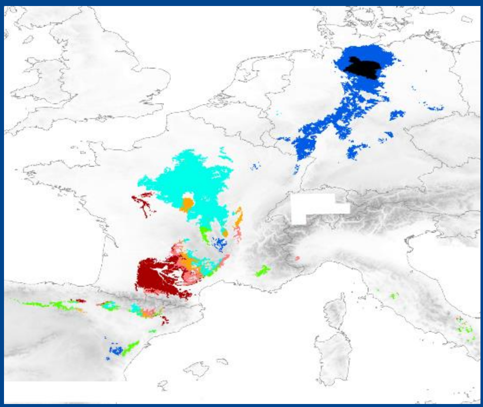
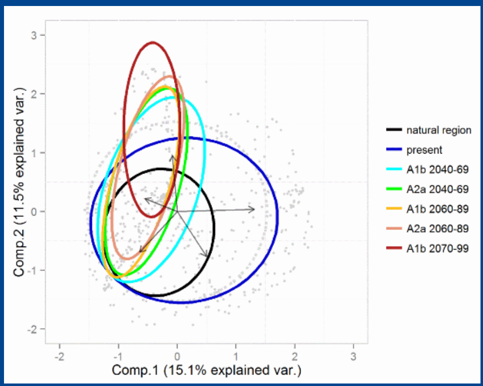
Umwelt und Raum Band 11





Christina Weiß & Michael Reich

Climate analogues: A method to assess the potential impact of climate change on Natura 2000 habitat diversity at the regional scale

Schriftenreihe Institut für Umweltplanung
Leibniz Universität Hannover

Umwelt und Raum Band 11

Climate analogues: A method to assess the potential impact of climate change on Natura 2000 habitat diversity at the regional scale

Christina Weiß & Michael Reich

Schriftenreihe Institut für Umweltplanung
Leibniz Universität Hannover

Bibliografische Information der Deutschen Nationalbibliothek

Die Deutsche Nationalbibliothek verzeichnet diese Publikation in der Deutschen Nationalbibliografie; detaillierte bibliografische Daten sind im Internet über http://dnb.ddb.de abrufbar.

1. Aufl. - Hannover: Institut für Umweltplanung, 2022

Herausgeber:	Institut für Umweltplanung Leibniz Universität Hannover Herrenhäuser Straße 2, 30419 Hannover www.umwelt.uni-hannover.de
Titelbilder:	oben: Overlaying of the climate analogues of the "Eastern Lowlands" for the different climate projections; mitte: PCA ordination biplot showing frequency and area of Natura 2000 habitats in the climate analogues of the different climate projections of the “Eastern Lowlands”; unten: Natura 2000 habitat type "4010 Northern Atlantic wet heaths with *Erica tetralix*" in the Natura 2000 site "Lüneburger Heide" in the natural region "Eastern Lowlands" (Foto: Christina Weiß)

ISSN (Online) 2366-5459

Umwelt und Raum	Band 11	1-32	Institut für Umweltplanung, Hannover 2022

Climate analogues: A method to assess the potential impact of climate change on Natura 2000 habitat diversity at the regional scale

Christina Weiß & Michael Reich

Abstract

The need and will to mitigate and adapt to climate change and its threats to biodiversity have risen. Nevertheless, the acting for the conservation of biodiversity remains hampered by knowledge gaps. E.g., for habitat types (in the sense of biotopes) the impact of climate change has been scarcely researched. There are many “species distribution models” (SDMs) that can project species distributions under climate change, but their application to contemporary habitat types poses considerable methodological problems.

Here we show the viability of the uncommon method of “climate analogues” to provide data to assess the potential impact of future climate change on habitat types for chosen regions, and the usability of the method compared to SDMs.

We assume climate analogues can reflect the potential future habitat data in the study regions when (1) plausibly located future climate analogues are found with relevant climate variables for the studied habitat types, and (2) habitat occurrences relate with their frequency and area to the climate reflected in the climate analogues. We tested the method for three landscapes in Germany using European Natura 2000 habitat data, analyzing five future climate conditions until 2100.

Future climate analogues were found southwest of the study regions, primarily in France. They progressed further southwest and from higher to lower elevations with increasing climate change. Ecologically sound habitat types remained stable, increased, and decreased in frequency and area parallel to the magnitude of climate change in the climate analogues.

Thus, we regard climate analogues as a viable method to estimate potential climate change induced changes of Natura 2000 habitat types at the regional scale. Nature conservation benefits from climate analogues as they are efficient, data-robust, and promote the implementation of actions, the exchange of conservation experiences, and international collaboration. They are an easy and powerful method to tackle the looming losses of habitat diversity from climate change.

1 Introduction

Warnings about the intensity of future climate change are becoming increasingly urgent (HÖHNE et al. 2020; RIPPLE et al. 2020; IPCC 2021; WORLD METEOROLOGICAL ORGANIZATION 2021), as are the warnings of the projected magnitude of caused biodiversity losses (WIENS 2016; IPBES 2019). Both have, together with observable heat and drought extremes (VOGEL et al. 2019; WORLD METEOROLOGICAL ORGANIZATION 2019), increased the public and political will to mitigate and adapt to climate change and its impacts on biodiversity (Fridays For Future, Extinction Rebellion, (HAGEDORN et al. 2019; DAVIES et al. 2021)). To mitigate the looming losses of biodiversity, knowledge is required about how biodiversity may change. Still, for the basic fundamental elements of biodiversity, such as habitat types, the possible threats of climate change remain little researched. In contrast to frequent research at the species level (JAESCHKE et al. 2014), the effect of climate change on habitats (in the sense of biotopes) has been scarcely investigated (EVANS 2012; ORLIKOWSKA et al. 2016). Possible changes have been assessed for selected habitat types (cf. BUSE et al. 2015), whereas assessments of complete sets of habitat types within a region have mostly been assessed in preliminary national and regional studies based only on expert judgements (VOS et al. 2013; WAGNER-LUECKER et al. 2014; though see BAATAR et al. 2019 who modelled vegetation communities of Austria). Thus, though habitat types contribute to what the UN defined as the third level of biodiversity (UNITED NATIONS 1992), the possible consequences of climate change for most habitat types remain unexplored (EVANS 2012).

The common method for assessing responses of biodiversity to climate change is species distribution modeling (SDM), also known as bioclimatic envelope modeling (BEM; ARAUJO et al. 2019; OVASKAINEN 2019). The advantages of SDMs are that they deliver geographically accurate views of large-scale shifts of the studied factors. However, when SDMs are applied to habitat types, problems arise. The first question to arise is whether the entire habitat or the constituting plant species should be used for modeling (direct vs. indirect approach), since the results can differ greatly depending on the approach (BITTNER et al. 2011; PRISCO et al. 2013).

The indirect approach is also called “stacked species modeling” as the modeling results of single species are overlaid to gain results for the habitat type (OVASKAINEN 2019). However, four out of five European plant species lack distribution data (LUOMUS 2014) so that many European habitat types cannot be modeled indirectly by their plant species (THUILLER et al. 2005; BITTNER et al. 2011; cf. BAATAR et al. 2019). A further shortcoming of indirect modeling is the difficulty of accounting for interactions (FERRIER and GUISAN 2006). Interactions influence the species composition of habitat types (e.g. via competition between plant species, interactions with pollinators, mycorrhiza, insects, pests, diseases etc.) but are challenging to integrate into models (OVASKAINEN 2019) and to be taken correctly into account when interpreting results (DORMANN et al. 2018). For the modeling of habitat types this challenge is serious because habitat types are defined by specific compositions of plant species (EUROPEAN COMMISSION DG ENVIRONMENT 2013), which result from the interplay among all ecosystem components.

The latest SDMs can project communities not only by simply stacking results for single species, but also considers interactions within the model, enabling more realistic results (FERRIER and GUISAN 2006; OVASKAINEN 2019). These models are called joint species distribution models (jSDMs, unlike the previously treated individual SDMs, called iSDMs (CARADIMA et al. 2019)). However, jSDMs still are not widely used (NIETO-LUGILDE et al. 2018; OVASKAINEN 2019) nor readily utilized as developing these models is not easy (DORMANN et al. 2018; OVASKAINEN

2019). Furthermore, most jSDMs (ZHANG et al. 2018) and studies focus on presence-absence data of the characteristic species that constitute the studied communities (NIETO-LUGILDE et al. 2018; cf. CARADIMA et al. 2019; NORBERG et al. 2019; TOBLER et al. 2019). However, for habitat types, presence-absence data is not sufficient, because proportion data of the characteristic plant species is required to assess changes of habitat types and to distinguish habitat types from each other. For example, among the following three habitat types in the interpretation manual of European Union habitats (EUROPEAN COMMISSION DG ENVIRONMENT 2013) the habitat structure changes from open to completely tree-covered: "Active raised bogs" are dominated by *Sphagnum* mosses (habitat code 7110), and "Northern Atlantic wet heaths with *Erica tetralix*" (4010) are dominated by *Erica tetralix*, whereas "Bog woodland" (91D0) is dominated by birch and pine. The list of plant species can be the same, only the proportions of plant species vary (EUROPEAN COMMISSION DG ENVIRONMENT 2013; DRACHENFELS 2021). Another example includes the succession from open grasslands (e.g. 6210) with scattered shrubs of *Juniperus communis* to a dense *Juniperus communis* shrub (5130) with only remnants of the open grassland.

Recently, jSDMs have been invented that can process proportion data (CLARK et al. 2017). To model habitat types, proportion data of at least the characteristic plant species is needed. However, when recording Natura 2000 habitats, there is no obligation to record proportional data, or even presence-absences, so that neither is area-wide available for e.g. Spain, France or Germany. Thus, there is not sufficient data to parameterize jSDMs for habitat type communities.

According to comparative studies (NIETO-LUGILDE et al. 2018; ZHANG et al. 2018; NORBERG et al. 2019), there is not yet a superior jSDM that performs best in all cases of community modeling. ZHANG et al. (ZHANG et al. 2018) even point out that further research should be carried out on how model performances vary between ecosystems. This could mean additional research effort for the alone 233 acknowledged habitat types of conservational value in the European Union (COUNCIL OF THE EUROPEAN COMMUNITIES 1992; EUROPEAN COMMISSION DG ENVIRONMENT 2013). Moreover, jSDMs remain computation intensive (NIETO-LUGILDE et al. 2018) and in the developmental stage. The best balance between thoroughness and simplicity is still trying to be found (MEROW et al. 2014; CARADIMA et al. 2019), as well as how to best cope with the lack of knowledge of ecological and environmental factors that each play a role.

As an alternative, there is the approach to model habitat types directly as a whole. In this direct approach a habitat type is treated like a species in a SDM (BITTNER et al. 2011). Whether the indirect or the direct approach yields better results depends on the habitat type, as performance varies among studies (BITTNER et al. 2011). However, the direct approach is simpler and faster than the indirect approach (FERRIER and GUISAN 2006). Still, each habitat type has to be parametrized individually. Furthermore, also the direct approach struggles to parametrize models when there are gaps in the distribution data of habitat types (cf. TOBLER et al. 2019).

In light of these difficulties in modeling habitat types with SDMs, we aimed to test whether the region-based method of "climate analogues" can yield viable data for assessing the impact of climate change on habitat types. Instead of modeling the future distribution of habitat types or their constituting species, the method models the future distribution of a study landscape under a future climate change scenario. The approach could be called "landscape distribution modeling". The future distributions of the study landscapes are called "future climate analogues". Thus, future climate analogues are regions which currently experience the climate conditions projected for a study region in a future climate change scenario. The idea is to anticipate from the future climate analogues what might happen to the habitat data in the study region in the future by comparing their habitat data, i.e. applying a space-for-time substitution (cf. PICKETT 1989; cf.

ELMENDORF et al. 2015). We assume that the simplicity of the modeling makes the method easy to apply and that the region-specific assessment offers added value for regional nature conservation.
So far, climate analogues have been applied to gain insights into shifts of clearly defined factors such as climate (OHLEMÜLLER et al. 2006; WILLIAMS et al. 2007; BURROWS et al. 2014) and single species (BERGMANN et al. 2009; BARTHOLY et al. 2012; BLOIS et al. 2013a; GUERIN et al. 2013; SYBERTZ and REICH 2015). Species are unambiguously described and the distribution data is often systematically recorded in fine grids so that species should show a strong relationship to climate. With habitat types the challenge is different.
Even the most comprehensive, and the most spatially and methodically finely resolved European database of habitat types, “Natura 2000”, lacks for many habitat types a consistent interpretation. Many habitat types are not clearly defined, definitions for different types sometimes overlap, some habitat types are too broad geographically and taxonomically, and others are too narrow, so that interpretations vary (DRACHENFELS 2001; EVANS 2006, 2010). Furthermore, the data is not collected in grids, but unsystematically, which will likely leave occurrences unrecorded. Both may weaken the relationship between habitat data and climate. Therefore it is unclear whether the occurrences of the Natura 2000 habitat types in the future climate analogues can be attributed to climate. There is the risk that the habitat data is too blurred and the data spatially too fragmentary to show a relation to climate.
To our knowledge, the climate analogues method has only been applied by SKOV et al. (SKOV et al. 2009) to plant communities, namely the potential natural vegetation of Denmark. Here the potential natural vegetation was unambiguously defined and widely recorded, so that it could show a good relation to climate. However, the authors did not aim to test a relation. Therefore, it remains unexplored as to whether the climate analogues method works for the contemporary habitat types of the Natura 2000 habitat database. We envisage that when there is a relation to climate, then the habitat data in the climate analogues can give insights into of what might happen to the habitats in the study regions in future.
The aim of this paper was to investigate whether the climate analogues method can provide viable results, from which the possible impact of climate change on Natura 2000 habitat types can be estimated in further steps, and to discuss the usability of the method for regional nature conservation. We assumed that the climate analogues method would provide viable results if the following two requirements were met:

(1) We can find plausibly located future climate analogues that reflect the climate conditions of the emission scenarios and time periods by using meaningful climate variables for the studied Natura 2000 habitat types.

(2) Frequency and area of Natura 2000 habitats in the future climate analogues are related to the climate conditions reflected in the future climate analogues.

We applied the climate analogues method to three study regions in Northern Germany, examining two different emission scenarios at four time periods from the present to the end of 21st century, and tested whether the method fulfilled the two requirements. We conclude with a discussion on the benefits and limitations of the method for regional nature conservation in mitigating the possible impact of future climate change on habitat types compared to approaches based on SDMs.

2 Data and Methods

2.1 Study regions

We chose three ecoregions in Germany, the Eastern, Central and Western Lowlands (Fig. 1 and S1 Database), with areas from 7,200 km² to 10,000 km², as study landscapes (FEDERAL AGENCY FOR NATURE CONSERVATION 2009). Ecoregions are landscape units that are consistent in physical environmental factors like elevation, slope, geology, soil, soil-water balance, and climate (SCHMITHÜSEN 1953-1965). Our study regions belong to the nemoral climate zone (MÜLLER-WESTERMEIER et al. 1999) and represent the easternmost end of the Atlantic biogeographical region in Central Europe (EUROPEAN ENVIRONMENT AGENCY 2016). Climatic factors follow a gradient from west to east across the study regions. Oceanity decreases from the adjacent Western and Central Lowlands to the 150 km distant Eastern Lowlands, which have more continental influences (MÜLLER-WESTERMEIER et al. 2001). Consequently, annual precipitation is higher in the Western and Central Lowlands than in the Eastern Lowlands (MÜLLER-WESTERMEIER et al. 1999). Likewise, winter and also summer temperatures are higher in the Western and Central Lowlands than in the Eastern Lowlands (MÜLLER-WESTERMEIER et al. 1999). The Western Lowlands are one of the warmest regions in Germany (MÜLLER-WESTERMEIER et al. 1999). Variation of the parameters within each ecoregion is low as a consequence of the flat topography. All three study regions are dominated by intense agriculture and forestry land-use. Geology and soils are dominated by deposits from the glacial period (MEISEL 1953-1965; MÜLLER 1953-1965; PFAFFEN 1953b-1965, 1953a-1965).

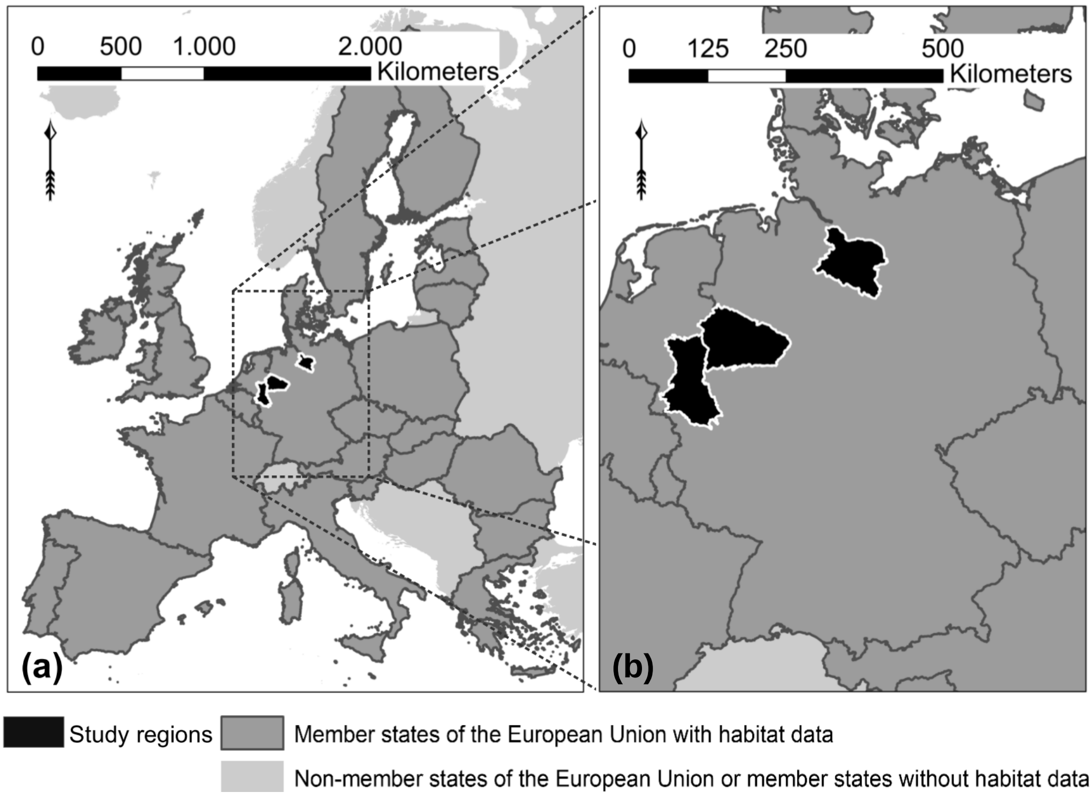


Fig. 1 **Study regions and European Union member states.** (a and b) Location of the three ecoregions within Germany chosen as study regions. (a) European Union member states with habitat data used as area for climate and habitat analyses. Ecoregions were taken from (FEDERAL AGENCY FOR NATURE CONSERVATION 2009).

2.2 Habitat data

Natura 2000 habitat data was obtained from the database of the European Environment Agency (EEA 2013), which provides occurrences and area of the Natura 2000 habitat types within designated Natura 2000 sites (details in S1 Text). We used the habitat data mapped from 2001-2006 as they fitted best to the climate reference period (1950-2000, see next section). After adjusting the data for our purpose (details in S1 Text), we based our analyses on 219 out of the 233 European Natura 2000 habitat types, for which about 130,000 occurrences in about 20,000 Natura 2000 sites were reported. Natura 2000 sites are hereafter referred to as N2k-sites.

2.3 Climate data

Future climate projections were taken from the database of the International Center for Tropical Agriculture (CIAT), providing 19 bioclimatic variables at a spatial resolution of 30 arc seconds (~1km) point data (HIJMANS et al. 2005; RAMIREZ and JARVIS 2008, 2010, 2012). The EU was covered by 8,759,914 climate points. We used simulations from the global circulation model MPI-ECHAM5 for the two most pessimistic climate scenarios SRES A2a and A1b of the 4th IPCC Assessment Report (IPCC 2007). They are similar to the two most pessimistic RCP scenarios of the 5th Assessment Report (IPCC 2008; COLLINS et al. 2013; KNUTTI and SEDLACEK 2013). We analyzed climate conditions for three future time periods: 2040-2069 and 2060-2089 for A1b and A2a and also 2070-2099 for A1b. A fourth time period represents the reference climate from 1950-2000, hereafter referred to as present climate. For this time period we used the Worldclim database (HIJMANS et al. 2005). Future and present climate data from CIAT and Worldclim are readily comparable because they are generated with the same methodology and resolution (RAMIREZ and JARVIS 2010).

