn about the benefits of using SDMs for connectivity modeling and further combine them with genetic data. It not only helped me to learn how landscape variations affect the spatial exchange of populations, but I also learned about the limitations of data and approaches, and how to bring these different sources of information in line to overcome these limitations and push the boundary of what is possible with the information and tools we have at hand. The next step would be to deepen that knowledge and explore the ideas and questions derived from it. First, it would be important to communicate the findings to practitioners in environmental planning to make use of the PCM framework for matrix-sensitive species such as the sand lizard. Further, more concrete assessments on SDM predictions and the genetic structure of the modeled species would be crucial to refine modeling practices in cases where modeling deviates from the available genetic information. Finally, it would be great to extend this framework to marine species, where ocean currents are a major factor driving dispersal and where research on this topic is far behind what has been done with terrestrial systems. I hope that I was able to contribute with my thesis to that new age of synthesis, as proposed by LI KA-SHING and quoted in the beginning of this section, and that I provided a proper vision for future work on a dynamic but fragile world.

SUMMARIES

“A good dissertation is a done dissertation. A great dissertation is a published dissertation. A perfect dissertation is neither.”

— @ACADEMICSSAY

Summary

Climate change and the intensification of human land use are generally accepted as leading factors for global biodiversity loss, and their synergistic effects could make species loss even worse. In particular, habitat loss and fragmentation can hamper the exchange among populations or even prevent it, but exchange is needed to counterbalance the effects of range shifting due to climate change. This can lead to negative demographic and genetic effects which can be tremendous for the affected populations.

To counteract these effects, and to develop more efficient conservation efforts, knowledge on population connectivity is mandatory. This thesis aims to contribute to this knowledge by linking tools from different disciplines for their application in conservation planning and spatial ecology. Introduced as *potential connectivity models* (PCMs) in Chapters 1 and 2, they will cover two main topics of the thesis: environmental planning and landscape genetics. After this, the use of genetic information for niche models is highlighted in the final part of the thesis.

Environmental Planning

Environmental planning is of particular importance for reducing environmental impacts due to human developments and maintaining biodiversity due to the designation of reserves and their management. However, the legislative roots in the European Union, despite being a unique effort to coordinate environmental policy across multiple countries, are strongly focusing on the design of protected areas, but neglecting their intended network nature. For this reason, Chapter 3 calls for more effort to revise the Natura 2000 network by better incorporating connectivity into their actions.

However, connectivity estimates could also contribute in unraveling effects not mutually acting at fine scales. Butterflies, for instance, are strongly declining in the grassland habitats of Central Europe. Therefore, the success of conservation measures on high-quality grassland habitats is controversially discussed. In Chapter 4, a comparison of changes in butterfly diversity and community structure on protected versus unprotected habitats shows strong species diversity losses and

remarkable shifts in community composition on both habitat types. Consequently, conservation measures on calcareous grasslands only partly archived their goal to maintain the high species diversity and functional complexity still observed in the 1970s. Even though connectivity was higher among vineyard fallows than among calcareous grasslands, the results were the same for both managed and unmanaged sites. The negative impacts of eutrophication and monotonization of the landscape, as well as climate change, are affecting all habitats—independent of management concepts. Therefore, management on conservation sites may buffer against these effects, but it is not sufficient for a full compensation.

Despite the large number of reserves and conservation sites that are designated and protected by law, potential habitats acting as inter-population connectivity corridors are mostly ignored in the common practice of environmental planning. In most cases, this is mainly caused by a lack of quantitative measures of functional connectivity available for the planning process. The use of fine-scale PCMs, derived from multispectral satellite data for the quantification of spatially explicit habitat corridors for matrix-sensitive species of conservation concern, can be a very helpful instrument for the planning process. The framework is illustrated in Chapter 5 by using the sand lizard (*Lacerta agilis*) in the metropolitan area of Cologne, Germany, as a case study. The model proved to be well-suited to identify connected—as well as isolated—populations within the study area. Furthermore, due to its fine resolution, the PCM was also able to detect small linear structures known to be important for inter-population connectivity for the species, such as railroad embankments. Thus, implementing PCMs will be helpful to overcome shortcomings in the common planning practice in matrix-sensitive species, and may help to counteract other aspects of global change.

Landscape Genetics

To understand how landscape characteristics affect gene flow in species with diverging ecological traits, it is important to analyze taxonomically-related sympatric species in the same landscape using identical methods. In central Europe, Hesperid butterflies of the genus *Thymelicus* represent such a system. In Chapter 6, PCMs with different sets of environmental variables were used, and results indicate that land use patterns influence population connectivity in the least mobile specialist, *T. acteon*. In contrast, populations of the highly mobile generalist, *T. lineola*, were panmictic, lacking any landscape-related effect on the weak genetic differentiation detected. In the species with ecological traits in between those of the congeners, *T. sylvestris*, climate had a strong impact on inter-population connectivity. The results show that closely related species representing a gradient of ecological traits also show genetic structures and landscape genetic relationships that gradually change from a geographical macro- to micro-scale. Thus, the type and magnitude of landscape effects on gene flow can strongly differ—even among closely-related species inhabiting the same landscape—and depend on their relative degree of specialization. In addition, the use of different genetic differentiation metrics makes it possible to detect recent changes in the relative importance of landscape factors affecting gene flow, which likely change as a result of contemporary habitat alterations.

Beside general patterns it is important to look also at local genetic effects. Because landscapes are dynamic entities, where processes are locally affected in manifold ways, genetic exchange is also likely to be affected by different locally-acting landscape elements, generating spatial nonstationarity in gene flow estimates as a result. Accounting for this source of uncertainty will enhance our understanding on how the landscape affects genetic exchange and which key landscape elements are driving it. Chapter 7 of this thesis proposes a method based on statistical learning theory that optimizes the relationship between genetic distances by combining the resistance surfaces of certain landscape elements. Using one of the above-mentioned Hesperid butterflies and the wolverine (*Gulo gulo*) as examples, this approach was introduced. The examples and literature review showed that this method would be valuable for landscape genetics, and should be applicable to any method that correlates genetic distances to a set of effective distances characterizing the landscape.

Genes to the niche!

The final part of the thesis deals with the implication genetic information can have on the conceptional roots of species distribution models (SDMs) also known as environmental niche models (ENMs). The technological revolution in the past 25 years now allows the analysis of species occurrence information in completely novel ways. ENMs appeared as a central tool in this regard, and they are frequently used to address questions related to global change. Despite their popularity, ENMs often suffer from a lack of biological realism and other methodological challenges. To this end, researchers have begun to integrate genetic information into ENMs. However, there is currently no conceptual framework that integrates population genetic information into the theoretical assumptions made for ENMs. Chapter 8 highlights five major reasons why the conceptual integration of genetic information in ENMs can improve model predictions and refine underlying theory. Specifically, genetic data can elucidate how environmental change alters functional connectivity, spatial genetic structure, hybridization, density-dependent priority effects, and source-sink dynamics. Thus, linking genetic and distribution data can lead to a better understanding why species respond to environmental change in a certain way, and improve our ability to forecast these responses. The chapter discusses these points in the context of modeling challenges in the era of the Anthropocene, where habitat fragmentation, biotic invasions, and climate change are major human-driven threads to global biodiversity. That overview shows that integrating different kind of genetic information into ENMs permits a more holistic view of niche theory and points to shortcomings associated with how niche theory is currently being implemented in ENMs.

Zusammenfassung

Klimawandel und eine stetig intensivere Landnutzung durch den Menschen sind allgemeinhin als treibende Faktoren hinter dem globalen Biodiversitätsverlust anerkannt. Betrachtet man beide Faktoren gemeinsam ist anzunehmen, dass sich dieser Verlust in Zukunft weiter verstärkt und damit sämtliche Befürchtungen übertrifft. Vor allem Habitatverlust und –fragmentierung sind sehr problematisch, da hierdurch der Austausch von Individuen zwischen Populationen gebremst oder gar komplett unterbunden wird. Dieser Austausch ist jedoch notwendig um die negativen Effekte des Klimawandels zu kompensieren, etwa indem sich Artareale verschieben könnten. Dies kann ungeheure negative Effekte auf demographische oder genetische Eigenschaften von betroffenen Populationen haben.

Um diesen Effekten entgegenzuwirken, und damit effektivere Schutzbemühungen zu entwickeln, ist Wissen zur Konnektivität von Populationen unerlässlich. Diese Dissertation soll einen Beitrag zu diesem Wissen leisten, indem Methoden verschiedener Fachdisziplinen zusammengeführt werden, um diese für die Umweltplanung und der Raumökologie anwendbar zu machen. Dieses in den Kapiteln 1 und 2 als „potentitelles Konnektivitätsmodell“ (PKM) eingeführte System soll in zwei wesentlichen Themenbereichen Anwendung finden: Umweltplanung und Landschaftsgenetik. Darüber hinaus soll in einem abschließenden dritten Teil der Nutzen genetischer Informationen für prädiktive Nischenmodelle hervorgehoben werden.

Umweltplanung

Umweltplanung ist von entscheidender Wichtigkeit, um negative Einflüsse von Bauvorhaben auf Tiere und Pflanzen sowie auf deren Habitate zu bewerten und gegebenenfalls zu kompensieren. Desweiteren soll erreicht werden Biodiversität als Ganzes durch die Ausweisung von Schutzgebieten und deren Management zu schützen. Die Europäische Union hat mit der FFH und der Vogelschutz-Richtlinie (Natura 2000) ein beispielloses staatenübergreifendes rechtliches Rahmenwerk für den Naturschutz geschaffen. Allerdings forcieren diese Richtlinien stark auf die Ausweisung von Schutzgebieten anstatt auch auf eine entsprechende räumliche

Vernetzung dieser Gebiete verbindlich einzugehen. Kapitel 3 stellt diesen Missstand in einem Kommentar auf eine entsprechende Facharbeit dar, die eine Vision für ein Natura 2020 aufstellt, hierbei jedoch den mangelhaften Bezug zur Konnektivität nicht andiskutiert.

Eine Quantifizierung von Konnektivität ist ebenfalls wichtig um Effekte auf lokaler Ebene von solchen auf größeren Skalenebenen zu unterscheiden. Beispielsweise sind viele Schmetterlingsarten in Offenlandlebensräumen in Mitteleuropa stark rückläufig. Der Erfolg von Schutzbemühungen wird daher kontrovers diskutiert. Kapitel 4 vergleicht Änderungen von Tagfalterzönosen in geschützten und ungeschützten Offenlandlebensräumen von 1970 bis heute. Wenngleich die Konnektivität höher zwischen ungeschützten Lebensräumen war sind die Ergebnisse sehr ähnlich bei allen Standorten: Tagfalterzönosen änderten sich von artenreichen zu artenärmeren und Generalist-dominierten Gesellschaften. Die negativen Effekte von Eutrophierung und Monotonisierung der Landschaft, sowie des Klimawandels beeinflussen sämtliche Habitate – ganz gleich wie deren Schutzbemühungen und Managementkonzepte aussehen. Daher ist es möglich mit einem Management geschützter Flächen (wie etwa einer extensiven Beweidung) großskalige Effekte abpuffern, jedoch lassen sich diese damit nicht Kompensieren.

Trotz der großen Zahl an Schutzgebieten und Bemühungen für deren Ausweisung, werden potentielle Vernetzungsstrukturen oftmals ignoriert in der Planungspraxis. Meistens ist dies darauf zurückzuführen, dass die Möglichkeiten solche Strukturen effektiv im Planungsprozess zu erfassen stark begrenzt sind. Feinskalige PKMs, die auf multispektralen Fernerkundungsdaten beruhen können einen hilfreichen Ansatz für die Umweltplanung darstellen, indem sie artrelevante Vernetzungsstrukturen räumlich explizit für strukturgebundene Arten abbilden können. Dieses Konzept wird in Kapitel 5 beispielhaft für die Zauneidechse (*Lacerta agilis,* L.) im Stadtgebiet von Köln vorgestellt. Das Modell zeigt sehr gut räumliche Vernetzungsstrukuren, wie beispielsweise Bahndämme an und bildet ebenfalls Habitate ab, in denen sich Populationen aufhalten. Diese Populationen können nun klar als gut vernetzt oder isoliert angesprochen werden. Durch die Implementierung von PKMs in der Planungspraxis lassen sich somit einige Unzulänglichkeiten in der Bewertung von strukturgebundenen Arten in Bezug auf die Vernetzung von Vorkommen sowie der Definition von lokalen Populationen beheben.

Landschaftsgenetik

Um zu verstehen, wie Landschaftselemente Genfluss von Arten mit unterschiedlichen ökologischen Eigenschaften beeinflussen ist es wichtig nah verwandte Arten in den gleichen Studienräumen vergleichend zu untersuchen. In Mitteleuropa stellen Dickkopffalter der Gattung *Thymelicus* ein solches System dar. Kapitel 6 untersucht mithilfe von PKMs welche Rolle verschiedene Landschaftselemente beim genetischen Austausch bei drei dieser Arten spielen. In der am wenigsten mobilen jedoch am stärksten spezialisierten Art *T. acteon* zeigte sich, dass Landnutzung ein wesentlicher Faktor für die genetische Vernetzung darstellt. Demgegenüber zeigte sich beim mobilen Generalisten *T. lineola* eine panmiktische genetische Struktur und somit keinerlei Korrelation mit irgendeinem der untersuchten Landschaftselemente. Bei der dritten Art, *T. sylvestris*, welche ökologisch zwischen seinen beiden Schwesternarten steht zeigte sich eine ausgeprägte zunehmende genetische Isolation mit der geographischen Distanz. Diese Korrelation bestand auch bei sämtlichen untersuchten Landschaftselementen. Weitaus am stärksten war diese jedoch mit den klimatischen Eigenschaften des Untersuchungsgebietes korreliert. Grundlegend deuten die Ergebnisse darauf hin, dass Arten mit graduell unterschiedlichen ökologischen Eigenschaften sich ebenfalls in ihren genetischen Antworten graduell unterscheiden. So in etwa mit der Skala, auf der die unterschiedlichen Landschaftselemente wirken. Während Landnutzung eher kleinräumig wirkt sind klimatische Charakteristika eher großräumig wirksam. Darüber hinaus beleuchtet das Kapitel die Bedeutung von der Verwendung unterschiedlicher genetischer Kennwerte bei solchen vergleichen, da mögliche Inkonsistenzen auf sich ändernde ökologische Gleichgewichte infolge menschlicher Eingriffe hinweisen können.

