Global warming threatens conservation status of alpine EU habitat types in the European Eastern Alps

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Abstract

At the European level, the Natura 2000 habitat network is the main instrument for preserving and protecting species and habitats. However, protected areas are fixed in location, and environmental conditions continually subject to change. Changing conditions force species to shift their geographic distribution or to adapt to new conditions, ultimately causing a change in the composition of the habitats' species. We modelled the response of two important alpine EU habitat types (6150, 6170) in the Styrian Eastern Alps to increasing temperatures using two representative concentration pathways (rcp 4.5 and rcp 8.5) of the regional climate model CCLM4-8-17 CLMcom. Our results confirmed that climate change within the next several decades will have an immediate and profound impact on the Alpine flora and their habitats. The niche models indicate a dramatic reduction in the habitat suitability of 15 habitat diagnostic species before the end of the twenty-first century. Habitat change was found to be slower inside protected areas in the first half of the twenty-first century, while in the second half of the twenty-first century, suitable habitat conditions either remained constant for the lower temperature scenario (rcp 4.5) or shifted to "outside" current protected areas in the severe scenario (rcp 8.5). Regions of rapidly changing habitat suitability and subsequently shifting species composition can be found both inside and outside of the protected area network. These developments may lead to the deterioration of the conservation status of habitat types and challenge the aims of the EU habitat directive.

Keywords Eastern alpine habitats · Natura 2000 · Protected areas · Climate change · Habitat suitability models

Introduction

Human impact on ecosystems has repeatedly been recognized as the main cause of rapid species and habitat loss. While several strategies have been developed to mitigate direct human impacts causing loss of biodiversity, it remains totally unclear how effective these strategies are in the context of the added impact of climate change. Because the projections

for future climate changes remain largely uncertain, the response of biodiversity to climatic changes is not fully understood, given the complexity of the interactions within those systems. Species are expected to adjust their geographical range due to climate change and many species have already shifted their ranges as a response to increasing temperatures (Parmesan and Yohe 2003; Pecl et al. 2017). Mountain ecosystems are particularly sensitive to global warming (Körner 2003; Gobiet et al. 2014; Pecl et al. 2017); moreover, changing land use is an additional threat (Körner 2003; Müller et al. 2017). For European alpine ecosystems, long-term monitoring programs show changes in vascular plant species richness (Erschbamer et al. 2009; Pauli et al. 2012; Steinbauer et al. 2018) and vegetation cover (Rogora et al. 2018; Lamprecht et al. 2018) across Europe's major mountain ranges. High declines are expected for cold-adapted alpine plants that are already living in the highest mountain regions as they are faced with limited migration options (Pauli et al. 2012), despite the fact that these areas are often within protection areas.

The European Alps, and especially the Eastern Alps, are of particular importance due to their species diversity and high

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levels of endemism (Tribtsch 2004; Essl et al. 2009). Large-scale networks, such as Natura 2000, provide long-term protection including the possibility for species to adapt or move to suitable habitat conditions (Araújo et al. 2011). Simulations suggest that habitat-based conservation strategies, such as site protection, may help to mitigate the negative impacts of climate change on biodiversity, but might not fully compensate for the total loss that climate change may cause (Wessely et al. 2017).

Only a few studies have examined the impacts of climate change on protected areas (Araújo et al. 2011; Fois et al. 2018). The Natura 2000 habitat network is the most important initiative at the European level that is working to counteract rapid biodiversity loss (Orlikowska et al. 2016). The network includes areas of high current nature conservation value, with the clear target of protecting the current biodiversity in the long term even under changing climatic conditions. Protected areas have been designated based on the assumption that the distribution of the target species and habitats will not significantly change. Indeed, climate change has not yet been implemented in most conservation strategies (Araújo et al. 2011; Jones et al. 2016). Assessing the effectiveness of site protection in the light of climate change is of particular importance to preserve species and habitats inside protected areas (Araújo et al. 2004; Hannah et al. 2007).