2.4 Testing the viability of the "climate analogues" method

For investigating the viability of the climate analogues method, we first tested whether plausibly located future climate analogues could be identified using meaningful climate variables for the studied habitat types (following four sub-sections, Fig. 2). We then tested whether habitats were related regarding their frequency and area to the climate reflected in the future climate analogues (last sub-section). This way it is possible to see whether the habitat data can serve as an image of what may happen to the habitats in the study regions in future (Fig. 2). Spatial analyses were processed with ArcMap 10 and statistical analyses with R 3.1.3 (R CORE TEAM 2015).

2.4.1 Selecting climate variables and characterizing climate change

We identified the most meaningful climate variables for the present distribution of the studied habitat types in two steps. First, we identified which of the 19 bioclimatic variables provided by Worldclim (HIJMANS et al. 2005), and the CIAT database (RAMIREZ and JARVIS 2008, 2012), best captured climatic variance in the EU. For this, we carried out a principal component analysis (PCA, function 'prcomp'; R CORE TEAM 2015) on the values of the standardized variables for all of the 8,7 million climate points of the EU. Variables representing gradients in temperature, precipitation, precipitation seasonality, and temperature range explained 90% of EU climate variance (S1 Table). Of these variables, in the second step, we selected the most relevant variables for habitat types in central and south-western Europe based on habitat literature (POTT

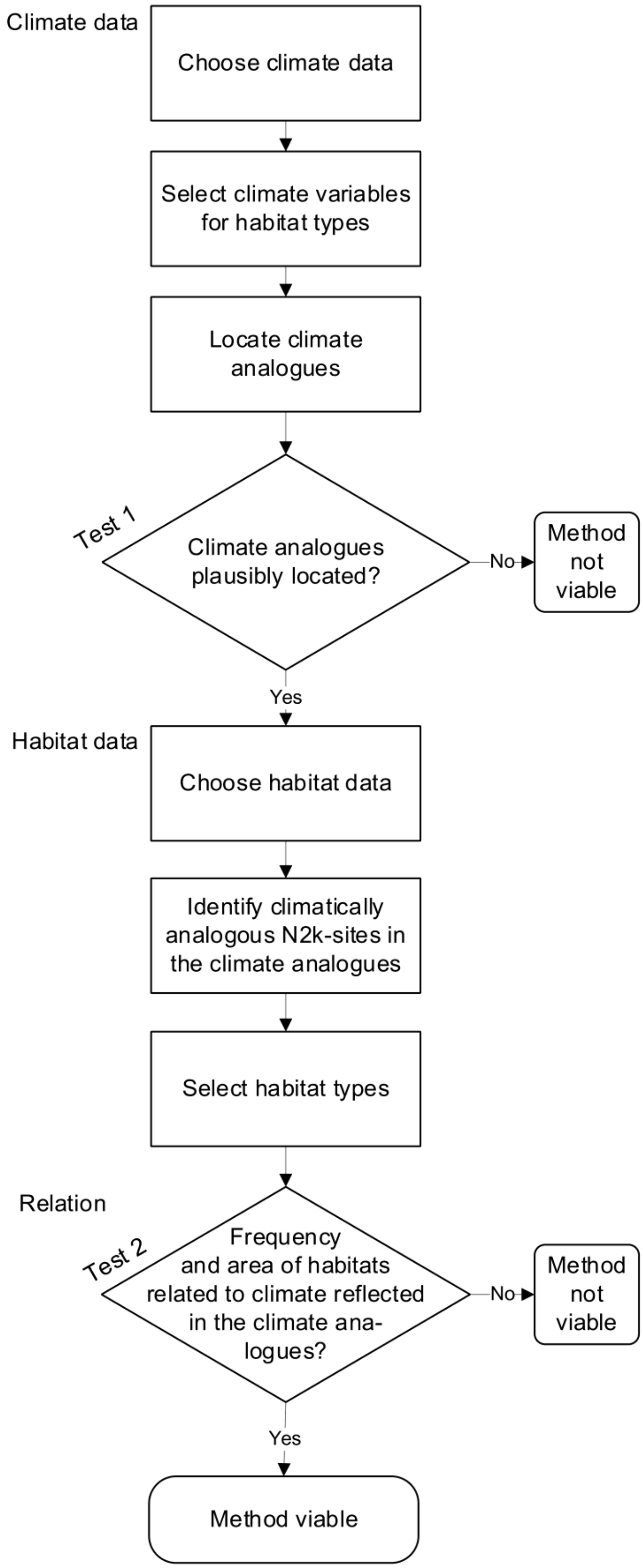


Fig. 2 Process for testing the viability of the climate analogues method with two tests.

1995; SSYMANK et al. 1998; ELLENBERG and LEUSCHNER 2010; EUROPEAN COMMISSION DG ENVIRONMENT 2013; DRACHENFELS 2014). Six climate variables were chosen as measures for moisture and temperature (Tab. 1). We further utilized these variables to analyze the character and magnitude of projected future climate change in the study regions (S2 Text).

Tab. 1 Bioclimatic variables used for the analyses.

Bioclimatic variable	Abbreviation
bio5 Max Temperature of Warmest Month	maxT_warmestM
bio10 Mean Temperature of Warmest Quarter	meanT_warmestQ
bio11 Mean Temperature of Coldest Quarter	meanT_coldestQ
bio12 Annual Precipitation	annPrecip
bio14 Precipitation of Driest Month	Precip_driestM
bio16 Precipitation of Wettest Quarter	Precip_wettestQ

The six out of 19 bioclimatic variables used from Worldclim (HIJMANS et al. 2005) and CIAT database (RAMIREZ and JARVIS 2008, 2012), which were chosen as meaningful for the studied habitat types and used for analyzing future climate change in the study regions and for searching climate analogues. Variable names and numbers refer to these in Worldclim/CIAT database.

The three chosen temperature variables showed, for all three study regions, a clear warming trend until the end of the 21st century (S1 Fig). There are two remarkable leaps in magnitude of warming. The first is from the present to all future temperature conditions and a second, smaller, from the last to the previous time period/scenario (S2 Fig, for numbers see S2 Table). The first leap is explained by the 40-year time gap between the present conditions (1950-2000) and the first assessed future time period in 2040-69, during which temperatures have already increased (IPCC 2018). The second leap results from the climate projections. The precipitation variables did not show any tendency as some future climate conditions were wetter and some drier than present conditions (S2 Fig and S3 Text). Thus, projected future climate change in the study regions is characterized by an increase in warming (further description in S3 Text). However, we also expect drier conditions for habitats in the growing season, see S4 Text for explanation.

For all three study areas, the temperature increased continuously for most future time periods and scenarios when the climate conditions were sorted first into time periods and subsequently into the scenarios A2a and A1b (S1 and S2 Fig). For this reason, we did not split any results according to scenarios but instead, interpreted results in one scenario-/timeline. The different time periods/scenarios are henceforth called “projections.”

2.4.2 Locating climate analogues (Test 1)

The first requirement for the viability of the method of climate analogues for habitat types is, whether plausible located climate analogues can be found for the study regions with the variables relevant for habitat types. To test this we used the following three steps. First, we selected the climate points within the study regions and extracted minimum and maximum future projected values of the six climate variables for each time period/scenario. Then we searched in the present climate data of all EU member states (Fig. 1) for climate point values within this range. Finally, if all six climate variables of a climate point were within the study region's future climate range, a climate point was defined as climatically analogous. The total of future climatically analogous climate points was identified as a "future climate analogue" of a time period/scenario. Comparisons between the habitats in the study regions and the future climate analogues were extended for the study regions to the entire area in Europe with the same climate conditions as the study region. In the following, the term "climate analogues", if not further specified, refers to present and future climate analogues together.

2.4.3 Identifying climatically analogous Natura 2000 sites (N2k-sites)

As exact locations of habitats were not available at the European scale, which would have enabled a distinct intersection with analogous climate points, we defined climatically analogous N2k-sites. We converted the climate points into trapezes (with the 30 arc seconds edge length of the point's data resolution) and defined N2k-sites as climatically analogous when a certain threshold of intersecting climatically analogous polygons was exceeded, depending on the area of the N2k-sites. We assumed that in "small" sites, climate differences are small and the non-analogous climate of one edge would only slightly deviate from the analogous climate of the other edge. Therefore, we considered an intersection of 25% as sufficient to be regarded as climatically analogous for N2k-sites smaller than 87 ha (we set area at 87 ha as this marks the 25% percentile of the area of the 2,125 N2k-sites, which intersected with any climate analogue of any study region, the 87 ha, is thus, defined by us as "small" sites). For all N2k-sites larger than 1,600 ha (75% percentile) we required an intersection of 50%. For all N2k-sites with an area in between, we linearly interpolated the required intersection. The quantities of climatically analogous N2k-sites within the climate analogues are listed in S3 Table.

2.4.4 Selecting habitat types

Out of the 219 habitat types in the European-wide database, 131 habitat types occurred in the study regions or their climatically analogous N2k-sites (S4 Table). We excluded 47 habitat types from further analysis because they require specific environmental conditions not found in the study regions or the climate analogues and would skew the results. Excluded were marine or coastal habitat types (27), habitat types on rocks or scree (10), sites rich in heavy metal or salt as long as salty soil is not induced by climate (2), alpine rivers (3), caves, tufa springs and karst habitat types (5). Further analysis was conducted with the remaining 84 habitat types (S4 Table). For the number of climatically analogous N2k-sites with occurrences of these habitat types see S3 Table.

2.4.5 The relation between habitats and climate (Test 2)

With our second method, we additionally tested for the viability of the climate analogues method. We aimed to find out whether frequency and area of the habitats in the N2k-sites were related to the magnitude of climate change reflected in the climate analogues. We analyzed this requirement via PCA ordinations ('prcomp'; R CORE TEAM 2015) of the habitat data in the climatically analogous N2k-sites in the climate analogues (shortened to: "habitat data in the climate analogues", S2 Database). The input data into the PCA was a matrix with one row for each N2k-site in the climate analogues, there were 84 columns for each of the 84 studied habitat types listing the total area the habitat type covered in the N2k-site. Results are shown in PCA ordination biplots ('ggbiplot'; VU 2015). In the biplots, each N2k-site is represented by one dot. Each dot contains information about which habitat types occur in this N2k-site and which area they cover. For more evident patterns, we coded the dots of the N2k-sites for projections and drew gravity ellipses, which envelope 2/3 of a projection's N2k-sites ('ggbiplot'; VU 2015) to show patterns. Some climate analogues overlapped or lay so close to each other that N2k-sites were climatically analogous to more than one climate analogue. These N2k-sites were included in the gravity ellipse of each of the different climate analogues. Patterns of the gravity ellipses were analyzed visually for detection of a relationship between climate and habitat data by examining the ellipses of the climate analogues, whether they were separated or not. Secondly, we examined whether they were aligned in an order that reflected the magnitude of climate change. To assess the plausibility of habitat changes identified in the PCA, habitat types that contributed to principal components by at least 0.4 were shown as arrows in the biplots.

We analyzed all principal components in biplots, which were in screeplots left the bend of the "elbow". For the Eastern Lowlands, this was the first nine principal components (PCs) out of 56, for the Central Lowlands, the first ten out of 70 and for the Western Lowlands, the first five out of 75 (S3 Fig). Presented here are only the biplots of the first two PCs because they sufficiently showed whether the habitats' frequency and area principally were related to the magnitude of climate change. The habitat data used for the PCAs were transformed using the Hellinger transformation (function 'decostand', package 'vegan'; OKSANEN et al. 2015) to reduce the problem of a calculated, virtual similarity of N2k-sites arising from absent habitats (LEGENDRE and GALLAGHER 2001; LEGENDRE and LEGENDRE 2012).

3 Results

To test the viability of the method of "climate analogues", we firstly tried to determine whether we could find plausible climate analogues with relevant climate variables for the studied Natura 2000 habitat types. Secondly, we sought to establish whether frequency and the area of habitats in the climate analogues were related to the magnitude of climate change reflected in the climate analogues. We found both viability requirements were met.

3.1 Location of future climate analogues

For all three study regions, future climate analogues were found in the south-western areas of the study regions, primarily in France, but also in northern Spain and central Italy (Fig. 3). Present climate analogues, which currently experience the same climate conditions as the study regions, were found geographically adjacent to the study regions (Fig. 3). Overlaying present and future climate analogues shows how, with increasing warming in the projections, the climate analogues shifted from north-western Germany in the present toward the south-west for the future (S4 Fig). They shifted partly over central France to south-western France and from higher to lower elevations around the Massif Central (France), the Pyrenees (France, Spain) and the Appennines (Italy).

For the study regions with a more oceanic climate, the Central and the Western Lowlands (S2 Table) (MÜLLER-WESTERMEIER et al. 2001), the present climate analogues were found closer to the coast than those of the more continental Eastern Lowlands (Fig. 3). Likewise, their future climate analogues were found more to the south and in lower elevations than those of the

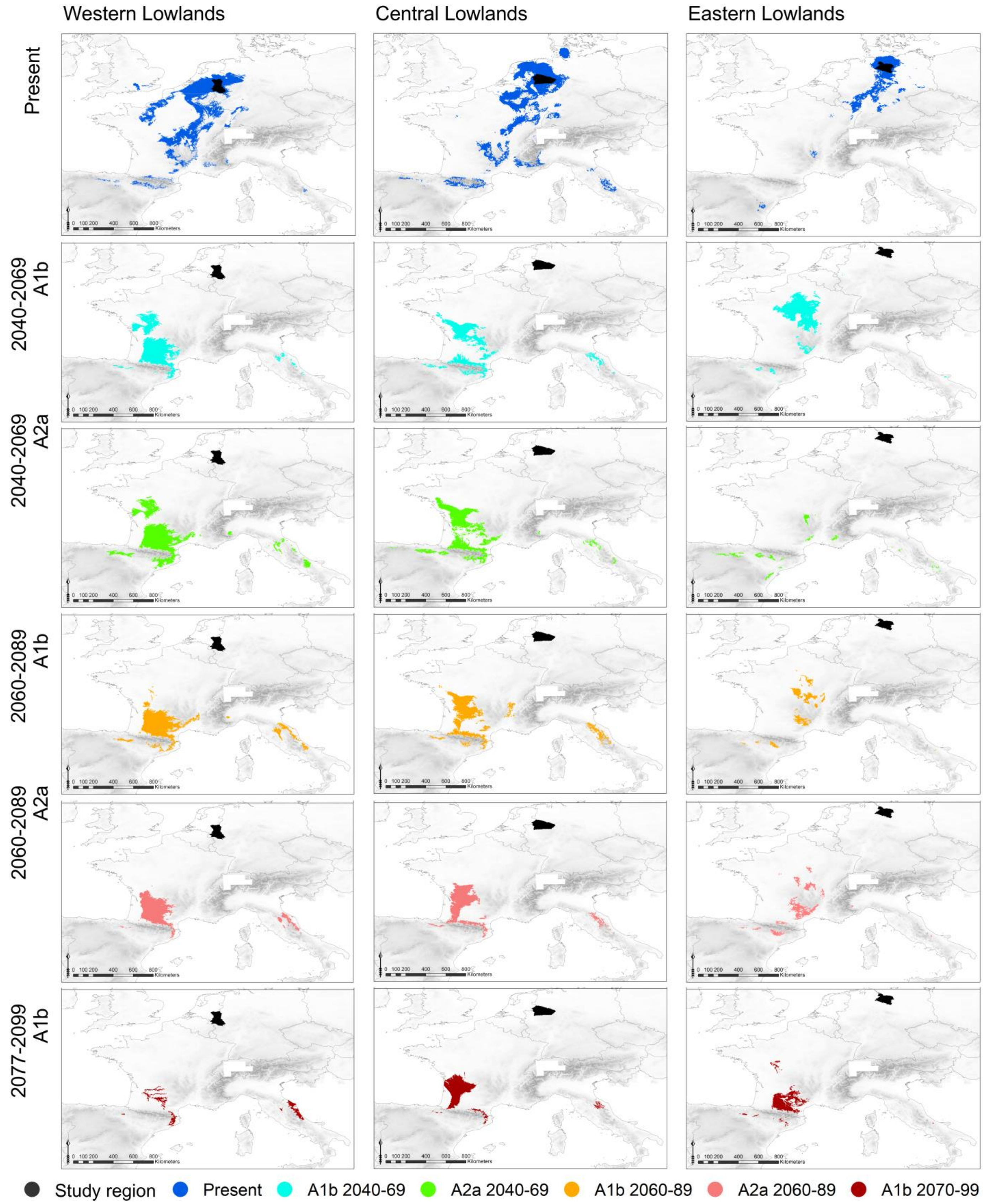


Fig. 3 **Present and future climate analogues of the three study regions for the different projections.** The size of the climate points constituting the climate analogues is not true to scale and appears in scattered areas denser than it really is. Map background shows elevation and indicates higher altitudes by darker gray. Elevation data is taken from JARVIS et al. (JARVIS et al. 2008).

Eastern Lowlands. The difference in locations of the climate analogues shows that the future climate analogues reflect differences in the climate of the study regions.
For the Eastern Lowlands, the geographical distance between present and future climate analogues was farther and the separation of the single future climate analogues was more distinctive than for the Central and Western Lowlands (Fig. 3).

3.2 Relation of occurrences of habitats to the climate in the climate analogues

To investigate whether frequency and area of habitats are related to climate, we interpreted PCA ordination biplots based on first and second component scores of frequency and area of habitats in the climatically analogous N2k-sites. The biplots showed three major results. First, although the ellipses of the habitat data of the different projections overlapped in large parts, the ellipses varied clearly in center, orientation, extension and eccentricity (Fig. 4A-C). This means that habitats differed in frequency and area between the climate analogues (explained by the first two axes with about 24 to 26% (Comp.s 1+2)). The second result is that the future climate analogues ellipses stretched in one direction and the ellipses of the most severe projections were farthest from the ellipses of the present climate analogue. This means that the order in magnitude of climate change was reflected in the habitat data in the climate analogues. The relationship can be seen most clearly in the biplot of the Eastern Lowlands (Fig. 4A, ellipses' centers and margins measured) and partly the Western Lowlands (Fig. 4C, ellipses' centers measured). Likewise, for the third result, there are two visible leaps in the position of the Eastern Lowlands ellipses, from present to future and between the last time period A1b7099 to the previous A2a6089. They correspond to the warming leaps of the climate data (see above under section 2.4.1). For the Central and Western Lowlands, the position of the ellipses divides only between the present and all future projections, so their habitat data reflects only the first warming leap.
The change of frequency and area of habitats in the climate analogues over the line of the projections was for all three study regions characterized by the same four to five Natura 2000 habitat types (Fig. 4D-F). The habitat type that was most related to the future climate analogues as it was most frequent/covered more area in the future climate analogues was "6210 Semi-natural dry grasslands and scrubland facies on calcareous substrates" (Fig. 4D-F). In the Eastern and Western Lowlands, this habitat type even increased over the line of the projections and led to the development trend of growing habitat change at the end of the 21st century (Fig. 4A,D,C,F). The habitat type 6210 is a grassland of warm and dry places (EUROPEAN COMMISSION DG ENVIRONMENT 2013). In contrast, the habitat types which were only related to the ellipses of the present climate analogues and decreased in the future climate analogues, were two beech forest habitat types and an oak-hornbeam forest habitat type ("9110 Luzulo-Fagetum beech forests", "9130 Asperulo-Fagetum beech forests", "9160 Sub-Atlantic and medio-European oak-hornbeam forests of the Carpinion betuli") (Fig. 4D-F). All three relate to temperate sites and at least mesophile or wetter moistured sites (EUROPEAN COMMISSION DG ENVIRONMENT 2013; DRACHENFELS 2014). Habitat types which did not apparently change in frequency or area between present and future climate analogues were a meadow habitat type, occurring on medium tempered and mesophile moistured places, and a riparian forest habitat type being independent from temperature, only dependent on periodic flooding of permanently flowing rivers ("6510 Lowland hay meadows (Alopecurus pratensis, Sanguisorba officinalis)", "91E0 Alluvial forests with Alnus glutinosa and Fraxinus excelsior (Alno-Padion, Alnion incanae, Salicion albae)") (cf. EUROPEAN COMMISSION DG ENVIRONMENT 2013; DRACHENFELS 2014)

(Fig. 4D-F). Increasing and decreasing habitat types fit in the warmer and drier conditions of the future climate analogues and indicate a relationship between habitats and climate.

