Global Ecology and Conservation 23 (2020) e01113

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: http://www.elsevier.com/locate/gecco

Original Research Article

Habitat availability disproportionally amplifies climate change risks for lowland compared to alpine species

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ARTICLE INFO

Article history:
Received 13 March 2020
Received in revised form 4 May 2020
Accepted 10 May 2020

Keywords:
Alpine and lowland species
Ecological niches
Habitats
Insects
Species distribution modelling
Vascular plants

ABSTRACT

Climate-driven range dynamics of species will interact with land use patterns that have reduced and fragmented habitat types needed for species' survival. This interaction could either amplify or mitigate the threats to species from climate change, but has so far been little explored. Here, we investigate whether shifts of suitable areas under future climatic conditions would increase or decrease the match between potential climatic ranges and the availability of appropriate habitat types. Using Central Europe (Austria, Liechtenstein, Switzerland, southern Germany, northern Italy) as study region, we applied "climatic" species distribution models to 51 species from three taxonomic groups (butterflies, grasshoppers, vascular plants) that are bound to natural or semi-natural habitats of either low or high elevations (i.e. those that mainly occur below or above the tree line) and pruned their distribution to appropriate habitats to predict species' current and future ranges in Central Europe. We found 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 lowland species, but generally increases for species of high elevation, especially for plants and butterflies. The observed pattern can be explained by a decrease of land use intensity towards higher elevations. The detected buffer effect of land use patterns for alpine species might, however, vanish in the long run as both climate and land-use interests may modify the spatial habitat pattern itself. We conclude that adjustment of land use practices by reducing the intensity in lowland areas, but maintaining moderate use at higher elevations appears the most sensible long-term strategy to reduce climate change effects on central European biodiversity.

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https://doi.org/10.1016/j.gecco.2020.e01113

1. Introduction

Climate warming and land use change are expected to be the two most important drivers of 21st century biodiversity loss (Pereira et al., 2010; IPBES, 2019). Indeed, many studies have already documented how species' populations have declined and/or shifted their geographical distributions in response to one of these two drivers (e.g. Walther et al., 2002; Parmesan and Yohe, 2003; Thuiller et al., 2005; Pauli et al., 2012; Jantz et al., 2015). In addition, their interactions are expected to create a "deadly anthropogenic cocktail" (Travis, 2003) as human degradation and fragmentation of (semi-)natural habitats may impede species migration.

Apart from hindering climate-driven range shifts, the interplay of land use and climate change may have additional effects on species' ranges and biodiversity patterns. In particular, climate change may shift climatically suitable ranges of species to regions where land use has already largely reduced or fragmented habitat types appropriate for the species. In contrast, some species might be able to colonize areas where appropriate habitat types are still larger and less fragmented than within current climatically suitable ranges. For example, a warmer climate might drive central European forest understorey species farther to the north-west of the continent, where land use intensification has greatly reduced the natural forest cover, or more to the north-east (Scandinavia), where forest cover is largely intact (Dullinger et al., 2015). As a consequence, purely climate based risk assessments will either under- or overestimate the actual threat to such species.

Whether and how the geographically varied availability of suitable habitat types will alter climate driven risks to species has been little explored so far (Titeux et al., 2016; Sirami et al., 2017; Dullinger et al., 2020). Idiosyncratic land use histories will certainly play an important role in this context, but some general trends might nevertheless be expected. In Europe, for example, land use intensity is highest in lowland areas, but much lower in the subalpine and alpine belts of mountain systems (Nogues-Bravo et al., 2008; Kampmann et al., 2012). It appears hence likely that shifts of potentially suitable climates could drive species confined to lowland habitats into areas where appropriate habitat types have been drastically reduced and fragmented. By contrast, if climate warming shifts a species range towards high altitudes, it may encounter more intact habitats there. As a corollary, the interplay with land use patterns could even buffer alpine species against climate-driven habitat loss to a certain degree and hence compensate for their expected higher vulnerability to climate change (e.g. Dirnböck et al., 2011; Engler et al., 2011; Wessely et al al., 2017). However, it is unknown if the smaller size of high altitude areas (Elsen and Tingley, 2015) counteracts such potential rescue effects.

Correlative species distribution models (SDMs) are the most frequently used tool to evaluate climate threats to biodiversity (e.g. Thuiller et al., 2005; Elith et al., 2010; Araújo et al., 2011; Engler et al., 2011). These models statistically relate occurrence data, which represent the realized niche of species, to environmental variables and are used to project altered (potential) species distributions in response to shifting climatic conditions. SDMs do not account for potential changes in biotic interactions as a consequence of environmental changes, nor do they account for a species' ability to track its changing environmental niche in geographic space due to e.g. dispersal limitation (Guisan and Thuiller, 2005). However, interactive effects of habitat availability can, in theory, be easily integrated into such models by using land-cover types as additional predictor variables (e.g. Dirnböck et al., 2003; Luoto et al., 2007; Stanton et al., 2012). In practice, this approach may face severe data limitations. Whereas climatic conditions are more or less continuously varying features of landscapes and can thus be interpolated from point measurements with reasonable accuracy at a broad range of different spatial grains (e.g. Zimmermann et al., 2009; Pradervand et al., 2014), land use patterns create complex mosaics of small units with often distinct boundaries that defy common downscaling procedures of available coarse-grain land-cover data (Titeux et al., 2016). Model accuracy is thus limited by the spatial resolution of both land-cover maps and species occurrence data. These limitations are particularly relevant when modelling species in regions which are strongly modified by long-lasting human land use like many cultural landscapes of Europe. Here, particularly the rare and endangered species are usually restricted to scattered remnants of natural and semi-natural habitats which often are (much) smaller than the grain size of species atlas or other occurrence datasets (e.g. Kurtto et al., 2013).

A way to circumvent this problem is overlaying the projections of coarser-grain species distribution models, which predict the response of species to climatic gradients, with finer-scale land-cover maps that represent the template of habitat types suitable to a particular species (e.g. Broennimann et al., 2006). This approach is particularly applicable where the ecology of species is well known and where they hence can be assigned to particular habitat types (e.g. Fordham et al., 2018). In this paper, we evaluate how species' potential ranges derived from climate-only projections are altered when additionally considering the availability of appropriate habitat types. We focus on 51 species stemming from three taxonomic groups (butterflies, grasshoppers, vascular plants) in a central European study region. We thereby address the following hypotheses: 1) Climate warming reduces the size of climatically suitable areas. 2) Geographically varied availability of appropriate habitat types alters purely climate-driven risks for species. 3) Climate effects on range sizes are weaker for lowland than for alpine species, but habitat effects show the opposite pattern.

2. Methods

2.1. Study area

The study area covers approximately 240,000 km^2 comprising the countries of Austria, Switzerland, Liechtenstein, the Federal States of Bavaria and Baden-Wurttemberg (Germany) and South Tyrol (Italy). Climate is mostly temperate humid with mean annual temperatures of 7.5–10.0 °C and annual precipitation sums of 600–1300 mm in the lowlands. In alpine regions annual mean temperatures decrease to <0 °C and precipitation sums may reach >2000 mm. A long history of human land use has transformed the natural vegetation cover of this landscape considerably (e.g. Ellenberg, 2009). Today, the lowlands are dominated by arable land and intensively used grasslands, with often only small remnants of (semi-)natural vegetation types like deciduous forests, wetlands or dry grasslands. By contrast, in mountain regions near-natural forests still cover considerable parts of the landscape (Kuttner et al., 2015). Above the tree line, natural alpine grasslands predominate, together with rock and scree vegetation.