Biodiversity responses to climate change have frequently been assessed using habitat suitability models (HSM). These calculate the change of species' range by relating current species occurrences to recent and future climate conditions (Guisan and Zimmermann 2000; Franklin 2010). EU habitat types are mainly defined by their typical species composition. Although habitats do not respond to environmental change as units, and species vary greatly in their rate of change (Chen et al. 2011), the effect of changing environmental conditions can be estimated by modelling habitat suitability for the characteristic species of a habitat type (Essl and Rabitsch 2013). Climate change impact models predict dramatic yet unevenly distributed habitat loss for alpine and subalpine species across Europe (Thuiller et al. 2005; Engler et al. 2011). Hybrid range dynamic models that account for fluctuating climate conditions (short-term trends) show much higher range loss and extinction rates (Hülber et al. 2016). Dullinger et al. (2012) and Cotto et al. (2017), taking demographic and evolutionary dynamics into account, predict a delay in species extinction due to species persistence and warn of the effects of long-term warming on mountain plant species.

Alpine environments are known to be particularly vulnerable to environmental changes. The effects of these changes can be even more pronounced especially in regions where the alpine belt is narrow as in the case of the Styrian Alps. In a regional case study, we therefore modelled the habitat suitability for 15 habitat diagnostic alpine species to investigate the response of environmental change on two alpine EU habitat

types in the Styrian Alps. Assuming an increase in temperature, we assessed (i) decadal change of habitat suitability for the species until the end of the twenty-first century for two emissions scenarios and (ii) the pixel-wise change rate of habitat suitability as a measure of regional variation of climate change effects on EU habitat types. We thereby addressed the following questions: (i) How does habitat suitability inside and outside of protected areas develop relative to the current situation? (ii) Is there regional variation in habitat suitability under rising temperatures? (iii) Is regional site protection sufficient to maintain the alpine flora of the European Eastern Alps after global warming?

Materials and methods

Study area

Styria is located at the easternmost part of the European Alps, where the mountain peaks are not covered by glaciers and are lower in comparison to the mountain peaks of the Central Alps. The altitudinal gradient ranges from 200 m a.s.l. at the south-eastern most point of the foreland to 2995 m a.s.l. at the highest peak of Mount Dachstein. Remarkable contrasts in geology, climatic conditions and glacial effects (Tribtsch and Schönschwetter 2003) explain the main distribution patterns of plant species in the Alps (Ozenda and Borel 2003). While the northern Alps generally have calcareous bedrock and are relatively humid, the Inner Alps are largely siliceous and more continental. The geological, climatic and historic conditions essentially apply for the Styrian Alps. The mean annual temperature ranges from -5 to 10 °C and mean annual precipitation from 700 to 2400 mm (Pilger et al. 2010). Detailed information about the geological situation of Styria can be found in Gasser et al. (2009).

Our study area, the Styrian Alps covers approximately 12,876 km², a substantial part of the Eastern Alps. In this part of the Alps (total area of the Alps ca. 200,000 km²), the alpine belt is fairly narrow, as all summits are below 3000 m above sea level (m a.s.l.). The alpine zone is not very extensive, and there are no glaciers (Dachstein glacier is not within the study region) or vegetation-free nival areas that can potentially serve as new habitats for alpine species. As a result, increasing temperatures will have a greater impact on alpine vegetation relative to the central or western part of the Alps.

Environmental data and pre-processing

When developing ecological models, the choice of appropriate environmental predictor variables is a crucial step towards ensuring accuracy and model realism (Mod et al. 2016). Moreover, highly correlated environmental data may lead to unstable estimates because related variables tend to overlap.

For this reason, we made a preselection of ecologically meaningful and less correlated variables (Spearman correlation $< |0.5|$, variance inflation factor < 2 ; Table 1). All environmental predictors have been downscaled or aggregated to a spatial resolution of 50 m. Table S 1 recapitulates the original resolution and the data source.