Neben solchen generellen Erkenntnissen ist es wichtig auch auf lokale Effekte zu achten. Landschaften sind dynamisch und damit räumlich sehr heterogen. Prozesse werden daher lokal in vielfältiger Weise beeinflusst. Genfluss als einer dieser Prozesse macht hierbei keine Ausnahme und kann durch lokale Landschaftscharakteristika unterschiedlich stark beeinflusst werden, die durch eine ganzheitliche Betrachtung, gemittelt über eine Untersuchungsregion, unter Umständen an Aussagekraft verlieren könnten. Dies führt letztlich zu räumlicher

Nonstationarität wodurch die nicht erklärte Varianz in einer Korrelation zwischen genetischer Distanz und der effektiven Distanz einzelner betrachteter Faktoren zunimmt. Diese potentielle Fehlerquelle zu berücksichtigen würde unser Verständnis darüber erweitern, wie die Landschaft als Ganzes genetischen Austausch beeinflusst und welche Landschaftselemente lokal dafür verantwortlich sind. Kapitel 7 der Dissertation stellt eine Methode vor die auf den Prinzipien des statistischen Lernens beruht und welche den Zusammenhang zwischen der Landschaft und des Genflusses optimiert. Hierdurch werden Werte von Widerstandslandschaften unterschiedlicher Landschaftselemente kombiniert und in eine einzige abhängige Variable überführt und iterativ optimiert bis die Varianz des Zusammenhangs minimiert wurde. Diese Methode wird im Kapitel 7 an zwei Fallbeispielen exemplarisch vorgestellt. Die Beispiele und ein Literaturvergleich zeigen, dass die Logik der Methode eine Bereicherung für landschaftsgenetische Untersuchungen hat und einfach für verschiedene Verfahren modifiziert werden könnte, welche genetische Distanzen mit effektiven Distanzen aus der Landschaft korrelieren.

Gene zu den Nischen!

Der letzte Teil der Doktorarbeit beschäftigt sich mit den Auswirkungen, die genetische Informationen auf die konzeptionellen Grundlagen von prädiktiven Nischenmodellen (SDMs & ENMs) haben können. Die technologische Revolution der vergangenen 25 Jahre ermöglicht nun völlig neue Wege zur Untersuchung von Arealsystemen. SDMs stellen hierbei ein zentrales Werkzeug dar, da diese häufig genutzt werden um Fragen zum Globalen Wandel zu beantworten. Trotz ihrer Popularität, fehlt es diesen Modellen, neben anderen methodischen Herausforderungen, oft an biologischer Relevanz. Um diesem Problem zu begegnen kombinieren Wissenschaftler nun SDMs vereinzelnd mit genetischen Informationen. Allerdings existiert bislang kein konzeptionelles Rahmenwerk, welches populationsgenetische Aspekte in die theoretischen Grundlagen von SDMs integriert. Kapitel 8 zeigt fünf Gründe, wieso eine konzeptionelle Integration von genetischer Information in SDMs sinnvoll ist, Modellvorhersagen verbessert und die den Modellen zugrundeliegende Theorie erweitert. Im Speziellen könnten genetische Daten zeigen, wie Veränderungen in der Umwelt auf funktionale Konnektivität, räumliche genetische Struktur, Hybridisierung, dichteabhängige Effekte sowie auf

Source-Sink Dynamiken wirken. Somit könnte diese Integration zu einem besseren Verständnis beitragen, wieso Arten auf bestimmte Änderungen reagieren wie sie es tun und verbessern die Möglichkeiten zur Vorhersage dieser Reaktionen. Dieses Kapitel illustriert diese Synthese mit Anthropozänen Beispielen, wo Habitatfragmentierung, biologische Invasionen, und der Klimawandel große Gefahren für die weltweite Biodiversität darstellen.

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“Everyone you will ever meet knows something you don’t”

— BILL NYE

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References

ABRAMS M 2000: The Advanced Spaceborn Thermal Emission and Reflection Radiometer (ASTER): data products for the high spatial resolution imager on NASA's Terra platform. Int J Remote Sens 21: 847–859.

ADDISON PFE, RUMPFF L, BAU SS, CAREY JM, CHEE YE, JARRAD FC, MCBRIDE MF, BURGMAN MA 2013: Practical solutions for making models indispensable in conservation decision-making. Div Distr 19:490–502.

ADRIAENSEN F, CHARDON JP, DE BLUST G, SWINNEN E, VILLALBA S, GULINCK H, MATTHYSEN E 2003: The application of 'least cost' modelling as a functional landscape model. Landsc Urban Plan 64: 233–247.

AGASYAN A, AVCI A, TUNIYEV B, LYMBERAKIS P, ANDRÉN C, COGALNICEANU D, WILKINSON J, ANANJEVA N, ÜZÜM N, ORLOV N, PODLOUCKY R, TUNIYEV S, KAYA U, CRNOBRNJA ISAILOVIC J, VOGRIN M, CORTI C, PÉREZ MELLADO V, SÁ-SOUSA P, CHEYLAN M, PLEGUEZUELOS J, KYEK M, WESTERSTRÖM A, NETTMANN HK, BORCZYK B, STERIJOVSKI B, SCHMIDT B 2010: Lacerta agilis, in: IUCN 2012. IUCN Red List of Threatened Species. Version 2012.2. Accessed via: www.iucnredlist.org.

AITKEN M 1996: A general maximum likelihood analysis of overdispersion in generalized linear models. Stat Comp 6: 251–262.

ALVARADO-SERRANO DF & KNOWLES LL 2014: Ecological niche models in phylogeographic studies: applications, advances and precautions. Mol Ecol Res 14: 233–248.

AMSELLEM L, NOYER JL, LE BOURGEOIS T, HOSSAERT-MCKEY M 2000: Comparison of genetic diversity of the invasive weed *Rubus alceifolius* Pior. (Rosaceae) in its native range and in areas of introduction, using amplified fragment length polymorphism (AFLP) markers. Mol Ecol 9: 443–455.

ANDERSEN LW, FOG K, DAMGAARD C 2004: Habitat fragmentation causes bottlenecks and inbreeding in the European tree frog (Hyla arborea). Proc R Soc B 271:1293–1302.

ANDERSON NJ, BUGMANN H, DEARING JA, GAILLARD M-J 2006: Linking palaeoenvironmental data and models to understand the past and predict the future. TREE 21: 696–704.

ANDRÉN H 1994: Effects on habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355–366.

ANGETTER LS, LÖTTERS S, RÖDDER D 2011: Climate niche shift in invasive species: the case of the brown anole. Biol J Linn Soc 104: 943–954.

ARAI K, TONOOKA H 2005: Radiometric performance evaluation of ASTER VNIR, SWIR and TIR. IEEE Trans Geosci Remote Sens 43: 2725–2732

ARAÚJO MB, CABEZA M, THULLIER W, HANNAH L, WILLIAMS PH 2004: Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. Glob Change Biol 10: 1618–1626.

ARAÚJO MB, PEARSON RG, THUILLER W, ERHARD M 2005: Validation of species-climate impact models under climate change. Glob Change Biol 11: 1504–1513.

ARNOLD ML 1997: Natural hybridization and evolution, Oxford.

AUBRY KB, MCKELVEY KS, COPELAND JP 2007: Distribution and broadscale habitat relations of the wolverine in the contiguous United States. J Wildl Manag 71: 2147–2158.

BAGUETTE M, STEVENS VM, CLOBERT J 2014: The pros and cons of applying the movement ecology paradigm for studying animal dispersal. Movement Ecol 2:13.

BALDWIN RA 2009: Use of maximum entropy modeling in wildlife research. Entropy 11: 854–866.

BALKENHOL N, WAITS LP, DEZZANI RJ 2009: Statistical approaches in landscape genetics: an evaluation of methods for linking landscape and genetic data. *Ecography* 32: 818–830.

BALKENHOL N, PARDINI R, CORNELIUS C, FERNANDES F, SOMMER S 2013: Landscape-level comparison of genetic diversity and differentiation in a small mammal inhabiting different fragmented landscapes of the Brazilian Atlantic Forest. Conserv Gen 14: 355–367.

BALKENHOL N, CUSHMAN SA, WAITS LP, STORFER A 2015a: Current status, future opportunities, and remaining challenges in landscape genetics. In: BALKENHOL N, CUSHMAN SA, STORFER AT, WAITS LP (eds): Landscape Genetics: concepts, methods, applications. Wiley.

BALKENHOL N, CUSHMAN SA, STORFER A, WAITS LP 2015b: Introduction to landscape genetics – concepts, methods, applications. In: BALKENHOL N, CUSHMAN SA, STORFER AT, WAITS LP (eds): Landscape Genetics: concepts, methods, applications. Wiley.

BALMER E, ERHARDT A 2000: Consequences of succession on extensively grazed grasslands for central European butterflies: Rethinking Conservation practices. Conserv Biol 14: 746–757.

BARTHOLMESS H, SCHLOTTMANN K, NOBEL W 2011: Immission measurements with diffusive samplers and lichen mappings to show the impact of nitrogen in the environment and its effects. Gefahrstoffe Reinhaltung der Luft 71: 165–172.

BEAUMONT LJ, HUGHES L, POULSEN M 2005: Predicting species distributions: use of climatic parameters in BIOCLIM and its impact on predictions of species' current and future distributions. Ecol Mod 186: 250–269.

BELL RC, PARRA JL, TONIONE M, HOSKIN CJ, MACKENZIE JB, WILLIAMS SE, MORITZ C 2010: Patterns of persistence and isolation indicate resilience to climate change in montane rainforest lizards. Mol Ecol 19: 2531–2544.

BELLARD C, BERTELSMEIER C, LEADLEY P, THUILLER W, COURCHAMP F 2012: Impacts of climate change on the future of biodiversity. Ecol Lett 15:365–377.

BENES J, KURAS T 1998: Long term diversity changes of butterflies and burnets of the Opavska pahorkatina Hills and Nizky Jesenik Mts. (Czech Republic). Casopis Slezskeho Muzea Opava 47: 245–270.

BENNETT AF, CROOKS KR, SANJAYAN M 2006: The future of connectivity conservation. In: *Connectivity conservation* (ed. CROOKS KR, SANJAYAN M). Cambridge University Press, Cambridge, pp. 676–694.

BERGLIND S-A 2000: Demography and management of relict Sand Lizard *Lacerta agilis* populations on the edge of extinction. Ecol Bull 48:123–142.

BERGLIND S-A 2004: Sand Lizard (*Lacerta agilis*) in central Sweden – modeling juvenile reintroduction and spatial management strategies for metapopulation establishment. In: AKCAKAYA HR et al. (eds) Species conservation and management: case studies. Oxford University Press.

BIELEFELD U 1985: Aufbau eines vernetzten Biotopsystems, Trocken- und Halbtrockenrasen in Rheinland-Pfalz. Ministerium für Soziales, Gesundheit und

Umwelt. Arten- und Biotopschutz - Aufbau eines vernetzten Biotopsystems. Ergebnis der Fachtagung 1984. Verlag Sommer, Lahnstein.

BINK FA 1992: Ecologische Atlas van de Dagvlinders van Noordwest-Europa. Schuyt & Co. Uitgevers en Importeurs, Haarlem.

BIVAND RS, PEBESMA E, GOMEZ-RUBIO V 2013: Applied spatial data analysis with R, Second edition. Springer.

BLANKE I 1999: Erfassung und Lebensweise der Zauneidechse (*Lacerta agilis*) an Bahnanlagen. Zeitschrift für Feldherpetologie 6:147–159.

BLANKE I (2010) Die Zauneidechse - Zwischen Licht und Schatten. Laurenti, Bielefeld, Germany.

BOLLIGER J, LANDER T, BALKENHOL N 2014: Landscape genetic since 2003: status, challenges and future directions. Landsc Ecol 29: 361–366.

BOTERO CA, WEISSING FJ, WRIGHT J, RUBENSTEIN DR 2015: Evolutionary tipping points in the capacity to adapt to environmental change. PNAS 112: 184–189.

BOURN NAD, THOMAS JA 2002: The challenge of conserving grassland insects at the margins of their range in Europe. Biol Conserv 104: 285–292.

BRAMBILLA M, FICETOLA GF 2012: Species distribution models as a tool to estimate reproductive parameters: a case study with a passerine bird species. J Anim Ecol 81: 781–787.

BRAUNISCH V, SEGELBACHER G, HIRZEL AH 2010: Modelling functional landscape connectivity from genetic population structure: a new spatially explicit approach. Molecular Ecology 19: 3664–3678.

BRAUNISCH V, COPPES J, ARLETTAZ R, SUCHANT R, SCHMID H, BOLLMANN K 2013: Selecting from correlated climate variables: a major source of uncertainty for predicting species distributions under climate change. Ecography 36: 971–983.

BROUAT C, CHEVALLIER H, MEUSNIER S, NOBLECOURT T, RASPLUS J-Y 2004: Specialization and habitat: spatial and environmental effects on abundance and genetic diversity of forest generalist and specialist *Carabus* species. Mol Ecol 13: 1815–1826.

BRUNSDON C, FOTHERINGHAM AS, CHARLTON ME 1996: Geographically weighted regression: a method for exploring spatial nonstationarity. *Geogr Analysis* 28: 281–298.

BURGGRAAFF P, KLEEFELD KD 1998: Historische Kulturlandschaft und Kulturlandschaftselemente: Ergebnisse aus dem F+E-Vorhaben 808 09 075 des Bundesamtes für Naturschutz. BfN-Schr.-Vertrieb im Landwirtschaftsverl, Münster.

BURNHAM KP, ANDERSON DR 2002: Model selection and multimodel inference: a practical information-theoretic approach. New York: Springer.

BURROUGH PA, MCDONNELL R 1998: Principles of geographical information systems. Oxford University Press, Oxford.

BUTCHART SHM, WALPOLE M, COLLEN B, VAN STRIEN A, SCHARLEMANN JPW, ALMOND REA, BAILLIE JEM, BOMHARD B, BROWN C, BRUNO J, CARPENTER KE, CARR GM, CHANSON J, CHENERY AM, CSIRKE J, DAVIDSON NC, DENTENER F, FOSTER M, GALLI A, GALLOWAY JN, GENOVESI P, GREGORY RD, HOCKINGS M, KAPOS V, LAMARQUE J-F, LEVERINGTON F, LOH J, MCGEOCH MA, MCRAE L, MINASYAN A, MORCILLO MH, OLDFIELD TEE, PAULY D, QUADER S, REVENGA C, SAUER JR, SKOLNIK B, SPEAR D, STANWELL-SMITH D, STUART SN, SYMES A, TIERNEY M, TYRRELL TD, VIÉ J-C, WATSON R 2010: Global biodiversity: Indicators of recent declines. *Science*, 328: 1164–1168.

CABRAL JS, KREFT H 2012: Linking ecological niche, community ecology and biogeography: insights from a mechanistic niche model. J Biogeogr 39: 2212–2224.

CALDWELL LK 1991: Analysis – assessment – decision: the anatomy of rational policymaking. Impact Assessment Bulletin 9:81–92.

CANTER L, ROSS B 2010: State of practice of cumulative effects assessment and management: the good, the bad and the ugly. Impact Assessment and Project Appraisal 28:261–268.

CARNAVAL AC, MORITZ C 2008: Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic forest. J Biogeogr 25: 1187–1201.

CASETTI E 1972: Generating models by the expansion method: applications to geographic research. *Geogr Analysis* 4: 81–91.