2.2. *Species distribution, current and future habitat data*

This study focuses on three taxonomic groups which have been selected because i) their distribution is particularly well-documented in Central Europe, and ii) they have fundamental, yet contrasting roles in ecosystems, i.e. forming the autotrophic basis (vascular plants), being important polyphagous herbivores in many non-forested habitats (grasshoppers), and being mostly mono- or oligophagous herbivores and important pollinators (butterflies). Across the entire study region, we collected 16,348, 17,138 and 47,017 occurrence records for 20 butterfly, 20 grasshopper and 20 vascular plant species. The distribution data are derived from national recording schemes and biodiversity databases supplemented by literature data (see Supplementary Information Table 4 of Wessely et al., 2017). Spatial resolution of occurrence data varied between point records and raster cells of 3 × 5 arc minutes (~32 km^2). We harmonized these data to a combined set of records (see Table S3) with a common resolution of 1 × 1 arc minutes (~2.6 km^2, see Appendix S1 for details). Species were selected according to the following criteria: i) to mainly represent cultural landscapes such as various sorts of grasslands (dry to wet, low to high intensity usage, elevational distribution) and some other non-forest vegetation types (e.g. mires, river alluviums), as well as from deciduous and coniferous forests; ii) to have well-known but contrasting ecological profiles (e.g. in terms of habitat affiliation, mobility) and covering a broad range of climate change vulnerabilities; and iii), to enable the parameterization of un-truncated SDMs, the study area should cover either the species' full climatic niches, or at least their warm range limits representing the trailing edge in case of climate change related shifts. To account for the last point, we compared SDM predictions of species' climatic niches against independent data from the full species range derived from the Global Biodiversity Information Facility GBIF (http://www.gbif.org). We removed nine out of 60 species (1 alpine/3 lowland butterflies, 2/2 grasshoppers and 0/1 plants) from further analyses because their predicted niches were narrower (at least along one of the climatic variables) than actual niches derived from the GBIF-data (see "Cross validation of climatic suitability models" in the Supplementary Methods of Wessely et al., 2017).

Information regarding habitat affiliation of the species was extracted from distribution databases and atlases as well as from a literature review. For vascular plant species, we used the information provided in the Austrian Vegetation Database (Willner et al., 2012), for grasshoppers, we used information on habitat affiliation in Baur et al. (2006), Zuna-Kratky et al. (2009) and supplemented it by information from the Austrian Orthoptera Database (Zuna-Kratky et al., 2017). For butterflies, we used information provided in SBN (1987), Ebert and Rennwald (1993), Settele et al. (2000), Huemer (2004), Bühler-Cortesi (2009), Stettmer et al. (2007), and Bräu et al. (2013).

This information on habitat affiliation was used to generate binary habitat layers (suitable/non-suitable) in the study area under both current and possible future land-cover. Maps of current land-cover were based on a fine-scaled habitat distribution map of the study area (Kuttner et al., 2015). Maps of future land-cover were derived from two land-cover projections for the year 2080 produced within the ALARM project (Settele et al., 2005; Spangenberg et al., 2012). The two projections represent future land-cover under a business-as-usual (GRAS = Growth Applied Strategy) and a sustainable (and SEDG = Sustainable European Development Goal) scenario of socio-economic development in Europe and were downscaled to 250 m spatial resolution using the method described in Dendoncker et al. (2006).

To harmonize the spatially and thematically coarser ALARM projections (250 m, 10 land-cover types) and the map of current habitat distribution (100 m resampled from the original resolution of 25 m, 19 classes), we used a re-classification approach. We first overlaid ALARM projections with a 250 m ALARM map of current land-cover to select all raster cells predicted to change their land-cover until 2080. To produce the finer-scaled future land-cover map, we then modified those 100 m cells of the finer habitat distribution map that spatially match the selected 250 m cells applying the following rules: cells predicted to be used as annual crop fields, permanent crop fields and built up areas (including roads) in the ALARM projections for 2080 were directly converted to these land-cover types. Cells predicted to be covered by grasslands in 2080 were converted to intensive grasslands and alpine grasslands at elevations below and above 1500 m a.s.l., respectively. Cells predicted to be covered by forests were converted either to coniferous or broadleaved forest according to the nature of the nearest forest cell in our land-cover map. Rocks and gravel alluviums along rivers were assumed to remain unchanged. For the SEDG scenario, which inherently assumes sustainable land use, we additionally presumed high nature value habitats like dry grasslands and wetlands to be sufficiently protected and thus to remain unchanged. Moreover, for the SEDG scenario we assumed alpine farming to be continued and thus no expansion of subalpine shrublands due to land abandonment. As simulations based on the two land-cover scenarios revealed similar results, we focus our presentation on the SEDG scenario henceforth.

Using the data sources mentioned above, species were moreover categorized according to their centre of distribution into alpine and lowland species, i.e. those that mainly occur above or below the tree line (see Table 1). We emphasize, that in order

Table 1
Habitat affiliation of the study species. Altitudinal Centre of Distribution ACD (a = alpine; l = lowland). Habitats (GRAVEL = River Alluviums; ALPGR = Alpine Grasslands; BLFO = Broad-leaved Forest; CFO = Coniferous Forest; DRY = Dry Grasslands; EXTGR = Extensive Grasslands; ROCK = Rocklands/Scree; SHRUB = Shrublands/krummholz Stands; WET = Wet Grasslands and Mires). Nomenclature of plants and insects follows Fischer et al. (2008) and Zulka (2005), respectively.

Species	ACD	GRAVEL	ALPGR	BLFO	CFO	DRY	EXTGR	ROCK	SHRUB	WET
Butterflies										
Boloria thore	l			X	X					
Boloria titania	a		X							X
Brenthis daphne	l			X						
Colias phicomone	a		X							
Erebia claudina	a									
Erebia nivalis	a		X					X		
Euphydryas maturna	l			X						
Lopinga achine	l			X						
Maculinea teleius	l									X
Melitaea asteria	a		X							
Oeneis glacialis	a		X					X		
Parnassius apollo	a					X		X		
Parnassius mnemosyne	l						X			
Parnassius phoebus	a		X						X	X
Pontia callidice	a		X					X		
Pyrgus armoricanus	l					X	X			
Grasshoppers										
Bohemanella frigida	a		X					X		
Chorthippus pullus	l	X								
Isophya brevicauda	l					X	X			
Metrioptera saussuriana	a		X							
Miramella alpina	a		X				X			
Miramella carinthiaca	a		X							
Miramella irena	a		X							
Nemobius sylvestris	l			X	X				X	
Oedipoda germanica	l					X		X		
Polysarcus denticauda	l					X	X			
Stauroderus scalaris	a					X	X			
Stenobothrus nigromaculatus	l					X				
Stenobothrus rubicundulus	a		X			X				
Stenobothrus stigmaticus	l					X	X			
vascular plants										
Alchemilla anisiaca	a		X					X	X	
Persicaria bistorta	l						X			X
Cerastium uniflorum	a		X					X		
Dianthus alpinus	a		X					X	X	
Drosera rotundifolia	l									X
Gentiana clusii	a		X					X	X	
Gentianellapraecox	l						X			
Gymnadenia conopsea	l		X			X	X	X	X	X
Jasione montana	l					X	X			
Leontopodium alpinum	a		X					X	X	
Nardus stricta	l		X				X	X	X	X
Phyteuma spicatum	l			X	X					
Polygala chamaebuxus	l	X			X	X		X	X	
Primula auricula	a		X					X		
Rhinanthus glacialis	a	X	X		X		X	X	X	
Saxifraga aizoides	a	X	X					X	X	X
Sibbaldia procumbens	a		X					X		
Trollius europaeus	l		X				X		X	X
Veronica fruticans	a		X					X	X	

to avoid truncated species niches in species distribution modelling, “lowland” species sensu this manuscript mainly comprise species that are most abundant in the (sub)montane elevation belt.

