

PUBLIZIERBARER ENDBERICHT

A) Projektdaten

Kurztitel	SPEC-Adapt
Langtitel:	Climate change driven species migration, conservation networks, and possible adaptation strategies
Program:	ACRP 4 th Call for Proposals
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Projektübersicht

1A) Executive Summary, English

Forthcoming climate change will severely alter the spatial distribution of species. However, it remains poorly understood to which extent species will be able to track climate change induced shifts in the highly fragmented Central European landscapes, particularly in the current nature reserves network. In Spec-Adapt we analyzed range dynamics of 60 exemplary species with contrasting ecological profiles from three different taxonomic groups (vascular plants, butterflies, grasshoppers) using a spatially and temporarily explicit simulation model (CATS).

As a spatially explicit, fine-grained habitat distribution map was necessary for this project, we created a new habitat distribution map for the entire study region, i.e. southern Central Europe. There, the premise was to create a harmonized map by incorporating various input data sources from federal institutes such as mapping campaigns and other supra-national and freely available data derived from satellite imagery or Open Street Map sources amongst others. Due to the lack of comparable maps and the extensive work that has been put in map creation which included plausibility checks, preparation and thematic harmonization of the applied base data, as well as modelling approaches to complement existing data sources and statistical evaluation on the goodness of the final map, a scientific article has been published (Kuttner et al. 2015) to make this habitat map also available to the larger scientific community. Moreover, we analysed how habitat availability interacts with climate change risks for species along an altitudinal gradient (i.e. lowland species compared to alpine ones) (Kuttner et al. in rev.).

Finally, we (a) analyzed the transient range shifts of the 60 study species in the study area (Austria, Switzerland, southern Germany, and South Tyrol) as driven by the climatic trends forecasted for the 21st century; (b) calculated the resulting range size changes within and outside the existing protected area network; (c) evaluated different strategies (protected areas, corridors, improvement of random plots in the matrix) to mitigate potential range losses, and (d) provided recommendations for adapting species conservation efforts and nature conservation networks management and design.

Species distribution modelling, as a first step of CATS simulations, demonstrated that while the potential climatic ranges of most species shrink under a warmer climate, the (proportional) match with appropriate habitat types remains largely unchanged for (sub)montane species but generally increases for species of high elevation, especially in case of plants and butterflies. This result highlights a so far hardly discussed interaction between climate change and land use patterns. We therefore summarized these results in a separate scientific paper which is currently in revision.

Overall, dynamic simulations with CATS suggested that (1) almost all modelled species will lose considerable parts of their suitable climate space under climate warming and a sizable minority (up to 25%) is even predicted to go extinct; (2) management, sensu restoration of semi-natural habitat types, can mitigate, but not fully compensate for this range loss in case of (sub)montane species; it will not, however, prevent predicted extinctions; (3) the mitigating effect of the (explored) management measures is negligible in case of high mountain species; (4) the more mobile taxonomic groups, butterflies and grasshoppers, profit more from management measures than the less mobile plants; (5) the spatial arrangement of restored habitats has only slight effects on management efficiency, with random placement performing worst. These results will soon be published in a scientific article (Wessely et al. in prep.).

Our integrative modelling approach – i.e. combining a dynamic modeling framework on species ecology and dispersal data with attributes (climatic and habitat suitability) of the study region under different scenarios of climate change and management, provided novel insights into the likely future range dynamics in the 21st century. We particularly conclude that even ambitious habitat restoration programs will not be able to fully compensate for the negative effects of climate warming on the modelled biota. For at least partial mitigation, adjustment of current elevational land use gradients with reduction of intensity and extensive habitat restoration in lowland areas, but maintenance or expansion of moderate use at higher elevations appears a sensible long-term strategy. In general, our approach in itself helps to advance concepts and simulations in conservation biology and may aid forthcoming conservation planning.

1A) Executive Summary, Deutsch

Fortschreitender Klimawandel wird die räumliche Verteilung von Tier- und Pflanzenarten stark verändern. Es ist jedoch unklar, wie sich der Klimawandel auf die Artverbreitungen in den stark fragmentierten mitteleuropäischen Landschaften und ihren gegenwärtigen Schutzgebietsnetzwerken auswirkt. In Spec-Adapt wurden deshalb Verbreitungsveränderungen von 60 beispielhaft ausgewählten Arten (Gefäßpflanzen, Schmetterlinge, Heuschrecken) mit unterschiedlichen ökologischen Eigenschaften mithilfe des räumlich und zeitlich expliziten Simulationsmodells CATS analysiert.

Zur Durchführung des Projekts erstellten wir eine räumlich explizite hochauflösende Lebensraumverbreitungskarte für das gesamte Untersuchungsgebiet, das heißt das südliche Mitteleuropa. Dabei war die Prämisse, eine harmonisierte Karte zu erstellen, indem verschiedene Eingangsdatenquellen aus Bundesinstituten und anderen Einrichtungen (z.B. Biotopkartierungen) sowie frei verfügbare von Satellitenbildern abgeleitete Daten und Open Street Map-Daten berücksichtigt wurden. Aufgrund des gegenwärtigen Mangels vergleichbarer Karten und der umfangreichen Arbeit, die in diese Lebensraumkarte investiert wurde (inkl. Plausibilitätskontrollen, Aufbereitung und thematische Harmonisierung der verwendeten Basisdaten, Modellierung zum Schließen von Datenlücken, und statistische Evaluierung der Qualität der fertigen Karte), wurde ein wissenschaftlicher Artikel veröffentlicht (Kuttner et al. 2015), um die Karte auch für weitere wissenschaftliche Anwendungen zur Verfügung zu stellen. Darüber hinaus analysierten wir, wie die Lebensraumverfügbarkeit mit Auswirkungen des Klimawandels auf die Arten entlang eines Höhengradienten in Wechselwirkung tritt (MS in Revision).

Schließlich analysierten wir (a) die Änderungen der Verbreitungsgebiete der 60 Tier- und Pflanzenarten im Studiengebiet (Österreich, Schweiz, Süd-Deutschland, Südtirol) unter dem für das 21. Jahrhundert prognostiziertem Klimawandel; (b) die daraus resultierenden Änderungen der Nettogrößen der Verbreitungsgebiete innerhalb und außerhalb des bestehenden Schutzgebietsnetzes; und (c) die Effektivität dreier Naturschutzstrategien (Schutzgebietsverbesserungen, ökologische Korridore, Maßnahmen in der Matrix) zur Reduzierung der klimawandelbedingten Arealverkleinerungen. Darauf aufbauend leiteten wir (d) Empfehlungen für Artenschutzbemühungen und Schutzgebietsnetzwerke und deren Management und Design ab.

Die Modellierung der Artverteilung als erster Schritt der CATS-Simulationen zeigte, dass die klimatisch geeigneten Gebiete für die meisten Arten unter wärmeren Klima schrumpfen. Die Verfügbarkeit der entsprechenden Lebensraumtypen bleibt dabei für (sub-)montane Arten weitgehend unverändert, für alpine Arten steigt sie jedoch an, insbesondere für Pflanzen und Schmetterlinge. Diese Ergebnisse lassen auf bisher kaum diskutierte Wechselwirkungen zwischen Klimawandel und Landnutzung schließen. Wir haben sie deshalb in einer eigenen wissenschaftlichen Veröffentlichung zusammengefasst, die derzeit in Überarbeitung ist.

Insgesamt ziegten die dynamische Simulationen mit CATS, dass (1) fast alle modellierten Arten erhebliche Teile ihrer klimatisch geeigneten Gebiete durch den Klimawandel verlieren und eine beträchtliche Minderheit (bis zu 25%) im Untersuchungsgebiet sogar aussterben wird; (2) Naturschutzmaßnahmen, d.h. Restaurieren von semi-natürlichen Lebensraumtypen, können diese Prozesse im Falle von vielen (sub-)montanen Arten mindern aber nicht vollständig kompensieren und Austerbeereignisse werden nicht gänzlich zu verhindern sein; (3) die mindernde Wirkung der untersuchten Naturschutzmaßnahmen ist bei alpinen Gebirgsarten vernachlässigbar; (4) die mobileren taxonomischen Gruppen, Schmetterlinge und Heuschrecken, profitieren mehr von den Naturschutzmaßnahmen als die weniger mobilen Gefäßpflanzen; (5) die räumliche Anordnung der restaurierten Lebensräume hat nur geringe Auswirkungen auf die Auswirkungen der Naturschutzmaßnahmen, Schutzgebietsverbesserungen und ökologische Korridore haben aber etwas stärkere Auswirkungen als Maßnahmen in der Matrix.

Unser integrativer Modellierungsansatz, d.h. eine dynamische Modellierung von ökologischen Daten und Verbreitungsdaten der Arten mit Attributen (Klima- und Habitateignung) des Untersuchungsgebiets unter Anwendung verschiedenen Klimawandelszenarien und Naturschutzstrategien, lieferte neue Erkenntnisse über die zu erwartende Dynamik der Artverbreitungen im 21. Jahrhundert. Wir folgern daraus, dass auch ambitionierte Habitatrestaurierungsprogramme nicht in der Lage sein werden, die negativen Auswirkungen der Klimaerwärmung auf Tier- und Pflanzenarten gänzlich zu kompensieren. Um eine teilweise Milderung zu erreichen, könnte die Anpassung der aktuellen Landnutzung-Höhengradienten durch Reduzierung der Nutzungsintensität und umfangreiche Wiederherstellung der Lebensräume im Flachland, sowie Beibehaltung oder Ausweitung moderater Nutzungsformen in höheren Lagen eine vernünftige langfristige Strategie darstellen. Der in Spec-Adapt entwickelte Ansatz sollte zur Weiterentwicklung von Konzepten und Simulationen in der Naturschutzbiologie beitragen und konkrete Hilfestellungen für die Naturschutzplanung bereitstellen.

2 Hintergrund und Zielsetzung

Ample empirical evidence now documents that plant and animal species are already moving their ranges in response to the last century's climatic trends. The pronounced warming predicted for the 21st century will probably accelerate these range dynamics. However, the climate may actually move at a rate (much) faster than many species will be able to track in today's heavily transformed and fragmented cultural landscapes. As refuges and as compensation, protected area networks are the most prominent strategy of biodiversity conservation, but the designation of protected areas has usually focused on conserving existing biodiversity patterns rather than taking into account the possible effects of climate change induced shifts of species ranges. Previously used static modeling approaches based on correlative habitat models were not able to assess the ability of these networks to cope with the dynamics of transient species ranges, although it is evident that these processes are crucially important as, for example, many sites which become climatically suitable to particular species might actually be unreachable due to dispersal limitations.

In this project, we tackled this question based on a spatially and temporarily explicit simulation model of range dynamics, applied to a suite of initially 60 species from three different taxonomic groups, i.e. 10 lowland and alpine species of each taxonomic group. The study design involved (a) the simulation of the transient range shifts of these species in Central Europe as driven by the climatic trends forecasted for the 21st century; (b) a calculation of the resulting range size changes of the individual species both within and outside the existing protected area network; (c) an evaluation of different strategies to mitigate potential range losses and to keep representation of these species within protected areas high, and (d) the provision of recommendations for adapting species conservation efforts and nature conservation networks management and design.

The study region comprised the countries Austria, Switzerland, southern Germany (Baden-Württemberg and Bavaria), and South Tyrol (Italy). The project focused on the three taxonomic group (vascular plants, grasshoppers, butterflies), which were selected based on data availability, relevance within ecological systems, knowledge of demographic and dispersal traits, and on importance in nature conservation contexts.

For each taxonomic group, selected species of contrasting ecological profiles (e.g. range size, ecological affiliation, mobility, nature conservation status) were analyzed to cover the range of climate change vulnerabilities. We initially selected 50 vascular plants, 22 grasshoppers and 20 butterflies as candidate species. To have a balanced sample, this initial set was then reduced to 20 species from each group, each including 10 species mainly occurring above the alpine treeline, and 10 species primarily occurring at (sub) montane elevations. The large number of modelled species allowed for testing range adaptation potential for species of differing key trait combinations and ecological profiles under climate change. Climatic data of the study region were downscaled to a resolution of 1 x 1 km for

both current conditions and future climatic scenarios (A1B and B2 scenarios run under different circulation models to 2100). The spatial distribution of different habitat types within the study region was derived from a lately established high-resolution habitat map. Spatial data of the national nature conservation networks were obtained from the national, respectively provincial nature conservation authorities. In addition, we collected distribution data of all selected species in the study region at the highest spatial resolution available (that is generally 3 x 5 geographic minutes (approx. 30 km²) for vascular plants, 1 x 1 geographic minutes (approx. 2 km²) for grasshoppers and butterflies), and complemented by precise point data from all taxonomic groups where available.