CHAN LM, BROWN JL, YODER AD 2011: Integrating statistical genetic and geospatial methods bring new power to phylogeography. Molecular Phylogenetics and Evolution 59: 523–537.

CHANDRA AK, RAGHAVAN R, RUZZO WL, SMOLENSKY R, TIWARI P 1997: The electrical resistance of a graph captures its commute and cover times. Comp complex 6: 312–340.

CHEN G, ZHAO K, MCDERMID GJ, HAY GJ 2012: The influence of sampling density on geographically weighted regression: a case study using forest canopy height and optical data. Int J Rem Sen 33: 2909–2924.

CONRADT L, ROPER TJ, THOMAS CD 2001: Dispersal behaviour of individuals in metapopulations of two British butterflies. Oikos 95: 416–424.

COPELAND JP, MCKELVEY KS, AUBRY KB, LANDA A, PERSSON J, INMAN RM, KREBS J, LOFROTH E, GOLDEN H, SQUIRES JR, MAGOUN A, SCHWARTZ MK, WILMOT J, COPELAND CL, YATES RE, KOJOLA I, MAY R 2010: The bioclimatic envelope of the wolverine: Do climatic constraints limit their geographic distribution? *Canadian* J Zool 88: 233–246.

CORD AF, RÖDDER D 2011: Inclusion of habitat availability in species distribution models through multi-temporal remote-sensing data? Ecol App 21: 3285–3298.

CORDELLIER M, PFENNINGER M 2009: Inferring the past to predict the future: climate modeling predictions and phylogeography for the freshwater gastropod *Radix balthica* (Pulmonata, Basommatophora). Mol Ecol 18: 534–544.

CORLETT RT 2014: The Anthropocene concept in ecology and conservation. TREE 30: 36–41.

COUNCIL OF THE EUROPEAN COMMISSION 1992: Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. Official Journal of the European Communities, Series L 206:7–49.

CRANDALL KA, BININDA-EMONDS ORP, MACE GM, WAYNE RK 2000: Considering evolutionary processes in conservation biology. TREE 15: 290–295.

CRAWFORD NG 2009: SMOGD: software for the measurement of genetic diversity. Mol Ecol Res 10: 556–557.

CRIST EP, CICONE RC 1984: Application of the Tasseled Cap Concept to Simulated Thematic Mapper Data, Photogr Engin Rem Sen 50:343–352.

CROOKS KR, SANJAYAN M (2006) Connectivity conservation. Cambridge University Press.

CUSHMAN SA, LANDGUTH RL 2010: Spurious correlations and inference in landscape genetics. Mol Ecol 19: 3592–3602.

CUSHMAN SA, WASSERMANN TN, LANDGUTH EL, SHIRK AJ 2013: Re-evaluating causal modeling with Mantel tests in landscape genetics. Diversity 5: 51–72.

DAWSON MN 2012: Parallel phylogeographic structure in ecologically similar sympatric sister taxa. Mol Ecol 21: 987–1004.

DE SMEDT P 2010: The use of impact assessment tools to support sustainable policy objectives in Europe. Ecol Soc 15:30.

DENNIS RLH, EALES H 1997: Patch occupancy in *Coenonympha tullia* (Müller 1764) (Lepidoptera: Satyrinae): Habitat quality matters as much as patch size and isolation. J Insect Conserv 1: 167–176.

DETWILER JT, CRISCIONE CD 2014: Recently introduced invasive geckos quickly reach population genetic equilibrium dynamics. Biol Inv 16: 2653–2667.

DEVICTOR V, VAN SWAAY C, BRERETON T, BROTONS L, CHAMBERLAIN D, HELIÖLÄ J, HERRANDO S, JULLIARD R, KUUSSAARI M, LINDSTRÖM Å, REIF J, ROY DB, SCHWEIGER O, SETTELE J, STEFANESCU C, VAN STRIEN A, VAN TURNHOUT C, VERMOUZEK Z, WALLISDE VRIES M, WYNHOFF I, JIGUET F 2012: Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Clime Change* 2:121–124.

DEVITT TJ, CAMERON DEVITT, SE, HOLLINGWORTH BD, MCGUIRE JA, MORITZ C 2013: Montane refugia predict population genetic structure in the Large-blotched *Ensatina* salamander. Mol Ecol 22: 1650–1665.

DEVKOTA ML, HATFIELD G, CHINTALA R 2014: Effect of sample size on the performance of ordinary least squares and geographically weighted regression. Br J Math & Comp Sci 4: 1–21.

DICKERSON W, MONTGOMERY J 1993: Substantive scientific and technical guidance for NEPA analysis: pitfalls in the real world. The Environmental Professional 15:7–11.

DIETZ JM, GILADI I 2009: Scale-dependence of habitat sources and sinks. In: LIU J, HULL V, MORZILLO AT, WIENS JA (eds): Sources, sinks and sustainability. Cambridge University Press.

DINIZ-FILHO JAF, BINI LM 2012: Thirty-five years of spatial autocorrelation analysis in population genetics: an essay in honour of Robert Sokal (1926-2012). Biol J Linn Soc 107: 721–736.

DOERR VAJ, BARRETT T, DOERR ED 2011: Connectivity, dispersal behavior and conservation under climate change: a response to Hogson et al. J Appl Ecol 48:143–147.

DORMANN CF, MCPHERSON JM, ARAÚJO MB, BIVAND R, BOLLIGER J, CARL G, DAVIES RG, HIRZEL A, JETZ W, KISSLING WD, KÜHN I, OHLEMÜLLER R, PERES-NETO PR, REINEKING B, SCHRÖDER B, SCHURR FM, WILSON R. 2007: Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30: 609–628.

DORMANN CF, SCHYMANSKI SJ, CABRAL J, CHUINE I, GRAHAM C, HARTIG F, KEARNEY M, MORIN X, RÖMERMANN C, SCHRÖDER B, SINGER A 2012: Correlation and process in species distribution models: bridging a dichotomy. J Biogeogr 39: 2219–2131.

DORMANN CF, ELITH J, BACHER S, BUCHMANN C, CARL G, CARRÉ G, GARCÍA MARQUÉZ JR, GRUBER B, LAFOURCADE B, LEITÃO PJ, MÜNKEMÜLLER T, MCCLEAN C, OSBORNE PE, REINEKING B, SCHRÖDER B, SKIDMORE AK, ZURELL D, LAUTENBACH S 2013: Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46.

DOVER J, SETTELE J 2009: The influences of landscape structure on butterfly distribution and movement: a review. J Insect Conserv 13: 3–27.

DOYLE PG, SNELL JL 1984: Random walks and electric networks. Mathematical Association of America.

DRIEZEN K, ADRIAESEN F, RONDININI C, DONCASTER CP, MATTHYSEN E 2007: Evaluating least-cost model predictions with empirical dispersal data: a case-study using radiotracking data of hedgehogs (Erinaceus europaeus). Ecol Mod 209:314–322.

DUDANIEC RY, SPEAR SF, RICHARDSON JS, STORFER A 2012: Current and historical drivers of landscape genetic structure differ in core and peripheral salamander populations. PLoS one 7: e36769.

DUFORET-FREBOURG N, BLUM MGB 2014: Nonstationarity patterns of isolation-by-distance: inferring measures of local genetic differentiation with Bayesian kriging. Evolution 68: 1110–1123.

DUINKER PN, BURBIDGE EL, BOARDLEY SR, GREIG LA 2013: Scientific dimensions of cumulative effects assessment: toward improvements in guidance for practice. Environ Rev 21: 40–52.

DYER RJ 2015a: Is there such a thing as landscape genetics? Mol Ecol 24: 3518–3528.

DYER RJ 2015b: Landscapes and plant population genetics. In: BALKENHOL N, CUSHMAN S, STORFER A, WAITS L (eds). Landscape genetics: concepts, methods, applications. Wiley.

EBERT G, RENNWALD E (eds) 1991: Die Schmetterlinge Baden-Württembergs, Band 1 und 2. Verlag Eugen Ulmer.

EEA. 2010: EEA Technical Report 12/2010, EU 2010 Biodiversity Baseline. http://www.eea.europa.eu/publications/eu-2010-biodiversity-baseline/. (visited Feb. 5, 2013)

ELITH J, GRAHAM CH, ANDERSON RP, DUDÍK M, FERRIER S, GUISAN A, HIJMANS RJ, HUETTMANN F, LEATHWICK JR, LEHMANN A, LI J, LOHMANN LG, LOISELLE BA, MANION G, MORITZ C, NAKAMURA M, NAKAZAWA Y, OVERTON JMCC, PETERSON AT, PHILLIPS SJ, RICHARDSON KS, SCACHETTI PEREIRA R, SCHAPIRE RE, SOBERÓN J, WILLIAMS S, WISZ MS, ZIMMERMANN NE 2006: Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129–151.

ELITH J, PHILLIPS SJ, HASTIE T, DUDÍK M, CHEE YE, YATES C 2011: A statistical explanation of MaxEnt for ecologists. Div Distr 17: 43–47.

ELLIS JR, PASHLEY CH, BURKE JM, MCCAULEY DE 2006: High genetic diversity in a rare and endangered sunflower as compared to a common congener. Mol Ecol 15: 2345–2355.

ELLWANGER G 2004: *Lacerta agilis* (Linnaeus, 1758), In: PETERSEN B, ELLWANGER G, BLESS R, BOYE P, SCHRÖDER E, SSYMANK A (eds): *Das europäische Schutzgebietssystem Natura 2000 - Ökologie und Verbreitung von Arten der FFH-Richtlinie in Deutschland* - Band 2: Wirbeltiere. BfN, Bonn Bad-Godesberg, pp 90–97.

ENGLER JO, RÖDDER D, ELLE O, HOCHKIRCH A, SECONDI J 2013: Species distribution models contribute to determine the effect of climate and interspecific interactions in moving hybrid zones. Journal of Evolutionary Biology 26: 2487–2496.

ENGLER JO, BALKENHOL N, FILZ KJ, HABEL JC, RÖDDER D 2014: Comparative landscape genetics of three closely related sympatric Hesperid butterflies with diverging ecological traits. PLoS one 9: e106526.

EU 1992: Council directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. *Official J.*, **L206** (July), 7–50.

EXCOFFIER L, LARVAL G, SCHNEIDER S 2005: Arlequin ver. 3.0: an integrated software package for population genetics data analysis. Evol Bioinform Onl 1: 47–50.

FAHRING L 2003: Effects of habitat fragmentation on biodiversity. Ann Rev Ecol Evol Syst 34:487–515.

FAGAN WF, CALABRESE JM 2006: Quantifying connectivity: balancing metric performance with data requirements. In: CROOKS KR, SANJAYAN M (eds) Connectivity conservation. Cambridge University Press.

FELSENSTEIN J 1985: Confidence limits on phylogenies: An approach using the bootstrap. *Evolution*, 39: 783–791.

FICETOLA GF, THUILLER W & MIAUD C 2007: Prediction and validation of the potential global distribution of a problematic alien invasive species – the American bullfrog. Div Distr 13: 476–485.

FICETOLA GF, MAIORANO L, FALCUCCI A, DENDONCKER N, BOITANI L, PADOA-SCHIOPPA E, MIAUD C, THUILLER W 2010: Knowing the past to predict the future: land-use change and the distribution of invasive bullfrogs. Glob Change Biol 16: 528–537.

FIELDING AH, BELL JF 1997: A review of methods for the assessment of prediction errors in conservation presence/absence models. Env Cons 24: 38–49.

FILZ KJ, ENGLER JO, STOFFELS J, WEITZEL M, SCHMITT T 2013a: Missing the target? A critical view on butterfly conservation efforts on calcareous grasslands. Biodiv Conserv 22: 2223–2241.

FILZ KJ, SCHMITT T & ENGLER JO 2013b: How fine is fine-scale? Questioning the use of fime-scale bioclimatic data in species distribution models to forecast abundance patterns in butterflies. Eur J Enthomol 110: 311–317.

FINGER A, ZACHOS FE, SCHMITT T, MEYER M, ASSMANN T, HABEL JC 2008: The genetic status of the Violet Copper *Lycaena helle* – a relict of the cold past in times of global warming. Ecography 32: 382–390.

FITHIAN W, HASTIE T 2013: Finite-sample equivalence in statistical models for presence-only data. Ann App Stat 7:1917–1939.

FISCHER J, LINDENMAYER DB 2007: Landscape modification and habitat fragmentation: a synthesis. Glob Ecol Biogeogr 16:265–280.

FORDHAM D, BROOK B, MORITZ C, NOGUÉS-BRAVO D 2014: Better forecasts of range dynamics using genetic data. TREE 29: 436–443.

FOSTER SA, GORR WL 1986: An adaptive filter for estimating spatially varying parameters: application to modeling police hours spent in response to calls for service. Manag Sci 32: 878–889.

FOTHERINGHAM AS, BRUNSDON C, CHARLTON ME 2002: Geographically weighted regression: the analysis of spatially varying relationships. Wiley.

FOURCADE Y, ENGLER JO, RÖDDER D, SECONDI J 2014: Mapping species distribution with MAXENT using a geographically biased sample of presence data: a performance assessment of methods for correcting sampling bias. PLoS one 9: e97122.

FRANKLIN J 2009: Mapping species distributions: Spatial inference and prediction. Cambridge University Press, Cambridge.

FURRER RD, PASINELLI G 2015: Empirical evidence for source-sink populations: a review on occurrence, assessments and implications. Biol Rev doi:10.1111/brv.12195.

GAEDICKE R, HEINICKE W (eds.) 1999: Verzeichnis der Schmetterlinge Deutschlands (Entomofauna Germanica 3). Entomologische Nachrichten und Berichte (Dresden) 5: 1–216.

GAGGIOTTI OE 1996: Population genetic models of source sink metapopulations. T Pop Biol 50: 178–208.

GAO BC 1995: Normalized Difference Water Index for Remote Sensing of Vegetation Liquid Water from Space. Proceedings of SPIE 2480: 225–236.

GASTON KJ 2003: The structure and dynamics of geographic ranges. Oxford University Press.

GAUDEUL M, GIRAUD T, KISS L, SHYKOFF JA 2011: Nuclear and Chloroplast microsatellites show multiple introductions in the worldwide invasion history of common ragweed, *Ambrosia artemisiifolia.* PLoS one 6:e17658.

GENELETTI D 2006: Some common shortcomings in the treatment of impacts of linear infrastructures on natural habitat. EIA Rev 26:257–267.

GERLACH G, JUETERBOCK A, KRAEMER P, DEPPERMANN J, HARMAND P 2010: Calculations of population differentiation based on G_{ST} and D: forget G_{ST} but not all of statistics! Mol Ecol 19: 3845–3852.

GILBERT-NORTON L, WILSON R, STEVENS JR, BEARD KH 2010: A meta-analytic review of corridor effectiveness. Conserv Biol 24: 660–668.

GITZENDANNER MA, SOLTIS PS 2000: Patterns of genetic variation in rare and widespread plant congeners. Am J Bot 87: 783–792.

