Accounting for tree line shift, glacier retreat and primary succession in mountain plant distribution models

Bradley Z. Carlson¹, Damien Georges¹, Antoine Rabatel², Christophe F. Randin³, Julien Renaud¹, Anne Delestrade⁵,⁶, Niklaus E. Zimmermann⁴, Philippe Choler¹,⁷† and Wilfried Thuiller¹†

¹Laboratoire d’Ecologie Alpine, UMR CNRS-UJF 5553, University Grenoble Alpes, BP 53, 38041 Grenoble, France, ²Laboratoire de Glaciologie et Géophysique de l’Environnement, UMR CNRS-UJF 5183, University Grenoble Alpes, BP 96, 38402 Grenoble, France, ³Botanisches Institut der Universität Basel, Schönbeinstrasse 6, 4056 Basel, Switzerland, ⁴Swiss Federal Research Institute WSL, Zürcherstr. 111, HL-E22, 8903 Birmensdorf, Switzerland, ⁵Centre de Recherche sur les Ecosystèmes d’Altitude, 67, lacets de Belvédère, 74400 Chamonix-Mont-Blanc, France, ⁶Laboratoire d’Ecologie Alpine, UMR CNRS-UJF 5553, University de Savoie, 73376 Le Bouget du Lac, France, ⁷Station Alpine J. Fourier, UMS CNRS-UJF 3370, University Grenoble Alpes, BP 53, 38041 Grenoble, France

†Co-senior authors.

ABSTRACT

Aim To incorporate changes in alpine land cover (tree line shift, glacier retreat and primary succession) into species distribution model (SDM) predictions for a selection of 31 high-elevation plants.

Location Chamonix Valley, French Alps.

Methods We fit linear mixed effects (LME) models to historical changes in forest and glacier cover and projected these trends forward to align with 21st century IPCC climate scenarios. We used a logistic function to model the probability of plant establishment in glacial forelands zones expected to become ice free between 2008 and 2051–2080. Habitat filtering consisted of intersecting land cover maps with climate-driven SDMs to refine habitat suitability predictions. SDM outputs for tree, heath and alpine species were compared based on whether habitat filtering during the prediction period was carried out using present-day (static) land cover, future (dynamic) land cover filters or no land cover filter (unfiltered). Species range change (SRC) was used to measure differences in habitat suitability predictions across methods.

Results LME predictions for 2021–2080 showed continued glacier retreat, tree line rise and primary succession in glacier forelands. SRC was highest in the unfiltered scenario (−10%), intermediate in the dynamic scenario (−15%) and lowest in the static scenario (−31%). Tree species were the only group predicted to gain overall range by 2051–2080. Although alpine plants lost range in all three land cover scenarios, new habitat made available by glacier retreat in the dynamic land cover scenario buffered alpine plant range loss due to climate change.

Main conclusions We provide a framework for combining trajectories of land cover change with SDM predictions. Our pilot study shows that incorporating shifts in land cover improves habitat suitability predictions and leads to contrasting outcomes of future mountain plant distribution. Alpine plants in particular may lose less suitable habitat than standard SDMs predict due to 21st century glacier retreat.

Keywords Chamonix Valley – French Alps, habitat filtering, land cover dynamics, remote sensing, species range change.

INTRODUCTION

High mountain environments are characterized by steep environmental gradients that lead to abrupt changes in land cover over short distances (Billings, 1973). The alpine tree line (Körner, 2007) and the alpine-nival ecotone (Gottfried et al., 1998) represent obvious and prominent boundaries in mountain landscapes that define areas of potential habitat for many plant species. Recent studies employing species distribution models (SDMs; Guisan & Thuiller, 2005) to predict
B. Z. Carlson et al.