Simulations of climate-change driven range dynamics were based on CATS, a recently developed modelling tool, which integrates features of species distribution models, demographic and dispersal models. CATS has a cellular automaton type structure, represents the study area as a regular grid of sites, and simulates local, i.e. per-grid-cell species abundance as a function of local site conditions and the exchange of individuals among cells. The first step in CATS application was fitting species distribution models (SDMs) of each study species under current climatic conditions. Upon substituting layers of current climatic variables with those of predicted future climates, fitted models project climate-induced changes in grid-cell suitability (= occurrence probability) over time which, in turn, drive the colonization of newly suitable and the extinction from no longer suitable sites (= grid cells).

The effects of management on future range dynamics was evaluated by assuming that certain proportions (1, 3, 5%) of intensively used land were restored as semi-natural habitat types (low-intensity grasslands, semi-natural deciduous forests) from current high intensity usage (mainly as arable land, high intensity grasslands, cultivated spruce forests). Restored habitats were placed following three different strategies: (a) 'improvement' of existing protected areas; (2) establishment of corridors among existing protected areas; (c) random placement in the landscape matrix. CATS simulations were then run under all possible combinations of spatial strategies and intensities.

3 Projektinhalt und Ergebnis(se)

We have drafted four manuscripts intended for publication in scientific journals (one published, one in press, one in revision, one in preparation) that outline the research's background, objective, methods, results and conclusions in detail. These manuscripts are annexed as part of the final report and comprise the main study results. Here, we provide an extended synthesis.

Initial situation / project motivation

Empirical evidence suggests that plant and animal species are already moving their ranges in response to the last century's climatic trends (e.g. Parmesan & Yohe 2003, Chen et al. 2011, Dawson et al. 2011). The pronounced warming predicted for the current century (IPCC 2007, Moss et al. 2010) will tend to accelerate these range dynamics. However, the climate may actually move at a rate (much) faster than many species will be able to track (Loarie et al. 2009). This is particularly likely in heavily transformed cultural landscapes where loss and fragmentation of suitable habitats additionally constrains the velocity of species migration (Pitelka et al. 1997, Sala et al. 2000, Higgins et al. 2003, Pearson & Dawson 2005). Consequently, the combination of habitat destruction and climate warming has been termed a 'deadly anthropogenic cocktail' for biodiversity (Travis 2003).

As a compensation of widespread habitat destruction and fragmentation in cultural landscapes, protected area networks are currently the most prominent strategy of biodiversity conservation with Europe having the most extensive such network worldwide (WCPA 2011). However, the designation of protected areas has usually focused on conserving existing biodiversity patterns and hardly ever taken into account the possible effects of climate change on species ranges (Araújo et al. 2004). Accordingly, recent evaluations have suggested that forthcoming climatic trends might undermine current European conservation efforts (Araújo et al. 2011). However, this, and similar evaluations (e.g. Hole et al. 2009) have used static modeling approaches based on correlative habitat models (Guisan & Thuiller 2005). They hence did not assess the ability of these networks to cope with the dynamics of transient species ranges which nevertheless might be crucially important as, for example, many sites which become climatically suitable to particular species might actually be unreachable for them due to dispersal limitation (e.g. Malcolm et al. 2002, Svenning & Skov 2007, Devictor et al. 2008, Dawson et al. 2011, Dullinger et al. 2012). Put it another way, environmental connectivity among protected areas might be a crucial factor for preserving biodiversity under climate change (Game et al. 2011); and improvement of such connectivity might either be achieved by a spatial re-arrangement of conservation areas or from an enhanced permeability of non-protected areas. The latter would involve a general shift in conservation policy as it defies the strict distinction between protected areas and an intensively used and transformed landscape matrix.

Project objectives

In Spec-Adapt, we tackled these research questions based on a recently developed spatially and temporarily explicit simulation model of range dynamics applied to a suite of 60 exemplary species from three different taxonomic groups (vascular plants, butterflies, grasshoppers). The study design involves (a) the simulation of the transient range shifts of these species in Central Europe (Austria, Switzerland, southern Germany) as driven by the climatic trends forecasted for the 21st century; (b) a calculation of the resulting range size changes of the individual species both within and outside the existing protected area network; (c) an evaluation of different strategies to mitigate potential range losses and to keep representation of these species within protected areas high, and (d) the provision of recommendations for adapting species conservation efforts and nature conservation networks management and design.

Activities performed, including methods employed

Study region

The study region comprised the countries Austria, and Switzerland, southern Germany (i.e. the federal states of Baden-Württemberg and Bavaria), and South Tyrol (Northern Italy) (Figure 1). We extend the study area beyond the borders of Austria (a) to cover a broader array of climates (temperate lowland to mountain climates), and (b) to take account of the trans-national character of biodiversity conservation under rapid environmental change. However, we exclude adjacent, but climatically and biogeographically differing regions to the South (Southern Alps and sub-mediterranean Europe) and Southeast (Pannonian Region) (a) to keep computational efforts feasible, and (b) because high quality distribution data of the selected taxonomic groups (see below) are not as easily, or not at all, available from these areas.

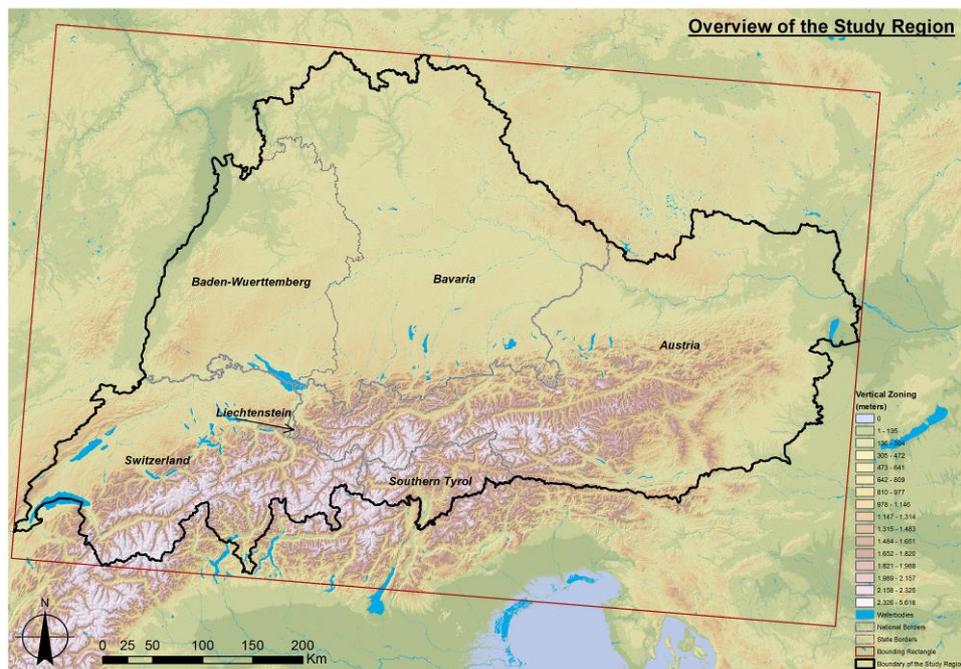


Figure 1. The study area, comprising Austria, Southern Germany (Bavaria and Baden-Wuerttemberg), Switzerland, and South Tyrol (Alto Adige, Northern Italy).

Study species selection

The project focused on three taxonomic groups, i.e. vascular plants, grasshoppers and butterflies. We have selected these groups based on data availability and accessibility, relevance within ecological systems, knowledge of functional demographic and dispersal traits, and on importance in nature conservation contexts:

- Vascular plants (appr. 3.500 native species in Central Europe) are the dominating primary producers in terrestrial ecosystems, and they form the energetic and structural basis for other organisms. Due to thorough floristic mapping projects in Central European countries (Niklfeld 1998), vascular plants species distributions are exceptionally well documented.
- Grasshoppers (Orthoptera, appr. 160 species in Central Europe), constitute one of the most important invertebrate groups in terrestrial habitats (e.g. grasslands, wetlands), are leading consumers of plant biomass, and thus play a key role in ecosystem processes (Ingrisch & Köhler 1998). Due to recently published (Thorens & Nadig 1997, Maas et al. 2002, Baur et al. 2006) or currently prepared national distribution atlases (www.orthoptera.at), supplemented by regional atlases (e.g. Detzel 1998, Schlumprecht & Waeber 2003, Zuna-Kratky et al. 2009, Illich et al. 2010), the distribution of grasshopper species within Central Europe is also very well documented.
- Butterflies (Macrolepidoptera partim, appr. 250 species in Central Europe) are important pollinators and encompass many enigmatic flagship species for nature conservation. Large central data bases (e.g. www.zobodat.at/, www.gbif.at), national (Reichl 1992, Bühler-Cortesi 2009, www.cscf.ch) and European distribution atlases

(Kudrna et al. 2011), an existing European risk assessment under climate change scenarios (Settele et al. 2010) and a European-wide monitoring program (<http://www.bc-europe.org/subcategory.asp?CatID=10&SubCatID=132>), provide an excellent data base for this taxonomic group.

From each taxonomic group, we selected a set of study species of contrasting ecological profiles (e.g. range size, ecological affiliation, mobility, nature conservation status, Table 1) to cover the range of climate change vulnerabilities (Rabitsch et al. 2010). Selected study species conformed to the following requirements: (1) their distribution and ecological requirements are well known, and (2) species distribution model (= SDM) parameterisation is possible, i.e. their ranges are (mostly) limited to the study area or to areas with similar climatic regimes. In particular, we did not consider southern European species with only peripheral occurrences in Central Europe. SDM parameterization for such species would have been difficult, as the study region would not have allowed sampling the whole climatic space of these species. However, these mostly thermophilic species will include many species of rather low vulnerability to climate change, and main responsibility for the conservation of these species lies not within the competence of Austria.

Table 1. Selected vascular plant (n=20), grasshopper (n=20) and butterflies species (n=20). Abbreviations: B=Butterflies; G=Grasshoppers; P=Plants. Trait abbreviations: a = alpine; l = lowland. Habitat abbreviations: ALLUV = Alluvions; ALPGR = Alpine Grasslands; BLFO = Broad-leaved Forest; CFO = Coniferous Forest; DRY = Dry Grasslands; EXTGR = Extensive Grasslands; ROCK = Rocks /Scree; SHRUB = Shrublands /Dwarf Tree Stands; WET = Wet Grasslands and Mires.