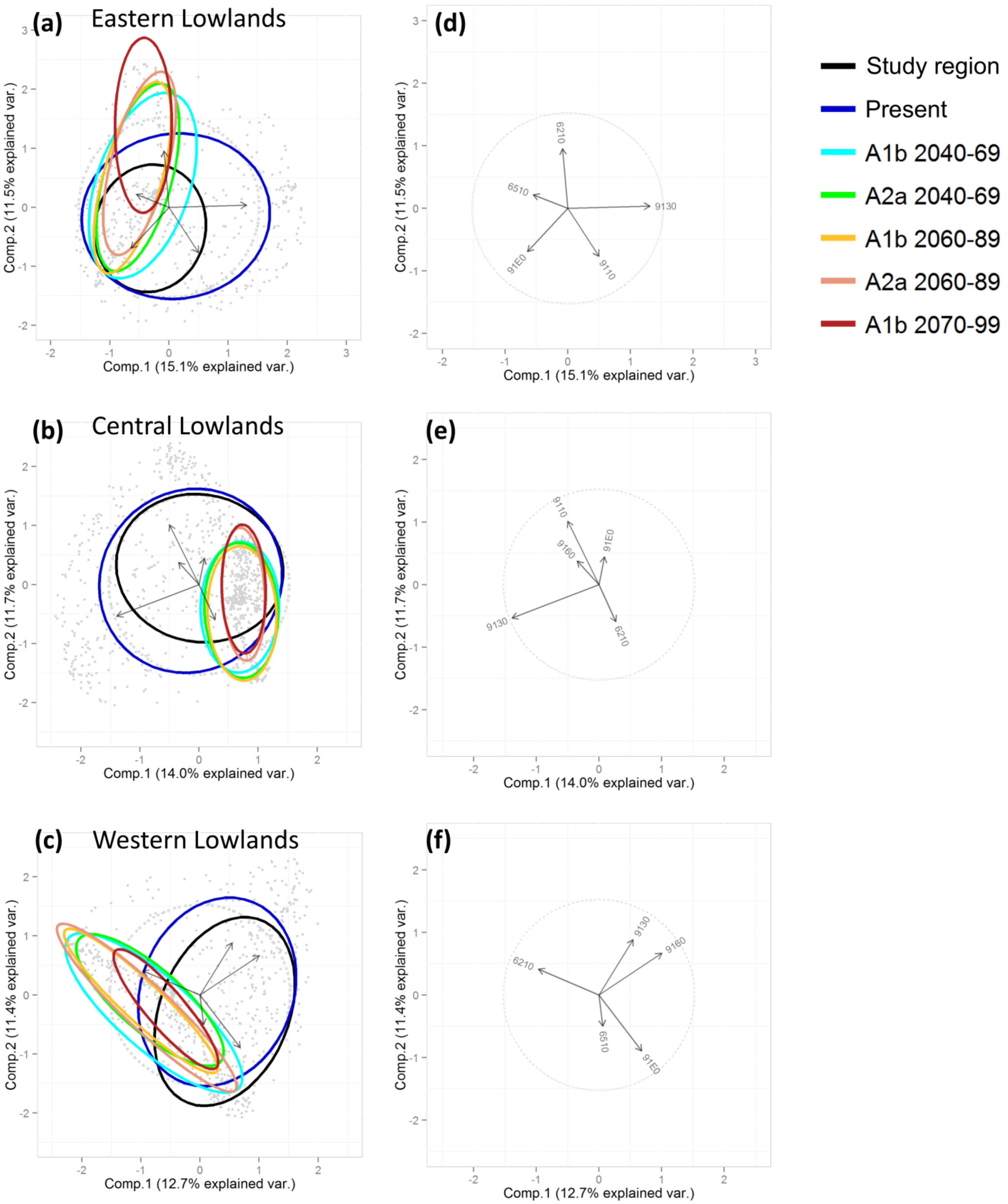


Fig. 4 **PCA ordination biplots of Natura 2000 habitats in the climate analogues.**
(a-c) Biplots showing frequency and area of habitats in the climate analogues of the different projections of the three study regions based on principal components 1 and 2. Each dot stands for a climatically analogous N2k-site with information about which habitat types occur and which area *[continued next page]*

they cover. Gravity ellipses envelope 2/3 of a climate analogue's N2k-sites dots and are coded according to time windows/scenarios. As some N2k-sites belong to more than one climate analogue some dots overlap and hide others, therefore dots are not distinguished. The dashed circle envelopes 2/3 of the total N2k-sites dots.

(d-f) The plots show which habitat types contribute to components 1 or 2 with at least 0.4. Numbers represent the Habitats Directive habitat code: 6210 Semi-natural dry grasslands and scrubland facies on calcareous substrates, 6510 Lowland hay meadows, 9110 Luzulo-Fagetum beech forests, 9130 Asperulo-Fagetum beech forests, 9160 Sub-Atlantic and medio-European oak or oak-hornbeam forests of the Carpinion betuli, 91E0 Alluvial forests with Alnus glutinosa and Fraxinus excelsior (Alno-Padion, Alnion incanae, Salicion albae).

(a-f): Analysis based for the Eastern Lowlands on n=618 N2k-sites and n=56 habitat types occurring in all present/future climate analogues; the Central Lowlands: n=982 N2k-sites and n=70 habitat types; the Western Lowlands: n=782 N2k-sites and n=75 habitat types.

4 Discussion

4.1 Method test

Our tests demonstrate that "climate analogues" are a viable method of providing results from which to assess the possible impact of climate change on Natura 2000 habitat types at the regional scale. Both requirements for the viability of the method were met. First, by using relevant climate variables for the studied habitat types, we found plausibly located future climate analogues, which reflected individual climate characteristics of the study regions. Secondly, frequency and area of Natura 2000 habitats were related to the climate reflected in the future climate analogues as they differed plausibly according to the climate conditions represented in the climate analogues.

4.1.1 Plausible location of the climate analogues

Future climate analogues formed a spatio-temporal series where, with increasing climate change, the analogues progressed toward the south-westward direction and moved downslope the mountains. This indicates that the farther the investigated future time horizon for the study region, the further south-west today's climate equivalents are found. This finding corresponds with observed range shifts of ecosystems (PARMESAN 2006; OLOFSSON et al. 2008; BELLARD et al. 2012), modeled uphill migration trends of habitat types (TRIVEDI et al. 2008), and projected climate shifts (OHLEMÜLLER et al. 2006; BURROWS et al. 2014). Exact locations vary, of course, due to different global (REAL et al. 2010; SHEPHERD 2014) and regional circulation models (cf. HALL 2014), scenarios, time periods and climate variables.

The climate analogues of the warmer oceanic study regions, in the present and in the future (Western and Central Lowlands, S2 Table), were found closer to the coast, more south and in lower elevations than those of the more continental study region (Eastern Lowlands). Thus, the climate analogues even reflected slightly varying climate characteristics of the three study regions. The climate analogues of the study region with a more homogeneous relief and thus a narrower climate range (Eastern Lowlands) were separated geographically more distinctly on the maps than those of the study regions with a more heterogeneous relief and a broader climate range (Central and Western Lowlands). This shows that climate analogues are geographically more precise the more climatically uniform the study region is and when searching climate analogues for hilly study regions, they should be identified separately for different altitudes and exposures.

4.1.2 Occurrences of habitats related to the climate change reflected in the future climate analogues

The Natura 2000 habitat data was plausibly related to the climate change reflected in the future climate analogues. For instance, the habitats clearly differed between the present and future climate analogues of all three study regions. For two study regions (the Eastern and partly the Western Lowlands) the differences clearly increased with an increasing magnitude of climate change. Additionally, the largest habitat changes were congruent with the largest leaps in warming (most clearly for the Eastern Lowlands but visible for all three study regions, the leap between present and future climate analogues). Differences were characterized by increasing, decreasing, and stable habitat types representing plausible ecological preferences that are in line with the expected climate changes of more dryness in the growing season and more warmth (cf. IPCC 2013). Specifically, the grassland habitat type (6210), which prefers warm and dry spots, was in all three study regions the most important representative of the habitat types that occurred with higher frequency/area in the future climate analogues. In contrast, two beech forest types (9110, 9130) and an oak-hornbeam forest type (9160) were the most important representatives of the habitat types that decreased in frequency/area in the future climate analogues. These forest habitat types prefer medium temperatures and a sufficient water balance (EUROPEAN COMMISSION DG ENVIRONMENT 2013). As these conditions are expected to lessen in the study regions in the future (see above under section 2.4.1), they were less frequently found in the future climate analogues. Hence, this decrease of habitat types reflects the difference in climate in the future climate analogues.

The results are consistent with other studies which have also identified vegetation that prefers “warm” and “dry” as likely to increase. Similarly, vegetation that prefers “cold” and “mesophile” was identified as likely to decrease (BERRY et al. 2003; SKOV et al. 2009; ESSL et al. 2012; BUSE et al. 2015; BILTON et al. 2016).

There was no change between present and future climate analogues in frequency and area of the likewise medium tempered and mesophile moistured meadow habitat type (6510). This is likely due to its broad definition (RODRIGUEZ-ROJO et al. 2014) which hides actual vegetation changes. The second habitat type that showed no difference in frequency and area between the present and future climate analogues was a riparian forest habitat type (91E0). The lack of change is explained by its independence from temperature and climatic moisture, as it occurs throughout Europe as azonal vegetation along rivers (ELLENBERG and LEUSCHNER 2010; analysis of EEA 2013 data). Thus, the stable reaction is ecologically sound.

The plausible differences and similarities show that the relation between the habitat and climate data in the future climate analogues was strong enough to outweigh possible weaknesses of the habitat data, which could be an unequal interpretation of occurrences (DRACHENFELS 2001; EVANS 2006, 2010) and a patchy web of records.

The relationship between the habitat data and the magnitude of climate change, reflected in the climate analogues, was most evident for the Eastern Lowlands (Fig. 4A-C). The less distinct development trend for the Central and Western Lowlands can be explained by reasons not related to climate (S5 Text). For how to refine the results of climate analogues refer also to S5 Text.

Habitats also relate to other physical environmental factors which may change in parallel with the climate (for example soil, geology, land-use, land-use history, topography). However, PEARSON and DAWSON (PEARSON and DAWSON 2003), as well as METZGER et al. (METZGER et al. 2005), have found that climate exerts a dominant role on the distribution of ecosystems on scales larger than 100 km (cf. also ARAÚJO and ROZENFELD 2014). The ecoregions, used as study regions in our research, are already more than 100 km in diameter (cf. Fig. 1) and their climate analogues spread across continental scales of more than 1,000 km (distances between study regions and climate analogues, cf. Fig. 3). Thus, frequency and area of habitat types in the climate analogues are expected to be mainly related to climate. Nevertheless, the influence of environmental factors on habitats' frequency and area should be clarified with more precise data (see below under section "Limitations").

We identified an anthropogenic grassland habitat type (6210) as the habitat type which increases the most. Hence, this increase could be caused not only by climate but also by land-use. However, as four natural forest habitat types (9110, 9130, 9160, 91E0) likewise showed plausible differences between present and future climate analogues, we view the relationship between habitats and climate confirmed.

Therefore, we are convinced that the results of the climate analogues method can be used to estimate the potential development trends of habitat types at the regional scale.

4.2 Benefits

For nature conservation at the regional scale, we see five technical and six practical benefits of applying the climate analogues method, compared to species distribution models (SDMs).

4.2.1 Technical benefits

- Climate analogues are **efficient**. Instead of modeling single habitat types, they model the study region of interest (SKOV et al. 2009). Thus, they save time and computational power (FERRIER and GUISAN 2006; KOPF et al. 2008; PRISCO et al. 2013). In a single comparative step, information on potential development trends for all habitat types within the study region and potentially immigrating habitat types is obtained. Habitat types are identified into three categories:
  - stable (occurring both in the study region and the future climate analogue),
  - potentially missing (occurring only in the study region),
  - potentially additionally occurring (occurring only in the future climate analogue

  In comparison, the use of SDMs requires more effort as each habitat type has to be modeled individually. Secondly, SDMs are usually only applied to the current habitat types of a study region (ACKERLY et al. 2015; cf. BAATAR et al. 2019). Consequently, potential immigrating habitat types remain undetected.
- Climate analogues **avoid technical problems** which are obstacles for SDMs: (a) missing proportion-data hinders community modeling of habitat types (cf. CLARK et al. 2017), (b) imprecise and broadly defined habitat types (MÜCHER et al. 2009; PRISCO et al. 2013), and missing distribution maps of species (THUILLER et al. 2005; MÜCHER et al. 2009) challenge parameterization of indirect models and, (c) gaps in distribution maps of habitat types and dispersed and low frequency habitat types pose problems to parameterization of direct models for habitat types.
- Climate analogues can be used for **controlling their own results**. For both SDMs and climate analogues it is problematic when true occurrences of habitats are not recorded (cf. SKOV et al. 2009) as the absence is likely mistaken as being climate caused (cf. ALESSI et al. 2019). Within the climate analogues, field assessments can confirm whether the mapping was poor or whether habitat types are really missing (cf. MÜCHER et al. 2009). Additionally,

regional, available data can be queried. This way, results can be verified in a manageable area. These procedures are less susceptible to false assumptions than the correcting of data-poor regions via modeling approaches (cf. EL-GABBAS and DORMANN 2018), which are needed for large scales.

- Climate analogues facilitate the **gathering of data, even of data-poor** influential factors such as land-use and land-use history (cf. BOU and VILAR 2019). Potential climate dependent changes in land-use (e.g. ways and demands of irrigation, usage of grasslands) can be identified for the study regions and integrated into management perspectives of habitat types, by using available regional data or gathering data within the climate analogues. In SDMs, land-use is usually ignored due to classification which is too coarse and the spatial grain of available large-scale data (TITEUX et al. 2016).
- Climate analogues can estimate the potential reaction of **rare habitat types**. Rare habitat types are challenging to model (NIETO-LUGILDE et al. 2018; cf. for species CARADIMA et al. 2019) but can be rated with climate analogues, provided that the occurrences are dense enough to fall into the climate analogues. Even when they are not, frequent habitat types in the climate analogues can reveal "shared patterns of [climate] (…) response" with ones that have low frequency, a trick which is also used by SDMs (FERRIER and GUISAN 2006: 401; CARADIMA et al. 2019).

4.2.2 Practical benefits

We see six practical benefits of climate analogues for nature conservation:

- With climate analogues, nature conservationists can anticipate possible future changes of their **complete regional set** of habitat types (cf. RAMIREZ-VILLEGAS et al. 2011). They can compare sensitivities and set priorities.
- Climate analogues support the **realization of measures** with their region-based approach (HANNAH et al. 2002; TRIVEDI et al. 2008). They visualize the abstract threat of climate change impacts for policy makers and the public when, on geographic maps, they link future time periods with distinct and real regions (FERRIER and GUISAN 2006; VELOZ et al. 2012). They reveal which habitat types are at risk in a study region and, thus, show conservationists where to take local actions (HELLER and ZAVALETA 2009). Furthermore, the ease of the approach enables the uptake of its results (cf. YATES et al. 2018). This can increase the will and responsibility of people to act and support nature conservation and push conservation activities forward (cf. KATI et al. 2015).
- Climate analogues enable **exchange and collaboration** as they highlight where additional expertise is needed. Conservationists can learn from colleagues in the future climate analogues, regarding the management of habitat types under a warmer and drier climate (cf. RAMIREZ-VILLEGAS et al. 2011). For example, they can copy how increasing conflicts of interests in water irrigation (cf. WADA et al. 2013) can be resolved and balanced between wetland habitats, water management and farming. Conservationists can coordinate migration measures for immigrating and emigrating habitat types with conservationists in the climate analogues and realize the need for international collaboration (cf. VAN TEEFFELEN et al. 2015).
- Climate analogues can determine the regions where **field experiments** can be conducted under future climate conditions (RAMIREZ-VILLEGAS et al. 2011). These are regarded as

especially important in further research (JAESCHKE et al. 2014; ALEXANDER et al. 2016). Further, habitats in the climate analogues represent biotic interactions across all ecosystem parts and levels, from trees to mosses, vertebrates to insects, soil organisms, fungi, mycorrhiza, pests, and diseases, etc., under future climate conditions. Scientists can study them in the field and assess their potential future relevance to the study regions. SDM cannot encompass biotic interactions comparably comprehensively in the modeling (RUSHING et al. 2019).

- The method is **easy** to apply. Climate analogues can be found with open access data (climate, habitats) and GIS. Online tools, such as the Climate Analogues online platform from the CGIAR (http://analogues.ciat.cgiar.org) or the Climate Wizard from the CCAFS (ccafs-climate.org/climatewizard; GIRVETZ et al. 2009), are available even for non-experts.
- **"II. Order future climate analogues"** can embed the regional assessments into a European context. For instance, some southern habitat types will lose their suitable climate conditions, as e.g. described for Laurus nobilis (cf. BERGER et al. 2007) which is characteristic for Natura 2000 habitat type 5230. These habitat types can be identified with "II. Order future climate analogues." These are the future climate analogues of a study region's future climate analogues (S5 Fig). Likewise, "Northern future climate analogues" (the CGIAR calls them "forward climate analogues", http://analogues.ciat.cgiar.org) can identify habitat types which may lose their suitable climate in the study regions and do not yet occur north of the study regions (S5 Fig). This information helps nature conservationists to discuss and develop European-wide conservation strategies.

4.3 Limitations

We see seven technical and four practical limitations of the climate analogues method compared to the use of SDMs.

4.3.1 Technical limitations

The technical limitations can be distinguished into uncertainties concerning the climate variables (predictor variables), the habitat data (response variables), and the output of the climate analogues (model evaluation; cf. ARAUJO et al. 2019).

Climate variables:

- We aimed to test the climate analogues method in principle but when applying the method, more emphasis needed to be placed on increasing the reliability of the results by reducing the uncertainty of the climate projections (cf. ARAUJO et al. 2019). For this, the natural **climate variability** should be covered with an ensemble of climate analogues. This ensemble should be searched for a variety of climate data that is based on different global climate models and different scenario runs with multiple realizations (PIERCE et al. 2009). However, for the analysis in this paper, two examples of climate projections and three future time periods were sufficient.
- The projection power of climate analogues is reduced by the mean-orientated climate data. **Extreme events** can alter plant communities (JENTSCH and BEIERKUHNLEIN 2008; KREYLING et al. 2008) but their magnitude and frequency is hidden by 30 year climate averages. As drought and heat events will likely increase in the future (IPCC 2013), the effect is not yet reflected in the habitat data of the future climate analogues. The effect of future climate

change may thus be worse than the future climate analogues suggest. However, SDMs work with the same mean-orientated data and have the same risk of underestimation, as long as they are not explicitly modeling the effects of extreme events.

- We have carefully chosen a set of **temperature and precipitation variables**, which represent climatic differences in Europe as decisive climatic characteristics for habitat types in order to define the climate analogues. However, variables for the soil water balance would be more meaningful than precipitation variables, as indicated by PIEDALLU et al. (PIEDALLU et al. 2013). However, to date, these data are not available. Furthermore, for individual habitat types, specific climate variables may be more decisive than the ones chosen, shifting the climate analogues from general climate analogues to specific ones. Compared to SDMs, which can parametrize the variables for each habitat type individually, this generality of variables is a weakness of the climate analogues method. However, since SDM studies use the same set of climate variables for all habitat types (PRISCO et al. 2013; cf. BAATAR et al. 2019) and plant species (cf. THUILLER et al. 2005; POMPE et al. 2008; ARAÚJO et al. 2011; GARCIA-VALDES et al. 2015), this generality is more of a theoretical weakness than a real one.

Habitat data and environmental data:

- Occurrences of habitats in the Natura 2000 habitat database are **spatially dissolved** to the extension of the N2k-site they lie in. This extension sets a limit to relations between habitats, climate and environmental factors (as, for example, N2k-sites may be hilly at one end and flat at the other, and thus have different climates, or have different soils or geology). For more precise relationships, data would be needed that provides the habitats' exact location within the N2k-site instead of giving only lists of habitat types that occur within the N2k-site. Since management plans record habitat occurrences in the N2k-sites as spatially distinct, a European habitat database uniting the data would be desirable. It should also encompass data on habitat occurrences outside the N2k-sites, which is still a dearth of (cf. MÜCHER et al. 2009).

  Additionally, soil and land-use data with a resolution of at least as fine as habitat patches (not yet available; cf. MÜCHER et al. 2009) would help to better understand how they influence the occurrence of habitats. Today, the only harmonized European Soil Database (ESDB; EUROPEAN COMMISSION AND THE EUROPEAN SOIL BUREAU NETWORK 2004) is still relatively coarse, particularly as habitat types are often found on special soil conditions (the ESDB's finest resolution are "Soil Mapping Units" at the scale of 1:1,000,000 these in turn contain up to 11 "Soil Typological Units" which are not spatially located (INRA et al. 1994)). Overlaying coarse patches of habitat data and soil data would amplify the geographic uncertainty in their relationship.

Output of the climate analogues method/ model evaluation:

- Stable habitat types have a high probability of being truly projected with climate analogues. However, it is hard to evaluate whether potentially missing and additionally occurring habitat types will become reality. Climate analogues do not provide information on how long disappearing habitat types may persist, whether and when potentially additionally occurring habitat types may reach the study region, or whether new communities will not instead be built (cf. HUNTLEY 1991; WALTHER 2010; BLONDER et al. 2017), ones which may not correspond anymore to the Natura 2000 habitat types.