Mountain plant occurrence have focused largely on bioclimatic variables, such as temperature, precipitation, edaphic conditions (Dubuis et al., 2013), or biotic predictors (Pellissier et al., 2010). Climate-driven SDMs, however, run the risk of generating spurious predictions if land cover and its temporal changes are not considered. In mountain landscapes, urban areas, tree cover, bare rock or glaciers may preclude the presence of certain plant species regardless of climate conditions. Previous mountain plant modelling studies have dealt with the problem of heterogeneous land cover in two ways, either focusing on small-extent study areas with consistent habitat types (e.g. Dullinger et al., 2011) or at broader scales, using present-day land cover maps to define areas of suitable habitat for mountain plants in the future (e.g. Randin et al., 2009; Engler et al., 2011).

The use of a present-day land cover map to filter predictions of species distribution in 2080 becomes problematic given that land cover in mountain environments is dynamic and known to change over comparably short time-scales. Abundant literature points to recent and ongoing phenomena of glacier retreat (e.g. Rabatel et al., 2012, 2013), tree line rise (Kullman, 2002; Harsh et al., 2009; Elliott, 2011) and upward shifts in alpine plant distribution in response to climate change (Gottfried et al., 2012). Land abandonment and land use intensification have been connected to the expansion of mountain tree species and the loss of grassland habitat in the Pyrenees and in the Alps (Gehrig-Fasel et al., 2007; Améztegui et al., 2010; Carlson et al., 2014). In alpine environments, climate-induced glacier retreat has caused the alpine-nival ecotone to shift upward and enabled rapid primary plant succession dynamics to occur during colonization of glacier forelands (Pauli et al., 2003; Boggs et al., 2010; Burga et al., 2010). Collectively, such land cover shifts have taken place over recent decades and can be expected to continue to play a strong role in shaping mountain landscapes during the prediction period considered by most modelling studies (the next 50–100 years).

The primary aim of this study was to refine climate-based SDM predictions using dynamic land cover maps, and to test this approach on a selection of 31 plants in the Chamonix Valley, French Alps. We considered tree line rise, glacier retreat and primary succession as relevant land cover changes in determining the distribution of high mountain plants. We sought to understand the effect of using modelled land cover to define suitable habitat for plants during a 2021–2080 century prediction period, and to compare these results to predictions generated by previous approaches (either no habitat filtering or static filtering based on a present-day land cover map). To model land cover, we used historical aerial photographs to document past shifts in forest and glacier extent and then projected these trends forward in time using a linear mixed modelling approach. We classified present-day SPOT satellite imagery to include other land cover classes in our analysis in addition to forest and glacier. A logistic model was used to predict the probability of plant colonization in ice-free areas following glacier retreat. For both present-day and future land cover maps, we defined favourable habitat for plant species during the prediction period using a typology of six land cover classes. Our pilot study tests this novel methodological approach on high-elevation plants of the French Alps and lays the groundwork to better account for shifts in land cover in future studies aimed at forecasting 21st century mountain plant distribution.

METHODS

Study area context

The study area included a 122 km² sector covering the south-eastern side of the Chamonix Valley and the French side of the Mont Blanc mountain range (Figs 1c and 2). The elevation gradient of the study area spans a range from approximately 1000 m above sea level (m a.s.l.) in the valley floor to 4122 m a.s.l. at the summit of the Aiguille Verte, over a horizontal distance of approximately 5 km (Fig. 2). Glaciers are currently estimated to cover 19% of the study area (23 km²). Vegetation is typical of a granitic landscape in the northern French Alps (e.g. Lauber & Wagner, 2008). As part of the interior Alps, the climate of the Mont Blanc range is classified as continental. The Mont Blanc side of the Chamonix Valley has no official protection status and thus has been subject to a high degree of human disturbance in the form of pastoral activities and mountain tourism since the late 19th century (Sauvy, 2001). Since the 1970s, many of the slopes surrounding the Chamonix Valley have also been developed for the ski industry by the Compagnie des Remontées Mécaniques de Chamonix-Mont-Blanc (Sauvy, 2001). Although the influence of land use on vegetation in the Chamonix Valley was not explicitly considered in this study, it is important to emphasize that observed vegetation dynamics took place in a context of a heavily human-altered landscape.