Species Name	Taxon	Trait	ALLUV	ALPGR	BLFO	CFO	DRY	EXTGR	ROCK	SHRUB	WET
<i>Aeropedellus variegatus</i>	G	a		X							
<i>Alchemilla anisiaca</i>	P	a		X					X	X	
<i>Arcyptera fusca</i>	G	a					X	X			
<i>Aster bellidiastrum</i>	P	a	X	X					X	X	
<i>Bistorta officinalis</i>	P	n						X			X
<i>Bohemanella frigida</i>	G	a		X					X		
<i>Boloria eunomia</i>	B	n									X
<i>Boloria thore</i>	B	n			X	X					
<i>Boloria titania</i>	B	a		X							X
<i>Brenthis daphne</i>	B	n			X						
<i>Bryodemella tuberculatum</i>	G	n	X								
<i>Cerastium uniflorum</i>	P	a		X					X		
<i>Chorthippus pullus</i>	G	n	X								
<i>Colias palaeno</i>	B	a								X	X
<i>Colias phicomone</i>	B	a		X							
<i>Conocephalus dorsalis</i>	G	n									X
<i>Dianthus alpinus</i>	P	a		X					X	X	
<i>Drosera rotundifolia</i>	P	n									X
<i>Erebia nivalis</i>	B	a		X					X		
<i>Euphydryas maturna</i>	B	n			X						
<i>Gentiana clusii</i>	P	a		X					X	X	
<i>Gentianella bohemica</i>	P	n						X			
<i>Gymnadenia conopsea</i>	P	n		X			X	X	X	X	X
<i>Isophya brevicauda</i>	G	n					X	X			
<i>Jasione montana</i>	P	n					X	X			
<i>Leontopodium alpinum</i>	P	a		X					X	X	
<i>Lopinga achine</i>	B	n			X						
<i>Lycaena helle</i>	B	n									X
<i>Maculinea teleius</i>	B	n									X
<i>Melitaea asteria</i>	B	a		X							

<i>Metrioptera saussuriana</i>	G	a		X						
<i>Miramella alpina</i>	G	a		X			X			
<i>Nardus stricta</i>	P	n		X			X	X	X	X
<i>Nemobius sylvestris</i>	G	n			X	X			X	
<i>Oedipoda germanica</i>	G	a					X			
<i>Oeneis glacialis</i>	B	a		X				X		
<i>Parnassius apollo</i>	B	a					X			
<i>Parnassius mnemosyne</i>	B	n					X			
<i>Parnassius phoebus</i>	B	a		X					X	X
<i>Pholidoptera fallax</i>	G	n					X	X		
<i>Phyteuma spicatum</i>	P	n			X	X				
<i>Plebeius optilete</i>	B	n							X	X
<i>Polygala chamaebuxus</i>	P	n	X			X	X	X	X	
<i>Polysarcus denticauda</i>	G	n					X			
<i>Pontia callidice</i>	B	a		X				X		
<i>Primula auricula</i>	P	a		X				X		
<i>Pyrgus armoricanus</i>	B	n					X	X		
<i>Rhinanthus glacialis</i>	P	a	X	X		X		X	X	
<i>Saxifraga aizoides</i>	P	a	X	X				X	X	X
<i>Selinum carvifolia</i>	P	n						X		X
<i>Sibbaldia procumbens</i>	P	a		X				X		
<i>Stauroderus scalaris</i>	G	a					X	X		
<i>Stenobothrus nigromaculatus</i>	G	n					X			
<i>Stenobothrus rubicundulus</i>	G	a		X			X			
<i>Stenobothrus stigmaticus</i>	G	n					X	X		
<i>Tetrix tuerki</i>	G	n	X							
<i>Trollius europaeus</i>	P	n		X				X	X	X
<i>Veronica fruticans</i>	P	a		X				X	X	

Distribution data

For all study species, we collected distribution data in the study region at the highest spatial resolution available which, generally, is 3x5 geographic minutes (appr. 30 km²) for vascular plants (Niklfeld 1998) and 1x1 geographic minutes (appr. 2 km²) for grasshoppers and butterflies (for ca. 70% of the study area). In total, we collected 16.328, 16.510 and 50.050 occurrence records for plant, butterfly and grasshopper species, respectively (Table 2). Different spatial resolutions in occurrence data of different origins were harmonized to a resolution of 1 x 1 geographic minutes (~ 2.3 km²).

Table 2. Overview on the distribution data used for the study. Additionally shown are the data sources.

	Species Name	AT ^{1,2}	BW ³	BAV ⁴	CH ⁵	ST ⁶	Total (species)	Data Sources
Grasshoppers	<i>Aeropedellus variegatus</i>	2	-	-	18	19	39	Datenbank AG Heuschrecken Österreichs, c/o Thomas Zuna-Kratky, Vienna, Austria ¹ Gefährdungsanalyse der Heuschrecken Deutschlands: Verbreitungsatlas, Gefährdungseinstufung und Schutzkonzepte, Germany ² Distribution database of Orthoptera in Germany, c/o Peter Detzel, Stephen Maas, Aloysius Staudt, Germany ³ Artenschutzkartierung Bayern - Bayer. Landesamt für Umwelt, Bayern ⁴
	<i>Arcyptera fusca</i>	106	19	45	172	77	419	
	<i>Bohemanella frigida</i>	56	-	-	133	120	309	
	<i>Bryodemella tuberculatum</i>	19	-	264	-	-	283	
	<i>Chorthippus pullus</i>	50	-	191	12	3	256	
	<i>Conocephalus dorsalis</i>	171	124	741	27	20	1083	
	<i>Isophya brevicauda</i>	106	-	-	-	-	106	
	<i>Metrioptera saussuriana</i>	35	-	-	235	-	270	
	<i>Miramella alpina</i>	571	603	410	502	64	2150	
	<i>Nemobius sylvestris</i>	450	1270	3216	679	157	5772	
	<i>Oedipoda germanica</i>	23	370	220	188	33	834	
	<i>Pholidoptera fallax</i>	210	-	-	21	-	231	
	<i>Polysarcus denticauda</i>	174	264	207	93	-	738	
	<i>Stauroderus scalaris</i>	190	794	1	502	266	1753	
<i>Stenobothrus nigromaculatus</i>	136	147	248	32	8	571		

	<i>Stenobothrus rubicundulus</i>	89	-	-	51	106	246	Centre Suisse de Cartographie de la Faune, Neuchâtel, Switzerland ⁵ Distribution database of Orthoptera in South Tyrol, Naturmuseum Südtirol, Italy ⁶
	<i>Stenobothrus stigmaticus</i>	280	472	551	5	-	1308	
	<i>Tetrix tuerki</i>	27	-	88	21	6	142	
	Subtotal (Taxon/country)	2695	4063	6182	2691	879	16510	
		AT ^{1,2}	BW ³	BAV ^{4,5,6}	CH ⁷	ST ⁸		
Vascular Plants	<i>Alchemilla anisiaca</i>	131	-	-	-	-	131	Database of Austrian Endemic Species, Environment Agency, Austria ¹
	<i>Aster bellidiastrum</i>	684	85	638	1330	296	3033	
	<i>Bistorta officinalis</i>	412	822	1227	1074	99	3634	Floristic Mapping Project of Austria, University Vienna, Austria ²
	<i>Cerastium uniflorum</i>	296	-	16	158	263	733	Staatliches Museum für Naturkunde Stuttgart, c/o Arno Wörz, Germany ³
	<i>Dianthus alpinus</i>	275	-	-	-	-	275	
	<i>Drosera rotundifolia</i>	436	140	1146	188	134	2044	Artenschutzkartierung Bayern - Bayerisches Landesamt für Umwelt, Germany ⁴
	<i>Gentiana clusii</i>	280	-	798	437	120	1635	
	<i>Gentianella bohemica</i>	36	-	146	-	-	182	Floristic Mapping Project of Bavaria, Germany ⁵
	<i>Gymnadenia conopsea</i>	941	971	2076	5804	1487	11279	
	<i>Jasione montana</i>	124	137	660	110	34	1065	Bayerisches Landesamt für Umwelt, Augsburg, Germany ⁶
	<i>Leontopodium alpinum</i>	130	-	55	286	238	709	
	<i>Nardus stricta</i>	1096	283	1494	1917	404	5194	Info Flora, c/o Botanischer Garten, Altenbergrain 21, 3013 Bern, Switzerland ⁷
	<i>Phyteuma spicatum</i>	645	1501	1650	1699	12	5507	
	<i>Polygala chamaebuxus</i>	552	18	817	1458	257	3102	Naturmuseum Südtirol, c/o Thomas Wilhelm, Italy ⁸
	<i>Primula auricula</i>	252	-	297	378	24	951	
	<i>Rhinanthus glacialis</i>	620	235	224	418	243	1740	
	<i>Saxifraga aizoides</i>	608	-	131	548	307	1594	
<i>Selinum carvifolia</i>	213	187	997	83	19	1499		
<i>Sibbaldia procumbens</i>	305	-	29	235	267	836		
<i>Trollius europaeus</i>	707	300	695	1790	374	3866		
<i>Veronica fruticans</i>	308	6	52	413	262	1041		
	Subtotal (Taxon/country)	9051	4685	13148	18326	4840	50050	
		AT ¹⁻⁵	BW ⁶	BAV ⁷	CH ⁸	ST ⁵		
Butterflies	<i>Boloria eunomia</i>	32	94	1484	-	4	1614	Article 17 report of the EU Habitats Directive ¹
	<i>Boloria thore</i>	32	1	297	105	7	442	
	<i>Boloria titania</i>	81	38	1269	521	1	1910	Database Heinz Habeler, Graz, Austria ²
	<i>Brenthis daphne</i>	84	197		279	10	570	Database Josef Pennerstorfer & Helmut Höttinger, Austria ³
	<i>Colias palaeno</i>	31	54	1628	279	20	2012	Database Endemic species of Austria, Environment Agency Austria ⁴
	<i>Colias phicomone</i>	68	-	462	428	77	1035	
	<i>Erebia nivalis</i>	72	-	-	8	5	85	Database Tiroler Landesmuseen Betriebsges. mbH, Innsbruck, Austria ⁵
	<i>Euphydryas maturna</i>	870	4	122	-	-	996	
	<i>Lopinga achine</i>	298	174	547	95	1	1115	Staatliches Museum für Naturkunde Karlsruhe, Germany ⁶
	<i>Lycaena helle</i>	53	8	281	76	-	418	
	<i>Maculinea teleius</i>	745	165	979	81	-	1970	Bayerisches Landesamt für Umwelt, Augsburg, Germany ⁷
	<i>Melitaea asteria</i>	41	-	-	21	5	67	
	<i>Oeneis glacialis</i>	21	-	77	191	18	307	Centre Suisse de Cartographie de la Faune, Neuchâtel, Switzerland ⁸
	<i>Parnassius apollo</i>	411	27	515	479	122	1554	
	<i>Parnassius mnemosyne</i>	538	33	166	148	-	885	
	<i>Parnassius phoebus</i>	34	-	6	219	57	316	
	<i>Plebeius optilete</i>	42	28	263	176	19	528	
<i>Pontia callidice</i>	17	-	22	185	21	245		
<i>Pyrgus armoricanus</i>	15	13	127	103	1	259		
	Subtotal (Taxon/country)	3485	836	8245	3394	368	16328	
	Total (country)	15231	9584	27575	24411	6087	82888	

Climate data

Maps of current climatic conditions were taken from WorldClim climate grids available online (www.worldclim.org). The WorldClim database provides monthly climate averages for the period of 1950-2000 for precipitation and temperature (minimum, average, maximum) (Hijmans et al. 2005). We scaled precipitation and temperature data down to 100 m

horizontal resolution by applying a statistical downscaling procedure (Zimmermann et al. 2009, Tabor & Williams 2010). Subsequently, we used these spatially refined temperature and precipitation grids to derive maps of six bioclimatic variables. To reduce collinearity among these variables we selected those that showed some independent variation across the study region (Pearson $r < |0.75|$, Dormann et al. 2013): the maximum temperature of the warmest month (bio5), the minimum temperature of the coldest month (bio6), the temperature annual range (bio7), as well as the precipitation seasonality (bio15), the precipitation sum of the wettest quarter (bio16) and the precipitation sum of the driest quarter (bio17).

Projections of monthly temperature and precipitation series until the end of the 21st century were taken from simulations of the regional climate downscaling experiment ENSEMBLE (<http://ensembles-eu.metoffice.com/papers.html>), which provides regional circulation models for Europe for the IPCC4 SRES scenario family (IPCC 2007). We selected: (i) The Hadley Centre Regional Climate Model (HadRM3.0) model runs (Collins et al. 2006), which are based on the Hadley Centre Coupled Model (hadcm3) general circulation model (GCM) for the A1B scenario with an original resolution of 25 km; (ii) The climate limited-area modelling community (CLM) model runs (Hollweg et al. 2008), based on the ECHAM5 GCM for the A1B scenario that have been generated by the Max Planck Institute at a resolution of ca. 35 km; and (iii) The Rossby Centre regional atmospheric climate model (RCA3) model runs (Kjellström et al. 2005), estimating from the Community Climate System Model (CCSM3) GCM for the B2 scenario and generated by the Swedish Meteorological and Hydrological Institute at a resolution of 50 km. These climate change scenarios differ in terms of projected severity of climate change, and henceforth are referred to as moderate climate change scenario ('ccsm3/B2'), severe climate change scenario ('echam5/A1B') and very severe climate change scenario ('hadcm3/A1B'). Using similar methods as for the current climatic dataset we downscaled and derived decadal averages of the six bioclimatic variables of interest.