Current and future climate data The representative concentration pathways (rcp) describe the greenhouse gas (GHG) concentration trajectories involving variables like socio-economic change, technological change, energy and land use, emissions of greenhouse gases and air pollutants. Emissions in rcp 4.5 are reaching the highest level around the middle of the century, whereas emissions in rcp 8.5 continue to rise throughout the twenty-first century (van Vuuren et al. 2011). We used two representative concentration pathways (rcp 4.5 and rcp 8.5) of the regional climate model CCLM4-8-17 provided by the climate limited-area modelling community (CLMcom). The dataset is based on daily mean temperature and precipitation values from the KNMI-RACMO22E regional climate model and uses scaled distribution mapping (SDM) for bias correction, which scales the observed distribution by simulated changes across the modelled distribution (Switanek et al. 2017). Daily average values of precipitation as well as minimum and maximum temperature for the period 1951–2100 with a spatial resolution of 1 km are available in netCDF format from the data portal of the Climate Change Centre Austria (CCCA). We first downscaled the daily climatic raster maps to a finer resolution of 50 m as a function of altitude, slope, northing and easting (see topographic variables) using robust regression (Evans 2018). Using the python module IRIS 1.13.0, we then calculated monthly averages for current (1951–2010) and decadal future time series. For each time series and each emission scenario, we calculated the maximum temperature of the warmest month (bio5, Hijmans et al. 2017, see Fig. 1) because the amplitude of temperature increase is more pronounced at this time of year, and the variable has a known impact on plant growth in alpine environments.

Geological data Major differences in vegetation patterns follow calcareous and non-calcareous bedrock, so geology is an essential determinant for Alpine plant species occurrence. The

Fig. 1 Temperature increase (maximum temperature of the warmest month, bio5) at the plot sites within the time period 2010–2100 for two emission scenarios (red, rcp 4.5; blue, rcp 8.5; see van Vuuren et al. 2011 for explanation; rcp, representative concentration pathway). We used generalized additive models with basis dimension of 3 to smooth the curves. The red and the blue area represent the 95% confidence interval for each scenario

geological map of Austria (KM 500 Austria) is provided by the geological federal institute and is available at the Austrian open data portal. For Styria, we first classified the geological map into either limestone or not limestone by assigning this dichotomous information for every pixel. We transformed the binary variable into a continuous one with a range from 0 to 1 (0 to 100%) by calculating the percentage of calcareous bedrock within a moving window. It calculates focal values for the neighbourhood of focal cells using a matrix of weights. The matrix does not need to be square, but the sides must be odd numbers. The size of the moving window affects the resulting smoothed geological variable and accounts for local variation. Too small window sizes result in sharp borders, but when the window size increases, the transition zone becomes more blurry, which comes closer to reality. Additionally, small window sizes would also give more weight to small limestone lenses, which are sparsely distributed in the central part of the Eastern Alps, where siliceous bedrock dominates. A window size of 89×99 pixel ($4.450 \text{ m} \times 4.950 \text{ m} = \sim 22 \text{ km}^2$) results in an acceptable outcome. This treatment of the binary geological variable allows to account for these small and isolated calcareous patches but did not overweight their impact. On the other hand, regions where calcareous bedrock dominates is given more weight. This weighing simultaneously affects the

Table 1 Spearman correlations and variance inflation factor (VIF) scores of the environmental variables used for the habitat suitability models

Name	Description	bio5	easting	geo	northing	swi	VIF
bio5	Maximum temperature of the warmest month	1.00	0.01	0.43	0.04	0.34	1.28
easting	Transformation of aspect; $\sin(\text{aspect})$	0.01	1.00	-0.04	-0.01	-0.07	1.01
geo	Geology	0.43	-0.04	1.00	-0.01	0.24	1.31
northing	Transformation of aspect; $\cos(\text{aspect})$	0.04	-0.01	-0.01	1.00	0.05	1.00
swi	Saga wetness index	0.34	-0.07	0.24	0.05	1.00	1.09

species' distribution, in so far that only widely distributed calcicolous species actually can be found in the isolated limestone patches.

Topographic variables Topography is a determining factor for meso-climatic site conditions. Topographic variables have been derived from a digital elevation model (DEM) available with a spatial resolution of 10 m at the Austrian open data portal. To include relief effects, we calculated slope and aspect using the terrain analysis tool “*Slope, aspect, curvature*” implemented in QGIS (QGIS Development Team 2018). The algorithm uses a 9-parameter second order polynomial and is described in Zevenbergen and Thorne (1987). In order to use circular aspect data in statistical models, we converted it into continuous variables “*northing*” and “*easting*” with a range from 1 to -1 . “*Northing*” is calculated as $\cos(\text{aspect})$ and “*easting*” as $\sin(\text{aspect})$. Soil moisture is one of the most important drivers of vegetation composition and structure (Raduła et al. 2018). We calculated the “*saga wetness index*” (SWI) as a modified “*topographic wetness index*” (TWI) using “*rsaga.wetness.index*” (Brenning et al. 2018) in R. The index is a proxy for water and nutrient accumulation.