2.3. Climate data

2.3.1. Current climatic conditions

Maps of current climatic conditions were taken from WorldClim climate grids available online (“http://www.worldclim.org”) at a resolution of 30 arc seconds (i.e. ~0.65 km^2). The WorldClim database provides monthly climate averages for the period of 1950–2000 for precipitation (mean) and temperature (minimum, average, maximum; Hijmans et al., 2005); this time period is representative for the climate before the onset of substantial climate warming in the study area in the early 21st century. We scaled precipitation and temperature data down to 100 m horizontal resolution using a moving window regression (supplementary information of Dullinger et al., 2012). Subsequently, we used these spatially refined temperature and precipitation grids to derive maps of the following six bioclimatic variables: 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).

2.3.2. Future climatic conditions

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). In detail, we used: (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), derived 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. For the sake of simplicity, the presented climate forecast scenarios are henceforth called ‘ccsm3/B2′, ‘echam5/A1B′ and ‘hadcm3/A1B’. As simulations based on these scenarios resulted in similar results, we focussed on the intermediate scenario (echam5) in the main text but provide results for other scenarios in Fig. S1. We applied a statistical downscaling procedure (Zimmermann et al., 2009, Tabor and Williams, 2010; see Appendix S2 for further details) and derived bioclimatic variables in the same way as for the current climate dataset for decadal time steps.

2.4. SDM parameterization

SDMs were calibrated by linking species distribution data with the current climatic conditions (named ‘base’ henceforth). To match SDMs to the spatial resolution of the land cover maps, we correlated species presence/absence in angular minute fields with the climate of the central 100 × 100 m cell of each minute field and subsequently projected climatic suitability at this finer resolution. Species distribution modelling was conducted within the *biomod2* modelling framework (Thuiller et al., 2009), run under R 3.0.2 (R Development Core Team, 2013). We selected the default set of parametric and non-parametric regression techniques and machine-learning algorithms in the ensemble modelling and forecast routines (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 split the available occurrence data into two subsets, one for calibrating the models (80%) and one for evaluating them (remaining 20%) using the True Skill Statistic score (TSS, Allouche et al., 2006). To avoid random effects of splitting, we repeated this procedure three times. Based on this set of 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 the period 2050–2090 (as mean of decadal ensemble predictions). Ensemble predictions were defined as the means of projected occurrence probabilities of single models. Finally, the ensemble predictions were translated into binary maps (presence/absence) using the threshold that maximizes the TSS score (Liu et al., 2005; see Appendix Table 1). These binary maps (100 m resolution) were evaluated using occurrence data on the coarsest resolution sampled (3 × 5 arc min). Thereby, a species was regarded to be present in a coarser grid cell if it was predicted to be present in more than 1% of its constituent 100 × 100 m cells.

2.5. Analyses

The current and future binary species projections (further referred to as climate-only projections) were overlaid with the current or future habitat maps to identify all cells that were both climatically suitable to a species and covered by an appropriate habitat type (referred to as habitat-filtered projections). Current and potential future range sizes were thus defined as the number of cells suitable to the species in either the climate-only or the habitat-filtered projections and were computed separately for each species under both current and future climatic conditions and current and future habitat distribution. We then regressed these potential range sizes of the 51 study species on climatic conditions (current and future), the type of projection (climate-only/habitat-filtered), the species' altitudinal centre of distribution (ACD; lowland/alpine) and all interactions of these factors. We used Linear Mixed-effects Models (LMMs) instead of (simple) linear regressions and allowed for random intercept terms for species to consider for potential non-independence among the four data records of each species (one for each combination of climatic conditions x type of projection). A regression including species nested in taxonomic group (i.e. butterflies, grasshoppers, plants) as grouping variable led to identical results because the variance explained by taxonomic group was zero (i.e. the variance in range size explained by the model was entirely allocated to species). Coefficients were estimated by optimizing the Restricted Maximum Likelihood criterion. Denominator degrees of freedom were calculated based on the Kenward-Roger's approximation. As we found interaction effects in this regression, we separately evaluated differences among the levels of one factor at all levels of the interacting factor. In particular, we evaluated differences in range size of species under current and future climatic conditions separately for climate-only and habitat-filtered projections of lowland and alpine species (i.e. four tests). We therefore used linear regressions after a visual inspection of near-normal distribution. Similarly, we tested for range size differences between habitat-filtered and climate-only projections of lowland and alpine species separately under current and future climate (hence also four tests). For the latter model, the response (i.e. the difference in range size between climate-only and habitat-filtered projection) was square root-transformed to meet the assumption of a normal distribution.

All statistical analyses were performed in R 3.0.2 (R Development Core Team, 2013) using the package *afex* (Singman et al., 2017) to fit LMM-models.

3. Results

3.1. Climate change effects on predicted range size

Climate change effects on range size (i.e. areas predicted to be climatically suitable) differed between lowland and alpine species (Table 2, Fig. 1a). While lowland species on average did not show a significant change in climatically suitable area between current and future climates (Table 3), for alpine species average losses in suitable area were 56% (Fig. 1a) in climate-only and 20% in habitat-filtered projections, respectively. This pattern was consistent across climate change scenarios (Fig. S1, Table S2). Differences among the taxonomic groups were considerable, however. Plants lost large parts of their range in the lowlands (mean ~45% and ~35% for climate-only and habitat-filtered projections, respectively) and alpine regions (70% and 15%; Fig. 1b). In contrast, grasshoppers and butterflies were predicted to gain range size in lowlands (30%–50%) but to lose range size in alpine regions (15%–55%). The magnitude of all these predicted changes were similar among climate change scenarios (data not shown).

3.2. Habitat filtering effects on predicted range size

Predicted suitable areas were significantly smaller (all $p < 0.001$) in habitat-filtered than in climate-only projections for both alpine and lowland species and under current as well as future climatic conditions (Fig. 2a). Accounting for habitat availability reduced predicted climatically suitable area by 77% and 73% for lowland species under current and future climates, respectively. For alpine species, effects were similar in magnitude under current (68%), but much less pronounced (39%) under future climatic conditions. This is in line with the less strong effects of climate change on habitat-filtered compared to climate-only projections for alpine species (Fig. 1a). Put another way, accounting for habitat availability affected range size predictions differently for alpine and lowland species and this difference became even more pronounced under a warming climate (cf. significant interaction terms in Table 2). Effects of habitat availability on range size showed only minor quantitative differences across climatic scenarios (73% and 37% for lowland and alpine species, respectively, under ccsm3/B2 and 71%/42% under hadcm3/A1B). Effects on alpine species were relatively uniform among the three taxonomic groups under current climate, but were stronger for butterflies under future climate (Fig. 2b). For lowland species, accounting for habitat availability caused range reductions of butterflies, grasshoppers and plants to be somewhat smaller, similar and higher, respectively, under current compared to future climatic conditions.

Table 2
Anova table of a linear mixed-effects model relating range size of 51 species from three taxonomic groups (grasshoppers, butterflies and vascular plant) to current and future (average of 2050–2090) climatic conditions, the type of projection (climate-only/habitat-filtered), the species' altitudinal centre of distribution (ACD; lowland/alpine) and their interactions. Denominator degrees of freedom were calculated based on the Kenward-Roger's approximation. Projections under future conditions are based on the climate forecast scenario echam5/A1B including and changes in habitat availability based on the land use scenario SEDG (Settele et al., 2005; Spangenberg et al., 2012). Other climate and land use scenarios are illustrated in Table S2.