Habitat distribution data

Several layers of environmental data were collected for the entire study area. The most important layers of environmental data were those for habitat types and protected areas. The map on habitat types combines several, partly fine grained datasets that have been gathered throughout the entire study region and consequently have been processed and harmonized in the frame of this study. The final version represents a very detailed map source with a spatial resolution of 25m (Figure 2). For the purpose of modelling within SPEC-Adapt, this habitat map has been finally resampled to 100m spatial resolution to meet with the operational level of CATS modelling tools. In WP5 – Task 5.2, this map with 100m resolution was altered according to the conservation management / climate change adaptation scenarios.

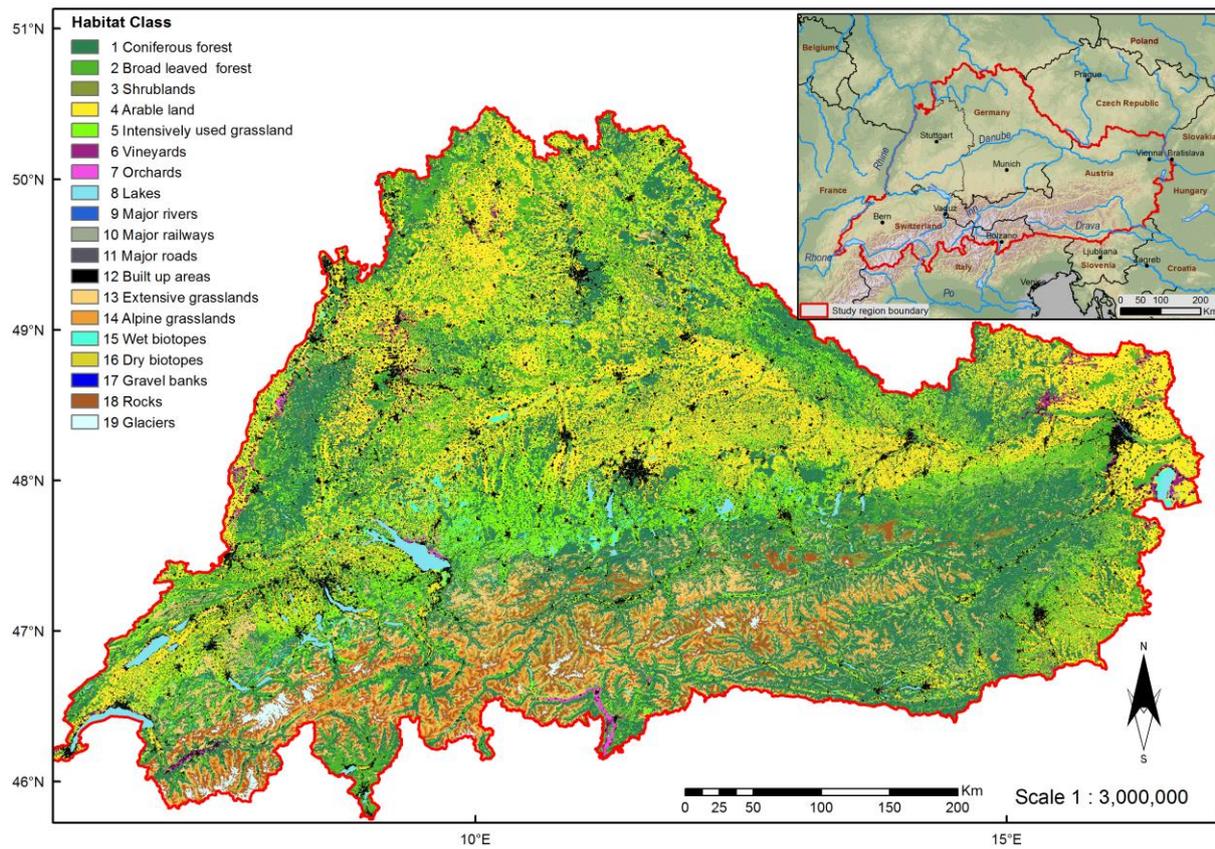


Figure 2. The final habitat distribution map of the study area, encompassing 19 different categories, thereof several are ecosystems of major conservation concern, for instance wet and dry habitats or extensive grasslands (Kuttner et al. 2015).

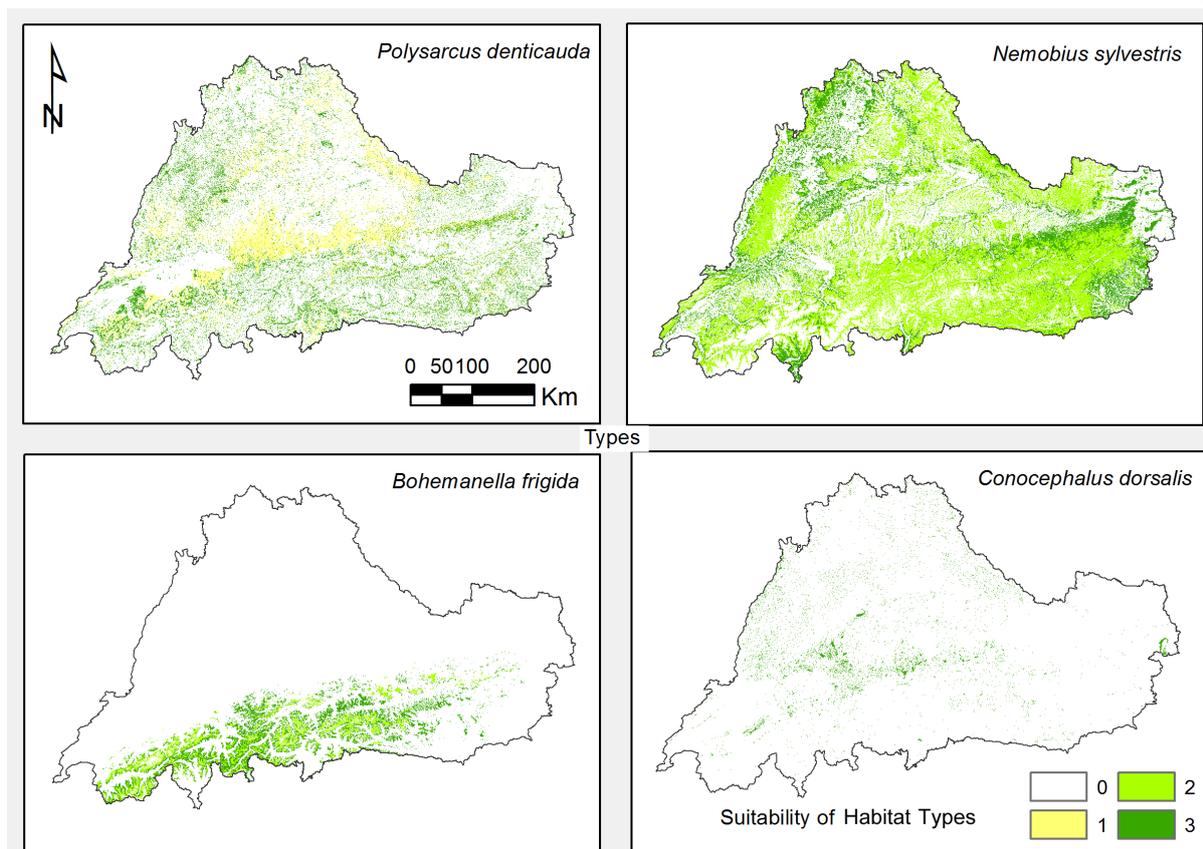


Figure 3. Four habitat suitability maps, exemplarily shown for grasshopper species of differing habitat requirements: *Polysarcus denticauda* inhabits dry and mesic extensive grasslands; *Nemobius sylvestris* is depending on forest cover; *Bohemanella frigida* occurs in rock outcrops and alpine grasslands while *Conocephalus dorsalis* is a very specialized species in wetland areas. The classification of habitat suitability follows a four-stage scale, ranging from “0” (not suitable = exclusion layer) up to “3” (main suitable habitat).

Nature conservation network data

We collected spatial data of the nature conservation networks within the study region (Figure 4). In particular, we collected these data for the European Natura 2000-network for southern Germany, Austria and South Tyrol (not applicable to Switzerland), the emerald network (for Switzerland) and for nationally designated nature reserve categories (i.e. national parks, nature reserves, biosphere reserves). Data on the nature reserve networks were obtained from the national, respectively provincial nature conservation authorities

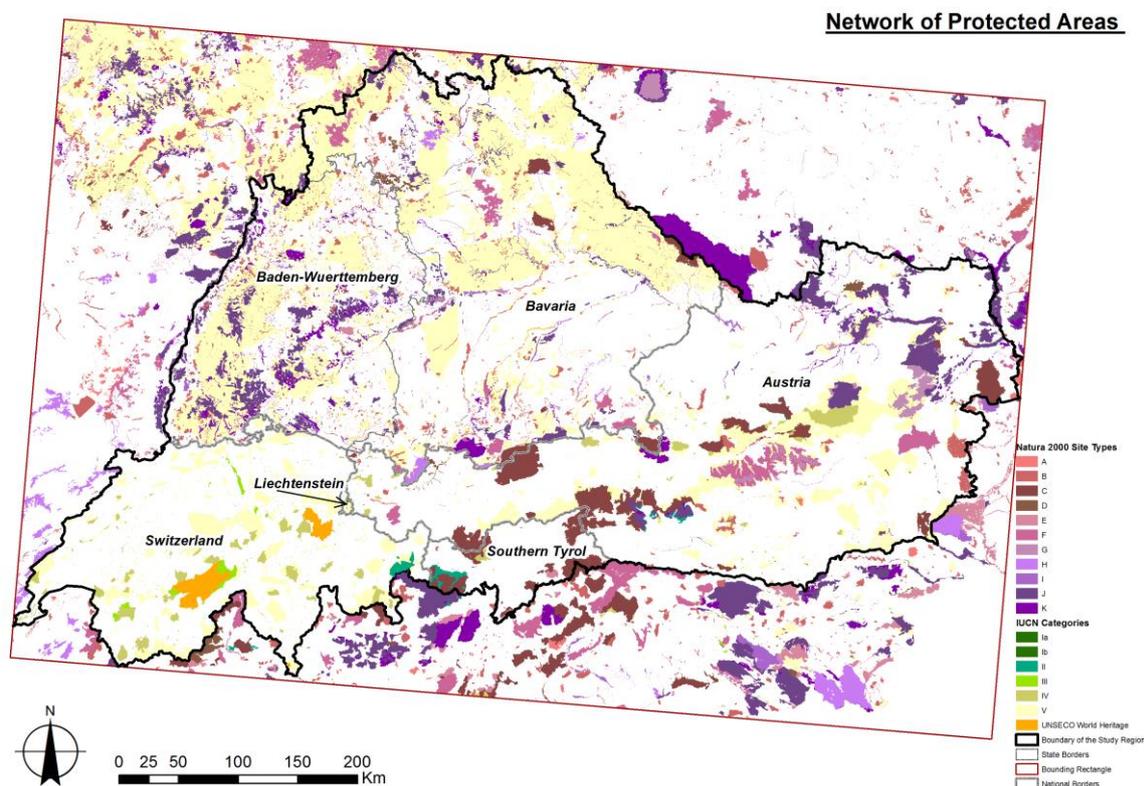


Figure 4. The network of the 18 most important categories of protected areas in the study area.

Generation of habitat suitability layers

Based on our newly established habitat distribution map, maps of suitable habitat were produced for all 60 study species (Figure 3). Therefore, we assigned, separately for each species, ordinal suitability values from “0” (not suitable = exclusion layer) up to “3” (optimal habitat) to each of the 19 habitat categories of the map. Assignment was based on a literature review and supplemented by expert knowledge. For vascular plant species, we used the Austrian Vegetation Database (Willner et al. 2012), for grasshoppers, Baur et al. (2006) and Zuna-Kratky et al. (2009) supplemented by the Austrian Orthoptera Database (Zuna-Kratky et al. unpubl.). In case of butterflies, we extracted information from SBN (1987), Ebert and Rennwald (1993), Settele et al. (2000), Huemer (2004), Bühler-Cortesi (2009), Stettmer et al. (2011), and Bräu et al. (2013). These maps subsequently served as base line for implementing management scenarios and as input for CATS simulations (see below).