Species plot data

Taxa selection focused on alpine vascular plant species (Table 2) that are regionally characteristic for the two EU habitats types (92/43/ECC, Habitat Directive) siliceous alpine and boreal grassland (6150), and alpine and subalpine calcareous grassland (6170). We thereby considered vegetation alliances (Grabherr and Mucina 1993) and included species from closely related alliances (e.g. *Saxifraga paniculata*, *Potentilla clusiana*) as well as regionally endemic species (e.g. *Campanula pulla*, *Potentilla clusiana*) to achieve higher level of congruence between vegetation relevés and the habitat characteristic species. In total, 4541 georeferenced plot data for the 15 species in the Styrian Alps were used. These came from the Austrian vegetation database (Willner et al. 2012) and were extended by our own vegetation plot data collected within the vegetation periods of 2016 and 2017 (Fig. 2a).

As plot sites might not have covered the study area homogeneously, we tested the value distribution of the used variables within our dataset (Fig. 3). We compared the median variable values used to calibrate the models at the plot sites ($n = 4541$) above 1800 m a.s.l., with the extracted variable values of random samples with the same sample size ($n = 4541$) in a 50-fold iteration. No significant differences were found, indicating that our dataset is representative.

Current and future habitat suitability

Modelling was performed in R (R Core Team 2018). The habitat suitability modelling procedure included four

modelling approaches: generalized linear models (GLM), boosted regression trees (BRT), random forest (RF) and Maxent, implemented in the biomod2 package (Thuiller et al. 2017). For each of the 15 alpine plant species, presence and automatically generated pseudo-absence points were correlated with the base line data set that are climatic data from the rcp 4.5 1951–2010 time series, terrain data and geological information. GLMs were calibrated as logistic regressions with quadratic interaction terms. Akaike Information Criterion (AIC) was used as a measure for a stepwise variable selection. For the BRTs, a maximum number of 1000 trees, an interaction depth of seven and shrinkage of 0.001 and three-fold cross-validation were set. RF and Maxent were run using the default settings.

For each species and modelling approach, an internal five-fold evaluation procedure was used by partitioning the model input data into a training (70%) and evaluation (30%) dataset. Two evaluation metrics, the True Skill Statistic (TSS) and the Receiver Operating Characteristic (ROC) were used to evaluate the accuracy of the models. The threshold-independent ROC (Fielding and Bell 1997), also known as Area Under the Curve (AUC), is a standard method used to assess the accuracy of predictive distribution models (Lobo et al. 2007). AUC values range from 0.5 to 1, where values of 0.5 are interpreted as random, values of 0.5–0.7 are considered low (poor model performance), values of 0.7–0.9 indicate moderate performance and above 0.9 high model performance (Swets 1988; Franklin 2010). Additionally, TSS accounts for both omission and commission errors, and success as a result of random guessing (Allouche et al. 2006). TSS ranges from -1 to $+1$, where $+1$ indicates perfect agreement and values of zero or less indicate a performance no better than random. Only models with $\text{TSS} > 0.7$ were used to build the final ensemble models. The mean probability by TSS of current and future occurrence (2020, 2030, ..., 2100) for each species was projected within each $50 \text{ m} \times 50 \text{ m}$ grid cell of the study area. Binary projections used the threshold that maximized the TSS evaluation score.

Analysis

For each species and projected time period, we counted pixels with suitable habitat conditions (see binary projections) as a measure of habitat loss over time. We quantified the loss of suitable habitats relative to the present amount of suitable habitats inside protected areas and relative to the total amount of suitable habitat in Styria. We used the current Natura 2000 coverage as a reference for site protection in Styria, because it is Europe's most important and effective network of protected areas and covers large parts of the mountainous regions in Styria. Figure 2b shows the borders of the Natura 2000 network. The coverage of the landscape above 600 m a.s.l. with Natura 2000 sites is ca. 65%. The highest parts of the protected area network (west and north in the map) are

Table 2 Modelled plant taxa with assigned habitat type code and evaluation metrics. The receiver operating characteristic (ROC) and true scale statistic (TSS) scores are averaged over 5 cross-validations, 5 pseudo-absence samplings and 4 modelling algorithms. Seventy and