Land cover mapping

Forest

Aerial photographs covering the study area were obtained for three dates (1952, 1979 and 2008; Fig. 1a). The 2008 mission consisted of 50-cm-resolution digital colour infrared (CIR) orthophotographs. The 1952 and 1979 missions were airborne paper photographs obtained from the French Institut National de l’Information Géographique et Forestière (IGN). Photographs were scanned at 1000 dpi resolution and then ortho-rectified using direct linear transformation in Erdas Imagine [version 9.2 (2011) Huntsville, AL, USA]. Approximately 25 ground control points (GCPs) were used per image, and it was ensured that the root mean square error was less than 5 m. For each date, an image mosaic was generated using histogram matching among images. Each mosaic was then imported into ArcGIS [version 10.1 (2010) Redlands, CA, USA] and ortho-rectified a second time using 200...
GCPs and the spline transformation method to ensure optimal superposition across dates. A supervised classification in eCognition Developer [version 8.0 (2012) Munich, Germany] was applied to the 1952, 1979 and 2008 mosaics to obtain a two-class forest/non-forest land cover map. Automated classification was then adjusted manually by comparison with the original mosaics, and forest cover maps were exported as 5-m raster layers.

Figure 1 Overview of the methodological approach utilised. Dashed lines represent data manipulation within a step, while solid arrows represent transitions between steps. LC = land cover; SDMs = species distribution models.

Figure 2 Example of using land cover to filter species distribution model predictions for the present-day period in the Chamonix Valley. (a) Predicted presence of *Picea abies* representing the unfiltered species distribution model output. (b) Predicted presence of *Picea abies* representing the species distribution model output filtered by present-day land cover. The dashed line on (b) indicates the extent of available land cover data.
Glacier

Glacier outlines were manually delineated for three historical dates: 1850, 1952 and 2008. Present-day moraine location was used as a signature to map maximum ice extent during the Little Ice Age, with 1850 being used as an approximate representative date (Gardent et al., 2012). Orthophotographs with a 50 cm resolution were used to map glacier extent in 1952 and 2008 at a scale of approximately 1 : 1000 (Gardent et al., 2012; Rabatel et al., 2012). This method, although more time-consuming than automatic delineation, enabled higher mapping accuracy, especially in the case of debris-covered glaciers.

Land cover modelling

A normalized Forestation Index (FI) and Glacier Index (GI) were calculated for pixel (i) and for each date (j) using the following formulas (eqn. 1 and 2):

\[ \text{FI}_{ij} = \frac{(F_{ij} - NF_{ij})}{(F_{ij} + NF_{ij})} \]  

(1)

\[ \text{GI}_{ij} = \frac{(G_{ij} - NG_{ij})}{(G_{ij} + NG_{ij})} \]  

(2)

where F represents forest area and NF non-forest area, and G represents glacier area and NG non-glacier area. Values ranged from -1.0 (non-forested or non-glaciated) to 1.0 (fully forested or fully glaciated). A hierarchical linear mixed effects (LME) model was used to analyse changes in FI over the last 60 years and changes in GI over the last 160 years (Fig. 1b). The longitudinal data set comprised N grid cells for which FI and GI were estimated for the three dates considered. Because there is the same number of repeated observations (n = 3) for all cells, and because the observations are made at fixed years, the design was balanced. The discrepancy in temporal extent between FI and GI analyses can be attributed to the lack of forest cover data for the mid-19th century. In the case of glaciers, we sought to consider to the longest available record in order to assess the hypothesis of linear recession over time.