Climatic suitability modeling

We parameterized SDMs within the BIOMOD framework (Thuiller et al. 2009) by correlating species presence-absence data to the five bioclimatic variables at the central 100 x 100 m of the angular minute field by means of eight modelling techniques (using BIOMODs default

settings): Generalized Linear Models (GLM), Generalized Additive Models (GAM), Boosted Regression Trees (GBM), Artificial Neural Networks (ANN), Random Forests (RF), Multivariate Adaptive Regression Splines (MARS), Maximum Entropy (MAXENT) and Flexible Discriminant Analysis (FDA). To evaluate model quality for each species and modelling technique, we randomly partitioned distribution data into a dataset for calibrating the models (80%) and one for evaluation (remaining 20%) using the True Skill Statistic score (TSS, Allouche, Tsoar et al. 2006). Based on the parameterized models, we subsequently generated ensemble projections of potential species distribution under current climate (mean of period 1950 – 2000) and under averaged decadal climatic conditions corresponding to the aforementioned climate change scenarios (i.e., 2020, 2030 ..., 2090). These ensemble projections were defined as mean consensus models of the projected occurrence probabilities of the selected (i.e., TSS > 0.5) single models. To produce a full annual time series of projected suitabilities for the whole study area grid we finally used linear interpolations between the decadal projections.

Design of conservation strategies

To test for the potential of conservation measures to counteract negative climate change impacts on species, we converted subsets of grid cells which currently are intensively used by agriculture or forestry into habitats of higher conservation value, and compared these strategies to a business-as-usual strategy, i.e., assuming no change in habitat distribution. We designed conservation strategies differing in the conservation effort, i.e., the number of converted grid cells, and their spatial allocation. Thereby, 1) in the protected area-strategy only grid cells within protected areas were converted. We selected protected areas with a minimum size of 1 ha from the Natura 2000 Network, nationally designated protected areas (CDDA; excluding areas of the IUCN category V because of their weak legal protection status) and biosphere reserves. For Switzerland, which lacks Natura 2000 sites, we included emerald sites, Swiss Parks of National Importance and UNESCO world natural heritage sites; 2) In the corridor-strategy we converted grid cells exclusively within linear corridors of two km breadth which were established to connect the 500 biggest protected areas and within these; 3) In the matrix- strategy we converted grid cells across the study area without any spatial preference to enhance landscape permeability. To account for the time necessary to establish new habitats, conversion of habitats was simulated to take place in the year 2030.

To represent a broad spectrum of plausible conservation efforts we implemented each conservation measure in three levels of efforts, i.e., a moderate (conversion of 1% of all grid cells of intensively used grasslands, arable lands and conifer plantations), a medium (conversion of 3% of all such grid cells), and an ambitious (conversion of 5% of all such grid cells) one. Intensively used grasslands as well as arable land were changed to extensively used grasslands (80% of converted grid cells), dry grasslands (10%) and wet grasslands (10%), while conifer plantations were transformed into deciduous forests. For the matrix-

strategy, grid cells were randomly chosen. Finally, to examine the efficiency of conservation strategies we compared simulated range dynamics based on these strategy with the ones based on the current distribution of habitats, i.e., the business-as-usual strategy (see below).

Simulations of spatio-temporal range dynamics

CATS ('Cellular Automaton-Type tool for simulating plant Spread'; Dullinger et al. 2012) is a spatially and temporarily explicit model operating on a two-dimensional grid (of 100 m mesh size in this case). CATS combines local species demographic rates scaled by occurrence probabilities for each grid cell with dispersal among grid cells. Dispersal is modelled as a combination of wind, exo- and endozoochoric dispersal for plant seeds and based on a correlated random walk within a species-specific maximum flight distance for ovipositing of adult insects. Time proceeds in annual steps. Changes in species' distribution across this grid are driven by the effects of annually changing site (=grid cell) suitabilities (i.e. changing occurrence probabilities as projected by the SDMs) on sub-routines that simulate the local demography of stage-structured cohorts and the eventually resulting local extinctions or colonizations of new sites.

Demographic modelling

Climate-dependence of local demography was modelled by linking demographic rates (seed persistence, germination, juvenile survival, maturation, fecundity and clonal reproduction) and carrying capacity to occurrence probabilities predicted by SDMs by means of sigmoidal functions. Demographic rates were confined by zero and a maximum value derived from literature and databases. Carrying capacity was reduced to 0% (classes 0 and 1 in Fig. 3), 10% (class 2) and 100 % (class 3) of its climatically determined value for cells that are unsuitable, marginally suitable and highly suitable, respectively, to the simulated species according to the habitat map. The rationale of this approach was that carrying capacity of a particular habitat is mainly determined by its proportional area that allows a species to establish a population, and that this proportional area is progressively reduced in less-well suited habitat categories of the habitat map. In addition, juvenile survival and clonal reproduction for plants as well as maturation for insects were modelled as density-dependent processes to account for intraspecific competition.

To account for uncertainty in parameters of demographic rates, we assigned each species two sets of maximum values representing the upper and lower end of a plausible range of values. The above mentioned definition of the sigmoidal function implies different responses of the two sets to environmental stress gradients: higher maximum values for demographic rates result in a stronger decrease with decreasing grid cell suitability allowing the species to grow faster under well suited conditions, but to be more sensitive to deteriorating conditions; and vice versa for the lower set of maximum demographic rate values. Put another way, the

two sets of values correspond (in relative terms) either to a more stress-sensitive (high values) or a more stress-tolerant (low values) demographic strategy.

Dispersal modelling

For wind dispersal of plant species we parameterized the analytical WALD kernel (Katul et al. 2005) based on measured seed traits and wind speed data from a meteorological station in the Central Alps of Austria. Exo- and endozoochorous plant kernels were parameterized based on correlated random walk simulations for one representative of a large ungulate dispersal vector in the study area, the chamois (*Rupicapra rupicapra* L.). During these random walk simulations 10,000 seeds per species were attached to the animals' furs or ingested and subsequently dropped or defecated after a time span corresponding to their surface structures and masses according to regression functions in Römermann et al. (2005) and Moussie (2004). Frequency distributions of the simulated distances between points of uptake and loss were then used to construct dispersal kernels. A detailed description of the dispersal kernel parameterization procedures can be found in (Dullinger et al. 2012). To account for uncertainties in species-specific dispersal rates, the proportion of seeds dispersed by the more far-reaching zoochorous kernels was assumed either as high (1 - 5%) or low (0.1 - 0.5%), hence setting upper and lower boundaries of a credible range of the dispersal ability of species.

We simulated ovipositioning of insects via a correlated random walk. Female adults first deposited 80% of eggs at their grid cell of origin. The consecutive dispersal of insects started in the direction of a randomly selected grid cell among those grid cells in the immediate 8-grid cell neighbourhood which represent the most suitable habitat. The directions of the following steps in the random walk were chosen via a von Mises distribution (with $\mu=0$, $\kappa=2$) (Mardia 1975) given the initial direction. At each step of the random walk (i.e., at each visited grid cell) the female deposited an egg cluster of random size (not extending 50% of eggs not deposited at the grid cell of origin) unless the grid cell represented an unsuitable habitat type (class 0 or 1 in Fig. 3). The random walk was continued until all eggs were deposited or the maximum flight distance was reached. Eggs not deposited when the maximum flight distance was reached were discarded. Due to the restricted number of possible (combinations of) grid cells that could be visited within the maximum flight distance, the number of random walks at each grid cell was restricted to 80. Thus, the overall female population of a grid cell was partitioned to the (max. 80) random walks conducted. Uncertainties in dispersal abilities of insects were regarded for via different maximum flight distances.

Simulation set up and simulation initialisation

To test for the effects of conservation measures on range sizes in 2090 we ran CATS for each of the 60 study species under a full factorial combination of (a) constant current climate and three climate change scenarios; (b) nine conservation strategies (implemented as three

approaches of spatial allocation x three levels of conservation effort) and a business-as-usual strategy (no conservation measures undertaken, i.e., the habitat configuration remains unconverted); and (c) two sets of demographic and dispersal parameters representing a more stress-tolerant and spatially conservative vs. a more stress-sensitive and spatially mobile strategy of each species. To account for stochastic elements in CATS, we averaged results derived from five replicated runs for further analyses.

Species habitat affiliations do not perfectly match those habitats for which spatially explicit information is available but limit species occurrences to microhabitats within broader habitat categories represented in our habitat distribution map. Thus, we used an iterative procedure that reduced the number of grid cells within the broad (suitable) categories of the map until the size of species' ranges did not fluctuate by more than 10% within 50 years of CATS simulation under current climatic conditions. This procedure was applied by re-classifying randomly selected suitable grid cells (but keeping grid cells with documented real species occurrence) – as unsuitable. This modified, restricted habitat suitability layer was used to generate initial distributions (see below) as well as in all simulation runs of the respective species.

All 4 x 10 x 2 x 5 (climate x restoration measures x demographic parameters x replication) simulation runs started with the same initial current distribution of the respective species. This current distribution was defined by overlaying SDM projections under current conditions (100 m resolution) with species occurrences (angular minute resolution). Species were assumed to be present in all 100 x 100 m grid cells, which were (1) projected to be suitable under current climatic conditions (for the technical definition of climate suitability of grid cells see (Dullinger et al. 2012)), (2) within angular minute fields where the species has actually been observed, and (3) representing a highly suitable or marginally suitable habitat. Initial population sizes at these grid cells were set to half of the carrying capacity. To accommodate these arbitrary population sizes to the actual local conditions we started simulations of range dynamics with a burn-in phase of 25 years run under constant current climatic conditions. This burn-in phase (which assumes grid cell suitability corresponding to mean climatic conditions of 1950 – 2000) was linked to suitability predictions based on the future climate projections (starting at 2010) by linear interpolation for the years 2000 to 2010.

Indices of distributional change

We quantified the effect of climate change and conservation measures on projected range sizes of species as $\log(\text{range size at 2090} / \text{range size at 2010})$ and $\log(\text{range size applying a conservation measure at 2090} / \text{range size without this measure at 2090})$. These log-ratios ensure changes in range size (i.e., increases or decreases) to be symmetric around zero. To compare the effects of conservation measures among habitats, species were assigned to all habitats classified as highly or moderately suitable (classes 2 and 3 in Fig. 3) for the respective species.

Results

We concentrate here on reporting the main project results regarding the effects of climate change on range dynamics and its possible mitigation by management measures as evaluated by CATS simulations. For the results from SDMs only see the annexed paper Kuttner et al. (in revision).

Species extinction events and their timing

We found that a substantial fraction of study species are projected to become extinct in the 21st century under climate change, particularly if climate change is severe (Figure 6). Alpine species were more likely to completely lose their range (20-27% of species; depending on the climate change scenario) than lowland (= (sub)montane) species (10-20%) and became extinct earlier. Among taxonomic groups, grasshoppers showed the highest number of species committed to extinction. These patterns were constant across climate change scenarios. In contrast, under constant climatic conditions no single species was predicted to go extinct. Overall, the effectiveness of all conservation strategies to delay or prevent extinction events under climate change was low: there was very little variation in the timing of projected extinction events and in the number of species projected to become extinct in the decades to come (Fig. 6).