  Persistence and migration will depend on adaptation, changes of biotic interactions (DOMINGUEZ-BEGINES et al. 2019), dispersal abilities, migration speeds of the habitats' single species (BRUELHEIDE 2003; THUILLER et al. 2008; WISZ et al. 2013) and, finally, it will be driven by the real courses of climate change and extreme weather events. Furthermore, these processes will be modified by invasive species that may change species compositions of habitat types, changes in land-use (ROUNSEVELL et al. 2006; AMEZTEGUI et al. 2016), and agricultural policies as, for example, described for grasslands by Finck et al. (FINCK et al. 2017). However, SDMs likewise struggle with uncertainty regarding these factors.

Concerning dispersal uncertainties, most SDMs assume two simple states until the studied time horizon, full dispersal and no dispersal (BITTNER et al. 2011; PRISCO et al. 2013; cf. BAATAR et al. 2019). Climate analogues are based on the same assumption of full dispersal for the potentially additionally occurring habitat types. How likely this is, needs to be discussed habitat-specific.

- SDMs geographically map the potential **future range** of habitat types and inform on whether the study region will be in the center, at the margin, or distant from the potential future range. This helps, for example, to estimate whether a potential additional habitat type may immigrate into the study region more quickly and more likely than others. This would be implied by a small distance between the leading edge of the habitat’s present range and the study region. Likewise, for a potentially disappearing habitat type, it may persist for a long time when the trailing edge of its future range is mapped not far from the study region. Climate analogues do not present range maps, but provide this information tailored to a study region. They provide the information via the distance between the future climate analogue and the present range of the habitat type.

- Compared to climate analogues, SDMs have the advantage that they are able to implement **migration rates** and biotic interactions into the modeling (COLLINGHAM and HUNTLEY 2000; e.g. FERRIER and GUISAN 2006). Implementing this into SDMs, has increasingly become the center of modeling research (ARAÚJO and LUOTO 2007; KISSLING et al. 2012; SNELL et al. 2014; GARCIA-VALDES et al. 2015; MOD et al. 2015; DORMANN et al. 2018; NIETO-LUGILDE et al. 2018). However, even for single species migration rates and biotic interactions are still difficult to predict (HUNTLEY 1991; THUILLER et al. 2008; WALTHER 2010; DORMANN et al. 2018) because they are known only for few plant species. Moreover, present-time conditions will likely alter in the course of climate change (BLOIS et al. 2013b). Additionally, these processes are affected by habitat connectivity, which will be modified by uncertain changes in land-use (cf. ROUNSEVELL et al. 2006). Thus, modeling the migration speed and change of biotic interactions of habitat types remains challenging. Apart from ecological questions, current habitat models become highly complex and require extensive computational power for the required spatial extent of future climate shifts (KISSLING et al. 2012; SNELL et al. 2014; DORMANN et al. 2018). Hence, though possible, it is still difficult to model processes that determine persistence, community change and migration of habitats.

4.3.2 Practical limitations

The four practical limitations of the climate analogues method for use in practical and strategic nature conservation planning are:

- The method provides statements about general trends, but it **does not provide any precise statements in terms of time or space**. However, we believe that the trends in habitat change that can be deduced from the data are adequate for conservation planning. Measures in nature conservation need time to show an effect, so that it is more important for conservationists to fit the measures to the general development trend than to know when certain stages of climate change will become reality. Climate analogues are useful to identify long-term trends (ELMENDORF et al. 2015) and to prepare for them with early low-input measures.

- Climate analogues serve **only the regional scale**. For international to continental conservation planning, SDMs are more appropriate as they can map changes of the potential future range of habitat types continental wide and identify potential migration corridors and core areas. The climate analogues, in contrast, discover only an extract of these potential future ranges. However, for the regional scale, the focus on the information that is directly relevant for the region makes the uptake of the results easy for regional actors and, thus, facilitates in the realization of actions.
- Climate analogues can be of different size and contain a varying number and size of N2k-sites. To test the relationship between habitat data and climate in this paper, the applied PCA is a robust method. However, when applying the method it should be tested whether a deviating number and area of N2k-sites within the present and future climate analogues may influence the **quantitative and qualitative comparisons** of the habitat data. Deviations could be equalized with rarefaction measures (e.g. LUDT et al. 2018; MCGLINN et al. 2019).
- For **climate-heterogeneous regions**, the climate analogues for the climate of different areas have to be determined separately and this means that the effort involved in this method rises.

5 Conclusions

Our results show “climate analogues” as a viable method to deliver results that can be subsequently used for assessing the potential impact of future climate change on Natura 2000 habitat types at the regional scale. We would argue that climate analogues are a powerful state-of-the-art method that offers regional nature conservation several important technical and practical benefits over species distribution models (SDMs). Whereas SDMs especially support planning at international scales, the climate analogues method empowers the regional level in implementing actions. THUILLER et al. (THUILLER et al. 2008: 146) stated that “[t]he conservation agenda is now moving on to consider adaptation to climate change and here a landscape approach is more applicable.” We believe that the climate analogues method provides a landscape approach. We regard the method as very appropriate to serve the rise in will of the public, politicians, and conservationists to take regional initiatives against the potential losses of biodiversity through future climate change.

Acknowledgements

We thank Carlos Navarro from the International Centre for Tropical Agriculture Colombia (CIAT) for giving us access to climate scenarios and acknowledge CGIAR Research Program on Climate Change, Agriculture and Food Security (CCAFS) for providing CIAT climate data sets. Danny Charbonneau from the European Commission, DG Environment, is thanked for providing the Natura 2000 database shapefiles from EUNIS-Database. Marc Van Liedekerke from the European Soil Data Centre (ESDAC) of the Joint Research Centre of the European Commission is thanked for giving us access to and answering questions related to the ESDB dataset. We also wish to thank Ingolf Kühn from the Helmholtz Centre for Environmental Research - UFZ, Ralf Ohlemüller from the University of Otago and Jessica Bergmann for providing climate data and analogues from ALARM project at the beginning of our research. We extend a special thanks to Martha Graf for improvements of a former version, Frank Schaarschmidt and Daniel Gerhard for their support in the statistical analysis, Louise von Falkenhayn for proofreading, two reviewers for valuable comments on the manuscript, and Katharina Niemann for supporting layout work.

References

ACKERLY DD, CORNWELL WK, WEISS SB, FLINT LE, FLINT AL (2015) A Geographic Mosaic of Climate Change Impacts on Terrestrial Vegetation: Which Areas Are Most at Risk? PLoS ONE, 10(6):e0130629

ALESSI N, TESITEL J, ZERBE S, SPADA F, AGRILLO E, WELLSTEIN C (2019) Ancient refugia and present-day habitat suitability of native laurophylls in Italy. J Veg Sci, 30(3):564–574

ALEXANDER JM, DIEZ JM, HART SP, LEVINE JM (2016) When Climate Reshuffles Competitors: A Call for Experimental Macroecology. Trends Ecol Evol, 31(11):831–841

AMEZTEGUI A, COLL L, BROTONS L, NINOT JM (2016) Land-use legacies rather than climate change are driving the recent upward shift of the mountain tree line in the Pyrenees. Glob Ecol Biogeogr, 25(3):263–273

ARAUJO MB, ANDERSON RP, MARCIA BARBOSA A, BEALE CM, DORMANN CF, EARLY R, GARCIA RA, GUISAN A, MAIORANO L, NAIMI B, O'HARA RB, ZIMMERMANN NE, RAHBEK C (2019) Standards for distribution models in biodiversity assessments. Science Advances, 5(1):eaat4858

ARAÚJO MB, ALAGADOR D, CABEZA M, NOGUÉS-BRAVO D, THUILLER W (2011) Climate change threatens European conservation areas. Ecol Lett, 14(5):484–492

ARAÚJO MB, LUOTO M (2007) The importance of biotic interactions for modelling species distributions under climate change. Glob Ecol Biogeogr, 16(6):743–753

ARAÚJO MB, ROZENFELD A (2014) The geographic scaling of biotic interactions. Ecography, 37(5):406–415

BAATAR U-O, DIRNBOECK T, ESSL F, MOSER D, WESSELY J, WILLNER W, JIMENEZ-ALFARO B, AGRILLO E, CSIKY J, INDREICA A, JANDT U, KACKI Z, SILC U, SKVORC Z, STANCIC Z, VALACHOVIC M, DULLINGER S (2019) Evaluating climatic threats to habitat types based on co-occurrence patterns of characteristic species. Basic Appl Ecol, 38:23–35

BARTHOLY J, PONGRACZ R, NAGY J, PIECZKA I, HUFNAGEL L (2012) Regional climate change impacts on wild animals' living territory in central Europe. Appl ecol and environ res, 10(2):107–120

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

BERGER S, SOEHLKE G, WALTHER G-R, POTT R (2007) Bioclimatic limits and range shifts of cold-hardy evergreen broad-leaved species at their northern distributional limit in Europe. Phytocoenologia, 37(3-4):523–539

BERGMANN J, POMPE S, OHLEMÜLLER R, FREIBERG M, KLOTZ S, KÜHN I (2009) The Iberian Peninsula as a potential source for the plant species pool in Germany under projected climate change. Plant Ecol, 207:191–201

BERRY PM, DAWSON TP, HARRISON PA, PEARSON RG, BUTT N (2003) The sensitivity and vulnerability of terrestrial habitats and species in Britain and Ireland to climate change. J Nat Conserv, 11(1):15–23

BILTON MC, METZ J, TIELBÖRGER K (2016) Climatic niche groups: A novel application of a common assumption predicting plant community response to climate change. Perspectives in Plant Ecology, Evolution and Systematics, 19:61–69

BITTNER T, JAESCHKE A, REINEKING B, BEIERKUHNLEIN C (2011) Comparing modelling approaches at two levels of biological organisation - Climate change impacts on selected Natura 2000 habitats. J Veg Sci, 22(4):699–710

BLOIS JL, WILLIAMS JW, FITZPATRICK MC, JACKSON ST, FERRIER S (2013a) Space can substitute for time in predicting climate-change effects on biodiversity. Proc Natl Acad Sci U S A, 110(23):9374–9379

BLOIS JL, ZARNETSKE PL, FITZPATRICK MC, FINNEGAN S (2013b) Climate Change and the Past, Present, and Future of Biotic Interactions. Science, 341(6145):499–504

BLONDER B, MOULTON DE, BLOIS J, ENQUIST BJ, GRAAE BJ, MACIAS-FAURIA M, MCGILL B, NOGUE S, ORDONEZ A, SANDEL B, SVENNING J-C (2017) Predictability in community dynamics. Ecol Lett, 20(3):293–306

BOU J, VILAR L (2019) Sessile oak forest plant community changes on the NE Iberian Peninsula over recent decades. J Plant Ecol, 12(5):894–906

BRUELHEIDE H (2003) Translocation of a montane meadow to simulate the potential impact of climate change. Appl Veg Sci, 6(1):23–34

BURROWS MT, SCHOEMAN DS, RICHARDSON AJ, MOLINOS JG, HOFFMANN AA, BUCKLEY LB, MOORE PJ, BROWN CJ, BRUNO JF, DUARTE CM, HALPERN BS, HOEGH-GULDBERG O, KAPPEL CV, KIESSLING W, O'CONNOR MI, PANDOLFI JM, PARMESAN C, SYDEMAN WJ, FERRIER S, WILLIAMS KJ, POLOCZANSKA ES (2014) Geographical limits to species-range shifts are suggested by climate velocity. Nature, 507(7493):492–495

BUSE J, BOCH S, HILGERSD J, GRIEBELER EM (2015) Conservation of threatened habitat types under future climate change - Lessons from plant-distribution models and current extinction trends in southern Germany. J Nat Conserv, 27:18–25

CARADIMA B, SCHUWIRTH N, REICHERT P (2019) From individual to joint species distribution models: A comparison of model complexity and predictive performance. J Biogeogr

CLARK JS, NEMERGUT D, SEYEDNASROLLAH B, TURNER PJ, ZHANG S (2017) Generalized joint attribute modeling for biodiversity analysis: Median-zero, multivariate, multifarious data. Ecol Monogr, 87(1):34–56

COLLINGHAM YC, HUNTLEY B (2000) Impacts of habitat fragmentation and patch size upon migration rates. Ecol Appl, 10(1):131–144

COLLINS M, KNUTTI R, ARBLASTER J, DUFRESNE J-L, FICHEFET T, FRIEDLINGSTEIN P, GAO X, GUTOWSKI WJ, JOHNS T, KRINNER G, SHONGWE M, TEBALDI C, WEAVER AJ, WEHNER M (2013) Long-term Climate Change: Projections, Commitments and Irreversibility. In: IPCC (ed) Climate Change 2013: The Physical Science Basis. Cambridge University Press, Cambridge

COUNCIL OF THE EUROPEAN COMMUNITIES (1992) Council directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. Available from https://eur-lex.europa.eu/legal-content/EN/TXT/PDF/?uri=CELEX:31992L0043&from=EN (accessed October 2021)

DAVIES AR, BROTO VC, HUGEL S (2021) Editorial: Is There a New Climate Politics? POLITICS AND GOVERNANCE, 9(2):1–7

Dominguez-Begines J, Deyn GB de, Garcia LV, Eisenhauer N, Gomez-Aparicio L (2019) Cascading spatial and trophic impacts of oak decline on the soil food web. J Ecol, 107(3):1199–1214

Dormann CF, Bobrowski M, Dehling DM, Harris DJ, Hartig F, Lischke H, Moretti MD, Pagel J, Pinkert S, Schleuning M, Schmidt SI, Sheppard CS, Steinbauer MJ, Zeuss D, Kraan C (2018) Biotic interactions in species distribution modelling: 10 questions to guide interpretation and avoid false conclusions. Glob Ecol Biogeogr, 27(9):1004–1016

Drachenfels O von (2001) Welchen Beitrag kann die FFH-Richtlinie zur Sicherung der Biotop-Vielfalt leisten?: Repräsentanz der Biotoptypen durch die Lebensraumtypen in Anhang I und die Habitate der Arten in Anhang II am Beispiel des Nordwestdeutschen Tieflands. Naturschutz und Landschaftsplanung, 33(7):205–212

Drachenfels O von (2014) Hinweise zur Definition und Kartierung der Lebensraumtypen von Anh. I der FFH-Richtlinie in Niedersachsen auf der Grundlage des Interpretation Manuals der Europäischen Kommission (Version EUR 27 vom April 2007). Available from http://www.nlwkn.niedersachsen.de/download/68728/Hinweise_zur_Definition_und_Kartierung_der_Lebensraumtypen_von_Anh._I_der_FFH-Richtlinie_in_Niedersachsen_Stand_Februar_2014_.pdf (accessed October 2021)

Drachenfels O von (2021) Kartierschlüssel für Biotoptypen in Niedersachsen unter besonderer Berücksichtigung der gesetzlich geschützten Biotope sowie der Lebensraumtypen von Anhang I der FFH-Richtlinie. Available from https://www.nlwkn.niedersachsen.de/download/111210/Den_Kartierschluessel_mit_Stand_Maerz_2021_koennen_Sie_sich_hier_herunterladen.pdf (accessed October 2021)

EEA (2013) Natura 2000 database - the European network of protected sites: Tabular data and spatial data, temporal coverage 2012, scale of spatial dataset: 1:100.000. [data]. Available from http://www.eea.europa.eu/data-and-maps/data/natura-4 (accessed October 2021)

El-Gabbas A, Dormann CF (2018) Improved species-occurrence predictions in data-poor regions: Using large-scale data and bias correction with down-weighted Poisson regression and Maxent. Ecography, 41(7):1161–1172

Ellenberg H, Leuschner C (2010) Vegetation Mitteleuropas mit den Alpen: In ökologischer, dynamischer und historischer Sicht. UTB Botanik, Ökologie, Agrar- und Forstwissenschaften, Geographie, vols 8104. Verlag Eugen Ulmer, Stuttgart

Elmendorf SC, Henry GHR, Hollister RD, Fosaa AM, Gould WA, Hermanutz L, Hofgaard A, Jonsdottir IS, Jorgenson JC, Levesque E, Magnusson B, Molau U, Myers-Smith IH, Oberbauer SF, Rixen C, Tweedie CE, Walker M (2015) Experiment, monitoring, and gradient methods used to infer climate change effects on plant communities yield consistent patterns. Proc Natl Acad Sci U S A, 112(2):448–452

Essl F, Dullinger S, Moser D, Rabitsch W, Kleinbauer I (2012) Vulnerability of mires under climate change: implications for nature conservation and climate change adaptation. Biodivers Conserv, 21(3):655–669

European Commission and the European Soil Bureau Network (2004) The European Soil Database distribution version 2.0: CD-ROM. Available from https://esdac.jrc.ec.europa.eu/resource-type/european-soil-database-soil-properties (accessed October 2021)

European Commission DG Environment (2013) Interpretation manual of European Union habitats. Version EUR 28. Available from

https://ec.europa.eu/environment/nature/legislation/habitatsdirective/docs/Int_Manual_EU28.pdf (accessed October 2021)
EUROPEAN ENVIRONMENT AGENCY (2016) Biogeographical regions in Europe. Available from https://www.eea.europa.eu/ds_resolveuid/9b7911cc33ad4a9c940847a7ff653a40 (accessed October 2018)
EVANS D (2006) The Habitats of the European Union Habitats Directive. Biol Environ, 106(3):167–173
EVANS D (2010) Interpreting the habitats of Annex I: past, present and future. Acta Botanica Gallica, 157(4):677–686
EVANS D (2012) The Habitats of Annex I and Climate Change. In: Ellwanger G., Ssymank A., Paulsch C. (eds) Natura 2000 and Climate Change – a Challenge. Naturschutz und Biologische Vielfalt, vols 118. BfN, Bonn, pp 73–82
FEDERAL AGENCY FOR NATURE CONSERVATION (2009) Naturräumliche Gliederung Deutschlands: Shape-file natbs.shp [data], Bonn
FERRIER S, GUISAN A (2006) Spatial modelling of biodiversity at the community level. J Appl Ecol, 43(3):393–404
FINCK P, HEINZE S, RATHS U, RIECKEN U, SSYMANK A (2017) Rote Liste der gefährdeten Biotoptypen Deutschlands. Naturschutz und Biologische Vielfalt, Heft 156. Bundesamt für Naturschutz; Landwirtschaftsverlag Münster, Bonn-Bad Godesberg, Münster
GARCIA-VALDES R, GOTELLI NJ, ZAVALA MA, PURVES DW, ARAÚJO MB (2015) Effects of climate, species interactions, and dispersal on decadal colonization and extinction rates of Iberian tree species. Ecol Model, 309:118–127
GIRVETZ EH, ZGANJAR C, RABER GT, MAURER EP, KAREIVA P, LAWLER JJ (2009) Applied Climate-Change Analysis: The Climate Wizard Tool. PLoS ONE, 4(12)
GUERIN GR, BIFFIN E, LOWE AJ (2013) Spatial modelling of species turnover identifies climate ecotones, climate change tipping points and vulnerable taxonomic groups. Ecography, 36(10):1086–1096
HAGEDORN G, LOEW T, SENEVIRATNE SI, LUCHT W, BECK M-L, HESSE J, KNUTTI R, QUASCHNING V, SCHLEIMER J-H, MATTAUCH L, BREYER C, HUEBENER H, KIRCHENGAST G, CHODURA A, CLAUSEN J, CREUTZIG F, DARBI M, DAUB C-H, EKARDT F, GOEPEL M, HARDT JN, HERTIN J, HICKLER T, KOEHNCKE A, KOESTER S, KROHMER J, KROMP-KOLB H, LEINFELDER R, MEDERAKE L, NEUHAUS M, RAHMSTORF S, SCHMIDT C, SCHNEIDER C, SCHNEIDER G, SEPPELT R, SPINDLER U, SPRINGMANN M, STAAB K, STOCKER TF, STEININGER K, HIRSCHHAUSEN E VON, WINTER S, WITTAU M, ZENS J (2019) The concerns of the young protesters are justified. A statement by Scientists for Future concerning the protests for more climate protection. Gaia, 28(2):79–87
HALL A (2014) Projecting regional change. Science, 346(6216):1461–1462
HANNAH L, MIDGLEY GF, MILLAR D (2002) Climate change-integrated conservation strategies. Glob Ecol Biogeogr, 11(6):485–495
HELLER NE, ZAVALETA ES (2009) Biodiversity management in the face of climate change: A review of 22 years of recommendations. Biol Conserv, 142(1):14–32
HIJMANS RJ, CAMERON SE, PARRA JL, JONES PG, JARVIS A (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol, 25:1965–1978
HÖHNE N, DEN ELZEN M, ROGELJ J, METZ B, FRANSEN T, KURAMOCHI T, OLHOFF A, ALCAMO J, WINKLER H, FU S, SCHAEFFER M, SCHAEFFER R, PETERS GP, MAXWELL S, DUBASH NK (2020) Emissions: World has four times the work or one-third of the time. Nature, 579(7797):25–28