	Df	F-value	p-value
projection	1, 147	58.85	<0.001
climate	1, 147	6.28	0.013
ACD	1, 49	4.25	0.044
projection: climate	1, 147	3.36	0.069
projection: ACD	1, 147	5.16	0.025
climate: ACD	1, 147	4.43	0.037
projection: climate: ACD	1, 147	2.63	0.107

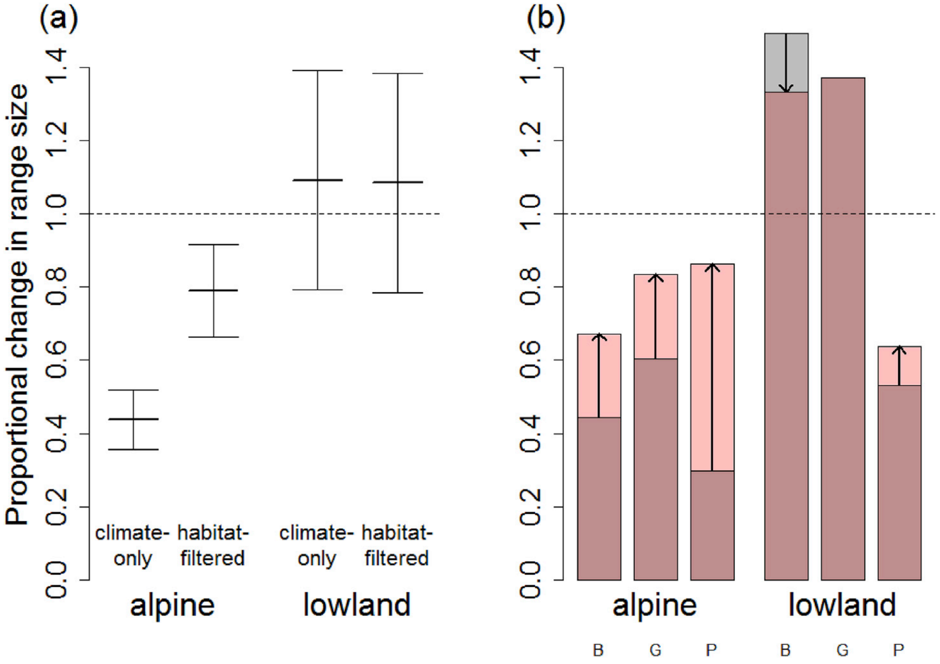

Fig. 1. Projected climate change effects on range size of 51 alpine and lowland species in Central Europe. Values represent changes in predicted suitable area between current and future (average of 2050–2090) climatic conditions calculated as proportions (future range/current range; mean ± SE; values < 1 indicate loss and >1 gain in area) for climate-only and habitat-filtered projections, respectively (a); the same proportions averaged over the three taxonomic groups (butterflies B, grasshoppers G, vascular plants P); b). Arrows indicate differences of climate change effects in climate-only (grey bars) and habitat-filtered projections (pink bars). Future climate and future land-cover are based on the climate scenarios echam5/A1B and the land use scenario SEDG (Settele et al., 2005; Spangenberg et al., 2012), respectively. Other climate forecast scenarios are illustrated in Fig. S1. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4. Discussion

Taken together, our results clearly demonstrate that climate change-induced losses in potential range size are much more pronounced for alpine than for lowland species. However, accounting for habitat availability considerably altered climate-based risk estimates, and this effect of habitat availability, differed considerably between lowland and alpine plants and insects. Alpine species appear to be buffered against climate induced range losses by habitat availability to a certain extent, because at the end of the 21st century the spatial match between climatically suitable ranges and the distribution of appropriate habitat types increases. In the case of lowland species this mitigating effect of land use was detectable only for plants. In contrast, butterflies showed gains in climatically suitable areas, which are used up by reduced habitat availability, and potential ranges size of lowland grasshoppers were hardly changed by accounting for habitat availability. However, effects of the availability of micro-refugia cannot be accounted for in large-scale studies. Thus, our estimated differences in climate change-effects on range sizes between lowland and alpine species might be overestimated to some degree. The topographically highly diverse alpine landscapes potentially facilitate survival within close spatial proximity more strongly than the more homogenous lowland regions (Scherrer and Körner, 2011).

4.1. Strong filtering-effects of habitat availability on species' range size under current climatic conditions

Our results clearly underpin that current land use in Central Europe represents a highly selective filter that allows the studied species to occupy only small fractions of their (macro)climatically suitable ranges, on average, under current climatic conditions. As expected, lowland and high-mountain regions differ considerably in this respect. Many (semi-)natural lowland habitats have become severely degraded, especially after World War II, by an array of measures like intensified application of fertilizers, herbicides and insecticides, multiple mowing of grasslands each year, land consolidation or amelioration techniques, or abandonment and afforestation of economically marginal sites (Poschlod et al., 2005; Graf et al., 2014). Consequently, habitat types characterized by low or moderate human usage, such as moderately fertilized grasslands, and/or by non-standard site conditions, such as dry and wet grasslands, have become increasingly rare throughout the study region (Henle et al., 2008; Čop et al., 2009; Janišová et al., 2011). Many of our study species are affiliated to such low-impact habitat types as they represent a characteristic part of the non-forest central European flora and fauna that has been shaped by land use over centuries (Tscharntke et al., 2005; van Swaay et al., 2006; Marini et al., 2008; Ellenberg, 2009). It is hence not surprising that the current land use intensity in central European lowlands imposes strong restrictions on the distribution of

Table 3
Regressions testing differences in range size under current and future (average of 2050–2090) climate. Regressions were run separately for species differing in their altitudinal centre of distribution and for projections not accounting (climate-only) or accounting for habitat suitability (habitat-filtered).

ACD	Projection	coef ±SE	t-value	p-value
Alpine	climate-only	37,903 ± 12,171	3.11	0.004
Alpine	habitat-filtered	5438 ± 2250	2.42	0.023
Lowland	climate-only	2880 ± 14,891	0.19	0.848
Lowland	habitat-filtered	888 ± 3963	0.22	0.825