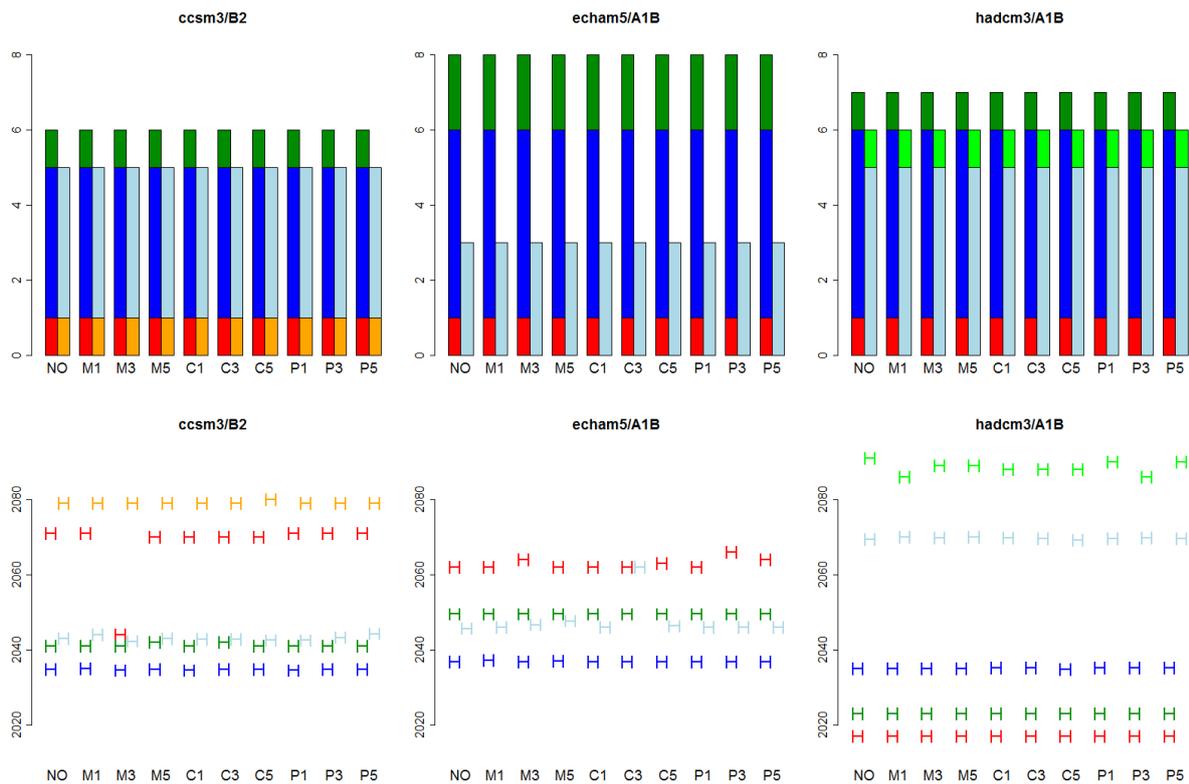


Figure 6. Comparison of the number of species predicted to go extinct during the 21st century (upper row) and the average year where extinction is simulated to happen (lower row) among conservation strategies under three climate change scenarios. Red, blue and green denote butterflies, grasshoppers and plants, respectively. Dark (left columns) and bright (right columns) colours represent alpine and lowland (i.e. (sub)montane) species, respectively. Labels refer to conservation strategies applied by converting intensively used habitats into habitats of higher conservation value within protected areas (P), within corridors connecting protected areas (C) and in the landscape matrix (M) assuming moderate (i.e., 1% of grid cells being converted; represented by P1, C1, M1), medium (3%) and ambitious (5%) conservation efforts. NO refers to the business-as-usual strategy, i.e., no conservation measure (i.e., habitat conversion) was applied.

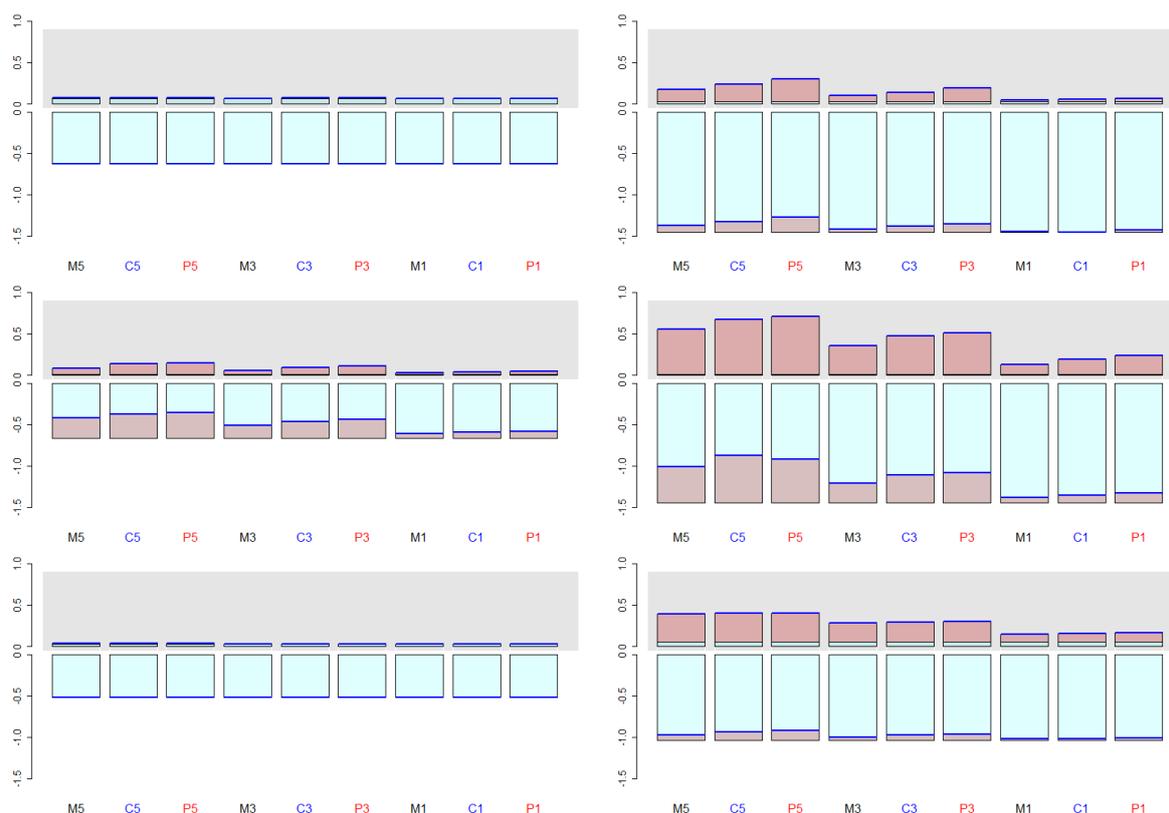


Figure 7. Effects of projected climate (turquoise bars) and conservation strategies (red bars) on range size of butterfly (upper panels), grasshopper (centre) and plant species (lower panels) until the end of the 21st century. Effects of climate change and conservation strategies were calculated as $\log(\text{range size at 2090} / \text{range size at 2010})$ and $\log(\text{range size applying a conservation scenario at 2090} / \text{range size of the business-as-usual strategy 2090})$, respectively. Thus negative values denote range losses, and positive ones range gains. The blue lines denote the net effects of climate and conservation strategies. Denoted are means computed separately for alpine (left column) and lowland (right) species of each taxonomic group. Simulations assuming current climatic conditions to be stable during the 21st century are indicated by a grey background, while bars in front of a white background are based on very strong climate change (hadcm3/A1B). Conservation strategies were applied by converting intensively used habitats into habitats of higher conservation value within protected areas (P; black label text), within corridors connecting protected areas (C; blue) and in the landscapes matrix (M; red). For each spatial allocation we assumed conservation efforts to be moderate (i.e., 1% of grid cells were converted; represented by P1, C1, M1), medium (3%) and ambitious (5%). Results are averaged over five simulation runs assuming a stress-sensitive demographic strategy of species. Species predicted to go extinct until 2090 were excluded.

Changes in range size

Under current climate mean range sizes of alpine as well as lowland species are predicted to change only marginally until the end of the 21st century for the three taxonomic groups (Figure 7). In contrast, under severe climate change (hadcm3) mean range sizes were projected to decrease to less than a half compared to current range sizes, even when species projected to go extinct during the 21st century were disregarded. While alpine butterflies, grasshoppers and plants lost on average 47%, 49% and 41% of their range, respectively, values for lowland species were 77%, 76% and 64%. The mitigating impacts of

conservation strategies on projected range sizes (Figure 7) were negligible for alpine species under current climate and all climate change scenarios – except for the grasshopper species *Miramella alpine* and, particularly, *Stauroderus scalaris*. In contrast, range sizes were projected to decrease less than under the business-as-usual scenario under each conservation strategy for lowland species. This mitigating effect was the higher the higher the conservation effort. Effects of corridor and protected area strategies generally did not significantly differ but were both higher than the effect of random placement of restored habitat. We found an interaction of climate and conservation strategy as mean effects of conservation measures were higher under current climate than under climate change (two-sample t-tests: $t = 4.86$, $p\text{-value} = 0.001$ for butterflies; $t=10.04$, $p<0.001$ for grasshoppers; and $t=7.07$, $p<0.001$ for plants). Furthermore, positive effects of conservation strategies on range sizes were lower for plants than for butterflies ($t=-2.32$, $p=0.049$) and grasshoppers ($t=-4.93$, $p=0.001$). As a result, conservation strategies had a positive effect on projected range sizes under current climate, but net changes in species range sizes were negative under all climate change scenarios due to the overwhelming effects of climate-driven range losses.

The importance of species ecology

Lowland species are generally simulated to increase their range size in response to conservation strategies under current climate, and, with the exception of plants, to face reduced range loss under climate change (Figure 8). Thirty to 60% of grasshopper species were projected to at least double their ranges (as compared to a business-as-usual scenario), while such a strong increase occurred only for one single butterfly and plant species, respectively. In contrast, range sizes of most alpine species did not respond to the conservation strategies (data not shown). We moreover found that the effects of the conservation strategies on range sizes differ strongly among species of different affiliations (Figure 9, left). Effects were weaker for forest species than for grassland species, whereupon dry and extensive grassland species responded stronger than species of wet grasslands. Range size gains (as compared to a business-as-usual scenario) of species of dry and extensive grasslands are stronger under current climate than under climate change (Figure 9, right). Among the latter, effects of conservation strategies are weakest under moderate climate change, and becomes more pronounced under severe climate change.

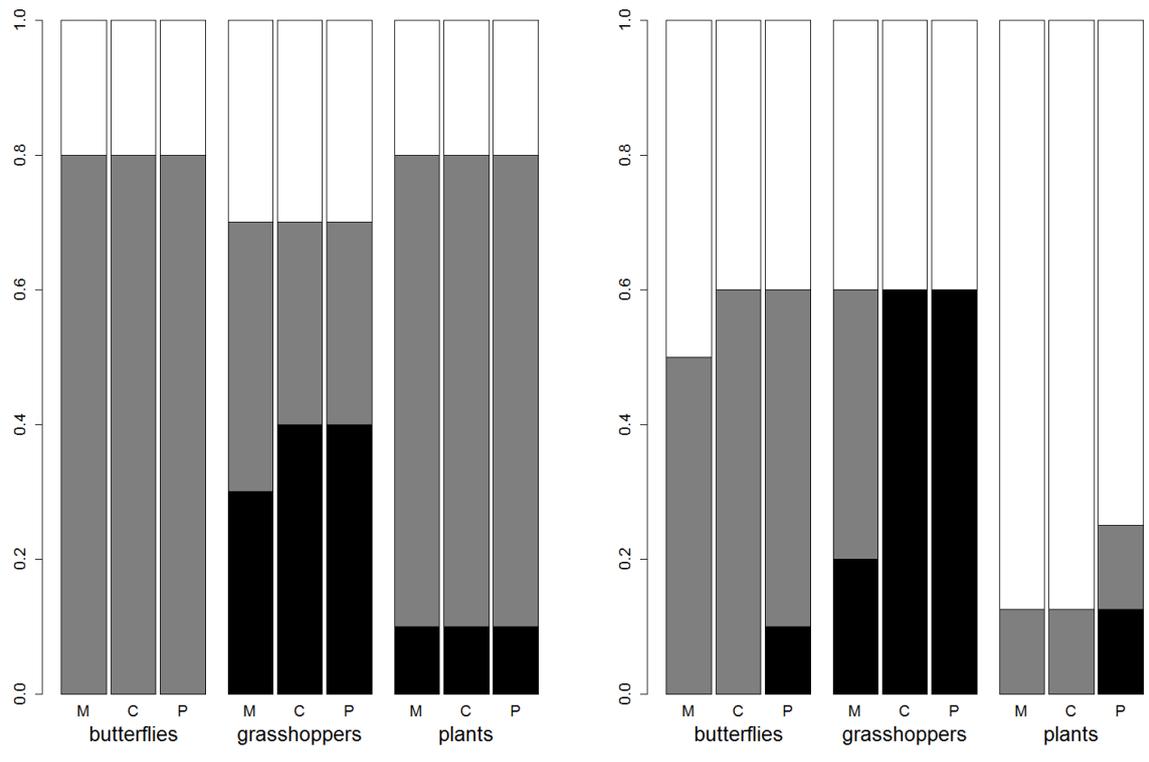


Figure 8. The impact of ambitious conservation efforts (i.e., conversion of 5% of the intensively used area) on projected range size of lowlands species at the end of the 21st century. White, grey and black bars represent the proportion of species responding marginally (gains or losses of range size <5%), moderately (gains in range size 5-100%) and strongly (gains in range size > 100%), respectively, to the conservation strategies applied in protected areas (P), corridors (C) and landscape matrices (M). Results were averaged across 5 simulation runs under current climate (left panel) and severe climate change (right panel; hadcm3/A1B). Under less severe climate change (ccsm3/B2, echam5/A1B) results were very similar and are therefore not shown.