GLANDT D, BISCHOFF W 1988: Biology and conservation of the Sand Lizard (*Lacerta agilis*). Mertensiella, 1:1–257

GOLDBERG CS, WAITS LP 2010: Comparative landscape genetics of two pond–breeding amphibian species in a highly modified agricultural landscape. Mol Ecol 19: 3650–3663.

GOLDSTEIN H 1987: Multilevel models in educational and social research. Oxford University Press.

GONTIER M 2006: Integrating landscape ecology in environmental impact assessment using GIS and ecological modeling. In: TRESS B, TRESS G, FRY G, OPDAM P (eds) From landscape research to landscape planning: aspects of integration, education and application, Bakkaveen, The Netherlands, pp 345–354.

GONTIER M, MÖRTBERG U, BALFORS B 2010: Comparing GIS-based habitat models for applications in EIA and SEA. EIA Rev 30:8–18.

GONZALEZ SC, SOTO-CENTENO JA, REED DL 2011: Population distribution models: species distributions are better modelled using biologically relevant data partitions. BMC Ecology 11: 20.

GOODWIN BJ 2003: Is landscape connectivity a dependent or independent variable? Landscape Ecol 18: 687–699.

GOSLEE SC, URBAN DL 2007: The *ecodist* package for dissimilarity-based analysis of ecological data. J Stat Softw 22: 1–19.

GOTELLI N, STANTON-GEDDES J 2015: Climate change, genetic markers and species distribution modelling. J Biogeogr 42: 1577–1585.

GROOT AT, CLASSEN A, INGLIS O, BLANCO CA, LÓPEZ JR. J, TÉRAN VARGAS A, SCHAL C, HECKEL DG, SCHÖFL G 2011: Genetic differentiation across North America in the generalist moth *Heliothis virescens* and the specialist *H. subflexa*. Mol Ecol 20: 2676–2692.

GUILLERA-ARROITA G, LAHOZ-MONFORT JJ, ELITH J, GORDON A, KUJALA H, LENTINI PE, MCCARTHY MA, TINGLEY R, WINTLE BA 2015: Is my species distribution model fit for purpose? Matching data and models to applications. Glob Ecol Biogeogr, 24: 276—292.

GUILLOT G, SANTOS F 2009: A computer program to simulate multilocus genotype data with spatially auto-correlated allele frequencies. Mol Ecol Res 9: 1112–1120.

GUILLOT G, MORTIER F, ESTOUP A 2005: Geneland: a program for landscape genetics. Mol Ecol Notes 5: 712–715.

GUISAN A, ZIMMERMAN NE 2000: Predictive habitat distribution models in ecology. Ecol Model 135: 147–186.

GUISAN A, THUILLER W 2005: Predicting species distributions: offering more than simple habitat models. Ecol Lett 8: 993–1003.

GUISAN A, GRAHAM CH, ELITH J, HUETTMANN F 2007: Sensitivity of predictive species distribution models to change in grain size. Div Dist 13: 332–340.

GUISAN A, TINGLEY R, BAUMGARTNER JB, NAUJOKAITIS-LEWIS I, SUTCLIFFE PR, TULLOCH AI, REAGAN TJ, BROTONS L, MCDONALD-MADDEN E, MANTYKA-PRINGLE C, MARTIN TG, RHODES JR, MAGGINI R, SETTERFIELD SA, ELITH J, SCHWARTZ MW, WINTLE BA, BROENNIMANN O, AUSTIN M, FERRIER S, KEARNEY MR, POSSINGHAM HP, BUCKLEY YM 2013: Predicting species distributions for conservation decisions. Ecol Lett 16:1424–1435.

HABEL JC, SCHMITT T 2009: The genetic consequences of different dispersal behaviours in Lycaenid butterfly species. Bull Entomol Res 99: 513–523.

HABEL JC, SCHMITT T 2012: The burden of genetic diversity. Biol Conserv 147: 270–274

HABEL JC, MEYER M, SCHMITT T, ASSMANN T 2008: Polymorphic microsatellite loci in the endangered butterfly *Lycaena helle* (Lepidoptera: Lycaenidae). Eur J Enthomol 105: 361–362.

HABEL JC, MEYER M, SCHMITT T 2009a: The genetic consequence of differing ecological demands of a generalist and a specialist butterfly species. Biodiv Conserv 18: 1895–1908.

HABEL JC, ZACHOS FE, FINGER A, MEYER M, LOUY D, ASSMANN T, SCHMITT T 2009b: Unprecedented long term genetic monomorphism in an endangered relict butterfly species. Conserv Gen 10: 1659–1665.

HABEL JC, RÖDDER D, SCHMITT T, NÈVE G 2011: Global warming will affect the genetic diversity and uniqueness of *Lycaena helle* populations. Glob Chan Biol 17: 194–205.

HABEL JC, RÖDDER D, LENS L, SCHMITT T 2013: The genetic signature of ecologically different grassland Lepidopterans. Biodiv Conserv 22: 2401–2411.

HADDAD NM, TEWKSBURY JJ 2005: Low-quality habitat corridors as movement conduits for two butterfly species. Ecol Appl 15: 250–257.

HALE ML, LURZ PWW, SHIRLEY MDF, RUSHTON S, FULLER RM, WOLFF K 2001: Impact of landscape management on the genetic structure of red squirrel populations. Science, 293:2246–2248.

HANSKI I 1994: A practical model of metapopulation dynamics. J Anim Ecol 63:151–162.

HANSKI I 1998: Metapopulation dynamics. Nature 396:41–49.

HANSKI I 1999: Metapopulation ecology. Oxford University Press.

HANSKI I, MOILANEN A, GYLLENBERG M 1996: Minimum viable metapopulation size. Am Nat 147:527–541.

HARRISON S 1991: Local extinction in a metapopulation context: an empirical evaluation. Biol J Linn Soc 42: 73–88.

HAUSMANN A, HASZPRUNAR G, GEGERER AH, SPEIDEL W, BEHOUNEK G, HERBERT PDN 2011: Now DNA-barcoded: the butterflies and larger moths of Germany. Spinxia 34: 47–58.

HEIKKINEN RK, LUOTO M, ARAÚJO MB, VIRKKALA R, THUILLER W, SYKES MT 2006: Methods and uncertainties in bioclimatic envelope modeling under climate change. Progr Phys Geogr 30:751–777.

HELLER R, SIEGISMUND HR 2009: Relationship between three measures of genetic differentiation G_{ST}, D_{EST} and G'_{ST}: how wrong have we been? Mol Ecol 18: 2080–2083.

HENDRY AP 2013: Key questions in the genetics and genomics of eco-evolutionary dynamics. Heredity 111: 456–466.

HERNANDEZ PA, GRAHAM CH, MASTER LL, ALBERT DL 2006: The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography 29: 773–785.

HEWITT GM 1996: Some genetic consequences of ice ages, and their role in divergence and speciation. Biol J Linn Soc 58: 247–276.

HIJMANS RJ, VAN ETTEN J 2012: raster: Geographic data analysis and modeling. R package version 2.3–12. http://CRAN.R-project.org/package=raster.

HIJMANS RJ, CAMERON SE, PARRA JL, JONES PG, JARVIS A 2005: Very high resolution interpolated climate surfaces for global land areas. Int J Climat 25: 1965–1978.

HILL J, STURM B 1991: Radiometric correction of multi-temporal Thematic Mapper data for the use in agricultural land-cover classification and vegetation monitoring. Int J Remote Sens 12: 1471–1491.

HILL J, MEHL W 2003: Geo- und radiometrische Aufbereitung multi- und hyperspektraler Daten zur Erzeugung langjähriger kalibrierter Zeitreihen. Photogramm Fernerkun 2003: 7–14.

HILL J, DIEMER C, STÖVER O, UDELHOVEN T 1999: A local correlation approach for the fusion of remote sensing data with different spatial resolutions in forestry applications. International Archives of Photogrammetry and Remote Sensing.

HOCHKIRCH A, SCHMITT T, BENINDE J, HIERY M, KINITZ T, KIRSCHEY J, MATENAAR D, ROHDE K, STOEFEN A, WAGNER N, ZINK A, LÖTTERS S, VEITH M, PROELSS A 2013: Europe needs a new vision for a Natura 2020 network. Conserv Lett 6:462–467.

HOF C, LEVINSKY I, ARAÚJO MB, RAHBEK C 2011: Rethinking species' ability to cope with rapid climate change. Glob Chan Biol 17: 2987–2990.

HOGSON JA, THOMAS CD, WINTLE BA, MOILANEN A 2009: Climate change, connectivity and conservation decision making: back to basics. J Appl Ecol 46:964–969.

HOGSON JA, MOILANEN A, WINTLE BA, THOMAS CD 2011: Habitat area, quality and connectivity: striking the balance for efficient conservation. J Appl Ecol 48:148–152.

HOLDEREGGER R, WAGNER HH 2006: A brief guide to landscape genetics. Landscape Ecol 21: 793–796.

HOLDEREGGER R, WAGNER HH 2008: Landscape genetics. Bioscience 58: 199–208.

HOLT RD 2009: Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. PNAS 106: 19659–19665.

HU XS, HE F, HUBBEL SP 2006: Neutral theory in macroecology and population genetics. Oikos 113: 548–556.

HUSEMANN M, COUSSEAU L, CALLENS T, MATTHYSEN E, VANGESTREL C, HALLMANN C, LENS L 2015: Post–fragmentation population structure in a cooperative breeding Afrotropical cloud forest bird: emergence of a source-sink population network. Mol Ecol 24: 1172–1187.

HUTCHINSON GE 1957: Concluding remarks. Cold Spring Harbor Symp. Quart. Biol. 22: 415–427.

IHLOW F, DAMBACH J, ENGLER JO, FLECKS M, HARTMANN T, NEKUM S, RAJAEI H, RÖDDER D 2012: On the brink of extinction? How climate change may affect global chelonian species richness and distribution. Glob Change Biol 18: 1520–1530.

IMS RA 1995: Movement patterns related to spatial structures. In: HANSSON L, FAHRING L, MERRIAM G (eds) Mosaic Landscapes and Ecological Processes. Chapman and Hall.

ITT 2008: ENVI version 4.5 software, 1133 Westchester Avenue, White Plains, NY 10604, USA.

JAMES G, WITTEN D, HASTIE T, TIBSHIRANI R 2013: An introduction to statistical learning – with applications in R. Springer.

JAMMALAMADAKA SR, SENGUPTA A 2001: Topics in Circular Statistics, Section 5.3. World Scientific Press, Singapore.

JAQUIÉRY J, BROQUET T, HIRZEL AH, YEARSLEY J, PERRIN N 2011: Inferring landscape effects on dispersal from genetic distances: how far can we go? Mol Ecol 20: 692-705.

JAY F, MANEL S, ALVAREZ N, DURAND EY, THUILLER W, HOLDEREGGER R, TABERLET P, FRANCOIS O 2012: Forecasting changes in population genetic structure of Alpine plants in response to global warming. Mol Ecol 21: 2353–2368.

JAYNES ET 1957: Information theory and statistical mechanics. Phys Rev 106: 620–630.

Jensen JR 2007: Remote Sensing of the Environment: An Earth Resource Perspective, 2nd Edition, Upper Saddle River: Prentice-Hall.

JIMÉNEZ-VALVERDE A 2011: Insights into the area under the receiver operating characteristic curve (AUC) as a discrimination measure in species distribution modelling. Glob Ecol Biogeogr 21: 498–507.

JIMÉNEZ-VALVERDE A, LOBO JM, HORTAL J 2008: Not as good as they seem: the importance of concepts in species distribution modeling. Div Distr 14:885–890.

JOHNSON DM 2004: Source-sink dynamics in a temporally heterogeneous environment. Ecology 85: 2037–2045.

JOHNSON ML, GAINES MS 1987: The selective basis for dispersal of the prairie vole, Microtus ochrogaster. Ecology 68:684–694.

JOHNSON JB, OMLAND KS 2004: Model selection in ecology and evolution. TREE 19: 101–108.

JOST L 2009: D vs. G_{ST}: Response to Heller and Siegismund (2009) and Ryman and Leimar (2009). Mol Ecol 18: 2088–2091.

KADLEC T, VRBA P, KEPKA P, SCHMITT T, KONVICKA M 2010: Tracking the decline of the once-common butterfly: delayed oviposition, demography and population genetics in ther hermit *Chazara briseis.* Anim Conserv 13: 172–183.

KASSEN R 2002: The experimental evolution of specialists, generalists, and the maintenance of diversity. J Evol Biol 15: 173–190.

KAUTH RJ, THOMAS GS 1976: The tasseled Cap -- A Graphic Description of the Spectral-Temporal Development of Agricultural Crops as Seen by LANDSAT. Proceedings of the Symposium on Machine Processing of Remotely Sensed Data.

KEARNEY M, PORTER W 2009: Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecol Lett 12: 334–350.

KEKKONEN J, SEPPÄ P, HANSKI IK, JENSEN H, VÄISÄNEN RA, BROMMER JE 2011: Low genetic differentiation in a sedentary bird: house sparrow population genetics in a contiguous landscape. Heredity 106: 183–190.

KETTUNEN M, TERRY A, TUCKER G, JONES A 2007: Guidance on the maintenance of landscape features of major importance for wild flora and fauna – Guidance on the implementation of Article 3 of the Birds Directive (79/409/EEC) and Article 10 of the Habitats Directive (92/43/EEC). Institute for European Environmental Policy (IEEP), Brussels, 114 pp. & Annexes.

KEYGHOBADI N 2007: The genetic implications of habitat fragmentation for animals. Can J Zool, 85:1049–1064.

KEYGHOBADI N, ROLAND J, MATTER SF, STROBECK C 2005: Among- and within-patch components of genetic diversity respond at different rates to habitat fragmentation: an empirical demonstration. Proc R Soc B 272: 553–560.

KLEIN HP, SCHUMACHER B, SCHUMACHER W 2001: Biodiversität und Naturschutz im Biologieunterricht. Praxis der Naturwissenschaften-Biologie in der Schule 4: 1–6.

KOLBE JJ, GLOR RE, RODRÍGUEZ SCHETTINO L, LARA AC, LARSON A, LOSOS JB 2004: Genetic variation increases during biological invasion by a Cuban lizard. Nature 431: 177–181.

KOLBE JJ, GLOR RE, SCHETTINO LR, LARA AC, LARSON A, LOSOS JB 2007: Multiple sources, admixture, and genetic variation in introduced *Anolis* lizard populations. Conserv Biol 21: 1612–1625.

KOLBE JJ, LARSON A, LOSOS JB, DE QUEIROZ K 2008: Admixture determines genetic diversity and population differentiation in the biological invasion of a lizard species. Biol Lett 4: 434–437.

KOZAK KH, GRAHAM CH, WIENS JJ 2008: Integrating GIS–based environmental data into evolutionary biology. TREE 23: 141–148.