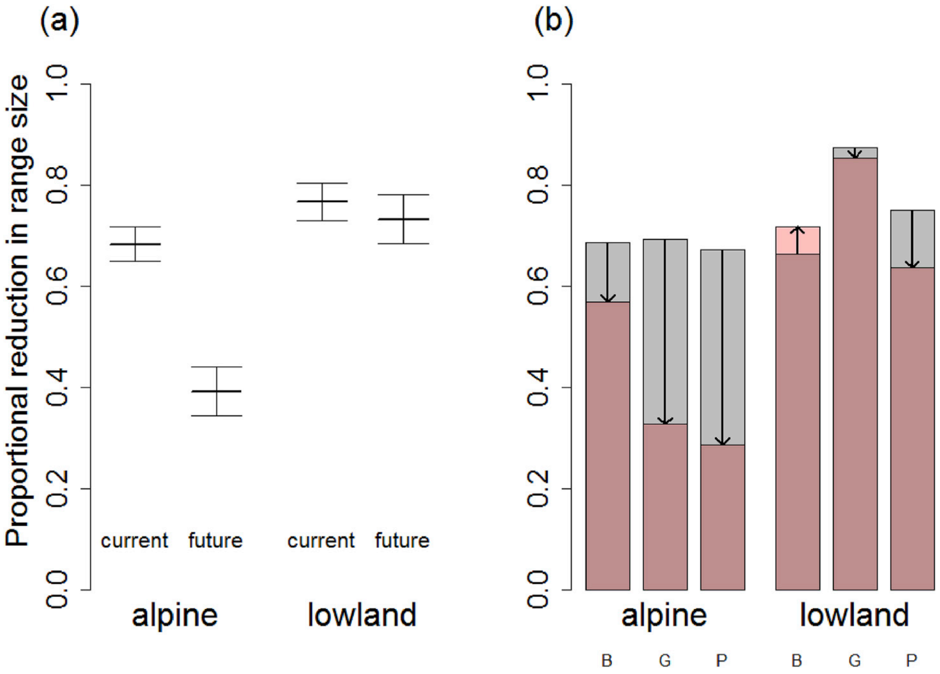

Fig. 2. Projected reduction of potential range size of 51 alpine and lowland species in Central Europe when considering habitat availability in addition to climatic suitability. Range reduction was calculated, separately for alpine and lowland species and under current and future climatic conditions, as 1 − range in habitat filtered projections/range in climate-only projections; mean ± SE, (a); and this same reduction averaged for the three taxonomic groups (butterflies B, grasshoppers G, vascular plants P); b). Arrows indicate how much accounting for habitat availability reduces potential range size under current (grey bars) as opposed to future climate and land use conditions (pink bars). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

these species even where climatic conditions would be highly suitable. At higher elevations, by contrast, land-cover is still dominated by semi-natural and natural habitat types, especially above the alpine tree line. While some of these habitat types, and hence the species affiliated to them, are naturally rare in the study area (e.g. snowbeds), others like forests (in the montane and subalpine belts) and grasslands (in the alpine belt) cover most of the terrain and the match between climatically suitable areas and appropriate habitat types is hence much higher for species of these habitat types at high elevations.

4.2. Opposing trends of habitat availability and climate change effects on range size along the elevation gradient

When climate warms, the majority of our study species are predicted to face a decline of their climatically suitable ranges. This predicted decline is stronger for alpine than for lowland species, a result in line with previous assessments of climate-induced risk to biodiversity (e.g. Engler et al., 2011). However, when accounting for habitat availability (and its predicted change) within the climatically suitable range this difference vanishes and lowland species appear as threatened by climate warming as high mountain species in terms of proportional range size loss (see also Thuiller et al., 2014). Put it differently, habitat availability buffers alpine, but not lowland species against climate warming because only for the former the spatial match of climatically suitable area and available habitats increases under future climates. We suspect that this apparent buffer effect of land use on alpine species arises because current climatically suitable ranges of many 'alpine' species include parts of the subalpine belt. Indeed, many of the alpine species in our study have climatic requirements that would allow them to thrive at lower elevations. They are mainly excluded from these lower elevations by biotic interactions, in particular by competition (e.g. Alexander et al., 2015), but can occasionally be found there if competitive intensity is reduced e.g. by natural or human disturbance like in avalanche paths or on summer pastures cleared from forests. Under climate warming, climatic ranges of these species are driven (further) upward in elevation, while the SEDG scenario predicts only marginal shifts of the tree line itself. As a corollary, the match between the area climatically suitable to these species and appropriate non-forest habitat types increases. Vice versa, climate warming drives lowland species upwards into montane and subalpine elevations where former agricultural land of marginal use has been afforested during the recent decades and forests have hence replaced grasslands and arable land as the predominant habitat type (e.g. Tasser et al., 2017). Species of low-intensity used grasslands and other low-intensity non-forest land use types will thus be driven from elevations where land use intensity is too high (lowlands) towards elevations where marginal agricultural lands have been abandoned. As a consequence, the match between climatically suitable ranges and appropriate habitats does not change.

Species differ in their ecological niche breadths and the distinction between lowland and alpine species is fuzzy. For our set of species, this distinction was based on the centre of their elevational distribution. Nevertheless, some species classified as lowland species sometimes occur above the tree line, too (e.g. *Polygala chamaebuxus*) and vice versa (e.g. *Aster bellidiastrum*). We hence suppose that our species selection has lessened the observable differences among elevational groups and that focussing on a comparison of lowland and alpine specialists in a strict sense would have demonstrated the apparent buffer effect even more clearly.

4.3. *Differences in habitat effects among taxonomic groups*

We found that the lack of appropriate habitats affects similar proportions of the ranges suitable to plants, grasshoppers and butterflies under current conditions (about 70%, markedly higher only in the case of lowland grasshoppers, see grey bars in Fig. 2b). However, in the future, the predicted buffer effect of habitat availability is more pronounced for alpine plants and grasshoppers than for alpine butterflies. In addition, lowland butterflies are predicted to face a further decrease in the availability of suitable habitats, while suitable habitats may rather increase for plants. Taken together, our models hence suggest that range loss from climate change is strongest for plants, but that, at the same time, habitat availability will compensate climate driven range loss most pronouncedly for this taxonomic group. However, the observed variation in the strength of habitat filter-effects on species of different taxonomic groups is difficult to assess, and warrants future research.

4.4. *Limits in predicting species' future range size*

Our results suggest a certain buffer effect of habitat patterns on climatic threats to alpine species. However, the match of climatically suitable areas with the availability of alpine (i.e. non-forest) habitats could be reduced by a rise of the alpine tree line in response to climate warming. Recent research has suggested that, on a landscape scale, changes to forest cover from land use will be much faster than the upward shift of the treeline in response to climate warming, which will be a matter of several centuries at least (Tasser et al., 2017; see also Dullinger et al., 2004; Harsch et al., 2009; Rabasa et al., 2013). Nevertheless, in the long run, the treeline will rise and this will eventually make climatic threats to the distribution of alpine species even more severe than predicted from SDMs that only account for climatic conditions (Dirnböck et al., 2011). On the other hand, a rising tree line may theoretically also open new areas for colonization by lowland forest species.

An inherent problem of modelling approaches – and even more of experimental studies – is the selection of representative species allowing for a generalisation of results to as large a fraction of the overall species pool as possible. Here, we included a mix of study species differing in range sizes, habitat affiliations and elevational distributions. Furthermore, we considered plants as well as two prominent orders of insects. Although the number of study species is rather small, we suppose that our main result, the (average) differential effect of land use patterns on climate-driven range shifts of lowland and alpine species, is robust for a larger set of species thriving in central European cultural landscapes.

The ecological requirements of our species do not perfectly match the habitat types distinguished in the habitat maps applied. In particular, several specialist species (e.g. snowbed specialists in plants or insects restricted to calcareous dry grasslands) actually inhabit only a subset of the broader defined habitats types (i.e. alpine and dry grasslands) derived from the map. This may have resulted in an over-prediction of their potential current and future ranges and, thus, and underestimation of the effects of habitat availability. The effects of such over-estimates on predictions for individual species can be severe, but as far as we see there is no indication that they should introduce a bias of any kind towards either lowland or alpine species. Again, we hence suppose that neglect of further habitat specialization in our models is unlikely to affect our conclusion that habitat availability buffers alpine and lowland species differently against climate induced range loss.