HUNTLEY B (1991) How Plants Respond to Climate Change - Migration Rates, Individualism and the Consequences for Plant Communities. Ann Bot, 67:15–22

INRA, UNIVERSITY OF GHENT, SSLRC, LRP (1994) A geographical knowledge database on soil properties for environmental studies based on 1:1,000,000 scale EC soil map data. Available from https://esdac.jrc.ec.europa.eu/ESDB_Archive/eusoils_docs/other/PTRDBprojRepFinal3.pdf (accessed October 2021)

IPBES (2019) Global Assessment on Biodiversity and Ecosystem Services: Chapter 2.2 Status and Trends – Nature. Unedited draft chapters 31 May 2019, Bonn. Available from https://www.ipbes.net/system/tdf/ipbes_global_assessment_chapter_2_2_nature_unedited_31may.pdf?file=1&type=node&id=35276 (accessed November 2019)

IPCC (2007) Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge

IPCC (2008) Klimaänderung 2007: Synthesebericht: Zusammenfassung für politische Entscheidungsträger. Available from https://www.ipcc.ch/site/assets/uploads/2018/05/IPCC2007-SYR-SPM-german.pdf (accessed September 2019)

IPCC (2013) Summary for Policymakers: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge, United Kingdom and New York, NY, USA

IPCC (2018) Summary for Policymakers: An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty, Genf. Available from https://www.ipcc.ch/sr15/ (accessed October 2019)

IPCC (2021) Summary for Policymakers. Cambridge University Press. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Available from https://www.ipcc.ch/report/ar6/wg1/ (accessed September 2021)

JAESCHKE A, BITTNER T, JENTSCH A, BEIERKUHNLEIN C (2014) The last decade in ecological climate change impact research: where are we now? Naturwissenschaften, 101(1):1–9

JARVIS A, REUTER HI, NELSON A, GUEVARA E (2008) Hole-filled SRTM for the globe: Version 4. [data]. Available from http://srtm.csi.cgiar.org (accessed September 2012)

JENTSCH A, BEIERKUHNLEIN C (2008) Research frontiers in climate change: Effects of extreme meteorological events on ecosystems. C. R. Geoscience, 340(9-10):621–628

KATI V, HOVARDAS T, DIETERICH M, IBISCH PL, MIHOK B, SELVA N (2015) The challenge of implementing the European network of protected areas Natura 2000. Conserv Biol, 29(1):260–270

KISSLING WD, DORMANN CF, GROENEVELD J, HICKLER T, KÜHN I, MCINERNY GJ, MONTOYA JM, ROEMERMANN C, SCHIFFERS K, SCHURR FM, SINGER A, SVENNING J-C, ZIMMERMANN NE, O'HARA RB (2012) Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. J Biogeogr, 39(12):2163–2178

KNUTTI R, SEDLACEK J (2013) Robustness and uncertainties in the new CMIP5 climate model projections. Nat Clim Chang, 3(4):369–373

KOPF S, HA-DUONG M, HALLEGATTE S (2008) Using maps of city analogues to display and interpret climate change scenarios and their uncertainty. Nat Hazards Earth Syst Sci, 8(4):905–918

KREYLING J, WENIGMANN, M. BEIERKUHNLEIN C., JENTSCH A (2008) Effects of Extreme Weather Events on Plant Productivity and Tissue Die-Back are Modified by Community Composition. Ecosystems, 11(5):752–763

LEGENDRE P, GALLAGHER ED (2001) Ecologically meaningful transformations for ordination of species data. Oecologia, 129(2):271–280

LEGENDRE P, LEGENDRE L (2012) Numerical ecology. Developments in environmental modelling, vols 24. Elsevier, Amsterdam

LUDT WB, MORGAN L, BISHOP J, CHAKRABARTY P (2018) A quantitative and statistical biological comparison of three semi-enclosed seas: The Red Sea, the Persian (Arabian) Gulf, and the Gulf of California. Mar Biodivers, 48(4):2119–2124

LUOMUS (2014) The database of Atlas Florae Europaeae. Available from http://www.luomus.fi/en/database-atlas-florae-europaeae (accessed October 2021)

MCGLINN DJ, XIAO X, MAY F, GOTELLI NJ, ENGEL T, BLOWES SA, KNIGHT TM, PURSCHKE O, CHASE JM, MCGILL BJ (2019) Measurement of Biodiversity (MoB): A method to separate the scale-dependent effects of species abundance distribution, density, and aggregation on diversity change. Methods Ecol Evol, 10(2):258–269

MEISEL S (1953-1965) 54 Westfälische Tieflandsbucht. 6. Lieferung, 1959. In: Meynen E., Schmithüsen J., Gellert J. F., Neef E., Müller-Miny H., Schultze J. H. (eds) Handbuch der naturräumlichen Gliederung Deutschlands. Veröffentlichungen des Instituts für Landeskunde und des deutschen Instituts für Länderkunde. Selbstverl. der Bundesanst. für Landeskunde und Raumforschung, Remagen, Bad Godesberg, pp 800–821

MEROW C, SMITH MJ, EDWARDS TC, JR., GUISAN A, MCMAHON SM, NORMAND S, THUILLER W, WUEEST RO, ZIMMERMANN NE, ELITH J (2014) What do we gain from simplicity versus complexity in species distribution models? Ecography, 37(12):1267–1281

METZGER MJ, BUNCE RGH, JONGMAN RHG, MÜCHER CA, WATKINS JW (2005) A climatic stratification of the environment of Europe. Glob Ecol Biogeogr, 14(6):549–563

MOD HK, LE ROUX PC, GUISAN A, LUOTO M (2015) Biotic interactions boost spatial models of species richness. Ecography, 38:1–9

MÜCHER CA, HENNEKENS SM, BUNCE RGH, SCHAMINÉE JHJ, SCHAEPMAN ME (2009) Modelling the spatial distribution of Natura 2000 habitats across Europe. Landsc Urban Plan, 92(2):148–159

MÜLLER T (1953-1965) 64 Lüneburger Heide. 7. Lieferung, 1965. In: Meynen E., Schmithüsen J., Gellert J. F., Neef E., Müller-Miny H., Schultze J. H. (eds) Handbuch der naturräumlichen Gliederung Deutschlands. Veröffentlichungen des Instituts für Landeskunde und des deutschen Instituts für Länderkunde. Selbstverl. der Bundesanst. für Landeskunde und Raumforschung, Remagen, Bad Godesberg, 959-670

MÜLLER-WESTERMEIER G, KREIS A, DITTMANN E (1999) Klimaatlas Bundesrepublik Deutschland: Teil 1. Lufttemperatur, Niederschlagshöhe, Sonnenscheindauer, Offenbach am Main. Selbstverlag des Deutschen Wetterdienstes. Available from https://www.dwd.de/DE/leistungen/pbfb_verlag_klimaatlas_brd/klimaatlas.html (accessed October 2019)

MÜLLER-WESTERMEIER G, KREIS A, DITTMANN E (2001) Klimaatlas Bundesrepublik Deutschland: Teil 2. Verdunstung, mittlere tägliche Extremwerte, Kontinentalität, Offenbach am Main. Deutscher Wetterdienst. Available from https://www.dwd.de/DE/leistungen/pbfb_verlag_klimaatlas_brd/klimaatlas.html (accessed October 2019)

NIETO-LUGILDE D, MAGUIRE KC, BLOIS JL, WILLIAMS JW, FITZPATRICK MC (2018) Multiresponse algorithms for community-level modelling: Review of theory, applications, and comparison to species distribution models. Methods Ecol Evol, 9(4):834–848

NORBERG A, ABREGO N, BLANCHET FG, ADLER FR, ANDERSON BJ, ANTTILA J, ARAUJO MB, DALLAS T, DUNSON D, ELITH J, FOSTER SD, FOX R, FRANKLIN J, GODSOE W, GUISAN A, O'HARA B, HILL NA, HOLT RD, HUI FKC, HUSBY M, KALAS JA, LEHIKOINEN A, LUOTO M, MOD HK, NEWELL G, RENNER I, ROSLIN T, SOININEN J, THUILLER W, VANHATALO J, WARTON D, WHITE M, ZIMMERMANN NE, GRAVEL D, OVASKAINEN O (2019) A comprehensive evaluation of predictive performance of 33 species distribution models at species and community levels. Ecol Monogr, 89(3):e01370

OHLEMÜLLER R, GRITTI E. S., SYKES MT, THOMAS CD (2006) Towards European climate risk surfaces: the extent and distribution of analogous and non-analogous climates 1931–2100. Glob Ecol Biogeogr, 15:395–405

OKSANEN J, BLANCHET FG, FRIENDLY M, KINDT R, LEGENDRE P, MCGLINN D, MINCHIN PR, O'HARA RB, SIMPSON GL, SOLYMOS P, STEVENS MHH, SZOECS E, WAGNER H (2015) Vegan: Community ecology package: R package version 2.2-1. Available from https://cran.r-project.org/package=vegan (accessed May 2015)

OLOFSSON J, HICKLER T, SYKES MT, ARAÚJO MB, BALETTO E, BERRY PM, BONELLI S, CABEZA M, DUBUIS A, GUISAN A, KÜHN I, KUJALA H, PIPER J, ROUNSEVELL MDA, SETTELE J, THUILLER W (2008) Climate change impacts on European biodiversity – observations and future projections: Climate change impacts on European biodiversity – MACIS Deliverable D 1.1. Available from https://circabc.europa.eu/sd/a/5d8d8d75-b406-43c6-bedb-b8a3a3272642/Policy%20analysis%20for%20biodiversity%20under%20climate%20change%20MACIS%20deliverable.pdf (accessed December 2019)

ORLIKOWSKA EH, ROBERGE J-M, BLICHARSKA M, MIKUSINSKI G (2016) Gaps in ecological research on the world's largest internationally coordinated network of protected areas: A review of Natura 2000. Biol Conserv, 200:216–227

OVASKAINEN O (2019) Species distribution models. In: Gelfand A. E., Fuentes M., Hoeting J. A., Smith R. L. (eds) Handbook of environmental and ecological statistics. Chapman & Hall/CRC handbooks of modern statistical methods. CRC Press, Boca Raton, FL, pp 277–299

PARMESAN C (2006) Ecological and Evolutionary Responses to Recent Climate Change. Annu Rev Ecol Evol Syst, 37(1):637–669

PEARSON RG, DAWSON TP (2003) Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? Glob Ecol Biogeogr, 12(5):361–371

PFAFFEN K (1953a-1965) 55 Niederrheinische Bucht. 6. Lieferung, 1959. In: Meynen E., Schmithüsen J., Gellert J. F., Neef E., Müller-Miny H., Schultze J. H. (eds) Handbuch der naturräumlichen Gliederung Deutschlands. Veröffentlichungen des Instituts für Landeskunde und des deutschen Instituts für Länderkunde. Selbstverl. der Bundesanst. für Landeskunde und Raumforschung, Remagen, Bad Godesberg, pp 822–844

PFAFFEN K (1953b-1965) 57 Niederrheinisches Tiefland. 6. Lieferung, 1959. In: Meynen E., Schmithüsen J., Gellert J. F., Neef E., Müller-Miny H., Schultze J. H. (eds) Handbuch der naturräumlichen Gliederung Deutschlands. Veröffentlichungen des Instituts für Landeskunde und des deutschen Instituts für Länderkunde. Selbstverl. der Bundesanst. für Landeskunde und Raumforschung, Remagen, Bad Godesberg, pp 852–881

PICKETT STA (1989) Space-for-time substitution as an alternative to long-term studies. Springer, New York

PIEDALLU C, GEGOUT J-C, PEREZ V, LEBOURGEOIS F (2013) Soil water balance performs better than climatic water variables in tree species distribution modelling. Glob Ecol Biogeogr, 22(4):470–482

PIERCE DW, BARNETT TP, SANTER BD, GLECKLER PJ (2009) Selecting global climate models for regional climate change studies. Proc Natl Acad Sci U S A, 106(21):8441–8446

POMPE S, HANSPACH J, BADECK FW, KLOTZ S, THUILLER W, KÜHN I (2008) Climate and land use change impacts on plant distributions in Germany. Biol Lett, 4:564–567

POTT R (1995) Die Pflanzengesellschaften Deutschlands. Ulmer, Stuttgart

PRISCO I, CARBONI M, ACOSTA, ALICIA T. R. (2013) The Fate of Threatened Coastal Dune Habitats in Italy under Climate Change Scenarios. PLoS One, 8(7):e68850

RAMIREZ J, JARVIS A (2008) High resolution statistically downscaled future climate surfaces: SRES A1B and A2a, based on IPCC AR4, bioclimatic parameters, 30yr averages 2060-2089, MPI-ECHAM5, 30 seconds. [data], Cali, Colombia. Available from http://gisweb.ciat.cgiar.org/GCMPage/download_sres.html (accessed April 2011)

RAMIREZ J, JARVIS A (2010) Downscaling Global Circulation Model Outputs: The Delta Method, Decision and Policy Analysis Working Paper No. 1, Cali, Colombia, No 1:1–18. Available from https://hdl.handle.net/10568/90731 (accessed November 2019)

RAMIREZ J, JARVIS A (2012) High resolution statistically downscaled future climate surfaces: SRES A1B and A2a, based on IPCC AR4, bioclimatic parameters, 30yr averages 2040-2069 and 2070-2099, MPI-ECHAM5, 30 arc-seconds, Delta Method IPCC AR4. [data], Cali, Colombia. Available from http://www.ccafs-climate.org/data/ (accessed August 2012)

RAMIREZ-VILLEGAS J, LAU C, KÖHLER A-K, SIGNER J, JARVIS A, ARNELL N, OSBORNE T, HOOKER J (2011) Climate Analogues: Finding tomorrow´s agriculture today: Working Paper No. 12, Cali, Colombia. Available from https://hdl.handle.net/10568/16420 (accessed November 2019)

REAL R, LUZ MÀRQUEZ A, OLIVERO J, ESTRADA A (2010) Species distribution models in climate change scenarios are still not useful for informing policy planning: an uncertainty assessment using fuzzy logic. Ecography, 33:304–314

RIPPLE WJ, WOLF C, NEWSOME TM, BARNARD P, MOOMAW WR (2020) World Scientists' Warning of a Climate Emergency. Bioscience, 70(1):8–12

RODRIGUEZ-ROJO MP, FERNANDEZ-GONZALEZ F, TICHY L, CHYTRY M (2014) Vegetation diversity of mesic grasslands (*Arrhenatheretalia*) in the Iberian Peninsula. Appl Veg Sci, 17(4):780–796

ROUNSEVELL MDA, REGINSTER I, ARAÚJO MB, CARTER TR, DENDONCKER N, EWERT F, HOUSE JI, KANKAANPÄÄ S, LEEMANS R, METZGER MJ, SCHMIT C, SMITH P, TUCK G (2006) A coherent set of future land use change scenarios for Europe. Agriculture Ecosystems & Environment, 114(1):57–68

RUSHING CS, ROYLE JA, ZIOLKOWSKI DJ, PARDIECK KL (2019) Modeling spatially and temporally complex range dynamics when detection is imperfect. Sci Rep, 9

SCHMITHÜSEN J (1953-1965) Einleitung: Grundsätzliches und Methodisches. In: Meynen E., Schmithüsen J., Gellert J. F., Neef E., Müller-Miny H., Schultze J. H. (eds) Handbuch der naturräumlichen Gliederung Deutschlands. Veröffentlichungen des Instituts für Landeskunde und des deutschen Instituts für Länderkunde. Selbstverl. der Bundesanst. für Landeskunde und Raumforschung, Remagen, Bad Godesberg, pp 1–44

SHEPHERD TG (2014) Atmospheric circulation as a source of uncertainty in climate change projections. Nat Geosci, 7(10):703–708

SKOV F, NYGAARD B, WIND P, BORCHSENIUS F, NORMAND S, BALSLEV H, FLØJGAARD C, SVENNING J-C (2009) Impacts of 21st century climate changes on flora and vegetation in Denmark. IOP Conf Ser: Earth Environ Sci, 8(1):1–13

SNELL RS, HUTH A, NABEL, J. E. M. S., BOCEDI G, TRAVIS JMJ, GRAVEL D, BUGMANN H, GUTIERREZ AG, HICKLER T, HIGGINS SI, REINEKING B, SCHERSTJANOI M, ZURBRIGGEN N, LISCHKE H (2014) Using dynamic vegetation models to simulate plant range shifts. Ecography, 37(12):1184–1197

SSYMANK A, HAUKE U, RÜCKRIEM C, SCHRÖDER E (1998) Das europäische Schutzgebietssystem NATURA 2000: BfN-Handbuch zur Umsetzung der Fauna-Flora-Habitat-Richtlinie (92/43/EWG) und der Vogelschutzrichtlinie (79/409/EWG). Schriftenreihe für Landschaftspflege und Naturschutz, vols 53. Bundesamt für Naturschutz, Bonn-Bad Godesberg

SYBERTZ J, REICH M (2015) Assessing Climate Change Induced Turnover in Bird Communities Using Climatically Analogous Regions. diversity, 7:36–59

THUILLER W, ALBERT C, ARAÚJO MB, BERRY PM, CABEZA M, GUISAN A, HICKLER T, MIDGLEY GF, PATERSON JS, SCHURR FM, SYKES MT, ZIMMERMANN NE (2008) Predicting global change impacts on plant species' distributions: Future challenges. Perspect Plant Ecol Evol Syst, 9(3-4):137–152

THUILLER W, LAVOREL S, ARAÚJO MB, SYKES MT, PRENTICE IC (2005) Climate change threats to plant diversity in Europe. Proc Natl Acad Sci U S A, 102(23):8245–8250

TITEUX N, HENLE K, MIHOUB J-B, REGOS A, GEIJZENDORFFER IR, CRAMER W, VERBURG PH, BROTONS L (2016) Biodiversity scenarios neglect future land-use changes. Glob Chang Biol, 22(7):2505–2515

TOBLER MW, KERY M, HUI FKC, GUILLERA-ARROITA G, KNAUS P, SATTLER T (2019) Joint species distribution models with species correlations and imperfect detection. Ecology, 100(8):e02754

TRIVEDI MR, MORECROFT MD, BERRY PM, DAWSON TP (2008) Potential effects of climate change on plant communities in three montane nature reserves in Scotland, UK. Biol Conserv, 141(6):1665–1675

UNITED NATIONS (1992) Convention on Biological Diversity. Available from https://www.cbd.int/doc/legal/cbd-en.pdf (accessed October 2021)

VAN TEEFFELEN A, MELLER L, VAN MINNEN J, VERMAAT J, CABEZA M (2015) How climate proof is the European Union's biodiversity policy? Reg Environ Change, 15(6):997–1010

VELOZ S, WILLIAMS JW, LORENZ D, NOTARO M, VAVRUS S, VIMONT DJ (2012) Identifying climatic analogs for Wisconsin under 21st-century climate-change scenarios. Clim Change, 112(3-4):1037–1058

VOGEL MM, ZSCHEISCHLER J, WARTENBURGER R, DEE D, SENEVIRATNE SI (2019) Concurrent 2018 Hot Extremes Across Northern Hemisphere Due to Human-Induced Climate Change. Earth's future, 7(7):692–703

VOS C, BOUWMA I, VERDONSCHOT P, GEERTSEMA W, VAN RIEL M (2013) Supplement: Managing climate change for the Natura 2000 network: Assessment of the vulnerability of Natura 2000 species and habitats for climate change: species and habitat types most at risk. Overall approach and the result of the analyses. Available from https://ec.europa.eu/environment/nature/climatechange/pdf/guidelines%20Supplement.pdf (accessed October 2021)

VU VQ (2015) ggbiplot: A ggplot2 based biplot: GitHub Repository. Available from http://github.com/vqv/ggbiplot (accessed April 2015)

WADA Y, WISSER D, EISNER S, FLOERKE M, GERTEN D, HADDELAND I, HANASAKI N, MASAKI Y, PORTMANN FT, STACKE T, TESSLER Z, SCHEWE J (2013) Multimodel projections and uncertainties of irrigation water demand under climate change. Geophys Res Lett, 40(17):4626–4632

WAGNER-LUECKER I, FOERSTER M, JANAUER G (2014) Assessment of Climate-Induced Impacts on Habitats. In: Rannow S. and Neubert M. (eds) Managing Protected Areas in Central and Eastern Europe Under Climate Change. Managing Protected Areas in Central and Eastern Europe Under Climate Change, vols 58. Springer, Dordrecht, pp 115–134

WALTHER G-R (2010) Community and ecosystem responses to recent climate change. Philos Trans R Soc B, 365(1549):2019–2024

WIENS JJ (2016) Climate-Related Local Extinctions Are Already Widespread among Plant and Animal Species. PLoS Biology, 14(12):e2001104

WILLIAMS JW, JACKSON ST, KUTZBACHT JE (2007) Projected distributions of novel and disappearing climates by 2100 AD. Proc Natl Acad Sci U S A, 104(14):5738–5742

WISZ MS, POTTIER J, KISSLING WD, PELLISSIER L, LENOIR J, DAMGAARD CF, DORMANN CF, FORCHHAMMER MC, GRYTNES J-A, GUISAN A, HEIKKINEN RK, HOYE TT, KÜHN I, LUOTO M, MAIORANO L, NILSSON M-C, NORMAND S, OCKINGER E, SCHMIDT NM, TERMANSEN M, TIMMERMANN A, WARDLE DA, AASTRUP P, SVENNING J-C (2013) The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. Biol Rev, 88(1):15–30

WORLD METEOROLOGICAL ORGANIZATION (2019) The Global Climate in 2015-2019, Genf. Available from https://library.wmo.int/doc_num.php?explnum_id=9936 (accessed October 2021)

WORLD METEOROLOGICAL ORGANIZATION (WMO) (2021) United in Science 2021: A multi-organization high-level compilation of the latest climate science information. Available from https://library.wmo.int/index.php?lvl=notice_display&id=21946#.YUIhGGb7TX0 (accessed September 2021)

YATES KL, BOUCHET PJ, CALEY MJ, MENGERSEN K, RANDIN CF, PARNELL S, FIELDING AH, BAMFORD AJ, BAN S, MARCIA BARBOSA A, DORMANN CF, ELITH J, EMBLING CB, ERVIN GN, FISHER R, GOULD S, GRAF RF, GREGR EJ, HALPIN PN, HEIKKINEN RK, HEINANEN S, JONES AR, KRISHNAKUMAR PK, LAURIA V, LOZANO-MONTES H, MANNOCCI L, MELLIN C, MESGARAN MB, MORENO-AMAT E, MORMEDE S, NOVACZEK E, OPPEL S, CRESPO GO, PETERSON AT, RAPACCIUOLO G, ROBERTS JJ, ROSS RE, SCALES KL, SCHOEMAN D, SNELGROVE P, SUNDBLAD G, THUILLER W, TORRES LG, VERBRUGGEN H, WANG L, WENGER S, WHITTINGHAM MJ, ZHARIKOV Y, ZURELL D, SEQUEIRA AMM (2018) Outstanding Challenges in the Transferability of Ecological Models. Trends Ecol Evol, 33(10):790–802

ZHANG C, CHEN Y, XU B, XUE Y, REN Y (2018) Comparing the prediction of joint species distribution models with respect to characteristics of sampling data. Ecography, 41(11):1876–1887

Supporting Information

S1 Database. Climate points that define the three study regions.