KOZAK KH, WIENS JJ 2007: Climatic zonation drives latitudinal variation in speciation mechanisms. Proc R Soc B 274: 2995–3003.

KRAMER-SCHADT S, NIEDBALLA J, PILGRIM JD, SCHRÖDER B, LINDENBORN J, REINFELDER V, STILLFRIED M, HECKMANN I, SCHARF AK, AUGERI DM, CHEYE SM, HEARN AJ, ROSS J, MACDONALD DW, MATHAI J, EATON J, MARSHALL AJ, SEMIADI G, RUSTAM R, BERNARD H, ALFRED R, SAMEJIMA H, DUCKWORTH JW, BREITENMOSER-WUERSTEN C, BELANT JL, HOFER H, WILTING A 2013: The importance of correcting for sampling bias in MaxEnt species distribution models. Divers. Dist. 19: 1366–1379.

KREMEN C, CAMERON A, MOILANEN A, PHILLIPS SJ, THOMAS CD, BEENTJE H, DRANSFIELD J, FISHER BL, GLAW F, GOOD TC, HARPER GJ, HIJMANS RJ, LEES DC, LOUIS E, NUSSBAUM RA, RAXWORTHY CJ, RAZAFIMPAHANANA A, SCHATZ GE, VENCES M, VIEITES DR, WRIGHT PC & ZJHRA ML 2008: Alinging conservation priorities across taxa in Madagascar with high–resolution planning tools. Science 320: 222–226.

KUDRNA O 2002: The distribution atlas of European butterflies. Oedippus 20: 1–342.

KUMAR S, NEI M, DUDLEY J, TAMURA K 2008: MEGA: a biologist-centric software for evolutionary analysis of DNA and protein sequences. *Briefings in bioinformatics*, **9**, 299–306.

KYLE JC, STROBECK C 2001: Genetic structure of North American wolverine (*Gulo gulo*) populations. Mol Ecol 10: 337–347.

LAMBECK RJ 1997: Focal species: A multi-species umbrella for nature conservation. Conserv Biol 11:849–856.

LANDGUTH EL, CUSHMAN SA 2010: CDPOP: a spatially explicit cost distance population genetics program. Mol Ecol Res 10: 156–161.

LANUV NRW 2010: FB 24 ABC Bewertungsbogen 07/10 – Lacerta agilis. http://www.naturschutz-fachinformationssysteme-nrw.de. Accessed 12 March 2010.

LAITA A, KOTIAHO JS, MÖNKKÖNEN M 2011: Graph-theoretic connectivity measures: what do they tell us about connectivity. Landsc Ecol 26:951–967.

LANDGUTH E, BALKENHOL N 2012: Relative sensitivity of neutral versus adaptive genetic data for assessing population differentiation. Conserv Gen 13: 1421–1426.

LAVERGNE S, MOLOFSKY J 2007: Increased genetic variation and evolutionary potential drive the success of an invasive grass. PNAS 104: 3883–3888.

LAURANCE WF 2009: Beyond island biogeography theory: understanding habitat fragmentation in the real world. In: Losos JB, Ricklefs RE, editors. The theory of island biogeography revisited. Princeton: Princeton University Press.

LEE-YAW JA, DAVIDSON A, MCRAE BH, GREEN DM 2009: Do landscape processes predict phylogeographic patterns in the wood frog? Mol Ecol 18: 1863–1874.

LENG L, ZHANG D 2011: Measuring population differentiation using Gst or D? A simulation study with microsatellite DNA markers under a finite island model and nonequilibrium conditions. Mol Ecol 20: 2494–2509.

LEVINS R 1969: Some demographic and genetic consequences of environmental heterogeneity for biological control. Bull Entomol Soc America 15: 237–240.

LEVY E, TOMKINS JL, LEBAS NR, KENNINGTON WJ 2013: Contrasting effects of landscape features on genetic structure in different geographic regions in the ornate dragon lizard, *Ctenophorus ornatus.* Mol Ecol 22: 3904–3915.

LEWIS SL, MASLIN MA 2015: Defining the Anthropocene. Nature 519: 171–180.

LICHSTEIN JW 2007: Multiple regression on distance matrices: a multivariate spatial analysis tool. Plant Ecol 188: 117–131.

LIU C, BERRY PM, DAWSON TP, PEARSON R 2005: Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28: 385–393.

LIZÉE MH, BONARDO R, MAUFFREY JF, BERTAUDIÈRE-MONTES V, TATONI T, DESCHAMPS-COTTIN M 2011: Relative importance of habitat and landscape scales on butterfly communities of urbanizing areas. CR Biol 334: 74–84

LOBO JM, JIMÉNEZ-VALVERDE A, REAL R 2008: AUC: a misleading measure of the performance of predictive distribution models. Glob Ecol Biogeogr 17: 145–151.

LOMOLINO MV, BROWN JH 2009: The reticulating phylogeny of island biogeography theory. Quart Rev Biol 84: 357–390.

LOUY D, HABEL JC, SCHMITT T, ASSMANN T, MEYER M, MÜLLER P 2007: Strongly diverging population genetic patterns of three skipper species: the role of habitat fragmentation and dispersal ability. Conserv Gen 8: 671–681.

MACARTHUR R-H, WILSON E-O 1967: The theory of island biogeography. Princeton: Princeton University Press.

MAES D, VAN DYCK H 2001: Butterfly Diversity loss in Flanders (north Belgium): Europe's worst case scenario? Biol Conserv 99: 263–276.

MAGOUN AJ, COPELAND JP 1998: Characteristics of wolverine reproductive den sites. J Wildl Manag 62: 1313–1320.

MAGUIRE DJ 1991: An overview and definition of GIS. In: Maguire DJ, Goodchild M, Rhinds D (eds) Geographical Information Systems: Principals and Applications, Longman, pp 9–20.

MANDELIK Y, DAYAN T, FEITELSON E 2005: Issues and dilemmas in ecological scoping: Scientific, procedural and economic perspectives. Impact Assessment and Project Appraisal 23:55–63.

MANEL S, HOLDEREGGER R 2013: Ten years of landscape genetics. TREE 28: 614–621.

MANEL S, SCHWARTZ MK, LUIKART G, TABERLET P 2003: Landscape genetics: combining landscape ecology and population genetics. TREE 18: 189–197.

MANEL S, JOOST S, EPPERSON BK, HOLDEREGGER R, STORFER A, ROSENBERG MS, SCRIBNER TM, BONIN A, FORTIN M-J 2010: Perspectives on the use of landscape genetic adaptive variation in the field. Mol Ecol 19: 3760–3772.

MARINI L, FONTANA P, KIMEK S, BATTISTI A, GASTON KJ 2009: Impact of farm size and topography on plant and insect diversity of manages grasslands in the Alps. Biol Conserv 142: 394–403.

MCINERNY GJ, ETIENNE RS 2013: ‘Niche’ or ‘distribution’ modeling? A response to Warren. TREE 28:191–192.

MCKINNEY ML, LOCKWOOD JL 1999: Biotic homogenization: a few winners replacing many loosers in the next mass extinction. TREE 14: 450–453.

MCRAE BH 2006: Isolation by resistance. Evolution 60: 1551–1561.

MCRAE BH, BEIER P 2007: Circuit theory predicts gene flow in plant and animal populations. PNAS 104: 19885–19890.

McRae BH, Dickson BG, Keitt TH, Shah VB 2008: Using circuit theory to model connectivity in ecology, evolution and conservation. Ecology 89: 2712–2724.

Meglécz E, Pecsenye K, Varga Z, Solignac M 1998: Comparison of differentiation pattern at allozyme and microsatellite loci in *Parnassius mnemosyne* (Lepidoptera) populations. Hereditas 128: 95–103.

Meglécz E, Solignac M 1998: Microsatellite loci for *Parnassius mnemosyne* (Lepidoptera). Hereditas 128: 179–180.

Meglécz E, Petenian F, Danchin E, Coer D'Acier A, Rasplus J-Y, Faure E 2004: High similarity between flanking regions of different microsatellites detected within each of two species of Lepidoptera: *Parnassius Apollo* and *Euphydrias aurinia*. Mol Ecol 13: 1693–1700.

Meirmans PG, Hedrick PW 2011: Assessing population structure F_{ST} and related measures. Mol Ecol Res 11: 5–18.

Merow C, Smith MJ, Silander Jr JA 2013: A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography 36:1058–1069.

Metzger J-P, Décamps H 1997: The structural connectivity threshold: a hypothesis in conservation biology at the landscape scale. Acta Oecologica 18:1–12.

Meyer CB, Thuiller W 2006: Accuracy of resource selection functions across spatial scales. Div Dist 12: 288–297.

Mimet A, Houet T, Julliard R, Simon L 2013: Assessing functional connectivity: a landscape approach for handling multiple ecological requirements. Methods Ecol Evol 4:453–463.

Moilanen A, Hanski I 1998: Metapopulation dynamics: effects of habitat quality and landscape structure. Ecology 79:2503–2515.

Moilanen A, Hanski I 2006: Connectivity and metapopulation dynamics in highly fragmented landscapes. In: Crooks KR, Sanjayan M (eds) Connectivity conservation, Cambridge University Press.

Moilanen A, Nieminen M 2002: Simple connectivity measures for metapopulation studies. Ecology 83:1131–1145.

MORITZ C 1994: Defining 'Evolutionary Significant Units' for conservation. TREE 9: 373–375.

MORRIS P, THERIVEL R 2001: Methods of environmental impact assessment. Spon.

MURPHY MA, EVANS JS, CUSHMAN SA, STORFER A 2008: Representing genetic variation as continuous surfaces: an approach for identifying spatial dependency in landscape genetic studies. Ecography 31: 685–697.

NAKAGAWA S, CUTHILL IC 2007: Effect size, confidence interval and statistical significance: a practical guide for biologists. Biol Rev Camb Philos Soc 82: 591–605.

NASA 2002: Landsat 7 science data users handbook, http://landsathandbook.gsfc.nasa.gov/pdfs/Landsat7_Handbook.pdf, Accessed 01 September 2011.

NICHOLSON E, OVASKAINEN O 2009: Conservation priorization using metapopulation models. In: MOILANAN A, WILSON KA, POSSINGHAM H (eds) Spatial conservation prioritization: Quantitative methods & computational tools. Oxford University Press.

NOGUÉS-BRAVO D 2009: Predicting the past distribution of species climatic niches. Glob Ecol Biogeogr 18:521–531.

OKSANEN J, BLANCHET FG, KINDT R, LEGENDRE P, MINCHIN PR, O'HARA RB, SIMPSON GL, SOLYMOS P, MHH STEVENS, WAGNER H 2014: vegan: Community Ecology Package. R package version 2.2-0. http://CRAN.R-project.org/package=vegan.

ONEY R, REINEKING B, O'NEILL G, KREYLING J 2013: Intraspecific variation buffers projected climate change impacts on *Pinus contorta.* Ecology & Evolution 3: 437–449.

ORTEGO J, RIORDAN EC, GUGGER PF, SORK VL 2012: Influence of environmental heterogeneity on genetic diversity and structure in an endemic southern Californian oak. Mol Ecol 21: 3210–3223.

PACKER L, ZAYED A, GRIXTI C, RUZ L, OWEN RE, VIVALLO F, TORO H 2005: Conservation genetics of potentially endangered mutualisms: reduced levels of genetic variation in specialist versus generalist bees. Conserv Biol 19: 195–202.

PÁEZ A, FARBER S, WHEELER D 2011: A simulation-based study of geographically weighted regression as a method for investigating spatially varying relationships. Environ Plann *A* 43: 2992–3010.

PAGEL J, SCHURR FM 2012: Forecasting species ranges by statistical estimation of ecological niches and spatial population dynamics. Glob Ecol Biogeogr 21: 293–304.

PALSBØLL PJ, BÉRUBÉ M, ALLENDORF FW 2007: Identification of management units using population genetic data. TREE 22: 11–16.

PARMESAN C 2006: Ecological and evolutionary responses to recent climate change. Annu Rev Ecol Syst 37: 637–669.

PARMESAN C, YOHE G 2003: A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.

PAVLACKY JR. DC, GOLDIZEN AW, PRENTIS PJ, NICHOLLS JA, LOWE AJ 2009: A landscape genetics approach for quantifying the relative influence of historic and contemporary habitat heterogeneity on the genetic connectivity of a rainforest bird. Mol Ecol 18: 2945–2960.

PEARMAN PB, D'AMEN M, GRAHAM CH, THUILLER W, ZIMMERMANN NE 2010: Within-taxon niche structure: niche conservatism, divergence and predicted effects of climate change. Ecography 33: 990–1003.

PEARSON RG, RAXWORTHY CJ, NAKAMURA M, PETERSON AT 2007: Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J Biogeogr 34:102–117.

PE'ER G, SALTZ D, THULKE HH, MOTRO U 2004: Response to topography in a hilltopping butterfly and implications for modeling nonrandom dispersal. Anim Behav 68: 825–839.

PE'ER G, HEINZ SK, FRANK K 2006: Connectivity in heterogeneous landscapes: analyzing the effect of topography. Landscape Ecol 21: 47–61.

PETERSON AT, VIEGLAIS DA 2001: Predicting species invasions using ecological niche modeling: new approaches from bioinformatics attack a pressing problem. BioScience 51: 363–371.

PETERSON AT, HOLT RD 2003: Niche differentiation in Mexican birds: using point occurrences to detect ecological innovation. Ecol Lett 6: 774–782.

PETERSON AT, SOBERÓN J, PEARSON RG, ANDERSON RP, MARTÍNEZ-MEYER E, NAKAMURA M, ARAÚJO MB 2011: Ecological niches and geographic distributions. Princeton University Press.

PETTERSON B 1985: Extinction of an isolated population of the middle spotted woodpecker *Dendrocopos medius* (L.) in Sweden and its relation to general theories on extinction. Biol Conserv 32:335–353.

PFEIFER M, DISNEY M, QUAIFE T, MARCHANT R 2012: Terrestrial ecosystems from space: a review of earth observation products for macroecology applications. Glob. Ecol Biogeogr. 21: 603–624.

PIN KOH L 2007: Impacts of land use change on South-east Asian forest butterflies: a review. J App Ecol 44: 703–713.

PHILLIPS SJ, DUDÍK M, SCHAPIRE RE 2004: A maximum entropy approach to species distribution modeling. Proceedings of the 21st International Conference on Machine Learning, Banff, Canada.

PHILLIPS SJ, ANDERSON RP, SCHAPIRE RE 2006: Maximum entropy modeling of species geographic distributions. Ecol Model 190: 231–259.

PHILLIPS SJ, DUDÍK M 2008: Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31: 161–175.

POELCHAU MF, HAMRICK JL 2012: Differential effects of landscape-level environmental features on genetic structure in three codistributed tree species in Central America. Mol Ecol 21: 4970–4982.

POLLARD E, YATES TJ 1993: Monitoring butterflies for ecology and conservation. The British Monitoring Scheme. Chapman & Hall.