Finally, we emphasize again that SDMs model realized and not fundamental niches. This implies that changes to trophic (e.g. distribution of host plants for larvae of butterflies, Schweiger et al., 2012) or competitive interactions (Alexander et al., 2015) that result from environmental changes are not explicitly accounted for. As already discussed, part of this neglect is compensated by filtering purely climatic projections by a habitat layer that, among other processes like disturbance, also captures presence or absence of competitors (e.g. trees for alpine herbs). However, many other possible effects of interactions on future realized niches remain unconsidered by SDMs. In addition, SDMs do not consider dispersal and thus it remains unclear if (and with which velocity) species will be able to track their changing environmental niche in space, even if it would remain unchanged. In mountain environments, for example, losses may occur with different velocities at lower and upper range margins creating substantial extinction debts at high elevations, in particular (cf. Dullinger et al., 2012; Rumpf et al., 2018, 2019). Whether and how much these lag times alter eventual outcomes of range shifts and hence realized ranges of the future is unknown. Short-time evaluations for mobile organisms like birds have shown that while more mechanistic and temporarily explicit models of range dynamics provide more accurate predictions when necessary parameters are well known, SDM results are still good approximations of proportional range size change (Fordham et al., 2018). However, whether these results hold under the pronounced and rapid climate change predicted by more severe scenarios is unclear (Zurell et al., 2016).

4.5. *Implications for species conservation under climate change*

The maintenance or even the intensification of traditional high-mountain summer pasturing has already been suggested as an important, although probably insufficient, land-use strategy to mitigate the negative long-term effects of climate warming on alpine species (cf. Dirnböck et al., 2003; Dullinger et al., 2003). Our results moreover suggest that the maintenance or re-vitalization of the currently declining traditional land use practices in montane and subalpine areas, particularly pasturing and hay-making (Chemini and Rizzoli, 2003), may also help species from current low-intensity land use types of the lowlands to find appropriate habitats when their climatic ranges are shifted upward in elevation. Taken together, a re-adjustment of land use intensity along the elevational gradient appears a sensible strategy to help a considerable part of the species of Central European cultural landscapes to cope with forthcoming climate warming to a certain extent: while decreasing land use intensity, combined with habitat restoration (Török et al., 2011; Prach et al., 2013; Joyce, 2014) will reduce the combined pressure from climate and land use in lowland areas, re-establishing low to moderately intensive traditional land use levels at higher elevations may conserve the necessary forest-free areas that species from lower elevations can colonize when climate warms. Such a mitigating strategy would, however, require that agricultural policies try to reverse current trends towards increasing disparities among regions of high intensity-land use and marginal areas where rural activities decline or vanish altogether.

Biosketch

Karl Hülber is a Senior Scientist at the University of Vienna, Department of Botany and Biodiversity Research. His research focuses on modelling the distribution of species and biodiversity patterns. He is also interested in the fields of evolutionary plant ecology with a particular focus on polyploid complexes.

Author contributions

F.E. and S.D. conceived the ideas and designed the study; M.K., D.M. F.E., W.R. and S.S. compiled the data; M.K., A.G. and J.W. run the models; K.H. analysed the data; and S.D., M.K. and K.H. wrote the paper. All authors commented on the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We acknowledge funding by the Austrian Climate and Energy Fund carried out within the framework of the “ACRP” Program (project number KR11AC0K00355). FE and SD acknowledge funding by the Austrian Science Foundation FWF (grant I 3757-B29). We are very grateful to the Floristic Mapping Projects of Austria, Switzerland, South Tyrol, Bavaria and Baden-Wurttemberg, the Austrian Working Group on Orthoptera, the Centre Suisse de Cartographie de la Faune, the Bayerisches Landesamt für Umwelt, the Tiroler Landesmuseen-Betriebsgesellschaft m.b.H., the Staatliches Museum für Naturkunde Karlsruhe, the Naturmuseum Südtirol, Heinz Habeler, Josef Pennerstorfer, Helmut Höttinger, Peter Detzel, Stephen Maas, Aloysius Staudt and all other colleagues and institutions that provided distribution data for this study. We appreciate the constructive comments by one anonymous reviewer.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2020.e01113.

References

Alexander, J.M., Diez, J.M., Levine, J.M., 2015. Novel competitors shape species’ responses to climate change. Nature 525, 515–518.
Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J. Appl. Ecol. 43, 1223–1232.
Araújo, M.B., Alagador, D., Cabeza, M., Nogués-Bravo, D., Thuiller, W., 2011. Climate change threatens European conservation areas. Ecol. Lett. 14, 484–492.
Baur, B., Baur, H., Roesti, C., Roesti, D., Thorens, P., 2006. Die Heuschrecken der Schweiz, first ed. Bern, Haupt.
Bräu, M., Bolz, R., Kolbeck, H., Nummer, A., Voith, J., Wolf, W., 2013. Tagfalter in Bayern, first ed. Ulmer, Stuttgart.

Broennimann, O., Thuiller, W., Hughes, G.O., Midgley, G.F., Alkemade, J.R.M., Guisan, A., 2006. Do geographic distribution, niche property and life form explain plants' vulnerability to global change? Global Change Biol. 12, 1079–1093.

Bühler-Cortesi, T., 2009. Schmetterlinge: Tagfalter der Schweiz, first ed. Bern, Haupt.

Chemini, C., Rizzoli, A., 2003. Land use change and biodiversity conservation in the Alps. J. Mt. Ecol. 7, 1–7.

Collins, M., Booth, B.B.B., Harris, G.R., Murphy, J.M., Sexton, D.M.H., Webb, M.J., 2006. Towards quantifying uncertainty in transient climate change. Clim. Dynam. 27, 127–147.

Čop, J., Vidrih, M., Hacin, J., 2009. Influence of cuting regime and fertilizer application on the botanical composition, yield and nutritive value of herbage of wet grasslands in Central Europe. Grass Forage Sci. 64, 454–465.

Dendoncker, N., Bogaert, P., Rounsevell, M., 2006. A statistical method to downscale aggregate land use data. J. Land Use Sci. 1, 63–82.

Dirnböck, T., Dullinger, S., Grabherr, G., 2003. A regional impact assessment of climate and land-use change on alpine vegetation. J. Biogeogr. 30, 401–417.

Dirnböck, T., Essl, F., Rabitsch, W., 2011. Disproportional risk for habitat loss of high-altitude endemic species under climate change. Global Change Biol. 17, 990–996.

Dullinger, S., Dirnböck, T., Greimler, J., Grabherr, G., 2003. A resampling approach for evaluating effects of pasture abandonment on subalpine plant species diversity. J. Veg. Sci. 14, 243–252.

Dullinger, S., Dirnböck, T., Grabherr, G., 2004. Modelling climate change-driven treeline shifts: relative effects of temperature increase, dispersal and invasibility. J. Ecol. 92, 241–252.

Dullinger, S., Gattringer, A., Thuiller, W., Moser, D., Zimmermann, N.E., Guisan, A., Willner, W., Plutzar, C., Leitner, M., Mang, T., Caccianiga, M., Dirnböck, T., Ertl, S., Fischer, A., Lenoir, J., Svenning, J.-C., Psomas, A., Schmatz, D.R., Silc, U., Vittoz, P., Hülber, K., 2012. Extinction debt of high-mountain plants under twenty-first-century climate change. Nat. Clim. Change 2, 619–622.

Dullinger, S., Dendoncker, N., Gattringer, A., Leitner, M., Mang, T., Moser, D., Mücher, C.A., Plutzar, C., Rounsevell, M., Willner, W., Zimmermann, N.E., Hülber, K., 2015. Modelling the effect of habitat fragmentation on climate-driven migration of European forest understorey plants. Divers. Distrib. 21, 1375–1387.

Dullinger, I., Gattringer, A., Wessely, J., Moser, D., Plutzar, C., Willner, W., Egger, C., Gaube, V., Haberl, H., Mayer, A., Bohner, A., Gilli, C., Pascher, K., Essl, F., Dullinger, S., 2020. A socio-ecological model for predicting impacts of land-use and climate change on regional plant diversity. Global Change Biol. https://doi.org/10.1111/gcb.14977.