The database contains a shapefile with the climate points from Worldclim climate data (HIJMANS ET AL. 2005) (30 arc seconds resolution) that intersect with the ecoregions, which were chosen as study regions. Ecoregions were taken from the ArcGIS shapefile of landscape units of the Federal Agency for Nature Conservation (FEDERAL AGENCY FOR NATURE CONSERVATION 2009). The intersecting climate points were selected with the ArcGIS 10 tool “Select by location”. The column "NATBS09_ID" gives the study region. "21" stands for the Eastern Lowlands, "32" for the Central Lowlands, "38" for the Western Lowlands. [zip file at http://doi.org/10.15488/11880]

S2 Database. Habitat data.

The database contains the habitat data of the climatically analogous N2k-sites in the present and future climate analogues of the three study regions with occurrences of the 84 analyzed habitat types. It is a matrix with one row for each N2k-site and the habitat types occurring in it and lists the total area each habitat type covers in the N2k-site. The database is based on the habitat data of the European Environment Agency (EEA 2013) which has been adjusted as described in S1 Text. Explanation of columns: SITECODE: N2k-site; 1430 … 9580 (habitat codes): total area the habitat type covers in the N2k-site (in ha); SR: the study region to which the climate analogue belongs to (21 = Eastern Lowlands, 32 = Central Lowlands, 38 = Western Lowlands); CA: the climate analogue the N2k-site is climatically analogous to; NATBS09_ID: the N2k-sites within the study region (21 = Eastern Lowlands, 32 = Central Lowlands, 38 = Western Lowlands). [zip file at http://doi.org/10.15488/11880]

S1 Text. Adjusting the habitat data.

The European-wide habitat data of the European Environment Agency (EEA 2013) consisted of two datasets: **(A) a polygon shapefile**, giving the locations of the Natura 2000 sites (N2k-sites); **(B) a database**, of the habitat types that occur in the N2k-sites, and the area they cover in these N2k-sites. We adjusted both datasets as following:

(A) Adjustment of the polygon shapefile: In the shapefile, we deleted N2k-sites lacking habitat-data, identical N2k-sites and appended habitat information of overlapping N2k-sites to one N2k-site (see details below in paragraph Adjustment of spatial data). Sites were deleted or combined as empty or overlapping sites distort statistics. For instance, if locations are included in the dataset twice, a location is given more weight than it actually has. Additionally, areas that overlap but which are not identical N2k-sites increase the chance of intersection with a climate analogue. Our final European-wide spatial data consisted of 21,357 non-overlapping N2k-sites on land area.

(B) Adjustment of the database: In the habitat database we corrected obvious typing errors of habitat type codes (2133, 2137 -> 2130; 5211 -> 5210; 6212 -> 6210; 9361 -> 9360; 9565 -> 9560; 21a0 -> 21A0; 91e0 -> 91E0) and deleted habitats coded as “non-present” in a N2k-site. Furthermore, we removed habitat occurrences with no indicated area (for example, 6,5% in the climate analogues of the Eastern Lowlands) or with implausible area (area of a single habitat larger than of its N2k-site; habitat occurences with negative area; see rule below in paragraph Adjustment of habitat area), for more powerful analyses on habitat area than only on presence/ absence data. Our final habitat database included area data for 219 different habitat types.

We linked the habitat data (B) to the N2k-sites (A), but there was no information about where exactly in an N2k-site the habitat types occurred. Therefore, we could not make a distinct intersection between single habitats and the climate and environmental factors of their location.

Adjustment of spatial data: The shapefile, giving the locations of the N2k-sites, consisted of spatial features for the N2k-sites. N2k-sites were designated as Special Protection Areas (SPA), Sites of Community Interest (SCI), or as both site types. For some of the N2k-sites, which were designated as both, were two separate, overlapping features (one for each site type) in the shapefile. In some cases, these two features were spatially identical, in other cases the feature of one site type was larger and contained the feature of the other site type. If one of these features lacked habitat data, we deleted the empty feature. For the features with habitat types listed, we proceeded as following:

a) When the overlapping features contained identical habitat types and were spatially identical, we kept only one feature. When one feature was larger, we only kept the larger feature.

b) When one feature contained more habitat types than the other and both features were spatially identical, we kept the feature with more habitat types. If one larger feature was containing a smaller feature we kept the feature with more habitat types, even if smaller.

c) When one feature contained habitat types that were missing in the other feature and both features were spatially identical we appended all habitat types into one feature. When one feature spatially contained the other feature, we appended all habitat types to the larger feature and deleted the smaller.

The original database consisted of 26,450 features and we deleted 19% of these original features for our analyses.

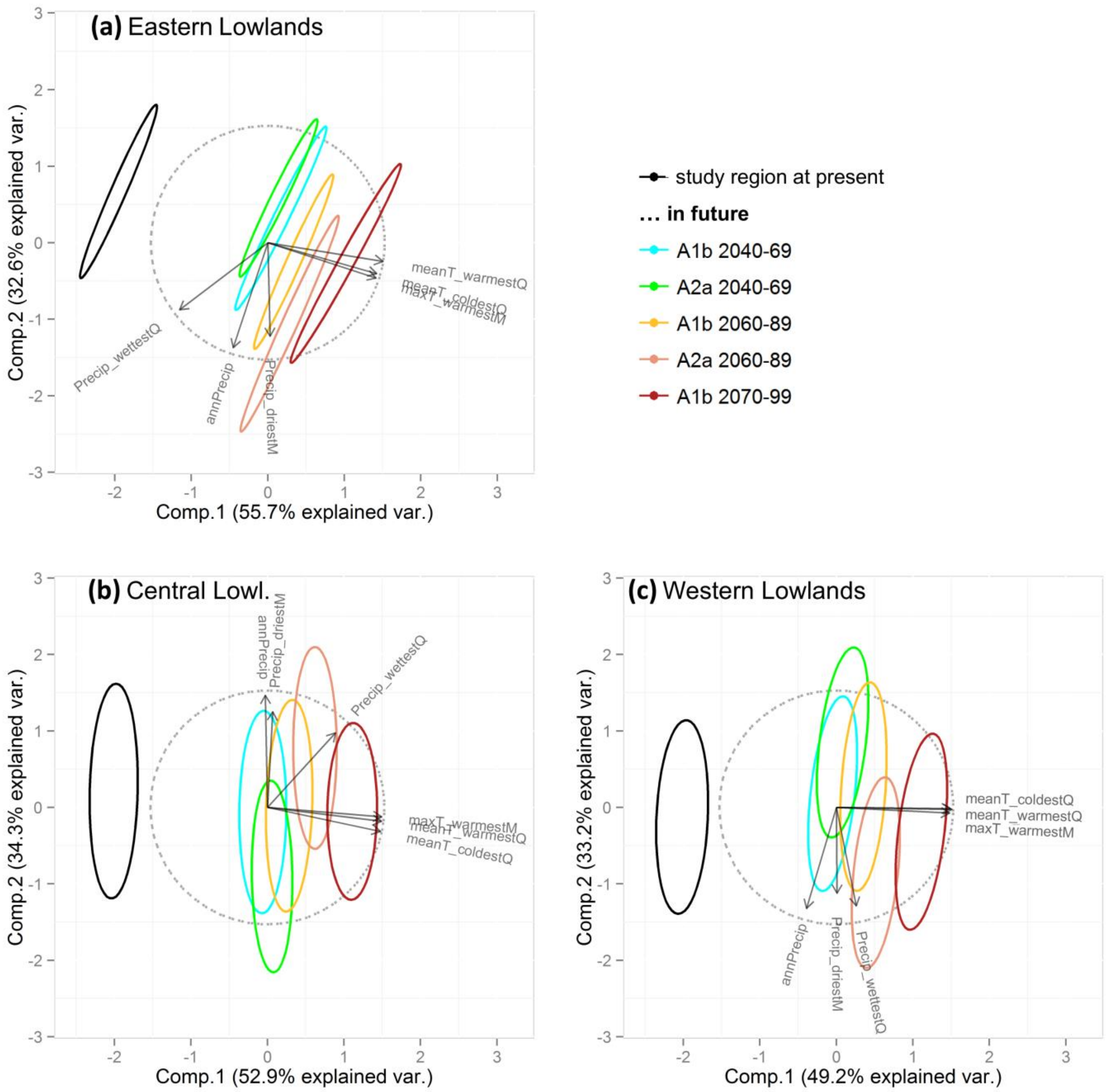
Adjustment of habitat area: We identified data errors in the habitat area by querying whether the area of a single habitat type exceeded the area of the N2k-site. Generally, we accepted an exceedance of less than 10%. However, forty-two habitat occurrences exceeded their N2k-site areas by more than 10%. For habitat occurrences in N2k-sites =< 1 ha, we accepted if the area of a single habitat was 247% larger than its N2k-site (18 habitat occurrences). For habitat occurrences in N2k-sites =< 546 ha, we accepted if the area of a single habitat was 28% larger than its N2k-site (15 habitat occurrences). Nine habitat occurrences exceeded their N2k-site areas by more than 52% (area of N2k-sites between 7 and 1670 ha). For four habitat occurrences, it was possible to correct the area by reviewing data sheets of regional administrations on the internet, the other five were deleted. One habitat occurrence was deleted because of negative area data.

S1 Table. Loadings from the PCA on the climate data in the EU. Loadings of the 19 bioclimatic variables on the first four principal components (PCs) from the PCA on the values of the standardized variables for all the 8,7 million climate points of the EU. The first two PCs explained 73% of the variance of the climate data, the first four PCs explained 90%. The first PC explains mainly a temperature gradient, the second PC a precipitation gradient, the third PC a gradient in precipitation seasonality, the fourth a gradient in temperature range.

	Comp.1	Comp.2	Comp.3	Comp.4
PrecipColdQuarter	0.24	0.25	-0.22	-0.03
PrecipWarmQuarter	-0.21	0.26	0.03	-0.24
PrecipDryQuarter	-0.04	0.35	0.26	-0.21
PrecipWetQuarter	0.14	0.28	-0.41	-0.15
PrecipSeasonality	0.14	-0.17	-0.55	0.11
PrecipDryMonth	-0.07	0.35	0.24	-0.19
PrecipWetMonth	0.15	0.26	-0.43	-0.17
AnnPrecipitation	0.1	0.37	-0.13	-0.19
MeanTempColdQuarter	0.35	-0.02	0.13	0.04
MeanTempWarmQuarter	0.26	-0.24	0	-0.16
MeanTempDryQuarter	0.34	-0.06	0.04	0
MeanTempWetQuarter	-0.1	-0.2	0	-0.17
TempAnnRange	-0.24	-0.22	-0.16	-0.35
MinTempColdMonth	0.35	0	0.14	0.09
MaxTempWarmMonth	0.23	-0.26	0.02	-0.29
TempSeasonality	-0.28	-0.18	-0.19	-0.2
Isothermality	0.29	0.07	0.22	-0.21
MeanTempRange	0.05	-0.2	0.08	-0.63
AnnMeanTemp	0.33	-0.11	0.09	-0.06

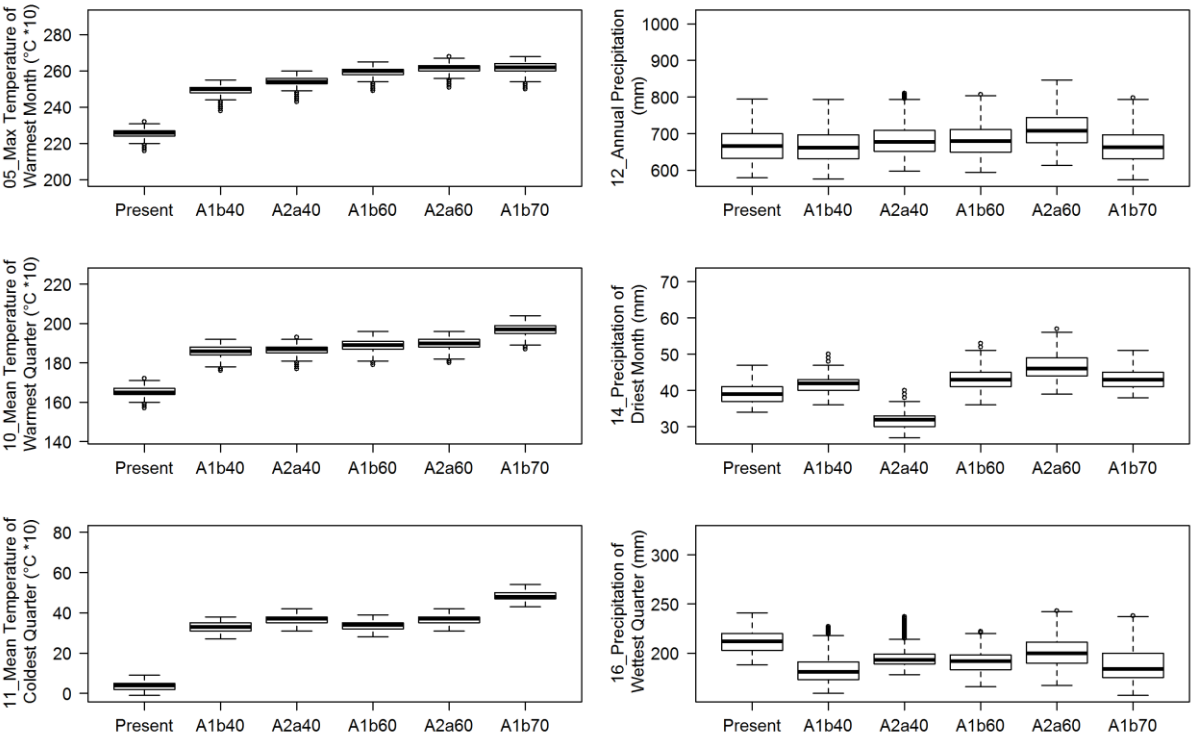
S2 Text. Method for characterizing climate change in the study regions.

As all of our analyses are subject to future climate conditions in the study regions, we analyzed the character and magnitude of the projected future climate change by carrying out PCAs (function 'prcomp') on the values of the six standardized climate variables of the 13,930 to 18,713 climate points in the study regions. In PCA ordination biplots ('ggbiplot') (VU 2015) we coded the climate points for time periods/scenarios and visually interpreted their patterns. To make patterns more evident we drew gravity ellipses, which envelope 2/3 of a time periods'/scenarios' climate points ('ggbiplot') (VU 2015). We analyzed the first principal components to the left of the bend in the PCA biplots as they explained the most variance in the data according to screeplots. These were in all three study regions the first two principal components.

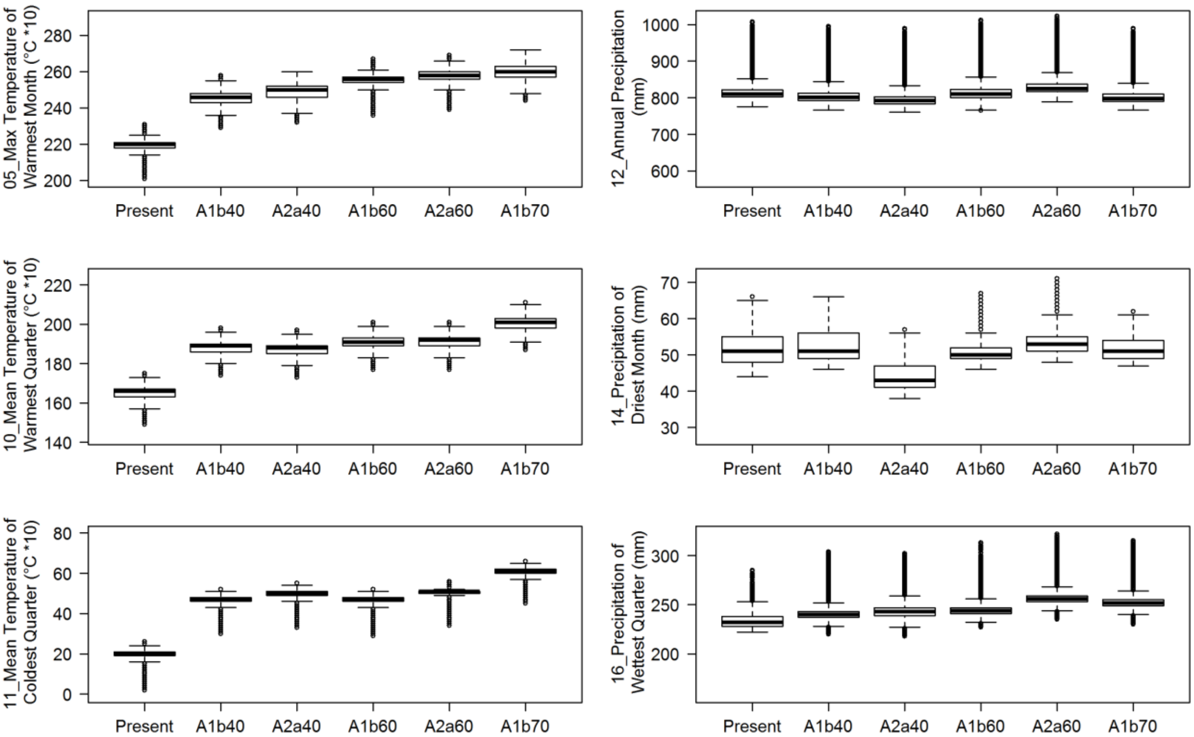


S1 Fig. PCA ordination biplots showing the climate conditions in the different time periods/ scenarios in the study regions. Climate conditions are characterized by six climate variables meaningful for the studied Natura 2000 habitat types. The biplots show principal components 1 and 2 and which variables load on these components, based on the climate points' values of all six climate variables within the three study regions (a-c). The number of climate points within the study regions are (a) n=13,930, (b) n=18,713, (c) n=15,379. Climate points have been removed to simplify the figures. Gravity ellipses envelope 2/3 of a time period's/scenario's climate points and are coded according to time periods/scenarios. The dashed circle envelopes 2/3 of the total climate points. Full names of climate variables are provided in Tab. 1.