Based on data exploration, it was hypothesized that FI and GI were dependent upon grid cell elevation, slope and date (eqn. 3 and 4):

\[ \text{FI}_{ij} = a_i + b_{i1}\text{SLOPE}_{ij} + b_{i2}\text{ELEV}_{ij} + b_{i3}\text{YEAR}_{ij} + b_{i4}\text{ELEV}_{ij} \times \text{YEAR}_{ij} + \nu_i + \nu_{ij} + \epsilon_{ij} \]  

(3)

\[ \text{GI}_{ij} = a_i + b_{i1}\text{SLOPE}_{ij} + b_{i2}\text{ELEV}_{ij} + b_{i3}\text{YEAR}_{ij} + b_{i4}\text{ELEV}_{ij} \times \text{YEAR}_{ij} + \nu_i + \nu_{ij} + \epsilon_{ij} \]  

(4)

where \( i \) corresponds to each pixel and \( j \) to each date considered, \( a \) represents model intercepts, \( b \) represents coefficients for the fixed effects SLOPE, ELEV and YEAR and their interaction, \( \nu \) are random effects and \( \epsilon \) is a cell-level error. Combined equations (3) and (4) have the form of a mixed linear model (Pinheiro & Bates, 2000).

LME models were fit at 1, 2, 3, 4 and 5 ha resolutions using the nlme library (Pinheiro et al., 2012) in the R software environment (R Core Team, 2013). Model performance was tested using AIC, log likelihood and Pearson’s correlation coefficients calculated between observed and predicted values. Random effects residuals were also considered for each model as an estimate of the explanatory power of input variables. Fitted models were then projected to the years 2021–2080, and model predictions were averaged to align with IPCC time periods 2021–2050 and 2051–2080. Continuous maps of FI and GI for the five resolutions considered were converted to point features and resampled to a baseline 100 m resolution using the kriging function in ArcGIS with a circular semivariogram. Future FI and GI were converted into binary forest/non-forest and glacier/non-glacier maps at 100 m resolution using the optimal threshold value that minimized false positives and maximized true positives for observed dates (Thuiller et al., 2009). Finally, projected maps of forest and glacier for 2021–2050 and for 2051–2080 were integrated with a current land cover map derived from SPOT satellite imagery so as to include urban areas, meadow and heath and bare ground (see Appendix S1).

A logistic regression model was used to predict the probability of plant colonization of glacier forelands following glacier retreat. Plant presence or absence based on the 2008 mosaic was detected at 100 m resolution within glacial forelands that became deglaciated between 1850 and 2008. Elevation, sum of annual solar radiation derived from a digital elevation model and distance to the front of the nearest glacier in 2008 were aggregated to grid cells, and a generalized linear model (GLM) was fit to observed data. After recalculating distance according to modelled ice extent, the GLM model was then applied to grid cells anticipated to become deglaciated between 2008 and 2051–2080. The aforementioned protocol was used to convert continuous probability values into a map of predicted plant presence–absence, and areas of presence were reclassified from bare ground to meadow/heath for the 2051–2080 land cover map. Accordingly, a seamless and dynamic land cover map from 2008 to 2051–2080 was generated 100 m resolution at the extent of the study area.

Species distribution model filtering

Species distribution models (SDMs) based on four bioclimatic variables and one regional climate scenario were calibrated at the scale of the French and Swiss Alps and were then projected at 100 m resolution for the prediction period (see Appendix S2, Fig. S1). In addition to climate suitability, land cover maps for 2008, 2021–2050 and 2051–2080 were used to define areas of favourable habitat for the 31 selected plant species. Favourable habitat for tree species was defined as forest land cover, while favourable habitat for alpine species was defined as meadow/heath and bare ground land cover. Favourable habitat for heath species was defined as bare ground, meadow/heath and forest land cover to enable