Ebert, G., Rennwald, E., 1993. Die Schmetterlinge Baden-Württembergs, first ed. In: Band 1 und 2. Ulmer, Stuttgart.

Elith, J., Kearney, M., Phillips, S., 2010. The art of modelling range-shifting species. Methods Ecol. Evol. 1, 330–342.

Ellenberg, H., 2009. Vegetation Ecology of Central Europe, 4th Edn. Translated by Gordon K. Strutt. Cambridge University Press, Cambridge.

Elsen, P.R., Tingley, M.W., 2015. Global mountain topography and the fate of montane species under climate change. Nat. Clim. Change 5, 772–776.

Engler, R., Randin, C.F., Thuiller, W., Dullinger, S., Zimmermann, N.E., Araújo, M.B., Pearman, P.B., Le Lay, G., Piedallu, C., Albert, C.H., Choler, P., Coldea, G., De Lamo, X., Dirnböck, T., Gégout, J.-C., Gómez-García, D., Grytnes, J.-A., Heegaard, E., Høistad, F., Nogués-Bravo, D., Normand, S., Puşcaş, M., Sebastià, M.-T., Stanisci, A., Theurillat, J.-P., Trivedi, M.R., Vittoz, P., Guisan, A., 2011. 21st century climate change threatens mountain flora unequally across Europe. Global Change Biol. 17, 2330–2341.

Fischer, M.A., Oswald, K., Adler, W., 2008. Exkursionsflora für Österreich, Liechtenstein und Lichtenstein. Land Oberösterreich, Linz.

Fordham, D.A., Bertelsmeier, C., Brook, B.W., Early, R., Neto, D., Brown, S.C., Ollier, S., Araujo, M.B., 2018. How complex should models be? Comparing correlative and range dynamics models. Global Change Biol. 24, 1357–1370.

Graf, R., Müller, M., Korner, P., Jenny, M., Jenni, L., 2014. 20% loss of unimproved farmland in 22 years in the Engadin, Swiss Alps. Agric. Ecosyst. Environ. 185, 48–58.

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8, 993–1009.

Harsch, M.A., Hulme, P.E., McGlone, M.S., Duncan, R.P., 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. Ecol. Lett. 12, 1040–1049.

Henle, K., Alard, D., Clitherow, J., Cobb, P., Firbank, L., Kull, T., McCracken, D., Moritz, R.F.A., Niemelä, J., Rebane, M., Wascher, D., Watt, A., Young, J., 2008. Identifying and managing the conflicts between agriculture and biodiversity conservation in Europe – a review. Agric. Ecosyst. Environ. 124, 60–71.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978.

Hollweg, H.-D., Böhm, U., Fast, I., Hennemuth, B., Keuler, K., Keup-Thiel, E., Lautenschlager, M., Legutke, S., Radtke, K., Rockel, B., Schubert, M., Will, A., Woldt, M., Wunram, C., 2008. Ensemble Simulations over Europe with the Regional Climate CLM Forced with IPCC AR4 Global Scenarios. Technical Report No. 3. Max Planck Institute for Meteorology, Hamburg.

Huemer, P., 2004. Die Tagfalter Südtirols, first ed. Folio, Bolzano.

IPBES, 2019. Global Assessment Report on Biodiversity and Ecosystem Services. https://ipbes.net/global-assessment.

IPCC, 2007. In: Parry, M.L., Canziani, O.F., Palutikof, J.P., J van der Linden, P., Hanson, C.E. (Eds.), 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 University Press, Cambridge.

Janišová, M., Bartha, S., Kiehl, K., Dengler, J., 2011. Advances in the conservation of dry grasslands: introduction to contributions from the seventh European Dry Grassland Meeting. Plant Biosyst. 145, 507–513.

Jantz, S.M., Barker, B., Brooks, T.M., Chini, L.P., Huang, Q., Moore, R.M., Noel, J., Hurtt, G.C., 2015. Future habitat loss and extinctions driven by land-use change in biodiversity hotspots under four scenarios of climate change mitigation. Conserv. Biol. 29, 1122–1131.

Joyce, C.B., 2014. Ecological consequences and restoration potential of abandoned wet grasslands. Ecol. Eng. 66, 91–102.

Kampmann, D., Lüscher, A., Konold, W., Herzog, F., 2012. Agri-environment scheme protects diversity of mountain grassland species. Land Use Pol. 29, 569–576.

Kjellström, E., Bärring, L., Gollvik, S., Hansson, U., Jones, C., Samuelsson, P., Rummukainen, M., Ullerstig, A.U.W., Wyser, K., 2005. A 140-year Simulation of European Climate with the New Version of the Rossby Centre Regional Atmospheric Climate Model (RCA3). *SMHI Reports Meteorology And Climatology No. 1*SMHI, Norrköping.

Kurtto, A., Sennikov, A.N., Lampinen, R. (Eds.), 2013. Atlas Florae Europaeae. Distribution of Vascular Plants in Europe. Rosaceae (Cydonia to Prunus, Excl. Sorbus), 1st Edn. The Committee for Mapping the Flora of Europe & Societas Biologica Fennica Vanamo (Helsiniki).

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.

Liu, C.R., Berry, P.M., Dawson, T.P., Pearson, R.G., 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28, 385–393.

Luoto, M., Virkala, R., Heikkinen, R.K., 2007. The role of land cover in bioclimatic models depends on spatial resolution. Global Ecol. Biogeogr. 16, 34–42.

Marini, L., Fontana, P., Scotton, M., Klimek, S., 2008. Vascular plant and Orthoptera diversity in relation to grassland management and landscape composition in the European Alps. J. Appl. Ecol. 45, 361–370.

Nogues-Bravo, D., Araujo, M.B., Romdal, T., Rahbek, C., 2008. Scale effects and human impact on the elevational species richness gradients. Nature 453, 216–219.

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

Pauli, H., Gottfried, M., Dullinger, S., Abdaladze, O., Akhalkatsi, M., Alonso, J.L.B., Coldea, G., Dick, J., Erschbamer, B., Calzado, R.F., Ghosn, D., Holten, J.I., Kanka, R., Kazakis, G., Kollár, J., Larsson, P., Moiseev, P., Moiseev, D., Molau, U., Mesa, J.M., Nagy, L., Pelino, G., Puşcaş, M., Rossi, G., Stanisci, A., Syverhuset, A.O., Theurillat, J.-P., Tomaselli, M., Unterluggauer, P., Villar, L., Vittoz, L., Grabherr, G., 2012. Recent plant diversity changes on Europe's mountain summits. Science 336, 353–355.

Pereira, H.M., Leadly, P.W., Proença, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarrés, J.F., Araújo, M.B., Balvanera, P., Biggs, R., Cheung, W.W.L., Chini, L., Cooper, H.D., Gilman, E.L., Guénette, S., Hurtt, G.C., Huntington, H.P., Mace, G.M., Oberdorff, T., Revenga, C., Rodrigues, P., Scholes, R.J., Sumaila, U.R., Walpole, M., 2010. Scenarios for global biodiversity in the 21st century. Science 330, 1496–1501.

Poschlod, P., Bakker, J.P., Kahmen, S., 2005. Changing land use and its impact on biodiversity. Basic Appl. Ecol. 6, 93–98.

Prach, K., Jongepierová, I., Řehounková, K., 2013. Large-scale restoration of dry grasslands on ex-arable land using a regional seed mixture: establishment of target species. Restor. Ecol. 21, 33–39.

Pradervand, J.-N., Dubuis, A., Pellissier, L., Guisan, A., Randin, C., 2014. Very high resolution environmental predictors in species distribution models: moving beyond topography? Prog. Phys. Geogr. 38, 79–96.