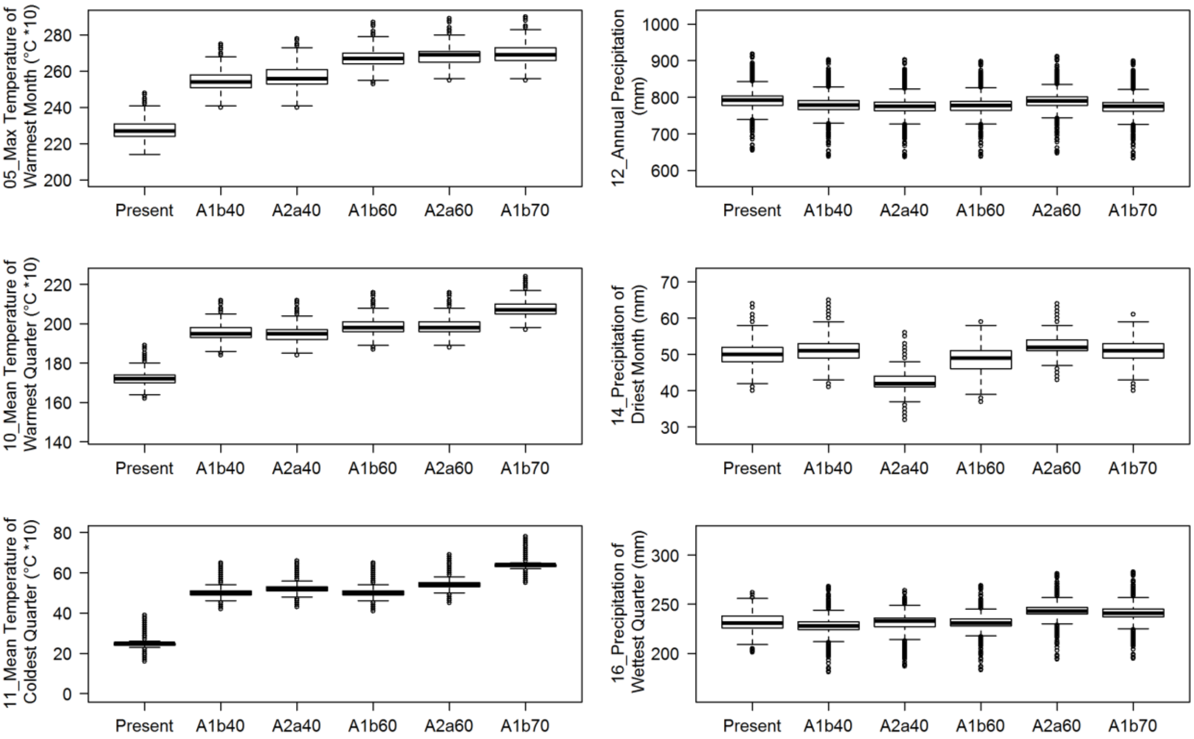
(a) Eastern Lowlands



(b) Central Lowlands



(c) Western Lowlands



S2 Fig. Boxplots showing the climate conditions in the different time periods/scenarios in the study regions. Boxplots are based on the climate change projections of the six chosen climate variables in the three study regions (a-c) from present time (1950-2000) to future 30-year averages (2040-2069, 2060-2089, 2070-2099). Analysis of n=13,930 climate points in the Eastern Lowlands, n=18,713 in the Central Lowlands and n=15,379 in the Western Lowlands. Data source for future scenario data: CIAT database (RAMIREZ and JARVIS 2008, 2012); for present: Worldclim database (HIJMANS et al. 2005). Variable numbers refer to variable numbers in Worldclim/CIAT database.

S2 Table. Climate conditions in the three study regions (a-c) in the different time periods/scenarios. Climate conditions and climate range of the six chosen climate variables within the study regions (a-c) at present and under future climate projections. Analysis of n=13,930 climate points in the Eastern Lowlands, n=18,713 in the Central Lowlands and n=15,379 in the Western Lowlands. Data source for future scenario data: CIAT database (RAMIREZ and JARVIS 2008, 2012); for present: Worldclim database (HIJMANS et al. 2005). Variable names and numbers refer to these in Worldclim/CIAT database.

(a) Eastern Lowlands

no.	climate variable			present 1950-2000	A1b 2040-2069	A2a 2040-2069	A1b 2060-2089	A2a 2060-2089	A1b 2070-2099
05	**Max Temperature of Warmest Month**	°C	min	21.6	23.8	24.3	24.9	25.1	25.0
			median	22.6	25.0	25.4	26.0	26.2	26.2
			mean	22.6	24.9	25.4	25.9	26.2	26.2
			max	23.2	25.5	26.0	26.5	26.8	26.8
			range	1.6	1.7	1.7	1.6	1.7	1.8
10	**Mean Temperature of Warmest Quarter**	°C	min	15.7	17.6	17.7	17.9	18.0	18.7
			median	16.5	18.6	18.7	18.9	19.0	19.7
			mean	16.5	18.6	18.7	18.9	19.0	19.7
			max	17.2	19.2	19.3	19.6	19.6	20.4
			range	1.5	1.6	1.6	1.7	1.6	1.7
11	**Mean Temperature of Coldest Quarter**	°C	min	-0.1	2.7	3.1	2.8	3.1	4.3
			median	0.4	3.3	3.7	3.4	3.7	4.8
			mean	0.4	3.3	3.7	3.4	3.7	4.9
			max	0.9	3.8	4.2	3.9	4.2	5.4
			range	1.0	1.1	1.1	1.1	1.1	1.1
12	**Annual Precipitation**	mm	min	580	576	598	594	613	574
			median	666	662	677	680	708	663
			mean	668	665	682	682	711	665
			max	795	794	810	807	846	798
			range	215	218	212	213	233	224
14	**Precipitation of Driest Month**	mm	min	34	36	27	36	39	38
			median	39	42	32	43	46	43
			mean	39	42	32	43	46	43
			max	47	50	40	53	57	51
			range	13	14	13	17	18	13
16	**Precipitation of Wettest Quarter**	mm	min	188	159	178	166	167	157
			median	212	181	193	192	200	184
			mean	212	183	196	191	201	187
			max	241	227	237	222	243	238
			range	53	68	59	56	76	81

(b) Central Lowlands

no.	climate variable			present 1950-2000	A1b 2040-2069	A2a 2040-2069	A1b 2060-2089	A2a 2060-2089	A1b 2070-2099
05	**Max Temperature of Warmest Month**	°C	min	20.1	22.9	23.2	23.6	23.9	24.4
			median	22.0	24.6	25.0	25.6	25.8	26.0
			mean	22.0	24.6	24.9	25.6	25.8	26.0
			max	23.1	25.8	26.0	26.7	26.9	27.2
			range	3.0	2.9	2.8	3.1	3.0	2.8
10	**Mean Temperature of Warmest Quarter**	°C	min	14.9	17.4	17.3	17.7	17.7	18.7
			median	16.6	18.9	18.8	19.1	19.2	20.1
			mean	16.5	18.8	18.7	19.1	19.1	20.1
			max	17.5	19.8	19.7	20.1	20.1	21.1
			range	2.6	2.4	2.4	2.4	2.4	2.4
11	**Mean Temperature of Coldest Quarter**	°C	min	0.2	3.0	3.3	2.9	3.4	4.5
			median	2.0	4.7	5.0	4.7	5.1	6.1
			mean	2.0	4.7	5.0	4.6	5.0	6.1
			max	2.6	5.2	5.5	5.2	5.6	6.6
			range	2.4	2.2	2.2	2.3	2.2	2.1
12	**Annual Precipitation**	mm	min	775	767	761	765	789	767
			median	811	801	792	810	825	798
			mean	816	807	797	814	831	804
			max	1007	995	989	1012	1023	990
			range	232	228	228	247	234	223
14	**Precipitation of Driest Month**	mm	min	44	46	38	46	48	47
			median	51	51	43	50	53	51
			mean	51	52	44	51	54	52
			max	66	66	57	67	71	62
			range	22	20	19	21	23	15
16	**Precipitation of Wettest Quarter**	mm	min	222	220	218	227	235	230
			median	232	240	243	244	256	252
			mean	234	241	243	246	257	252
			max	285	304	302	313	322	315
			range	63	84	84	86	87	85

(c) Western Lowlands

no.	climate variable			present 1950-2000	A1b 2040-2069	A2a 2040-2069	A1b 2060-2089	A2a 2060-2089	A1b 2070-2099
05	**Max Temperature of Warmest Month**	°C	min	21.4	24.0	24.0	25.3	25.5	25.5
			median	22.7	25.4	25.6	26.7	26.9	26.9
			mean	22.8	25.4	25.7	26.7	26.9	26.9
			max	24.8	27.5	27.8	28.7	28.9	29.0
			range	3.4	3.5	3.8	3.4	3.4	3.5
10	**Mean Temperature of Warmest Quarter**	°C	min	16.2	18.4	18.4	18.7	18.8	19.7
			median	17.2	19.5	19.5	19.8	19.8	20.7
			mean	17.2	19.5	19.5	19.8	19.8	20.7
			max	18.9	21.2	21.2	21.6	21.6	22.4
			range	2.7	2.8	2.8	2.9	2.8	2.7
11	**Mean Temperature of Coldest Quarter**	°C	min	1.6	4.2	4.3	4.1	4.5	5.5
			median	2.5	5.0	5.2	5.0	5.4	6.4
			mean	2.5	5.0	5.2	5.0	5.4	6.3
			max	3.9	6.5	6.6	6.5	6.9	7.8
			range	2.3	2.3	2.3	2.4	2.4	2.3
12	**Annual Precipitation**	mm	min	655	638	637	638	647	634
			median	792	779	776	778	790	775
			mean	791	779	775	777	790	775
			max	919	903	903	898	912	899
			range	264	265	266	260	265	265
14	**Precipitation of Driest Month**	mm	min	40	41	32	37	43	40
			median	50	51	42	49	52	51
			mean	50	51	43	48	53	51
			max	64	65	56	59	64	61
			range	24	24	24	22	21	21
16	**Precipitation of Wettest Quarter**	mm	min	201	181	187	183	194	195
			median	231	228	233	231	243	241
			mean	232	228	231	231	243	240
			max	262	268	264	269	281	283
			range	61	87	77	86	87	88

S3 Text. Characteristics of climate change in the study regions.

The six chosen climate variables distinguished the present and future climate conditions of the different time periods/scenarios in the study regions. The ellipses representing the climate data of a time period/climate scenario were considerably separated in the PCA ordination biplots (S1 Fig). The first two axes (Comp.1+2) explained more than 80% of the variance. The first axis contributed the greatest proportion with between 49 and 56%, and represented the temperature variables, showing for all three study regions a clear warming trend until the end of the 21st century (cf. S2 Fig and S4 Table). The second axis was formed by the precipitation variables, but partly without change from present conditions and generally without displaying a trend until the end of the 21st century (S2 Fig and S4 Table).

S4 Text. Assumption of drier conditions in the future study regions.

Although our climate variables did not indicate a clear precipitation change, we also anticipate drier conditions within the growing season by the end of the 21st century for three reasons. The first reason is that higher future precipitations can be outweighed (ACKERLY et al. 2015) by the increasing future temperatures. This would cause higher evapotranspiration which decreases the water balance (MCCABE and WOLOCK 2015). The second reason is that future precipitation is likely to fall more often in heavy precipitation events (COLLINS et al. 2013), which increases runoff and lowers water storage in the soils (MCCABE and WOLOCK 2015). The third reason is that single and series of dry years can be hidden within 30year averages of generally higher precipitation than today (JACOB et al. 2008).

S3 Table. N2k-sites in the three study regions and their climate analogues. Number of climatically analogous N2k-sites with occurrences of the 84 analyzed habitat types. N2k-sites can be part of more than one climate analogue.

	Within the study region	Present	A1b 2040-2069	A2a 2040-2069	A1b 2060-2089	A2a 2060-2089	A1b 2070-2099	total
Eastern Lowlands	51	498	70	14	27	28	16	618
Central Lowlands	103	816	65	81	88	69	64	982
Western Lowlands	93	560	80	142	105	82	27	782

S4 Table. Natura 2000 habitat types. List of the 131 Natura 2000 habitat types occurring in the three study regions and their climate analogues, and documentation about which of them were chosen for further analyses as they do not require special environmental conditions (geologically, pedogenically, etc.). An asterisk (*) indicates priority habitat types according to the Habitats Directive 92/43/EWG. EL= Eastern Lowlands, CL=Central Lowlands, WL=Western Lowlands. Further explanations at the end of the table.

Code		Habitat type	chosen for analysis
1110		Sandbanks which are slightly covered by sea water all the time	1
1130		Estuaries	1
1140		Mudflats and sandflats not covered by seawater at low tide	1
1150	*	Coastal lagoons	1
1160		Large shallow inlets and bays	1
1170		Reefs	1
1210		Annual vegetation of drift lines	1
1220		Perennial vegetation of stony banks	1
1230		Vegetated sea cliffs of the Atlantic and Baltic Coasts	1
1240		Vegetated sea cliffs of the Mediterranean coasts with endemic *Limonium spp.*	1
1310		Salicornia and other annuals colonizing mud and sand	1,3
1320		Spartina swards (*Spartinion maritimae*)	1
1330		Atlantic salt meadows (*Glauco-Puccinellietalia maritimae*)	1
1340	*	Inland salt meadows	3
1410		Mediterranean salt meadows (*Juncetalia maritimi*)	1,3
1420		Mediterranean and thermo-Atlantic halophilous scrubs (*Sarcocornetea fruticosi*)	1
1430		Halo-nitrophilous scrubs (*Pegano-Salsoletea*)	yes
1510	*	Mediterranean salt steppes (*Limonietalia*)	yes
1520	*	Iberian gypsum vegetation (*Gypsophiletalia*)	yes
2110		Embryonic shifting dunes	1
2120		Shifting dunes along the shoreline with *Ammophila arenaria* ("white dunes")	1
2130	*	Fixed coastal dunes with herbaceous vegetation ("grey dunes")	1
2140	*	Decalcified fixed dunes with *Empetrum nigrum*	1
2160		Dunes with *Hippophae rhamnoides*	1
2170		Dunes with *Salix repens ssp. argentea* (*Salicion arenariae*)	1
2180		Wooded dunes of the Atlantic, Continental and Boreal region	1
2190		Humid dune slacks	1
2230		Malcolmietalia dune grasslands	1
2240		Brachypodietalia dune grasslands with annuals	1
2270	*	Wooded dunes with *Pinus pinea* and/or *Pinus pinaster*	1
2310		Dry sand heaths with *Calluna* and *Genista*	yes
2320		Dry sand heaths with *Calluna* and *Empetrum nigrum*	yes
2330		Inland dunes with open *Corynephorus* and *Agrostis grasslands*	yes
3110		Oligotrophic waters containing very few minerals of sandy plains (*Littorelletalia uniflorae*)	yes
3120		Oligotrophic waters containing very few minerals generally on sandy soils of the West Mediterranean, with	yes
3130		Oligotrophic to mesotrophic standing waters with vegetation of the *Littorelletea uniflorae* and/or of the *Isoeto-Nanojuncetea*	yes
3140		Hard oligo-mesotrophic waters with benthic vegetation of *Chara spp.*	yes
3150		Natural eutrophic lakes with *Magnopotamion* or *Hydrocharition* - type vegetation	yes
3160		Natural dystrophic lakes and ponds	yes
3170	*	Mediterranean temporary ponds	yes
3180	*	Turloughs	4
3190		Lakes of gypsum karst	4
3220		Alpine rivers and the herbaceous vegetation along their banks	7
3230		Alpine rivers and their ligneous vegetation with *Myricaria germanica*	7
3240		Alpine rivers and their ligneous vegetation with *Salix elaeagnos*	7

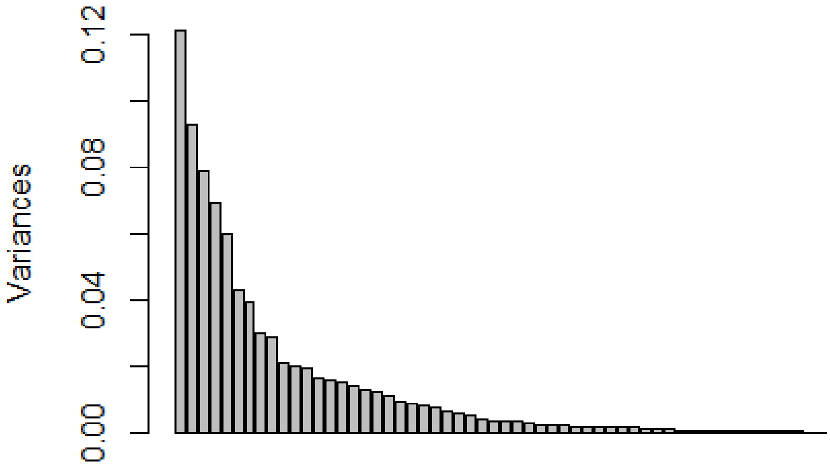
Code		Habitat type	chosen for analysis
3250		Constantly flowing Mediterranean rivers with *Glaucium flavum*	yes
3260		Water courses of plain to montane levels with the *Ranunculion fluitantis* and *Callitricho-Batrachion*	yes
3270		Rivers with muddy banks with *Chenopodion rubri p.p.* and *Bidention p.p.* vegetation	yes
3280		Constantly flowing Mediterranean rivers with *Paspalo-Agrostidion* species and hanging curtains of *Salix* and	yes
3290		Intermittently flowing Mediterranean rivers of the *Paspalo-Agrostidion*	yes
4010		Northern Atlantic wet heaths with *Erica tetralix*	yes
4020	*	Temperate Atlantic wet heaths with *Erica ciliaris* and *Erica tetralix*	yes
4030		European dry heaths	yes
4060		Alpine and Boreal heaths	yes
4090		Endemic oro-Mediterranean heaths with gorse	yes
40A0	*	Subcontinental peri-Pannonic scrub	yes
5110		Stable xerothermophilous formations with *Buxus sempervirens* on rock slopes (*Berberidion p.p.*)	2
5120		Mountain *Cytisus purgans* formations	yes
5130		*Juniperus communis* formations on heaths or calcareous grasslands	yes
5210		Arborescent matorral with *Juniperus spp.*	yes
5230	*	Arborescent matorral with *Laurus nobilis*	yes
5320		Low formations of *Euphorbia* close to cliffs	1
5330		Thermo-Mediterranean and pre-desert scrub	yes
6110	*	Rupicolous calcareous or basophilic grasslands of the *Alysso-Sedion albi*	yes
6120	*	Xeric sand calcareous grasslands	yes
6130		Calaminarian grasslands of the *Violetalia calaminariae*	3
6140		Siliceous Pyrenean *Festuca eskia* grasslands	yes
6170		Alpine and subalpine calcareous grasslands	yes
6210	(*)	Semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*) (* important	yes
6220	*	Pseudo-steppe with grasses and annuals of the *Thero-Brachypodietea*	yes
6230	*	Species-rich *Nardus* grasslands, on silicious substrates in mountain areas (and submountain areas in	yes
6240	*	Sub-Pannonic steppic grasslands	yes
6310		Dehesas with evergreen *Quercus spp.*	yes
6410		*Molinia* meadows on calcareous, peaty or clayey-silt-laden soils (*Molinion caeruleae*)	yes
6420		Mediterranean tall humid grasslands of the *Molinio-Holoschoenion*	yes
6430		Hydrophilous tall herb fringe communities of plains and of the montane to alpine levels	yes
6440		Alluvial meadows of river valleys of the *Cnidion dubii*	yes
6510		Lowland hay meadows (*Alopecurus pratensis, Sanguisorba officinalis*)	yes
6520		Mountain hay meadows	yes
7110	*	Active raised bogs	yes
7120		Degraded raised bogs still capable of natural regeneration	yes
7140		Transition mires and quaking bogs	yes
7150		Depressions on peat substrates of the *Rhynchosporion*	yes
7210	*	Calcareous fens with *Cladium mariscus* and species of the *Caricion davallianae*	yes
7220	*	Petrifying springs with tufa formation (*Cratoneurion*)	4
7230		Alkaline fens	yes
8110		Siliceous scree of the montane to snow levels (*Androsacetalia alpinae* and *Galeopsietalia ladani*)	2
8120		Calcareous and calcshist screes of the montane to alpine levels (*Thlaspietea rotundifolii*)	2
8130		Western Mediterranean and thermophilous scree	2
8150		Medio-European upland siliceous screes	2
8160	*	Medio-European calcareous scree of hill and montane levels	2
8210		Calcareous rocky slopes with chasmophytic vegetation	2
8220		Siliceous rocky slopes with chasmophytic vegetation	2
8230		Siliceous rock with pioneer vegetation of the *Sedo-Scleranthion* or of the *Sedo albi-Veronicion dillenii*	2
8240	*	Limestone pavements	4
8310		Caves not open to the public	4
9110		*Luzulo-Fagetum* beech forests	yes
9120		Atlantic acidophilous beech forests with *Ilex* and sometimes also *Taxus* in the shrublayer (*Quercion robori-petraeae* or *Ilici-Fagenion*)	yes
9130		Asperulo-Fagetum beech forests	yes
9140		Medio-European subalpine beech woods with *Acer* and *Rumex arifolius*	yes
9150		Medio-European limestone beech forests of the *Cephalanthero-Fagion*	yes
9160		Sub-Atlantic and medio-European oak or oak-hornbeam forests of the *Carpinion betuli*	yes