30% of the data were used for model calibration and validation, respectively. Only models with a mean TSS > 0.7 have been used to build ensemble models

Species name	Abbreviation	HD code	Description of the habitat	Number of points	BRT		GLM		Max		RF	
					ROC	TSS	ROC	TSS	ROC	TSS	ROC	TSS
<i>Agrostis rupestris</i>	agrupe	6150	Siliceous alpine and boreal grassland	255	0.97	0.88	0.97	0.88	0.97	0.87	0.97	0.86
<i>Carex curvula</i>	carcur	6150	Siliceous alpine and boreal grassland	199	0.98	0.94	0.98	0.95	0.96	0.89	0.98	0.92
<i>Oreochloa distica</i>	oreodist	6150	Siliceous alpine and boreal grassland	285	0.99	0.95	0.99	0.95	0.98	0.91	0.99	0.94
<i>Primula glutinosa</i>	priglut	6150	Siliceous alpine and boreal grassland	69	0.98	0.96	0.98	0.95	0.92	0.81	0.98	0.92
<i>Primula minima</i>	primini	6150	Siliceous alpine and boreal grassland	285	0.99	0.93	0.99	0.93	0.94	0.85	0.98	0.91
<i>Valeriana celtica</i> <i>ssp. norica</i>	valcelt	6150	Siliceous alpine and boreal grassland	316	0.98	0.92	0.99	0.93	0.97	0.9	0.98	0.91
<i>Campanula pulla</i>	campull	6170	Alpine and subalpine calcareous grassland	212	0.98	0.91	0.98	0.91	0.97	0.88	0.97	0.88
<i>Carex firma</i>	carfirm	6170	Alpine and subalpine calcareous grassland	546	0.98	0.91	0.98	0.9	0.97	0.86	0.98	0.9
<i>Dryas octopetala</i>	dryocto	6170	Alpine and subalpine calcareous grassland	529	0.98	0.89	0.98	0.9	0.96	0.85	0.98	0.9
<i>Galium noricum</i>	galnori	6170	Alpine and subalpine calcareous grassland	330	0.99	0.92	0.99	0.92	0.97	0.9	0.99	0.91
<i>Primula clusiana</i>	priclus	6170	Alpine and subalpine calcareous grassland	383	0.98	0.92	0.99	0.92	0.98	0.89	0.99	0.92
<i>Sesleria albicans</i>	sesalbi	6170	Alpine and subalpine calcareous grassland	610	0.97	0.85	0.97	0.82	0.93	0.75	0.97	0.85
<i>Silene acaulis</i>	silacu	6170	Alpine and subalpine calcareous grassland	189	0.98	0.92	0.99	0.92	0.97	0.88	0.98	0.91
<i>Potentilla clusiana</i>	potclus	6170	Alpine and subalpine calcareous grassland	158	0.98	0.9	0.98	0.9	0.97	0.89	0.97	0.88
<i>Saxifraga paniculata</i>	saxpani	6170	Alpine and subalpine calcareous grassland	175	0.98	0.89	0.98	0.91	0.97	0.86	0.97	0.88
Sum/mean				4541	0.98	0.91	0.98	0.91	0.96	0.87	0.98	0.9

BRT boosted regression tree, GLM generalized linear model, Max maximum entropy, RF random forest

responsible for the protection of the two EU habitats types 6150 (siliceous Alps, especially Niedere Tauern) and 6170 (Northern Calcareous Alps) studied.

The effects of rising temperatures on habitat suitability for alpine plant species were quantified as the rate of change of habitat suitability for each species over time by pixel-wise linear regression. For all species and at each pixel location, we performed a linear regression analysis for the model projections across the decades. We calculated the slope to get the direction (increase/decrease) and the magnitude (how much) of the trend. The resulting trend maps visualize the impact intensity of temperature increase for the modelled species per decade. By averaging the resulting single species' trend maps according to their assignment to EU habitat types, we subsequently calculated trend maps for each of the habitat types.

Results

The calibrated HSMs show high performance for all modelling algorithms, with mean score values of ROC and TSS for

GBM, GLM, Maxent and RF ranging from 0.87 to 0.98. The variation in model variable importance was high for the environmental variables (Fig. S 1).