Diversity and Distributions, 1–13, © 2014 John Wiley & Sons Ltd
both understorey coexistence of heath and forest (e.g. Nilsson & Wardle, 2005) and expansion of heath into non-vegetated areas, as has been observed in the study area during recent years (personal observation, A. Delestrade). For each species and for three dates (2008, 2021–2050 and 2051–2080), SDM outputs were multiplied by a binary habitat filter (0 for non-favourable, 1 for favourable) that excluded species from areas designated as unsuitable (Fig. 1d). Three scenarios were considered: (1) a static land cover filter, which consisted of multiplying the 2008 land cover map with SDM outputs for 2021–2050 and for 2051–2080, (2) a dynamic land cover filter, which consisted of multiplying SDM outputs for 2021–2050 and for 2051–2080, and (3) unfiltered SDM outputs that were not intersected with land cover data. Predicted species range change (SRC; % predicted range gain – % predicted range loss) was used to assess the effect of land cover filtering on habitat suitability predictions. Finally, a pairwise Wilcoxon rank sum was used to test for differences in SRC results among unfiltered, dynamic and static land cover scenarios.

RESULTS

Past and future land cover change

Historical land cover consistently reflected increasing forest cover as well as the diminishing extent of glaciers (Table 2). Glaciers covered 30% of the study area in 1850 as compared to 19% in 2008, whereas relative forest cover increased from 17% in 1952 to 26% of the study area in 2008. Observed forest expansion can be fit by a positive linear trajectory ($P < 0.001$) between 1952 and 2008, while glacier expansion can be fit by a negative linear trend ($P < 0.001$) between 1850 and 2008. Historical shifts at the scale of the study area thus supported the use of a linear model to predict future trends in land cover dynamics (Fig. 3). Among the five resolutions that were tested, the 300-m-resolution FI model and 100-m-resolution GI model were retained to model forest and glacier extent over time (see Appendix S3; Tables S1 and S2). Predicted land cover scenarios for forest and glacier reflected ongoing forest expansion and glacier retreat (Table 1). Although glacier cover continued to decrease at a roughly constant rate during the prediction period, increase in forest cover between 2021–2050 and 2051–2080 slackened (<2 km$^2$ gain) in comparison with observed historical changes. Forest expansion was particularly noticeable in the vicinity of the Col de Balme (see inset in Fig. 4). The model for plant succession predicted the expansion of meadow/heath communities in 2051–2080 (see the Mer de Glace inset, Fig. 4).

Land cover filtering of species distribution models

For the duration of the prediction period and for all species considered, proportional loss in suitable habitat was equivalent across land cover scenarios (57–58%) (Table 2). Proportional gain in suitable habitat was highest for unfiltered SDMs (49%), intermediate when the dynamic filter was applied (43%) and lowest in the case of the static filter (27%). Absolute range gain and loss were substantially higher in the unfiltered scenario, however, given that current and future species distributions in this scenario were not restricted by land cover maps. Overall species range change...
SRC was highest in the unfiltered scenario (−10%), intermediate in the dynamic scenario (−15%) and lowest in the static scenario (−31%). Pairwise differences in SRC among unfiltered, dynamic and static scenarios were significant (P < 0.001). Delta SRC between dynamic and static filtering methods was highest among tree species (+25%), followed by alpine plants (+20%), and was surprisingly low among heath species (+2%; Table 2).

Application of the three different land cover scenarios (dynamic, static and unfiltered) led to contrasting range gain predictions for the three plant groups considered (tree, heath and alpine). Pinus cembra, a pioneer tree species in the Chamonix Valley, gained 101 ha in the dynamic scenario as compared to only 10 ha in the static scenario. Below the tree line, montane species such as Fagus sylvatica gained substantially more range in the dynamic land cover scenario. As a group, tree species gained the most range in 2021–2050 when the dynamic filter was applied (Fig. 5a). However, as rates of modelled forest expansion declined for the 2051–2080 period, median species range gain for trees shifted to being higher in the case of the unfiltered SDM. When compared to the static scenario, heath species gained more range over the prediction period in the dynamic scenario due to modelled glacier retreat and primary succession. In the dynamic scenario, montane shrubs such as Salix caprea gained the most range (+2318 ha) while the expansion of more cryophilous subalpine species such as Empetrum nigrum was restricted by thermal limits and glacier cover (+34 ha; Table 2). Throughout the prediction period, alpine plants gained the most range in the case of the dynamic filter, even as compared to the unfiltered scenario (Fig. 5a). Expected gain in suitable habitat for alpine plants was therefore higher based on combined climate and land cover change relative to climate change alone. Across land cover scenarios, suitable habitat loss was greatest for alpine/nival species such as Ranunculus glacialis and Saxifraga oppositifolia and was lowest for transition subalpine/alpine species such as Trifolium alpinum and Dryas octopetala (Table 1).