POLUS E, VANDEWOESTIJNE S, CHOUTT J, BAGUETTE M 2007: Tracking the effects of one century of habitat loss and fragmentation on calcareous grassland butterfly communities. Biodiv Conserv 16: 3423–3436.

POSSINGHAM HP, ANDELMAN SJ, NOON BR, TROMBULAK S, PULLIAM HR 2001: Making smart conservation decisions. In: SOULE MA, ORIANS GH (eds) Conservation Biology: Research priorities for the next decade. Island Press, pp 225–244.

POULOS HM, CHERNOFF B, FULLER PL, BUTMAN D 2012: Ensemble forecasting of potential habitat for tree invasive fished. Aquatic Invasions 7: 59–72.

POWER DM 1972: Number of bird species on the California islands. Evolution 26: 451–463.

PULLIAM HR 1988: Sources and sinks: empirical evidence and population consequences. In: RHODES OE, CHESSER RK, SMITH MH (eds): Population dynamics in ecological space and time. University of Chicago Press.

PULLIAM HR 2000: On the relationship between niche and distribution. Ecol Lett 3: 349–361.

R DEVELOPMENT CORE TEAM 2010: R: a language and environment for statistical computing URL: http://www.R-project.org.

R DEVELOPMENT CORE TEAM 2012: R: a language and environment for statistical computing. Available: http://www.R-project.org.

R CORE TEAM 2013: R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

RAEYMAEKERS JAM, LENS L, VAN DEN BROECK F, VAN DONGEN S, VOLCKAERT FAM 2012: Quantifying population structure on short timescales. Mol Ecol 21: 3458–3473.

RÁKOSY L, SCHMITT T 2011: Are butterflies and moths suitable ecological indicator systems for restoration measures of semi–natural calcareous grassland habitats? Ecol Indic 11: 1040–1045.

REINHARDT R, THUST R 1988: Zur ökologische Klassifizierung und zum Gefährdungsgrad der Tagfalter der DDR. Entomologische Nachrichten und Berichte 32: 199–206.

RHODES JR, WIEGAND T, MCALPINE CA, CALLAGHAN J, LUNNEY D, BOWEN M, POSSINGHAM HP 2006: Modeling species' distributions to improve conservation in semiurban landscapes: Koala case study. Conserv Biol 20:449–459.

RICHARDS ZT, VAN OPPEN MJH 2012: Rarity and genetic diversity in Indo-Pacific *Acropora* corals. Ecol Evol 2: 1867–1888.

RICHARDSON JL 2012: Divergent landscape effects on population connectivity in two co-occurring amphibian species. Mol Ecol 21: 4437–4451.

RICHARDSON JL, URBAN MC, BOLNICK DI, SKELLY DK 2014: Microgeographic adaptation and the spatial scale of evolution. TREE 29: 165-176.

ROBERGE JM, ANGELSTAM P 2004: Usefulness of the umbrella species concept as a conservation tool. Conserv Biol 18:76–85.

ROBERTS DA, YAMAGUCHI Y, LYON RJP 1985: Calibration of Airborne Imaging Spectrometer data to percent reflectance using field measurements. Proceedings of the 19th International Symposium of Remote Sensing of the Environment, Ann Arbor, MI, October 21–25, 1985.

RÖDDER D, LÖTTERS S 2010: Explanative power of variables used in species distribution modeling: an issue of general model transferability or niche shift in the invasive Greenhouse frog (Eleutherodactylus planirostris). Naturwiss 97:781–796.

RÖDDER D, SCHULTE U 2010: Potential loss of genetic variability despite well established network of reserves: the case of the Iberian endemic Lacerta schreiberi. Biodiv Conserv 19:2651–2666.

RÖDDER D, SCHMIDTLEIN S, VEITH M, LÖTTERS S 2009: Alien invasive slider turtle in unpredicted habitat: a matter of niche shift or of predictors studied? PLoS one e7843.

RÖDDER D, ENGLER JO, BONKE R, WEINSHEIMER F, PERTEL W 2010: Fading of the last giants: an assessment of habitat availability of the Sunda gharial *Tomistoma schlegelii* and coverage with protected areas. Aquatic Conserv 20:678–684.

RÖDDER D, LAWING AM, FLECKS M, AHMADZADEH F, DAMBACH J, ENGLER JO, HABEL JC, HARTMANN T, HÖRNES D, IHLOW F, SCHIDELKO K, STIELS D, POLLY PD 2013: Evaluating the Significance of Paleophylogeographic Species Distribution Models in Reconstructing Quaternary Range-Shifts of Nearctic Chelonians. PLoS one e72855.

ROW JR, BLOUIN-DEMERS G, LOUGHEED SC 2010: Habitat distribution influences dispersal and fine-scale genetic population structure of eastern foxsnakes (*Mintonius gloydi*) across a fragmented landscape. Mol Ecol 19: 5157–5171.

ROUSE JW, HAAS RH, SCHELL JA, DEERING DW 1974: Monitoring Vegetation Systems in the Great Plains with ERTS. Third ERTS Symposium, NASA SP-351 I: 309–317.

Rubio L, Bodin Ö, Brotons L, Saura S 2015: Connectivity conservation priorities for individual patches evaluated in the present landscape: how durable and effective are they in the long term. Ecography 38: 782–791.

Ryman N, Leimar O 2009: G_{ST} is still a useful measure of genetic differentiation – a comment on Jost's *D*. *Mol Ecol* 18: 2084–2087.

Saitou N, Nei M 1987: The neighbor-joining method: A new method for reconstructing phylogenetic trees. Mol Biol Evol 4: 406–425.

Savolainen O, Lascoux M, Merilä J 2013: Ecological genomics of local adaptation. Nature Rev Genet 14: 807–820.

Sawyer SC, Epps CW, Brashares JS 2011: Placing linkages among fragmented habitats: do least-cost models reflect how animals use landscapes? J App Ecol 48:668–678.

Schaller J 1990: Geographical information system applications in environmental impact assessment, in: Scholten HJ, Stillwell JCH (eds). Geographical information systems for urban and regional planning. Kluwer Academic Publishers, pp 107–117.

Schidelko K, Stiels D, Rödder D 2011: Historical stability of diversity patterns in African estrildid finches (Estrildidae). Biol J Linn Soc 102: 455–470.

Schmidt A 2010: Die Großschmetterlinge (Macrolepidoptera s.l.) des Landes Rheinland-Pfalz. Standart-Faunenliste mit integriertem Rote Liste-Vorschlag. Melanargia 22: 121–277.

Schmitt T, Rákosy L 2007: Changes of traditional agrarian landscape and their conservation implications: a case study of butterflies in Romania. Divers Distrib 13: 855–862.

Schmitt T, Augenstein B, Finger A 2008: The influence of changes in viticulture management on the butterfly (Lepidoptera) diversity in a wine growing region of southwestern Germany. Eur J Entomol 105: 249–255.

Schnitter P, Eichen C, Ellwanger G, Neukirchen M, Schröder E 2006: Empfehlungen für die Erfassung und Bewertung von Arten als Basis für das Monitoring nach Artikel 11 und 17 der FFH-Richtlinie in Deutschland. – Berichte des Landesamtes für Umweltschutz Sachsen-Anhalt (Halle), Sonderheft 2.

Schurr FM, Pagel J, Cabral JS, Groeneveld J, Bykova O, O'Hara RB, Hartig F, Kissling WD, Linder HP, Midgley GF, Schröder B, Singer A, Zimmermann NF 2012: How to understand species' niches and range dynamics: a demographic research agenda for biogeography. J Biogeogr 39: 2146–2162.

Schwartz MK, Luikart G, Waples RS 2007: Genetic monitoring as a promising tool for conservation and management. TREE 22: 25–33.

Schwenk K, Brede N, Streit B 2008: Introduction. Extent, processes and evolutionary impact of interspecific hybridization in animals. Phil Transact B 363: 2805–2811.

Schwenk WS, Donovan TM 2011: A multispecies framework for landscape conservation planning. Conserv Biol 25: 1010–1021.

Scoble J, Lowe A 2010: A case for incorporating phylogeography and landscape genetics into species distribution modeling approaches to improve climate adaptation and conservation planning. Div Dist 16: 343–353.

Segelbacher G, Cushman SA, Epperson BK, Fortin M-J, Francois O, Hardy OJ, Holderegger R, Taberlet P, Waits LP, Manel S 2010: Applications of landscape genetics in conservation biology: concepts and challenges. Conserv Genet 11: 375–385.

Seiferling IS, Proulx R, Peres-Neto PR, Fahring L, Messier C 2012: Measuring Protected-Area Isolation and Correlations of Isolation with Land-Use Intensity and Protection Status. Conserv Biol 26: 610–618.

Settele J, Feldmann R, Reinhardt R 1999: Die Tagfalter Deutschlands-Ein Handbuch für Freilandökologen, Umweltplaner und Naturschützer. Ulmer, Stuttgart.

Severns PM, Liston A, Wilson MV 2011: Habitat fragmentation, genetic diversity, and inbreeding depression in a threatened grassland legume: is genetic rescue necessary? Conserv Gen 12: 881–893.

Shirk AJ, Wallin DO, Cushman SA, Rice CG, Warheit KI 2010: Inferring landscape effects on gene flow: a new model selection framework. Mol Ecol 19: 3603–3619.

Short-Bull RA, Cushman SA, Mace R, Chilton T, Kendall KC, Landguth EL, Schwartz MK, McKelvey K, Allendorf FW, Luikart G 2011: Why replication is important in landscape genetics: American black bear in the Rocky Mountains. Mol Ecol 20: 1092–1107.

SINGLETON PH, GAINES WL, LEHMKUHL JF 2002: Landscape permeability for large carnivores in Washington: a geographic information system weighted-distance and least–cost corridor assessment. U.S. Forest Service Research Paper PNW-RP-549.

SKELLY DK, JOSEPH LN, POSSINGHAM HP, FREIDENBURG LK, FARRUGIA TH, KINNISON MT, HENDRY AP 2007: Evolutionary responses to climate change. Conserv Biol 21: 1353–1355.

SMITH SA, DONOGHUE MJ 2010: Combining Historical Biogeography with Niche Modeling in the Caprifolium Clade of Lonicera (Caprifoliaceae, Dispacales). Systematic Biology 59: 322–341.

SOBERÓN JM 2007: Grinnellian and Eltonian niches and geographic distributions of species. Ecol Lett 10: 1115–1123.

SOBERÓN JM 2010: Niche and area of distribution modeling: a population ecology perspective. Ecography 33:159–167.

SOBERÓN JM 2014: Commentary on ditch, stitch and pitch: the niche is here to stay. J Biogeogr 41: 414–417.

SOBERÓN JM & NAKAMURA M 2009: Niches and distributional areas: concepts, methods, and assumptions. PNAS 106: 19644–19650.

SPEAR SF, BALKENHOL N, FORTIN MJ, MCRAE BH, SCRIBNER K 2010: Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. Mol Ecol 19:3576–3591.

SPEAR SF, CRISAFULLI CM, STORFER A 2012: Genetic structure among coastal tailed frog populations at Mount St. Helens is moderated by post-disturbance management. *Ecol App* 22: 856–869.

STEELE CA, BAUMSTEIGER J, STORFER A 2009: Influence of life-history variation on the genetic structure of two sympatric salamander taxa. Mol Ecol 18: 1629–1639.

STEFFEN W, BROADGATE W, DEUTSCH L, GAFFNEY O, LUDWIG C 2015a: The trajectory of the Anthropocene: The great acceleration. The Anthropocene Review 2:81–98.

STEFFEN W, RICHARDSON K, ROCKSTRÖM J, CORNELL SE, FETZER I, BENNETT EM, BIGGS R, CARPENTER SR, DE VRIES W, DE WIT CA, FOLKE C, GERTEN D, HEINKE J, MACE GM, PERSSON LM, RAMANATHAN V, REYERS B, SÖRLIN S. 2015b: Planetary boundaries: Guiding human development on a changing planet. Science 347: 1259855.

STIELS D, SCHIDELKO K, ENGLER JO, VAN DEN ELZEN R, RÖDDER D 2011: Predicting the potential distribution of the invasive common waxbill Estrilda astrild (Passeriformes: Estrildidae). J Ornithol 152: 769–780.

STORFER A, MURPHY MA, EVANS JS, GOLDBERG CS, ROBINSON S, SPEAR SF, DEZZANI D, DELMELLE E, VIERLING L, WAITS LP 2007: Putting the 'landscape' in landscape genetics. *Heredity*, **98**, 128–142.

STORFER A, MURPHY MA, SPEAR SF, HOLDEREGGER R, WAITS LP 2010: Landscape genetics: where are we now? Mol Ecol 19: 3496–3514.

SUTCLIFFE OL, BAKKESTUEN V, FRY G, STABBETORP OE 2003: Modelling the benefits of farmland restoration: methodology and application to butterfly movement. Landsc Urban Plan 63: 15–31.

SWETS JA 1988: Measuring the accuracy of diagnostic systems. Science 240: 1285–1293.

SYFERT MM, SMITH MJ, COOMES DA 2013: The effects of sampling bias and model complexity on the predictive performance of MaxEnt species distribution models. PLoS one 8: e055158.

TAMURA K, NEI M, KUMAR S 2004: Prospects for inferring very large phylogenies by using the neighbor–joining method. PNAS 101: 11030–11035.

TAMURA K, PETERSON D, PETERSON N, STECHER G, NEI M, KUMAR S 2011: MEGA5: Molecular Evolutionary Genetics Analysis using Maximum Likelihood, Evolutionary Distance, and Maximum Parsimony Methods. Mol Biol Evol 28: 2731–2739.

TANRÉ D, DEROO C, DUHAUT P, HERMAN M, MORCRETTE JJ, PERBOS J, DESCHAMPS PY 1990: Description of a computer code to simulate the satellite signal in the solar spectrum the 5 S code. Int J Rem Sens 11: 659–668

TAYLOR PD, FAHRING L, WITH KA 2006: Landscape connectivity: a return to the basics. In: CROOKS KR, SANJAYAN MA (Eds.) Connectivity conservation. Cambridge University Press.

TEMPLETON AR, SHAW K, ROUTMAN E, DAVIS SK 1990: The genetic consequences of habitat fragmentation. Annals of the Missouri Botanical Garden, 77:13–27.

THERIVEL R, ROSS B 2007: Cumulative effects assessment: Does scale matter? EIA Rev 27:365–385.

THOMAS JA 1995: The conservation of declining butterfly populations in Britain and Europe: priorities, problems and successes. Biol J Linn Soc 56: 55–72.

THOMAS K, KEELER-WOLF T, FRANKLIN J 2002: A comparison of fine- and coarse-resolution environmental variables toward predicting vegetation distribution in the Mojave Desert. In: SCOTT JM, et al., eds. Predicting species occurrences: issues of accuracy and scale. Covello, CA: Island Press, 133–139.

THOMAS CD 2013: The Anthropocene could raise biological diversity. Nature 507:7.