Code		Habitat type	chosen for analysis
9170		*Galio-Carpinetum* oak-hornbeam forests	yes
9180	*	*Tilio-Acerion* forests of slopes, screes and ravines	2
9190		Old acidophilous oak woods with *Quercus robur* on sandy plains	yes
91AA		Eastern white oak woods	yes
91B0		Thermophilous *Fraxinus angustifolia* woods	yes
91D0	*	Bog woodland	yes
91E0	*	Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (*Alno-Padion, Alnion incanae, Salicion albae*)	yes
91F0		Riparian mixed forests of *Quercus robur, Ulmus laevis* and *Ulmus minor, Fraxinus excelsior* or *Fraxinus angustifolia* , along the great rivers (*Ulmenion minoris*)	yes
91L0		Illyrian oak-hornbeam forests (*Erythronio-Carpinion*)	yes
91M0		Pannonian-Balkanic turkey oak -sessile oak forests	yes
91U0		Sarmatic steppe pine forest	yes
9210	*	Apeninne beech forests with *Taxus* and *Ilex*	yes
9220	*	Apennine beech forests with *Abies alba* and beech forests with *Abies nebrodensis*	yes
9230		Galicio-Portuguese oak woods with *Quercus robur* and *Quercus pyrenaica*	yes
9240		*Quercus faginea* and *Quercus canariensis* Iberian woods	yes
9260		*Castanea sativa* woods	yes
92A0		*Salix alba* and *Populus alba* galleries	yes
92D0		Southern riparian galleries and thickets (*Nerio-Tamaricetea* and *Securinegion tinctoriae*)	yes
9330		*Quercus suber* forests	yes
9340		*Quercus ilex* and *Quercus rotundifolia* forests	yes
9380		Forests of *Ilex aquifolium*	yes
9410		Acidophilous *Picea forests* of the montane to alpine levels (*Vaccinio-Piceetea*)	yes
9420		Alpine *Larix decidua* and/or *Pinus cembra* forests	yes
9430		Subalpine and montane *Pinus uncinata forests* (* if on gypsum or limestone)	yes
9510	*	Southern Apennine *Abies alba* forests	yes
9530	*	(Sub-) Mediterranean pine forests with endemic black pines	yes
9540		Mediterranean pine forests with endemic Mesogean pines	yes
9560	*	Endemic forests with *Juniperus spp.*	yes
9580	*	Mediterranean *Taxus baccata* woods	yes

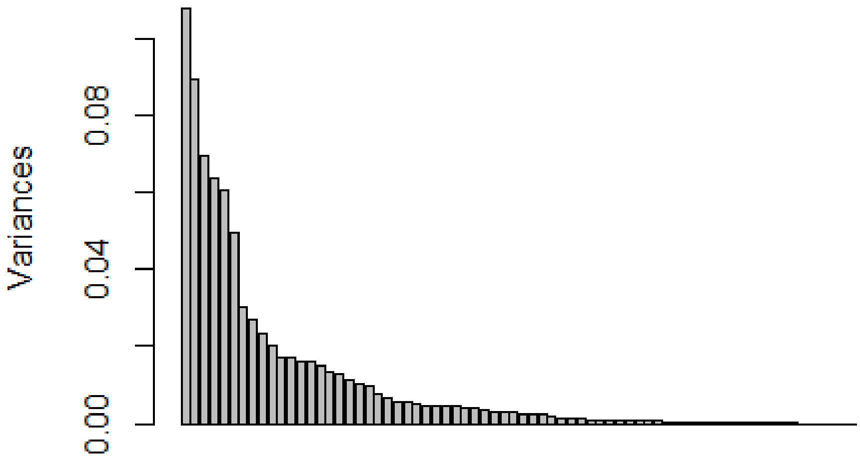
Explanation of the column “chosen for analysis”:

yes	chosen for further analyses because none of the following reasons relevant:
1	marine or coastal habitats
2	geologically special site: rocky or on scree
3	pedogenically special site: rich in heavy metal or salt (as long as salty soil is not induced by climate)
4	geologically dominated habitats: karst or caves or tufa springs
7	alpine rivers with steep gradients and quick flow

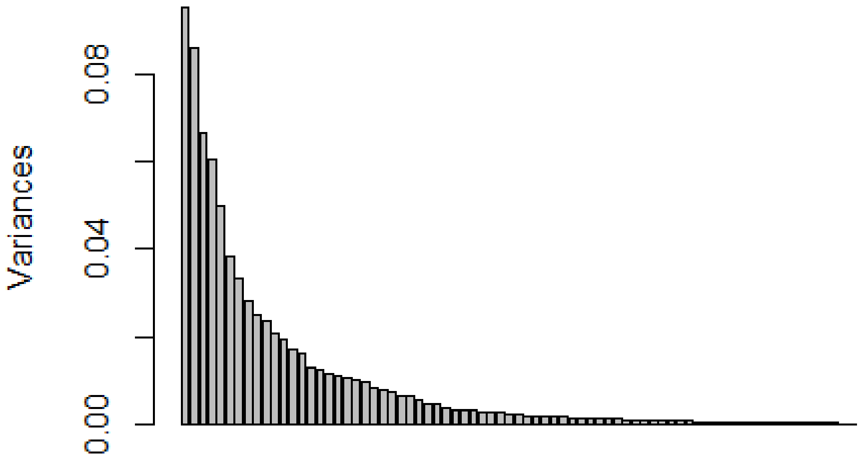
a) Eastern Lowlands



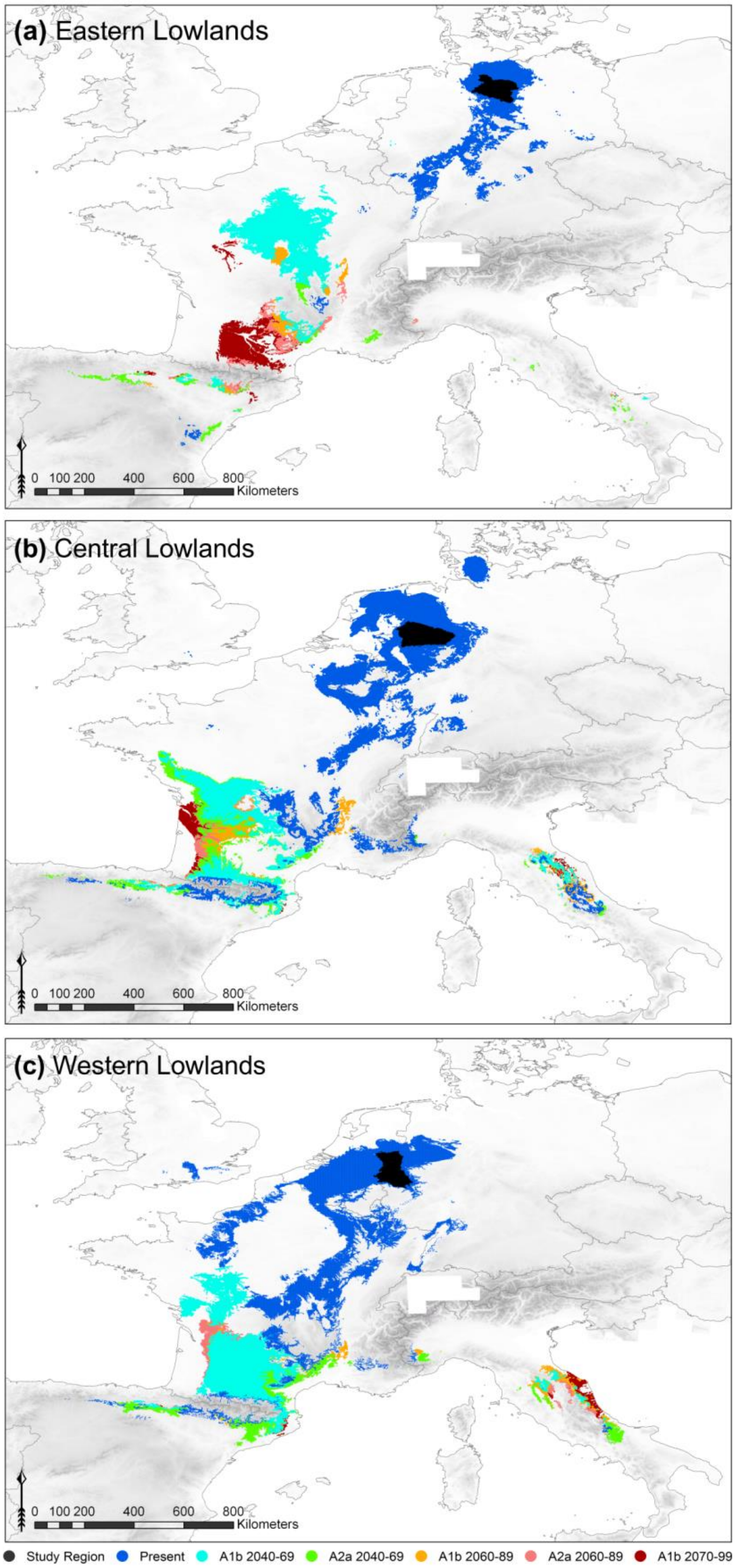
b) Central Lowlands



c) Western Lowlands



S3 Fig. Screeplots. Screeplots for the three study regions (a-c) showing the variances of the principal components that were identified in PCAs on the habitat types occurring in the three study regions and their present and future climate analogues. The number of habitat types, and thus the number of principal components, was for the Eastern Lowlands 56, for the Central Lowlands 70 and for the Western Lowlands 75. We regarded in (a) the first nine, in (b) the first ten, and in (c) the first five principal components as left of the bend of the “elbow”.



S4 Fig. Overlaying of all of the climate analogues for the different climate projections. Overlaying is shown for the three study regions (a-c) and begins with the most severe projection (A1b 2070-99) at the bottom until present on top (cf. order in legend). The size of the climate points constituting the climate analogues is not true to scale and appears in scattered areas denser than it really is. Map background shows elevation and indicates higher altitudes by darker gray. Elevation data is taken from JARVIS et al. (JARVIS et al. 2008).

S5 Text. Explanation of a less clear relation between habitat data and climate of two study regions.

In the PCA biplots, the habitat data in the future climate analogues of the Central and the Western Lowlands showed a less distinct development trend over the line of the projections of increasing climate change than the habitat data in the future climate analogues of the Eastern Lowlands (Fig. 4A-C). Additionally, the habitat data in the last projection did not change in accordance to the magnitude of projected warming (S2 Fig). This less distinct development trend and reaction can be explained by two reasons not related to climate.

The first reason is the wider climate range of the study regions of the Central and the Western Lowlands (S4 Table). The wider range caused overlapping future climate analogues, mainly in southwestern France (S4 Fig). This had an effect on the habitat data in the climate analogues because N2k-sites are not equally distributed and most N2k-sites occurred in the overlapping parts. As a result, the different climate analogues contained many identical N2k-sites making the habitat data of different future climate analogues appear more similar, blurring a sharp trend over the line of the projections. The second reason for a less distinct development trend of the habitat data over the line of the projections is because most of the N2k-sites in the climate analogues were rivers and floodplains and their habitat types are less influenced by climate than most of the upland habitat types (BRECKLE 2002). As a result, the habitat data in the future climate analogues of the Central and Western Lowlands changed less distinctly from future climate analogue to future climate analogue over the line of the projections than in the Eastern Lowlands. Additionally, the habitat data reflected climate conditions less clearly than in the Eastern Lowlands.

We conclude that unclear relations can be caused by three climate-independent problems: firstly, overlapping climate analogues, secondly, low density of N2k-sites and, thirdly, underrepresentation of certain habitat types (e.g. upland habitat types) in the N2k-sites data. However, they can be mitigated.

Overlapping climate analogues can be disentangled by searching the climate analogues of the study regions separately for different altitudes. To attain clear relations of habitats with climate, larger climate analogues are helpful. They can be enlarged by widening the scanned area south- and eastwards (cf. KOPF et al. 2008; FITZPATRICK and HARGROVE 2009). If this does not result in larger climate analogues, they may not exist in the present climate. In this case, the method cannot be used, but neither could the alternative method of bioclimatic envelope modeling (BEM)/ species distribution modelling (SDM). Blurred relationships are because of an under-representation of certain (e.g. upland) habitat types (third problem). These can be mitigated by remapping in the field within and outside the N2k-sites to detect habitat occurrences that are not reported in the data. These additional reports would also refine the differences between spatially slightly varying climate analogues and this would also reduce the problem of small and overlapping climate analogues. To sharpen the relationship between climate and habitat data more precise habitat data is needed, as well as knowledge about the habitats' locations within the N2k-sites instead of simply lists of habitat types. This would assist by refining and multiplying the datasets.

However, missing analogous climate, coarse enviromental data and fragmentary habitat data are likewise problems for SDM (WILLIAMS et al. 2007; FITZPATRICK and HARGROVE 2009; ARAÚJO et al. 2011; AMEZTEGUI et al. 2016; NIETO-LUGILDE et al. 2018).

S5 Fig. II. Order future climate analogues. "II. Order future southern climate analogues" and "Northern climate analogues" help to identify changes of habitat types in a European context.

References

ACKERLY DD, CORNWELL WK, WEISS SB, FLINT LE, FLINT AL (2015) A Geographic Mosaic of Climate Change Impacts on Terrestrial Vegetation: Which Areas Are Most at Risk? PLoS ONE, 10(6):e0130629

AMEZTEGUI A, COLL L, BROTONS L, NINOT JM (2016) Land-use legacies rather than climate change are driving the recent upward shift of the mountain tree line in the Pyrenees. Glob Ecol Biogeogr, 25(3):263–273

ARAÚJO MB, ALAGADOR D, CABEZA M, NOGUÉS-BRAVO D, THUILLER W (2011) Climate change threatens European conservation areas. Ecol Lett, 14(5):484–492

BRECKLE S-W (2002) Walter's vegetation of the earth: The ecological systems of the geo-biosphere. Springer, Berlin

COLLINS M, KNUTTI R, ARBLASTER J, DUFRESNE J-L, FICHEFET T, FRIEDLINGSTEIN P, GAO X, GUTOWSKI WJ, JOHNS T, KRINNER G, SHONGWE M, TEBALDI C, WEAVER AJ, WEHNER M (2013) Long-term Climate Change: Projections, Commitments and Irreversibility. In: IPCC (ed) Climate Change 2013: The Physical Science Basis. Cambridge University Press, Cambridge

EEA (2013) Natura 2000 database - the European network of protected sites: Tabular data and spatial data, temporal coverage 2012, scale of spatial dataset: 1:100.000. [data]. Available from http://www.eea.europa.eu/data-and-maps/data/natura-4 (accessed March 2022)

FEDERAL AGENCY FOR NATURE CONSERVATION (2009) Naturräumliche Gliederung Deutschlands: Shape-file natbs.shp [data], Bonn

FITZPATRICK MC, HARGROVE WW (2009) The projection of species distribution models and the problem of non-analog climate. Biodivers Conserv, 18(8):2255–2261

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

JACOB D, GÖTTEL H, KOTLARSKI S, LORENZ P, SIECK P (2008) Klimaauswirkungen und Anpassung in Deutschland - Phase 1: Erstellung regionaler Klimaszenarien für Deutschland. Erarbeitet im Auftrag des Umweltbundesamtes. Climate Change, Dessau-Roßlau

JARVIS A, REUTER HI, NELSON A, GUEVARA E (2008) Hole-filled SRTM for the globe: Version 4. [data]. Available from http://srtm.csi.cgiar.org (accessed September 2012)

KOPF S, HA-DUONG M, HALLEGATTE S (2008) Using maps of city analogues to display and interpret climate change scenarios and their uncertainty. Nat Hazards Earth Syst Sci, 8(4):905–918

MCCABE GJ, WOLOCK DM (2015) Increasing Northern Hemisphere water deficit. Clim Change, 132(2):237–249

NIETO-LUGILDE D, MAGUIRE KC, BLOIS JL, WILLIAMS JW, FITZPATRICK MC (2018) Multiresponse algorithms for community-level modelling: Review of theory, applications, and comparison to species distribution models. Methods Ecol Evol, 9(4):834–848

RAMIREZ J, JARVIS A (2008) High resolution statistically downscaled future climate surfaces: SRES A1B and A2a, based on IPCC AR4, bioclimatic parameters, 30yr averages 2060-2089, MPI-ECHAM5, 30 seconds. [data], Cali, Colombia. Available from http://gisweb.ciat.cgiar.org/GCMPage/download_sres.html (accessed April 2011)

RAMIREZ J, JARVIS A (2012) High resolution statistically downscaled future climate surfaces: SRES A1B and A2a, based on IPCC AR4, bioclimatic parameters, 30yr averages 2040-2069 and 2070-2099, MPI-ECHAM5, 30 arc-seconds, Delta Method IPCC AR4. [data], Cali, Colombia. Available from http://www.ccafs-climate.org/data/ (accessed August 2012)

VU VQ (2015) ggbiplot: A ggplot2 based biplot: GitHub Repository. Available from http://github.com/vqv/ggbiplot (accessed April 2015)

WILLIAMS JW, JACKSON ST, KUTZBACHT JE (2007) Projected distributions of novel and disappearing climates by 2100 AD. Proc Natl Acad Sci U S A, 104(14):5738–5742

Umwelt und Raum

Schriftenreihe Institut für Umweltplanung

Leibniz Universität Hannover

Bislang in der Schriftenreihe erschienen:

Band 1: Reich, M. & S. Rüter (Hrsg.)
Energiepflanzenanbau und Naturschutz
Cuvillier, 2010, 165 Seiten
ISBN 978-3-86955-473-0

Band 2: Reich, M. & S. Rüter (Hrsg.)
Auswirkungen des großflächigen Anbaus von Energiepflanzen auf die Tierwelt der Agrarlandschaft
Cuvillier, 2011, 244 Seiten
ISBN 978-3-86955-606-2

Band 3: Urban, B., C. v. Haaren, H. Kanning, J. Krahl & A. Munack
Methode zur Bewertung der Biodiversität in Ökobilanzen am Beispiel biogener Kraftstoffe
Cuvillier, 2011, 210 Seiten
ISBN 978-3-86955-697-0

Band 4: Brinkmann, R., O. Behr, I. Niermann & M. Reich (Hrsg.)
Entwicklung von Methoden zur Untersuchung und Reduktion des Kollisionsrisikos von Fledermäusen an Onshore-Windenergieanlagen
Cuvillier, 2011, 457 Seiten
ISBN 978-3-86955-753-3

Band 5: Stowasser, A.
Potenziale und Optimierungsmöglichkeiten bei der Auswahl und Anwendung ingenieurbiologischer Bauweisen im Wasserbau
Cuvillier, 2011, 404 Seiten
ISBN 978-3-86955-795-3

Band 6: Werpup, A.
Biotoptypenbasierte Gehölzansaaten – Eine Begrünungsmethode zur ingenieurbiologischen Sicherung von oberbodenlosen Verkehrswege-böschungen
Cuvillier, 2013, 253 Seiten
ISBN 978-3-95404-409-2

Band 7: Behr, O., R. Brinkmann, F. Korner-Nievergelt, M. Nagy, I. Niermann, M. Reich & R. Simon (Hrsg.)
Reduktion des Kollisionsrisikos von Fledermäusen an Onshore-Windenergieanlagen (RENEBAT II)
2016, 369 Seiten
DOI: http://dx.doi.org/10.15488/263

Band 8: Bredemeier, B., M. Schmehl, M. Rode, J. Geldermann & C. v. Haaren
Biodiversität und Landschaftsbild in der Ökobilanzierung von Biogasanlagen
2017, 75 Seiten
DOI: https://doi.org/10.15488/3862

Band 9: Wix, N., M. Rode & M. Reich (Hrsg.)
Blühstreifen - Biodiversität und produktionsintegrierte Kompensation
2018, 322 Seiten
DOI: http://dx.doi.org/10.15488/3683

Band 10: Sybertz, J. & M. Reich
Tierarten im Klimawandel in Harz und Lüneburger Heide
2018, 91 Seiten
DOI: https://doi.org/10.15488/4236

iup Institut für Umweltplanung

Leibniz Universität Hannover

ISSN (Online) 2366-5459