Trees were the only species group to maintain average positive SRC throughout the prediction period in all three scenarios (Fig. 5b). Heath species exhibited neutral SRC across scenarios for 2021–2050, which shifted to negative

Table 1 Relative cover of forest and glacier for observed (1850 to 2008) and predicted (2021–2080) time periods (− indicates that no data were available for this date).

<table>
<thead>
<tr>
<th>Year</th>
<th>Forest % Cover</th>
<th>Forest Area (km²)</th>
<th>Glacier % Cover</th>
<th>Glacier Area (km²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Observed</td>
<td>1850</td>
<td>17</td>
<td>30</td>
<td>36.87</td>
</tr>
<tr>
<td></td>
<td>1952</td>
<td>20</td>
<td>22</td>
<td>26.71</td>
</tr>
<tr>
<td></td>
<td>1979</td>
<td>26</td>
<td>–</td>
<td>22.96</td>
</tr>
<tr>
<td></td>
<td>2008</td>
<td>36</td>
<td>19</td>
<td>22.96</td>
</tr>
<tr>
<td>Predicted</td>
<td>2021–2050</td>
<td>36</td>
<td>14</td>
<td>16.61</td>
</tr>
<tr>
<td></td>
<td>2051–2080</td>
<td>37</td>
<td>10</td>
<td>11.73</td>
</tr>
</tbody>
</table>

Figure 4 Land cover filters used to define areas of favourable habitat for the 36 plant species considered: (a) 2008 (b) 2021–2050 and (c) 2051–2080. Inset maps represent modelled plant succession dynamics on the foreland of the Mer de Glace Glacier and in the Col de Balme agro-pastoral area.
Table 2 Predicted range change in 2051–2080 relative to current distributions for dynamic, static and unfiltered land cover scenarios by species and vegetation group