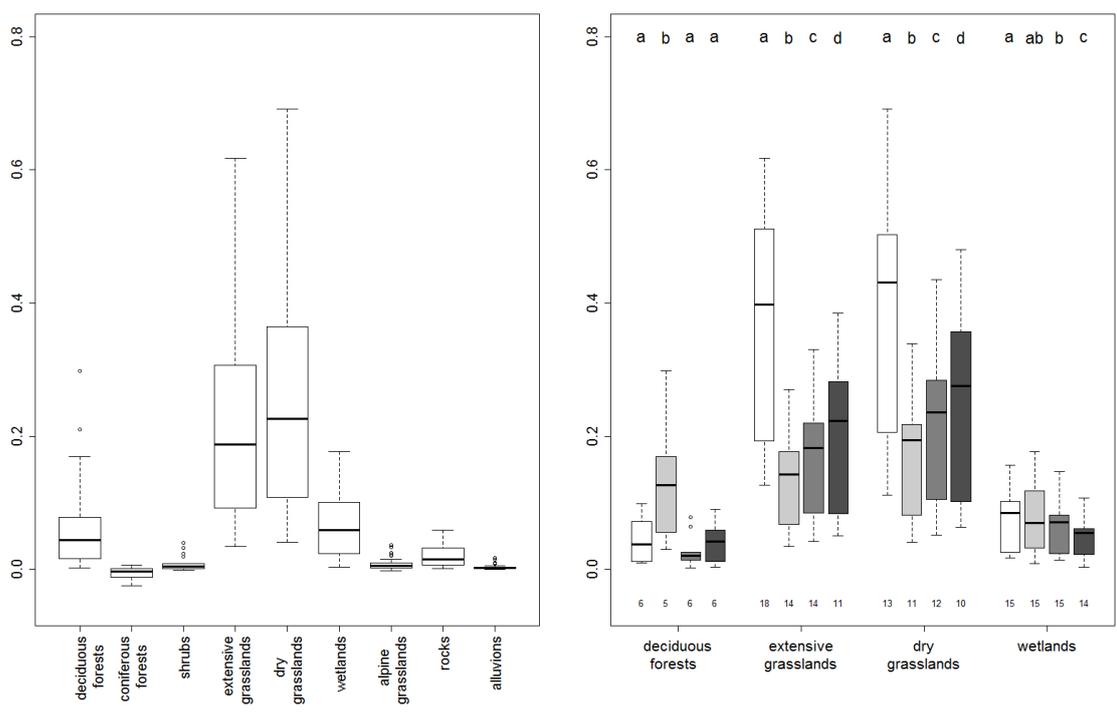


Figure 9. Effects of conservation strategies compared among species with different habitat affiliations. Boxplots represent the variation in mean effects (averaged across species) across the nine conservation strategies (three spatial allocation patterns x three efforts). These were pooled for current and predicted future climate (left panel) and shown separately (right panel) for current climate (white), for moderate (ccsm3/B2; light grey), strong (echam5/A1B; medium grey) and very strong (hadcm3/A1B; dark grey) climate change. Only semi-natural habitats whose size was increased by the applied conservation strategies are shown. Note that species were assigned to each habitat being moderately or highly suitable to the respective species. Values at the bottom denote the number of species represented by each boxplot. Lower case letters indicate significant differences of conservation effects derived from paired t-tests. Results are average across 5 simulation runs assuming a stress-sensitive demographic strategy of species. Species predicted to go extinct until 2090 were excluded.

4 Schlussfolgerungen und Empfehlungen

Considering the interacting effects of global climate and land use change is of crucial importance in the assessment of future species' threats of range losses or extinction. For 60 species of three taxonomic groups we simulated the effects of conservation strategies (i.e., combining three spatial configurations and three levels of effort) under current climate and three future climate scenarios. As the application of species-specific conservation strategies for a set of species is not feasible, we designed common conservation strategies on a landscape level, by transforming anthropogenic habitats (intensively used grasslands, arable lands and conifer plantations) into habitats of high conservation value.

Extinction

Our results indicate that these conservation strategies can neither prevent nor significantly delay species' extinctions caused by climatic deterioration during the 21st century. Even in case of ambitious conservation efforts, i.e. the conversion of 5% of the overall study area, no species could be protected from extinction. We assume the time necessary to implement conservation measures after the decision making to be about 20 years and hence applied the conservation strategies in 2030. At that time climate induced range losses were already severe for several species. Thus, the implementation of conservation measures was likely too late for these species.

This finding shows that the identification of threatened species not affected by 'general-purpose habitat restoration' is highly important. Furthermore, there is no systematic review of response times to conservation strategies (Akçakaya et al. 2014). We argue that with 'general-purpose habitat restoration' at regional scales, as implemented in our simulations, response times are likely to be much longer, as the single species requirements are only to be met by part of the measures. Therefore, we recommend further analyses of response times to different conservation efforts.

Conservation mitigates climate losses only for lowland species

For species primarily occurring at (sub) montane elevations (within our study area), conservation measures can reduce climate change induced range loss and hence secure viable population sizes that buffer against environmental, demographic or genetic stochasticity (Peer et al. 2014). For alpine species, the conservation measures showed no or very limited effects, because there is little intensively used land to restore. This finding implies that for species of high altitudes, habitat restoration is a largely inappropriate conservation measure. Instead, the results of Kuttner et al. (in revision) suggest that maintenance of low or moderately intensive land use and upper montane and subalpine elevations can be beneficial for many species, especially those adapted to non-forest habitats from lower elevations which are forced to migrate upslope under climate warming.

Spatial arrangement of conservation measures matters

Our simulations indicate that increasing the overall permeability of the landscape (i.e., the matrix scenario) has significantly less effect than either improving habitat suitability in protected areas or increasing their connectivity. Hence, the spatial configuration of restored habitats is important. If climate change leads to a slow range shift, restoration measures which increase aggregation of suitable habitats in protected areas perform best, as most modelled species already occur there. On the other hand, if the species range shifts outside of protected areas, aggregated suitable habitats along corridors result in the strongest effect, as they lead to faster and directed migrations. Although increasing the overall permeability of the landscape is also a strategy to support dispersal, it results in diffuse undirected migration which furthermore includes larger dispersal distances.

Implications for species conservation

We found that even ambitious habitat restoration programs will not be able to fully compensate for the negative effects of climate warming on the modelled biota. This is a troublesome result as it shows that there likely are severe limits to compensate for the negative impacts of climate change on species by improving habitat suitability or landscape connectivity.

For at least partial mitigation, adjustment of current elevational land use gradients with reduction of intensity and extensive habitat restoration in lowland areas, but maintenance or expansion of moderate use at higher elevations appears a sensible long-term strategy. Further, our results underpin the necessity to supplement the tested conservation strategies with species-specific conservation programmes.

In general, our approach in itself helps to advance concepts and simulations in conservation biology and may aid forthcoming conservation planning.

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B) Projektdetails

5 Methodik

Work Package 1: Species selection, collection and harmonization of distribution data

Initially, a total of 50 plant, 22 grasshopper and 20 butterfly species were selected to cover a range of different ecological profiles enabling tests for different climate change vulnerabilities and the potential for adaptation. We also considered distribution data quality and availability for the selection. Of this species data set, we subsequently subsampled 60 species for the full set of analyses (Table 1), i.e. 10 lowland and alpine species for each taxonomic group. This approach ensured a balanced representation of study species of each taxonomic group along an altitudinal gradient.

Distributional data were collected for the 50 plant, 22 grasshopper, and 20 butterfly species for the entire study area (Austria, Bavaria, Baden-Wuerttemberg, and Switzerland, SouthTyrol, Figure 1). As we obtained species distribution data from various federal institutions, research groups and databases, spatial reference systems partly differed and resolution of the data was ranging from precise point data up to grid mapping specifications on angular minute or quadrant (i.e. 3 x 5 angular minutes) level. We consequently chose the minute field grid for data harmonization purposes: Fine-scaled point data was assigned to the centroid of the underlying minute field. We applied the same procedure for the minute-field data while in case of the coarser quadrant data we randomly selected one minute field within the target quadrant for the assignment. In case of overlapping data provision we always selected the finer-scaled and more recent data source. We set a threshold year for the occurrence data applied within this study by 1990; older records have not been considered. Within every quadrant where a target species was not recorded we randomly set one minute-field as 'absent' and assigned all remaining fields as 'NULL' (i.e. No Data). Further, to avoid double counting we cleared the database and only kept the most recent entries. This procedure was iteratively conducted for all individual target species datasets to establish a standardized input table, consisting of 105,428 rows that regularly covered the entire study region of approx. 240,000 km².

Work Package 2: Collection of demographic traits for dynamic modelling

Demographic parameter values for plant, grasshopper and butterfly species were collected by extracting species-specific data from databases and literature. The lower and upper boundaries of the range of probable parameter values were determined using expert opinion of taxonomic group experts.

Work Package 3: Collection of environmental data and climate change scenarios

Current climate was mapped as 100 m raster data, downscaled from 1 km Worldclim climate grids. Worldclim provides long-term monthly climate averages for the period of 1950–2000 for precipitation and minimum, average and maximum temperature and a series of nineteen bioclimatic variables directly derived from the monthly grids. We first downscaled monthly base maps to a spatial resolution of 100 m to better represent the topographic variation of climate in our study area. In a second step we used these downscaled temperature and precipitation grids to re-generate maps of five bioclimatic variables which (1) have an obvious impact on organisms in mountain environments; and (2) showed some independent variation across the study area (Pearson $r < |0.75|$): the maximum temperature of the warmest month (bio5), the minimum temperature of the coldest month (bio6), the temperature annual range (bio7), as well as the precipitation seasonality (bio15), the precipitation sum of the wettest quarter (bio16) and the precipitation sum of the driest quarter (bio17). The downscaling procedure can be summarized as follows: at the 1 km spatial resolution, we analysed the dependency of precipitation and temperature on elevation by means of linear regressions in circular moving windows of 15 and 25 km radius, respectively. We chose smaller moving windows for precipitation, because of the better fit in cross-validation exercises. By doing so, we extracted the hidden lapse rates and '0 m above sea level' temperature and precipitation intercepts inherent in the Worldclim maps. We stored lapse rates and intercepts to the center cell of each window position and then spatially interpolated these regression parameters to a 100 m resolution by means of inverse distance-weighted interpolation. Finally, the interpolated regression parameters were applied for back conversion to climate maps using a 100 m digital elevation model, which was aggregated from the 90 m SRTM DEM3 version 4.0 in ArcGrid. In summary, this procedure allowed us to, first, extract the hidden regression parameters of the Worldclim maps, and, second, to spatially scale them to the resolution of 100 m.