THOMAS CD, CAMERON A, GREEN RE, BAKKENES M, BEAUMONT IJ, COLLINGHAM YC, ERASMUS BFN, FERREIRA DE SIQUEIRA M, GRAINGER A, HANNAH L, HUGHES L, HUNTLEY B, VAN JAARSVELD AS, MIDGELY GE, MILES L, ORTEGA–HUERTA MA, PETERSON AT, PHILLIPS OL, WILLIAMS SE 2004: Extinction risk from climate change. Nature 427:145–148.

TILMAN D, MAY RM, LEHMAN CL, NOWAK MA 1994: Habitat destruction and the extinction dept. Nature 371:65–66.

TISCHENDORF L, FAHRING L 2000: On the usage and measurement of landscape connectivity. Oikos 90: 7–19.

TRAVIS JMJ 2003: Climate change and habitat destruction: a deadly anthropogenic cocktail. Proc R Soc B 270: 467–473.

TURNER MG 2010: Disturbance and landscape dynamics in a changing world. Ecology 91: 2833–2849.

VALLADARES F, MATESANZ S, GUILHAUMON F, ARAÚJO MB, BALAGUER L, BENITO-GAZÓN M, CORNWELL W, GIANOLI E, VAN KLEUNEN M, NAYA DE, NICOTRA AB, POORTER H, ZAVALA MA 2014: The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. Ecol Lett 17: 1351–1364.

VAN DYCK H, BAGUETTE M 2005: Dispersal behaviour in fragmented landscapes: routine or special movements? Basic App Ecol 6: 535–545.

VAN ETTEN J 2011: gdistance: distances and routes on geographical grids. R package, version 1.1-1. http://CRAN.R-project.org/package=gdistance.

VAN GILS H, WESTINGA E, CARAFA M, ANTONUCCI A, CIASCHETTI G 2014: Where the bears roam in Majella National Park, Italy. J Nat Conserv 22: 23–34.

VAN HELSDINGEN PJ, WILLEMSE L, SPEIGHT MCD 1996: Background information on invertebrates of the Habitats Directive and the Bern Convention; Part 1: Crustacaea, Coleoptera and Lepidoptera. Nature and Environment No. 79. Council of Europe Publishing.

VAN SWAAY CAM 2002: The importance of calcareous grasslands for butterflies in Europe. Biol Conserv 104: 315–318.

VAN SWAAY CAM, WARREN MS 2006: Prime butterfly areas of Europe: an initial selection of priority sites for conservation. J Insect Conserv 10: 5–11.

VAN SWAAY CAM, NOWICKI P, SETTELE J, VAN STRIEN AJ 2008: Butterfly monitoring in Europe: methods, applications and perspectives. Biodivers Conserv 17: 3455–3469.

VAN SWAAY CAM, MAES D, COLLINS S, MUNGUIRA M, ŠAŠIĆ M, SETTELE J, VEROVNIK R, WARREN M, WIEMERS M, WYNHOFF I, CUTTELOD A 2011: Applying IUCN criteria to invertebrates: How red is the Red List of European butterflies? Biol Conserv 144: 470–478.

VANDERWAL J, SHOO LP, JOHNSON CN & WILLIAMS SE 2009: Abundance and the environmental niche: Environmental Suitability estimated from Niche Models predicts the upper limit of local abundance. Am Nat 174: 282–291.

VAPNIK V 2013: The nature of statistical learning theory. Springer.

VOGT P, FERRARI JR, LOOKINGBILL TR, GARDNER RH, RIITTERS KH, OSTAPOWICZ K 2009: Mapping functional connectivity. Ecol Indicators 9:64–71.

VOS CC, VERBOOM J, OPDAM PFM, TER BRAAK CJF, BERGERS PJM 2001: Towards ecologically scaled landscape indices. Am Nat 157:24–41.

WAGNER HH, FORTIN M-J 2013: A conceptual framework for the spatial analysis of landscape genetic data. Conserv Genet 14: 253–261.

WAITS LP, CUSHMAN SA, SPEAR SF 2015: Applications of landscape genetics to connectivity research in terrestrial animals. In: BALKENHOL N, CUSHMAN S, STORFER A, WAITS L (eds). Landscape genetics: concepts, methods, applications. Wiley.

WALLISDEVRIES MF, POSCHLOD P, WILLEMS JH 2002: Challenges for the conservation of calcareous grasslands in northwestern Europe: Integrating the requirements of flora and fauna. Biol Conserv 104: 265–273.

WANG Y-H, YANG K-C, BRIDGMAN CL, LIN L-K 2008: Habitat suitability modelling to correlate gene flow with landscape connectivity. Landsc Ecol 23: 989–1000.

WANG IJ, SAVAGE WK, SHAFFER HB 2009: Landscape genetics and least-cost path analysis reveal unexpected dispersal routes in the California tiger salamander (Ambystoma californiense). Mol Ecol 18: 1365–1374.

WARREN DL 2012: In defense of 'niche modeling'. TREE 27:497–500.

WARREN DL 2013: 'Niche modeling': that uncomfortable sensation means it's working. A reply to McInerny and Etienne. TREE 28:193–194.

WARREN MS 1993a: A review of butterfly conservation in central southern Britain: I. Protection, evaluation and extinction on prime sites. Biol Conserv 64: 25–35.

WARREN MS 1993b: A review of butterfly conservation in central southern Britain: II. Site management and habitat selection of key species. Biol Conserv 64: 37–49.

WARREN MS 1997: Conserving Lepidoptera in a changing environment: a perspective from Western Europe. J Insect Conserv 1: i–iv.

WARREN MS, HILL JK, THOMAS JA, ASHER J, FOX R, HUNTLEY B, ROY DB, TELFER MG, JEFFCOATE S, HARDING P, JEFFCOATE G, WILLIS SG, GREATOREX-DAVIES JN, MOSS D, THOMAS CD 2001: Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature 414: 65–69.

WASSERMANN TN, CUSHMAN SA, SHIRK AS, LANDGUTH EL, LITTELL JS 2012: Simulating the effects of climate change on population connectivity of American marten (*Martes americana*) in the northern Rocky Mountains, USA. Landscape Ecol 27: 211–225.

WATERS JM, FRASER CI, HEWITT GM 2013: Founder takes all: density-dependent processes structure biodiversity. TREE 28: 78–85.

WEIBULL AC, BENGTSSON J, NOHLGREN E 2000: Diversity of butterflies in the agricultural landscape: the role of farming system and landscape heterogeneity. Ecography 23: 743–750.

WEISS SB, MURPHY DD, WHITE RR 1988: Sun, slope, and butterflies: topographic determinants of habitat quality for *Euphydryas editha*. Ecology 69: 1486–1496.

WEMDZIO M 2011: Nachträgliche Anordnung bei der Gefährdung von Fledermäusen durch Windenergieanlagen unter besonderer Berücksichtigung der lokalen Population. Natur und Recht 33: 464–468.

WENZEL M, SCHMITT T, WEITZEL M, SEITZ A 2006: The severe decline of butterflies on western calcareous grasslands during the last 30 years: A conservation problem. Biol Conserv 128: 542–552.

WICKHAM H 2012: scales: Scale functions for graphics. R package version 0.2.3. http://CRAN.R-project.org/package=scales.

WILSON DE 1982: in *Wild Mammals of North America*, CHAPMAN JA, FELDHAMMER GA (eds), Johns Hopkins University Press, pp 644–652.

WILSON K, CABEZA M, KLEIN CJ 2009: Fundamental Concepts of Spatial Conservation Prioritization. In: Moilanen A, Wilson K, Possingham HP (eds) Spatial Conservation Prioritization: quantitative methods and computational tools. Oxford Universtiy Press, pp. 16–27.

WISZ MS, HIJMANS RJ, LI J, PETERSON AT, GRAHAM CH, GUISAN A 2008: Effects of sample size on the performance of species distribution models. Divers Distrib 14: 763–773.

WRIGHT S 1943: Isolation by distance. Genetics 28: 114–138.

WRIGHT S 1965: The interpretation of population structure by F-statistics with special regard to systems of mating. Evolution 19: 395–420.

WU JJ 2012: Landscape Ecology. In: LEEMANS R (ed) Ecological Systems – Selected Entries from the Encyclopedia of Sustainability Science and Technology, Springer.

WULDER MA 1998: Optical remote-sensing techniques for the assessment of forest inventory and biophysical parameters. Prog Phys Geogr 22: 449–476.

WYNHOFF I, VAN SWAAY CAM 1995. Threatened and vulnerable butterflies in the Netherlands. Wageningen: De Vlinderstichting.

YAMAGUSHI Y, KAHLE A, TSU H, KAWAKAMI T, PNIEL M 1998: Overview of ASTER instrument on EOS-AM1 platform. IEEE Trans Geosci Remote Sens 36:1026–1071.

YAMAGUCHI Y, FUJISADA H, KUDOH M, KAWAKAMI T, TSU H, KAHLE AB, PNIEL M 1999: ASTER instrument characterization and operation scenario. Adv Space Res 23: 1415–1424.

ZACHOS FE, ALTHOFF C, STEYNITZ YV, ECKERT I, HARTL GB 2007: Genetic analysis of an isolated red deer (*Cervus elaphus*) population showing signs of inbreeding depression. Eur J Wildl Res 53: 61–67.

ZANG D–X 2004: Lepidopteran microsatellite DNA: redundant but promising. Trends Ecol Evol 19: 507–509.

ZEBISCH M, GROTHMANN T, SCHRÖTER D, HASSE C, FRITSCH U, CRAMER W 2005: Klimawandel in Deutschland: Vulnerabilität und Anpassungsstrategien klimasensitiver Systeme. Forschungsbericht 201 41 253 Umweltbundesamt.

Curriculum Vitae

Personal information

Name: Engler
Surname: Jan Oliver

Home Address:

Current position:
Work Addresses:

Nationality:
Date of Birth:
Place of origin:

Education

since 01/2013	PhD student; Zoological Researchmuseum Alexander Koenig, Bonn, Germany
10/2005-03/2012	Diploma degree & intermediate diploma in applied biogeography, Trier University, Trier, Germany. Major subjects: Biogeography, Geobotany, Soil Science, Geology

Work experience

since 2013	Affiliated researcher at the Department of Wildlife Sciences, University of Göttingen, Göttingen, Germany
since 2007	Freelance work for several consulting and planning agencies: *ANUVA Stadt- und Umweltplanung, Architekturbüro Ernst & Partner, BioConsult SH, Büro Sieber, Ecoda Umweltgutachten, egp GmbH, Grontmij GmbH, Hortulus GmbH, KBH Architektur, Landschaftsökologische*

	Arbeitsgemeinschaft Schäfer & Wey, Landschaftsökologie Scholtes, Stadtplanungsamt Trier, Umwelt- und Verbraucherschutzamt Köln
2011-2012	Affiliated researcher at the Zoological Researchmuseum Alexander Koenig, Bonn, Germany
2007-2010	Student research assistant at the University of Trier Dpts. Biogeography, Geobotany, Geology, Environmental specimen bank
2010	Intern at Oikostat GmbH, Switzerland (four weeks)
2008	Student research assistant at the Max Planck Institute of evolutionary anthropology – Dpt. Primatology, Leipzig, Germany
2007	Intern at the Nationalpark Berchtesgaden, Germany (six weeks)
2006	Student research assistant at the Institute of Avian Research „Vogelwarte Helgoland“ Inselstation Helgoland, Germany
1999	Intern at the Biological Institute Helgoland, Germany (three weeks)

Grants & Awards

As of November 2015 I attracted 86868€ of funding, next to the following awards:

2015	Hans-Löhrl Award, German Ornithological Society
2014	Peerage of Science reviewer award
2009	Best student talk award at the 142th annual meeting of the German Ornithological Society, Pörtschach, Austria

Service

Journal Reviewer:	Avian Research, Biological Invasions, Biotropica, Bird Conservation International, Bird Study, Ecography, Ecological Modelling, Ecology & Evolution, Herpetological Journal, Journal of Animal Ecology, Journal of Biogeography, Journal of Heredity, Journal of Ornithology, Mammalian Biology, Marine Ecology Progress Series, Molecular Ecology, Northwestern Journal of Zoology, Oecologia, Organisms, Diversity & Evolution, Peerage of Science, PeerJ, PLoS one, Salamandra, Spatial and Spatio-temporal Epidemiology

Positions in professional societies

since 2015	Council member of the European Ornithologists Union
since 2015	Member of the Scientific Program Committee for the 11th European Ornithological Conference, Turku, Finland 2017
since 2013	Co-founder and spokesman of the special interest group "Spatial Ecology and Biogeography" of the German Ornithological Society
since 2013	Co-founder and spokesman of the special interest group for early career researcher "EOU Fledgelings" of the European Ornithologists Union
since 2014	Founder and co-editor of the research news section of the ornithological journal *VOGELWARTE*
2014-2015	Member of the Scientific Program Committee for the 10th European Ornithological Conference, Badajoz, Spain 2015

Contributions to scientific meetings

Organized events at conferences, symposia, or workshops

2015	Student talk & poster competition, 10th European Ornithological Conference, Badajoz, Spain (with M Weissensteiner)
	Meet-the-editors event, 10th European Ornithological Conference, Badajoz, Spain (with M Weissensteiner)
	Roundtable: Macroecology, global change and the state of modeling avian distributions. 10th European Ornithological Conference, Badajoz, Spain (with D Stiels & M Brambilla)
	Workshop: Towards the 'next generation' of species distribution modeling: emerging themes and methods. 7th Conference of the International Biogeography Society, Bayreuth, Germany (with A Cord, T Václavíc, D Rödder & J Chipperfield)
2014	Symposium: A decade of Landscape Genetics: Linking functional connectivity across trophic scales. 44th Conference of the German Ecological Society, Hildesheim, Germany (with H Edelhoff)

2013	Workshop: Challenges in avian species distribution modeling: A brief guide to MaxEnt for ornithologists. Conference of the German Ornithological Society, Regensburg, Germany (with D Stiels & K Schidelko)
2012	Workshop: Introduction into the anylsis and visualization of environmental data with GIS, German Zoological Society, Trier, Germany (with O Elle, A Hochkirch, N Wagner)
2011	Workshop: Habitat analysis and modeling. German Ornithological Society, Giessen, Germany (with T Gottschalk & O Elle)
	Symposium: Dispersal meets Biogeography: How dispersal affects range dynamic processes. 8th European Ornithological Conference, Riga, Latvia. (with M Delgado & D Arlt)
	Symposium: Predictive modeling in ornithology – recent problems, novel solutions, and future challenges. 8th European Ornithological Conference, Riga, Latvia. (with K Schidelko, D Stiels, M Barbet-Massin & D Rödder)

Talks (past 5 years, presented by myself)

Engler JO, Rödder D, Habel JC & Balkenhol N (2014): Assessing landscape mediated gene-flow in three sympatric Hesperid butterflies with diverging ecological traits. 44. Conference of the German Ecological Society (GfÖ), 10.9.2014, Hildesheim, Germany

Engler JO, Secondi J, Rödder D, Dawson DA & Hochkirch (2014): Exploring moving range edges in parapatric distributed passerines: From climate, genes and biotic interactions. 26. International Ornithological Congress, 16.8.2014, Tokyo, Japan.