In general, our habitat models indicate a dramatic reduction of suitable habitat for all 15 plant species by the end of the twenty-first century under both emission scenarios (Fig. 4, Fig. S 2a, b). Assuming that the selected species properly represent the respective habitat type, even inside the Natura 2000 network (Fig. 5a, b), the suitable habitat conditions for the EU habitat types siliceous alpine grasslands (6150) and calcareous alpine grasslands (6170) will have decreased in the range of 50 to 90%, by the middle of the twenty-first century. From the middle of the twenty-first century onwards, the habitat decline stabilizes in the rcp 4.5 scenario, after a warming of about 2.5 degrees. By this time, calcareous alpine grasslands (6170) have lost 60%, and the siliceous alpine grasslands (6150) 85% of their suitable habitat. In the rcp 8.5 scenario, the decline continues until 2080, by which time calcareous alpine grasslands (6170) will have lost a projected 80%, and the siliceous alpine grasslands (6150) 95% of their suitable habitat in the study area.

Fig. 2 **a** Distribution of 4541 vegetation plot sites used for calibrating the habitat suitability models. The data set was compiled from the Austrian vegetation database (black dots; Willner et al. 2012) and has been extended by own relevés (red dots). **b** Location of Natura 2000 protected areas in

Styria (black lines). The base map shows the percentage of limestone above 600 m a.s.l.; red indicates no limestone, shades of blue indicate different proportions of limestone

The current Natura 2000 coverage for calcareous alpine grasslands and siliceous alpine grasslands is high, around 50 to 80%, respectively (Fig. 5c, d). With increasing temperatures, habitat loss occurs more slowly inside protected areas than outside them in the first half of the twenty-first century as the ratio of suitable habitats inside to total suitable habitat in Styria shifts towards greater representation inside the Natura 2000 protected area network. In the second half of the twenty-first century, suitable habitat conditions are highly reduced, the ratio between “inside” and “outside” stays constant for the weaker scenario (rcp 4.5) but is shifted to “outside” in the severe scenario (rcp 8.5).

The change rate of habitat suitability for species of the two EU habitat types studied in response to increasing temperatures is regionally different and independent of whether species are located inside or outside the Natura 2000 network of protected areas (Fig. 6). Regions with rapid change can be found inside and outside the protected area network.

Discussion

With increasing temperatures, an upslope shift of species and ecosystems change due to species redistribution is expected and has already been observed within long-term studies (Erschbamer et al. 2009; Pauli et al. 2012; Rogora et al. 2018; Steinbauer et al. 2018). Our regional study confirms that climate change will have a strong impact on the Alpine flora and their habitats in Styria, as soon as within in the next several decades. Currently, and during the first half of the twenty-first century, the models predict a rapid loss of habitat suitability. This loss is more pronounced in siliceous alpine grasslands (6150) than in calcareous alpine grasslands (6170). If temperatures rise moderately in the first half

Fig. 3 Comparison of the value distribution for the variables used in the habitat suitability models at the plot sites (red box plots; $n = 4541$) and for 50 iterations of random samples (blue boxplots; $50 \times n = 4541$) within the study area and above 1800 m a.s.l. with a spatial resolution of $50 \text{ m} \times 50 \text{ m}$. Maximum temperature of the warmest month (bio 5), topographic variables (northing and easting), wetness index (swi)

Fig. 4 Predicted average reduction of suitable habitat for 15 alpine plants for two climate change scenarios (rcp 4.5 and rcp 8.5; rcp, representative concentration pathway) until 2100 in Styria. The points are showing the actual range size of species in the particular decade. The smoothed lines represent the results of a local regression (loess) using the mean range size for all species per decade and emission scenario. The red and the blue area represent the 95% confidence interval for each scenario

of the twenty-first century, species within the Natura 2000 network will remain viable longer as the deterioration of habitat quality is slower inside the network than outside of it. With a 2.5 degree rise in temperature habitat, decline stabilizes after 60% of calcareous grassland habitat and 85% of siliceous grassland habitat has been lost. If the temperature increase is greater than 2.5 degrees, habitat suitability decreases dramatically relative to the current climate suitability for all modelled species, with up to 95% loss. These tendencies are more visible for the siliceous grassland, despite the Natura 2000 network having greater coverage of this vegetation type than of calcareous grassland. Even inside the protected areas, strong shifts in the species composition are visible in the models. This implies that the conservation status of the habitat types deteriorates, as they no longer correspond with the definition of the EU habitat type. This development is not in compliance with the habitat directive, which contains a no-deterioration clause. The legal consequences for the member states are completely uncertain.