Projections of monthly temperature and precipitation series for the 2001 to 2100 time span were taken from simulations that the Max Planck Institute has generated based on a regional circulation model. Specifically, we used the climate limited-area modelling community model runs, which were fed by output from the ECHAM5 general circulation model for the A1B scenario. This output is available as a 1961–2100 daily or monthly data series in NetCDF format at a 20' (~36 km) spatial resolution, and was downloaded from the CERA world data centre for climate in Hamburg (<http://cerawww.dkrz.de/CERA>). We downloaded the monthly averages, and then calculated monthly anomalies for temperature (min, average, max) and precipitation (sum) against a 1961–2000 monthly mean of the same CLM simulation output. By doing so we hence calculated the changing climate series relative to the same baseline time span available from Worldclim1. Anomalies for temperature were expressed as absolute differences, while precipitation anomalies were calculated as relative differences. These anomalies were then scaled in a first step to a 1 km, and in a second step to a 100 m spatial resolution. Next we added (temperatures) or multiplied (precipitation) the anomalies at the 100 m spatial resolution with the downscaled 100 m climate maps in order to generate

monthly climate time series for our study area. By this we had derived a time series of future climate data at a 100 m spatial and a monthly temporal resolution. Finally, we re-calculated the five bioclimatic variables for the full time series 2001–2100 and then smoothed these series by a nine-years moving average to measure climatic suitability of sites by mid-term climatic conditions rather than by annual fluctuations.

Work Package 4: Re-coding and adaptation of the CATS modelling environment

The main tasks in this WP was the re-coding and adapting the CATS modelling software to represent the specific requirements of animal species, as CATS has been originally designed and programmed for vascular plant species. For this purpose, we re-coded and implemented new demographic modules and dispersal kernels within CATS which were based on the life history traits of grasshoppers and butterflies.

With respect to demography, stages of butterfly and grasshopper development were restricted to eggs and adults because the mobility of larval stages of the selected insect species is marginal at the spatial resolution of our 100 x 100 m grid cells. The two stages were linked by the processes of maturation, defined as the probability of an embryo within an egg to pass through all larval stages and survive until the reproductive stage; and fecundity, defined as the number of eggs produced by an average female individual. Both processes were linked to habitat suitability, as projected by the SDMs, in the same way as in the case of plants, i.e. by sigmoid functions with inflection points set to binary occurrence thresholds (Dullinger et al. 2012).

Dispersal of insect species was implemented by random walks that were executed on the fly within CATS simulation runs. For details see description under 2.2.3 of this report (subheading Dispersal modelling).

Work Package 5: Simulation of species range dynamics under climate change

Species distribution models (SDMs) were calibrated by linking pre-processed species distribution data (see also WP1) with the current climate conditions (named 'base' from here on) at the central 100 × 100 m raster cell of each angular minute field across the study region. Based on these parameterized models, we subsequently generated ensemble projections of potential species distribution under current climate (mean of period 1950 – 1999) and under climatic conditions corresponding to the aforementioned climate forecast scenarios for ten consecutive centuries from 2001 – 2090 by applying the previously smoothed nine-year moving average bioclimatic datasets. Visualization of SDM outcomes is exemplified in Figure 5 by showing the base projection and future forecasts for the grasshopper species *Tetrix tuerki*.

For further details on SDM modelling see description under 2.2.3 of this report (subheading Climatic suitability modelling).

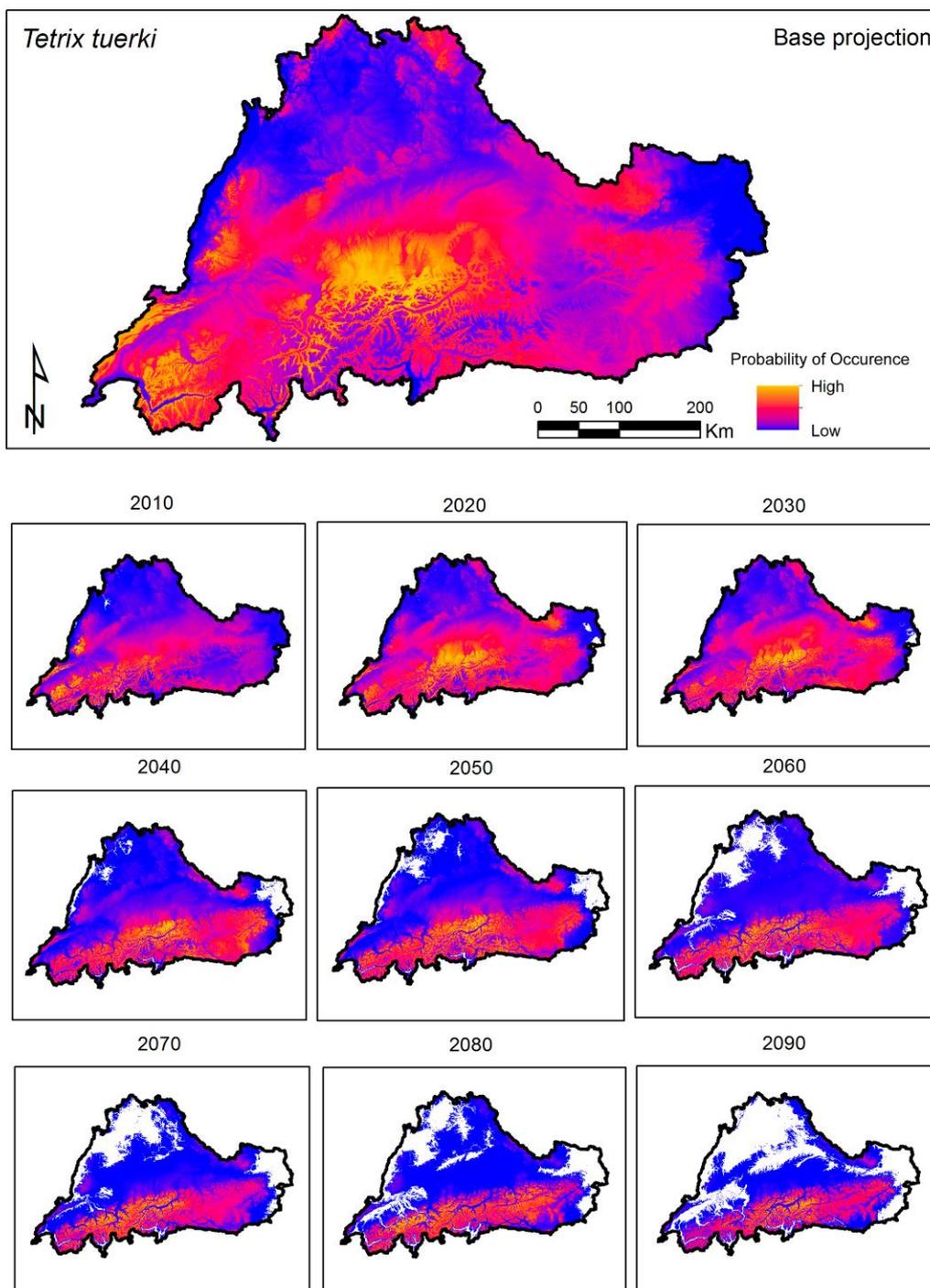


Figure 5. Base and future projections for every decade applying the A1B-ECHAM5 global circulation model, here exemplarily displayed for the grasshopper species *Tetrix tuerki*. A decrease in occurrence probability is predicted under climate change.

Work Package 6: Recommendations for management

We have tested nine management scenarios representing a factorial combination of three levels of management intensity with three different spatial allocation strategies. To represent

a broad spectrum of plausible conservation efforts we implemented each conservation measure in three levels of efforts, i.e. a moderate (conversion of 1% of all grid cells of intensively used grasslands, arable lands and conifer plantations), a medium (conversion of 3% of all such grid cells), and an ambitious (conversion of 5% of all such grid cells) one. These management scenarios represent a landscape corridor approach, a landscape matrix approach and the strengthening of the current protected area network. For further details see description under 2.2.3 of this report (subheading *Design of conservation strategies*).

Work Package 7: Synthesis and publication

Project results were already (Kuttner et al. 2015) published, are currently in press (Essl et al. 2016), in revision (Kuttner et al. in rev.), or in preparation (Wessely et al. in prep) for peer-reviewed scientific journals, have been presented at scientific conferences (e.g. oral presentations at the Austrian Climate Days 2015 and 2016), and in journals and magazines intended for conservation managers and decision makers in the nature conservation sector (e.g. https://www.klimafonds.gv.at/assets/Uploads/Broschren/ACRP-in-Essence/KLIEN_ACRP_Biodiversitaet.pdf).

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Kuttner M, Hülber K, Moser D, Rabitsch W, Schindler S, Wessely J, Gattringer A, Essl F, Dullinger S (in review.) Habitat availability disproportionately amplifies climate change risks for lowland compared to alpine species. *Diversity and Distributions*.

6 Arbeits- und Zeitplan

Phase 1

In phase 1 of the project, the study species were selected and species data were gathered at a high-resolution for the full study region. In addition, the collection and preparation of the

relevant functional traits for the study species was done. Finally, the relevant climatic and environmental data for the study region were compiled and processed.

Phase 2

In phase 2, all necessary updates of the CATS framework have been implemented and subsequently habitat distribution modelling initialization of parametrization of CATS has been done. In addition, the Central European Habitat map has been compiled and published.

Phase 3

In phase 3, the conservation scenarios have been designed and implemented, and CATS modelling has been performed. The second manuscript (Kuttner et al. in revision) has been written and submitted.

Phase 4

The final CATS modelling work has been done, the project findings have been interpreted in the context of climate change, adaptation measures and future species risks and the third (Wessely et al. in prep.) and fourth (Essl et al. in press) publications have been drafted.

7 Publikationen und Disseminierungsaktivitäten

Kuttner M, Essl F, Peterseil J, Dullinger S, Rabitsch W, Schindler S, Hülber K, Gattringer A & Moser D (2015) A new high-resolution habitat distribution map for Austria, Liechtenstein, southern Germany, South Tyrol and Switzerland. *Eco.Mont* 7:18-29.

Kuttner M, Hülber K, Moser D, Rabitsch W, Schindler S, Wessely J, Gattringer A, Essl F, Dullinger S (in review.) Habitat availability disproportionately amplifies climate change risks for lowland compared to alpine species. *Diversity and Distributions*.

Wessely J, Hülber K, Gattringer A, Kuttner M, Moser D, Rabitsch W, Schindler S, Dullinger S & Essl F (in prep.) The limits of conservation strategies to mitigate climate change-induced range losses.

Essl F, Hülber K, Gattringer A, Kuttner M, Moser D, Rabitsch W, Schindler S, Wessely J & Dullinger S (in press) Können Naturschutzmaßnahmen die klimawandelbedingte Risiken für Arten kompensieren? Das Projekt Spec-Adapt. *Natur und Landschaft*.

A manuscript, summarizing the entire process of environmental data collection, harmonization and map creation of the aforementioned habitat map and entitled “A new high-resolution habitat distribution map for Austria, Liechtenstein, southern Germany, South Tyrol and Switzerland” has been published in issue 7/2 of the scientific journal “eco.mont”: <http://epub.oeaw.ac.at/?arp=0x00324710>.

A manuscript, dealing with changes in the potential distribution ranges within the subsets of lowland and alpine species is currently under revision (Kuttner et al. in rev.). The manuscript

is entitled “Habitat availability disproportionately amplifies climate change risks for lowland compared to alpine species” and was submitted to the scientific journal “Diversity and Distributions” by late November 2015 (Kuttner et al. in rev.). We have received the largely favourable reviews in early April 2016, and will submit the revised manuscript in the weeks to come.

The publication on the main results of the dynamic modelling results is currently in preparation (Wessely et al. in prep.) and will be soon submitted to a scientific journal.

The publication of Essl et al. (in press) summarizes the approach and major outcomes of Spec-Adapt in German language and is published in the leading German-speaking conservation journal “Natur und Landschaft”.

Diese Projektbeschreibung wurde von der Fördernehmerin/dem Fördernehmer erstellt. Für die Richtigkeit, Vollständigkeit und Aktualität der Inhalte übernimmt der Klima- und Energiefonds keine Haftung.