R Development Core Team, 2013. *R*: A Language and Environment for Statistical Computing. *R* Foundation for Statistical Computing, Vienna.

Rabasa, S.G., Granda, E., Benavides, R., Kunstler, G., Espelta, J.M., Ogaya, R., Penuelas, J., Scherer-Lorenzen, M., Gil, W., Grodzki, W., Ambrozy, S., Bergh, J., Hodar, J.A., Zamora, R., Valladares, F., 2013. Disparity in elevational shifts of European trees in response to recent climate warming. Global Change Biol. 19, 2490–2499.

Rumpf, S.B., Hülber, K., Klonner, G., Moser, D., Schütz, M., Wessely, J., Willner, W., Zimmermann, N.E., Dullinger, S., 2018. Climate-driven range dynamics of mountain plants decrease with elevation. Proc. Natl. Acad. Sci. U.S.A. 115, 1848–1853.

Rumpf, S., Hülber, K., Zimmermann, N.E., Dullinger, S., 2019. Elevational rear edges shifted at least as much as leading edges over the last century. Global Ecol. Biogeogr. 28, 533–543.

Scherrer, D., Körner, C., 2011. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. J. Biogeogr. 38, 406–416.

Schweiger, O., Heikkinen, R.K., Harpke, A., Hickler, T., Klotz, S., Kudrna, O., Kühn, I., Pöyry, O., Settele, J., 2012. Increasing range mismatching of interacting species under global change is related to their ecological characteristics. Global Ecol. Biogeogr. 21, 88–99.

SBN, 1987. Tagfalter und ihre Lebensräume: Arten, Gefährdung, Schutz, first ed. Schweizerischer Bund für Naturschutz, Basel.

Settele, J., Feldmann, R., Reinhardt, R., 2000. Die Tagfalter Deutschlands, 1st edn. Ulmer, Stuttgart.

Settele, J., Hammen, V., Hulme, P., et al., 2005. ALARM: assessing LArge-scale environmental Risks for biodiversity with tested Methods. Gaia 14, 69–72.

Singman, H., Bolker, B., Westfall, J., Aust, F., 2017. afex: analysis of Factorial Experiments. R package version 0.17. https://CRAN.R-project.org/package=afex.

Sirami, C., Caplat, P., Popy, S., Clamens, A., Arlettaz, R., Jiguet, F., Brotons, L., Martin, J.L., 2017. Impacts of global change on species distributions: obstacles and solutions to integrate climate and land use. Global Ecol. Biogeogr. 26, 385–394.

Spangenberg, J.H., Bondeau, A., Carter, T.R., Fronzek, S., Jaeger, J., Jylhä, K., Kühn, I., Omann, I., Paul, A., Reginster, I., Rounsevell, M., Schweiger, O., Stocker, A., Sykes, M.T., Settele, J., 2012. Scenarios for investigating risks to biodiversity. Global Ecol. Biogeogr. 21, 5–18.

Stanton, J.C., Pearson, R.G., Horning, N., Ersts, P., Akçakaya, H.R., 2012. Combining static and dynamic variables in species distribution models under climate change. Methods Ecol. Evol. 3, 349–357.

Stettmer, C., Bräu, M., Gros, P., Wanninger, O., 2007. Die Tagfalter Bayerns und Österreichs, second ed. Bayerische Akademie für Naturschutz und Landschaftspflege (ANL), Laufen.

Tabor, K., Williams, J.W., 2010. Globally downscaled climate projections for assessing the conservation impacts of climate change. Ecol. Appl. 20, 554–565.

Tasser, E., Leitinger, G., Tappeiner, U., 2017. Climate change versus land-use change – what effects the mountain landscape more? Land Use Pol. 60, 60–72.

Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T., Prentice, I.C., 2005. Climate change threats to plant diversity in Europe. Proc. Natl. Acad. Sci. Unit. States Am. 102, 8245–8250.

Thuiller, W., Lafourcade, B., Engler, B., Araújo, M.B., 2009. BIOMOD – a platform for ensemble forecasting of species distributions. Ecography 32, 369-3.

Thuiller, W., Guégue, M., Georges, D., Bonet, R., Chalmandrier, L., Garraud, L., Renaud, J., Roquet, C., Van Es, J., Zimmermann, N.E., Lavergne, S., 2014. Are different facets of plant diversity well protected against climate and land cover changes? A test study in the French Alps. Ecography 37, 1254–1266.

Titeux, N., Henle, K., Mihoub, J.B., Regos, A., Geijzendorffer, I.R., Cramer, W., Verburg, P.H., Brotons, L., 2016. Biodiversity scenarios neglect future land-use changes. Global Change Biol. 22, 2505–2515.

Török, P., Vida, E., Deák, B., Lengyel, S., Tóthmérész, B., 2011. Grassland restoration on former croplands in Europe: an assessment of applicability of techniques and costs. Biodivers. Conserv. 20, 2311–2332.

Travis, J.M.J., 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. Proc. Biol. Sci. 270, 467–473.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. Ecol. Lett. 8, 857–874.

van Swaay, C.A.M., Warren, M.S., Loïs, G., 2006. Biotope use and trends of European butterflies. J. Insect Conserv. 10, 189–209.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. Nature 416, 389–395.

Wessely, J., Hülber, K., Gattringer, A., Kuttner, M., Moser, D., Rabitsch, W., Schindler, S., Dullinger, S., Essl, F., 2017. Habitat-based conservation strategies cannot compensate for climate-change-induced range loss. Nat. Clim. Change 7, 823–828.

Willner, W., Berg, C., Heiselmayer, P., 2012. In: Dengler, J., Oldeland, J., Jansen, F., Chytrý, M., Ewald, J., Finckh, M., Glöckler, F., Lopez-Gonzalez, G., Peet, R.K., Schaminée, J.H.J. (Eds.), Austrian Vegetation Database. *Vegetation Databases for the 21st Century*, vol. 4. 3*Biodiversity & Ecology*.

Zimmermann, N.E., Yoccoz, N.G., Edwards, T.C., Meier, E.S., Thuiller, W., Guisan, A., Schmatz, D.E., Pearman, P.B., 2009. Climatic extremes improve predictions of spatial patterns of tree species. Proc. Natl. Acad. Sci. Unit. States Am. 106, 19723–19728.

Zulka, K.P., 2005. Rote listen gefährdeter tiere österreichs. Band 14/1: teil 1: säugetiere, vögel, heuschrecken, wasserkäfer, netzflügler, schnabelfliegen, tagfalter. In: Bundesministerium für Land- und Forstwirtschaft, Umwelt und Wasserwirtschaft.

Zuna-Kratky, T., Karner-Ranner, E., Lederer, E., Braun, B., Berg, H.-M., Denner, M., Bieringer, G., Ranner, A., Zechner, L., 2009. Verbreitungsatlas der Heuschrecken und Fangschrecken Ostösterreichs, first ed. Naturhistorisches Museum Wien, Wien.

Zuna-Kratky, T., Landmann, A., Illich, I., Zechner, L., Essl, F., Lechner, K., Ortner, A., Weißmair, W., Wöss, G., 2017. Die Heuschrecken Österreichs. Biologiezentrum, Linz.

Zurell, D., Thuiller, W., Pagel, J., Cabral, J.S., Münkemüller, T., Gravel, D., Dullinger, S., Normand, S., Schiffers, K.H., Moore, K.A., Zimmermann, N.E., 2016. Benchmarking novel approaches for modelling species range dynamics. Global Change Biol. 22, 2651–2664.