The upslope shift of species is limited in mountainous ecosystems. In areas like the Styrian Alps where summits comprise the alpine belt, and there are no glaciers or vegetation-free nival areas, rising temperatures will inevitably lead to a shrinking of the alpine habitat, as demonstrated by our models. Even the protection of large areas cannot impede this process.

Small-scale situations with special microclimates might buffer the negative effects of rising macroclimate temperatures and delay the movement or extinction of cold-adapted species (Scherrer and Körner 2011; de Frenne et al. 2013; Maclean et al. 2015). Such microrefugia can act as stepping

Fig. 5 Percent decrease of potential habitat suitability for species grouped by EU habitat types (6150, siliceous alpine and boreal grassland; 6170, alpine and subalpine calcareous grassland) relative to recent amount of suitable habitats inside Natura 2000 (**a** rcp 4.5, **b** rcp 8.5) and relative to the total amount of suitable habitats within Styria (**c** rcp 4.5, **d** rcp 8.5).

stones that might facilitate future range expansions (Patsiou et al. 2014). This is not included in our models and could somewhat mitigate the strong negative results. It suggests that protected areas should be as large as possible, complex and geomorphologically diverse.

Inertia of ecological systems (von Holle et al. 2003) that leads to time-lag phenomena like the extinction debt (Dullinger et al. 2012) were not included in our models. Plants can survive for a restricted time even if the habitat is no longer suitable. This effect can trigger a delay in plant migration. Such an effect would reduce the negative result of our models. On the other hand, negative effects of land use, including the sports and leisure industry, which can affect habitat suitability (Theurillat and Guisan 2001), were also not considered in the models. These would accelerate the negative effects we describe.

Value distribution is indicated by points. The colour represents the EU habitat types. The smoothed lines represent the results of a local regression (loess) using the mean habitat suitability for all species assigned to the respective habitat type. rcp, representative concentration pathway

One important area of uncertainty missing from our models is precipitation. In the climate data, all precipitation scenarios for our study area weakened the model quality, so we omitted precipitation values from the models. Heimann and Sept (2000) indicate in their precipitation models that the Western Alps will become significantly drier in the twenty-first century, whereas the Eastern Alps show only slight changes. The precipitation regime will get more Mediterranean, with more precipitation in winter and less in summer (Beniston 2005; Gobiet et al. 2014). Rising temperatures will cause more precipitation to fall as rain instead of snow (Beniston 2005; Gobiet et al. 2014). For the vegetation, the resulting, drier conditions during the warm time of the year are likely to be comparable to the effect of an increase in temperature. Consequently, in this regional

Fig. 6 The maps show the result of a pixel-wise time series trend analysis of species grouped by EU habitat type. **a, b** Siliceous alpine and boreal grassland (6150) for rcp 4.5 and rcp 8.5, respectively; **c, d** alpine and subalpine calcareous grassland (6170) for rcp 4.5 and rcp 8.5,

respectively. Red lines represent the Natura 2000 network of protected areas. Habitat suitability changes regardless of location inside or outside of the protected network. The intensity of the change corresponds to the intensity of the grey colour. rcp, representative concentration pathway

context, with only slight changes in precipitation, temperature is the stronger climatic driver for the habitat change.

Changing environmental conditions require species to migrate, persist or adapt (Berg et al. 2010); thus, connectivity, landscape heterogeneity and matrix quality play an important future role (Gillson et al. 2013; Jones et al. 2016). Our models show that protected areas can provide suitable habitat conditions longer during moderate times but cannot stop the changes in habitat quality. Newly designed protected areas need to account for maximization of the climate space (Schloss et al. 2011), including a maximum of abiotic diversity (geology, soils and hydrology) and structural diversity (elevation, topography, habitats). Future conservation sites are reliant on functional landscapes which will likely remain viable over long time frames and provide the diverse environmental gradients and regimes necessary for biodiversity to respond to global change (Poiani et al. 2000). These considerations are also of national or international importance. The rise in global temperatures

needs to be limited to two degrees if we are to maintain alpine diversity beyond the twenty-first century in sufficiently large habitats.

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