Engler JO, Balkenhol N, Habel JC & Rödder D (2014): Combining species distribution models with population genetic data: Good for Landscape Genetics but also good for Macroecology? 8. Meeting of the SIG Macroecology of the German Ecological Society (GfÖ), 4.3.2014, Halle (Saale), Germany.

Engler JO, Secondi J, Rödder D, Dawson DA & Hochkirch (2014): Exploring moving range edges in parapatric distributed passerines: From climate, genes and biotic interactions. 2. Early Career Conference of the International Biogeography Society (IBS), 9.1.2014, Canberra, Australia.

Rödder D, Lawing AM, Flecks M, Ahmadzadeh F, Dambach J, **Engler JO**, Habel J-C, Hartmann T, Hörnes D, Ihlow F, Schidelko K, Stiels D & Polly PD (2013): Evaluating the impact of glacial cycles on Nearctic Chelonians‘ species richness, distribution, and phylogeographic patterns using palaeophylogeographic models (PPGMs). 7th Meeting of the SIG Macroecology of the German Ecological Society (GfÖ), 13.3.-15.3.2013, Göttingen, Germany.

Twietmeyer S & **Engler JO** (2013): Arealdynamik des Orpheusspötters in NRW: Ausbreitung, Ortstreue und populationsgenetische Charakteristika. Annual meeting 2013 of the North Rhine-Westphalian Ornithological Society (NOW), 3.3.2013, Recklinghausen, Germany.

Engler JO, Secondi J, Dawson DA, Elle O & Hochkirch A (2012): Populationsgenetische Effekte entlang sich bewegender Arealränder zweier parapatrisch verbreiteter Spötter (Genus: Hippolais): Welche Rolle spielen Langstrecken-Dispersal und „surfende" Allele? 145th Conference of the German Ornithological Society, 3.10.-8.10.2012, Saarbrücken, Germany.

Flecks M, Lawing AM, Ahmadzadeh F, Dambach J, **Engler JO**, Habel J-C, Hartmann T, Hörnes D, Ihlow F, Schidelko K, Stiels D, Polly PD, & Rödder D (2012): Extinct during the past, yet still alive? Evaluating the impact of glacial cycles on species richness, distribution, and phylogeographic patterns on Nearctic Chelonians. 7th World Congress of Herpetology, 8.-14.8.2012, Vancouver, Canada.

Engler, JO, Ihlow F, Dambach J, Flecks M, Hartmann T, Nekum S, Rajaei H & Rödder D (2012): On the brink of extinktion? How climate change may affect global chelonian species richness and dirstibution. 7th World Congress of Herpetology, 8.-14.8.2012, Vancouver, Canada.

Twietmeyer S & **Engler JO** (2012): Das Orpheusspötterprojekt Trier. Jahresversammlung des NABU Landesverband Rheinland-Pfalz, 10.3.2012, Worms, Germany.

Engler JO (2011): Wie konservativ sind saisonale Nischen bei ziehenden Singvögeln. 2nd Ornithological Students Congress 25.-27.11.2011, Seewiesen, Germany.

Engler JO, Secondi J, Dawson DA, Hochkirch A & Elle O (2011): Range expansion and the often neglected role of long distance dispersal in a migrating bird. 8th Conference of the European Ornithologists' Union, 27.-30.8.2011, Riga, Latvia.

Engler JO, Elle O & Rödder D (2010): Der Eine geht, der Andere kommt: Untersuchung der Arealdynamik von Orpheus- und Gelbspötter mittels Artverbreitungsmodellen. 143th Conference of the German Ornithological Society, 29.9.-3.10.2010, Helgoland, Germany.

Engler JO, Twietmeyer S, Roderus D, Lemke H & Elle O (2010): Wie funktionieren Arealexpansionen? Konzeption und erste Ergebnisse einer Studie an südwestdeutschen Orpheusspöttern (*Hippolais polyglotta*). Annual meeting of the Arbeitskreis Biogeographie of the VGDH, 07.-09.05.2010, Trier, Germany.

Engler JO (2010): Which factors facilitating range expansions? Theory, practice and first results on Melodious Warblers (*Hippolais polyglotta*) in Southwest Germany. Invited talk held at 09.02.2010 at the Max Planck Institute of Ornithology, Radolfzell, Germany.

Engler JO (2010): Wie funktionieren Arealexpansionen? Theorie, Planung und erste Ergebnisse an Südwestdeutschen Orpheusspöttern (*Hippolais polyglotta*). Invited talk held at the Swiss Ornithological Institute, Sempach, Switzerland (22.01.2010).

Poster (past 5 years, presented by myself)

Engler JO, Rödder D, Stiels D & Förschler MI (2015): On the duality of seasonal niches in migratory birds: the case of the citril finch (Carduelis citrinella). 10th European Ornithologist Conference, 26.8.2015, Badajoz, Spanien.

Engler JO, Rödder D, Habel JC & Balkenhol N (2015): Linking species distribution models to landscape genetics: comparison of landscape effects on gene flow in three diverging Thymelicus skippers. Annual Conference of the Society for Molecular Biology and Evolution (SMBE), 14.7.2015, Vienna, Austria.

Engler JO, Rödder D, Habel JC & Balkenhol N (2014): Linking species distribution models to landscape genetics: comparison of landscape effects on gene flow in three diverging Thymelicus skippers. Spring School: A practical, hands-on introduction to Landscape Genetics, 15.3.2014, Göttingen, Germany.

Engler JO, Habel JC (2013): East African Zosterops ssp in space and time: comparative analyses reveal multiple drivers of speciation in a yet cryptic species complex. 9th Conference of the European Ornithologists' Union (EOU), 28.8.-31.8., Norwich, UK.

Engler JO, Lawing AM, Ihlow F, Polly PD & Rödder D (2013): Learning from the past to predict the future: Linking palaeophylogeographic models with future climate change risk assessments in Nearctic Chelonians. 6th international conference of the International Biogeography Society (IBS), 9.1.-13.1.2013, Miami, USA.

Engler JO, Secondi J, Dawson DA, Elle O & Hochkirch A (2012): Population genetics reveal the role of long distance dispersal and allele surfing in contact zone movement in two parapatric distributed Hippolais sister species. 5th North American Ornithological Conference, 14.-18.8.2012, Vancouver, Canada.

Engler JO, Secondi J, Grossiard F, Elle O & Rödder D (2011): Contact zone on the move: is range expansion in Melodious Warblers driven by climate change or biological interaction? 144th Conference of the German Ornithological Society, 29.9. - 4.10.2011, Potsdam, Germany.

Engler JO, Secondi J, Grossiard F, Elle O & Rödder D (2011): Contact zone on the move: is range expansion in Melodious Warblers driven by climate change or biological interaction? 8th European Ornithologists Conference, 27.-30.8.2011, Riga, Latvia.

Scientific Publications

Google Scholar metrics (as of Nov 2015): 272 citations; h-index: 10

Accepted / in press:

32. Dambach J, Raupach MJ, Leese F, Schwarzer J, **Engler JO** (in press): Ocean currents determine functional connectivity in a deep-sea shrimp. Marine Ecology.

2015

31. **Engler JO**, Twietmeyer S, Secondi J, Elle O, Hochkirch A. Analytical limits of hybrid identification using genetic markers: an empirical and simulation study in *Hippolais* warblers. *BioRxiv preprint* http://dx.doi.org/10.1101/026781.

30. **Engler JO**, Secondi J, Dawson DA, Elle O & Hochkirch A (minor revision): Assessing the genetic consequences of moving range edges in a pair of parapatric distributed *Hippolais* warblers *Ecography* doi:10.1111/ecog.01520.

29. Teixeira RL, Ferreira RB, Silva-Soares T, Mageski MM, Pertel W, Rödder D, Hoffman de Barros E & **Engler JO** (2015): Anuran community of a cocoa agroecosystem in southeastern Brazil. *Salamandra* 51: 259-262.

28. Stiels D, Gaißler B, Schidelko K, **Engler JO**, Rödder D (2015): The importance of niche-overlap analysis for species distribution models of non-native species – an example with four Estrildid finch species (Passeriformes: Estrildidae). *Ibis* 157: 75-90.

2014

27. **Engler JO**, Husemann M (2014): Data constraints, bias and the (mis-)use of scientometrics for predicting academic success: A comment on van Dijk et al. *Proceedings of Peerage of Science* e8.

26. **Engler JO**, Cord AF, Dieker P, Wägele JW, Rödder D (2014): Accounting for the 'network' in the Natura 2000 network: A response to Hochkirch et al. 2013. *arXiv*:1408.7076.

25. **Engler JO**, Filz K, Balkenhol N, Habel JC & Rödder D (2014): Comparative Landscape Genetics of Three Closely Related Sympatric Hesperid Butterflies with Diverging Ecological Traits. *PLoS one* 9: e106526.

24. **Engler JO**, Sacher T, Elle O, Coppack T & Bairlein F (2014): No evidence of sex-biased dispersal in an island population of Common Blackbirds *Turdus merula*. *Ibis* 156: 885-891.

23. Fourcade Y, **Engler JO**, Rödder D, Secondi J, (2014): Mapping species distributions with MAXENT using a geographically biased sample of presence data: A performance assessment of methods for correcting sampling bias. *PLoS one* 9: e97122.

22. **Engler JO**, Rödder D, Stiels D & Förschler MI (2014): Suitable, reachable but not colonized: Current breeding range limitations in an endemic European mountainous songbird. *Journal of Ornithology* 155: 657-669.

21. Jacob SS, Rödder D, **Engler JO**, Shaaf S, Özkan H, Blattner F & Kilian B (2014): Evolutionary history of Wild Barley (*Hordeum vulgare* subsp. *spontaneum*) analyzed using multilocus sequence data and paleodistribution modeling. *Genome Biology and Evolution* 6: 685-702.

20. **Engler JO**, Secondi J, Dawson DA, Roderus D, Elle O & Hochkirch A (2014): Cross-species utility of 22 microsatellite markers in the Melodious Warbler (*Hippolais polyglotta*). *Avian Biology Research* 7: 91-98.

19. **Engler JO** (2014): First record of a wintering Swainson's Warbler *Limnothlypis swainsonii* (Audubon, 1834) for Florida and the United States. *Florida Field Naturalist* 42: 29-32.

2013

18. **Engler JO**, Rödder D, Elle O, Hochkirch A & Secondi J (2013): Species distribution models contribute to determine the effect of climate and interspecific interactions in moving hybrid zones. *Journal of Evolutionary Biology* 26: 2487-2496.

17. **Engler JO**, Roderus D, Elle O, Secondi J & Hochkirch A (2013): Temporal comparison of the genetic structure in newly founded populations along the expansive range edge of the Melodious Warbler (*Hippolais polyglotta*). *Vogelwarte* 51: 179-184. (German with English summary)

16. Fourcade Y, **Engler JO**, Rödder D, Secondi J (2013): Confronting expert-based and modelled distributions for species with uncertain conservation status. A case study from the corncrake (*Crex crex*). *Biological Conservation* 167: 161-171.

15. Rödder D, Lawing AM, Flecks M, Ahmadzadeh F, Dambach J, **Engler JO**, Habel J-C, Hartmann T, Hörnes D, Ihlow F, Schidelko K, Stiels D & Polly PD. (2013): Evaluating the Significance of Paleophylogeographic Species Distribution Models in Reconstructing Quaternary Range-shifts of Nearctic Chelonians. *PLoS one* 8: e72855.

14. Ahmadzadeh F, Flecks M, Rödder D, Böhme W, Ilgaz C, Harris DJ, **Engler JO**, Üzüm N, Carretero MA, (2013): Multiple dispersal out of Anatolia: biogeography and evolution of oriental green lizards. *Biological Journal of the Linnean Society* 110: 398-408.

13. Ahmadzadeh F, Flecks M, Carretero MA, Böhme W, Ilgaz C, **Engler JO**, Harris DJ, Üzüm N, Rödder D, (2013): Rapid lizard radiation lacking niche conservatism: ecological diversification within a complex landscape. *Journal of Biogeography* 40:1807-1818.

12. Werner P, Lötters S, Schmidt BR, **Engler JO** & Rödder D (2013): The role of climate for the range limits of parapatric European land salamanders. *Ecography* 36: 1127-1137.

11. Filz KJ, **Engler JO**, Weitzel M, Schmitt T. (2013): Missing the target? butterfly conservation efforts on calcareous grasslands in south-western Germany. *Biodiversity Conservation* 22: 2223-2241.

10. Filz KJ, Schmitt T, **Engler JO** (2013): How fine is fine scale? Questioning the use of fine-scale bioclimatic data in species distribution models used for forecasting abundance patterns in butterflies. *European Journal of Entomology* 110: 311-317.

2012

9. **Engler JO** & Rödder D (2012): Disentangling inter- and extrapolation uncertainties in species distribution models: A novel visualization technique for spatial variations of predictor correlations. *Biodiversity Informatics* 8: 30-40.

8. Habel JC, **Engler JO**, Rödder D & Schmitt T (2012): Contrasting genetic and morphologic responses on recent population decline in two burnet moths (Lepidoptera, Zygaenidae). *Conservation Genetics* 13: 1293-1304.

7. Habel JC, **Engler JO**, Rödder D & Schmitt T (2012): Landscape genetics of a recent population extirpation in a burnet moth species. *Conservation Genetics* 13: 247-255.

6. Ihlow F, Dambach J, **Engler JO**, Flecks M, Hartmann T, Nekum S, Rajaei H & Rödder D (2012): On the brink to extinction: How climate change threatens global turtle diversity. *Global Change Biology* 18: 1520-1530.

2011

5. Rödder D & **Engler JO** (2011): Quantitative metrics of overlap in Grinnellian niches: advances and possible drawbacks. *Global Ecology and Biogeography* 20: 915-927.

4. **Engler J**, Abt K & Buhk C (2011): Seed characteristics and germination limitations in the highly invasive *Fallopia japonica* s.l. (Polygonaceae). *Ecological Research* 26: 555-562.

3. Stiels D, Schidelko K, **Engler JO**, van den Elzen R & Rödder D (2011): Predicting the potential distribution of the invasive common

waxbill Estrilda astrild (Passeriformes: Estrildidae). *Journal of Ornithology* 152: 769-780.

2010

2. Rödder D, **Engler JO**, Bonke R, Weinsheimer F & Pertel W (2010): Fading of the last giants: an assessment of habitat availability of the Sunda Gharial *Tomistoma schlegelii* and coverage with protected areas. *Aquatic Conservation: Marine and Freshwater Ecosystems* 20: 678-684.

2009

1. Abt K & **Engler J** (2009): Rapid increase of the grey seal (Halichoerus grypus) breeding stock at Helgoland. *Helgoland Marine Research* 63: 177-180.