<table>
<thead>
<tr>
<th>Species</th>
<th>Dynamic LC</th>
<th>Static LC</th>
<th>Unfiltered</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Loss (ha)</td>
<td>Stable (ha)</td>
<td>Gain (ha)</td>
</tr>
<tr>
<td>Tree</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Populus tremula</td>
<td>27</td>
<td>1659</td>
<td>1196</td>
</tr>
<tr>
<td>Betula pendula</td>
<td>854</td>
<td>1193</td>
<td>216</td>
</tr>
<tr>
<td>Betula alba</td>
<td>1696</td>
<td>332</td>
<td>506</td>
</tr>
<tr>
<td>Alnus incana</td>
<td>0</td>
<td>442</td>
<td>1528</td>
</tr>
<tr>
<td>Acer pseudoplatanus</td>
<td>490</td>
<td>2073</td>
<td>1799</td>
</tr>
<tr>
<td>Larix decidua</td>
<td>407</td>
<td>1608</td>
<td>728</td>
</tr>
<tr>
<td>Picea abies</td>
<td>517</td>
<td>2836</td>
<td>1009</td>
</tr>
<tr>
<td>Pinus cembra</td>
<td>1692</td>
<td>574</td>
<td>101</td>
</tr>
<tr>
<td>Pinus uncinata</td>
<td>1306</td>
<td>822</td>
<td>1029</td>
</tr>
<tr>
<td>Fagus sylvatica</td>
<td>237</td>
<td>1332</td>
<td>2756</td>
</tr>
<tr>
<td>Heath</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Salix caprea</td>
<td>197</td>
<td>3530</td>
<td>2318</td>
</tr>
<tr>
<td>Arctostaphylos uvaursi</td>
<td>2491</td>
<td>766</td>
<td>1560</td>
</tr>
<tr>
<td>Calluna vulgaris</td>
<td>363</td>
<td>10</td>
<td>22</td>
</tr>
<tr>
<td>Rhododendrum ferrugineum</td>
<td>2224</td>
<td>2268</td>
<td>328</td>
</tr>
<tr>
<td>Vaccinium myrtillus</td>
<td>2239</td>
<td>3260</td>
<td>683</td>
</tr>
<tr>
<td>Vaccinium uliginosum</td>
<td>3433</td>
<td>5</td>
<td>40</td>
</tr>
<tr>
<td>Vaccinium vitisidae</td>
<td>2412</td>
<td>3294</td>
<td>179</td>
</tr>
<tr>
<td>Empetrum nigrum</td>
<td>3661</td>
<td>629</td>
<td>34</td>
</tr>
<tr>
<td>Sorbus chamaemespilus</td>
<td>3377</td>
<td>340</td>
<td>1375</td>
</tr>
<tr>
<td>Juniperus sibirica</td>
<td>2181</td>
<td>1744</td>
<td>555</td>
</tr>
<tr>
<td>Alpine</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ranunculus glacialis</td>
<td>2353</td>
<td>393</td>
<td>956</td>
</tr>
<tr>
<td>Dryas octopetala</td>
<td>1115</td>
<td>1908</td>
<td>1873</td>
</tr>
<tr>
<td>Salix herbacea</td>
<td>2539</td>
<td>674</td>
<td>1081</td>
</tr>
<tr>
<td>Linaria alpina</td>
<td>2177</td>
<td>862</td>
<td>1094</td>
</tr>
<tr>
<td>Carex curvula</td>
<td>3256</td>
<td>205</td>
<td>706</td>
</tr>
<tr>
<td>Silene acaulis</td>
<td>2172</td>
<td>1256</td>
<td>1311</td>
</tr>
<tr>
<td>Festuca halleri</td>
<td>3276</td>
<td>110</td>
<td>669</td>
</tr>
<tr>
<td>Sedum alpestre</td>
<td>3330</td>
<td>153</td>
<td>621</td>
</tr>
<tr>
<td>Trifolium alpinum</td>
<td>1399</td>
<td>2010</td>
<td>797</td>
</tr>
<tr>
<td>Gentiana acutis</td>
<td>1784</td>
<td>1808</td>
<td>823</td>
</tr>
<tr>
<td>Saxifraga oppositifolia</td>
<td>3592</td>
<td>14</td>
<td>9</td>
</tr>
<tr>
<td>Mean</td>
<td>1832.16</td>
<td>1229.35</td>
<td>900.06</td>
</tr>
</tbody>
</table>

Combining SDMs with mountain land cover dynamics
The main finding of this study was to show that the consideration of historical trends in land cover projected forward to the 21st century significantly altered SDM predictions for mountain plants. To the best of our knowledge, this approach is unique in that it combines historical remote sensing with species distribution models in a high mountain context. It differs from previous attempts to refine SDM predictions in alpine environments that used very high-resolution explanatory variables (Randin et al., 2009) or that took into account mechanistic processes such as the lag time associated with plant dispersal (Dullinger et al., 2012), although ideally these different approaches should be combined (Carlson et al., 2013). Our results support the conclusion that mountain plants could lose less range due to climate change than standard SDMs predict (Randin et al., 2009; Engler et al., 2011).

### DISCUSSION

The main finding of this study was to show that the consideration of historical trends in land cover projected forward to the 21st century significantly altered SDM predictions for mountain plants. To the best of our knowledge, this approach is unique in that it combines historical remote sensing with species distribution models in a high mountain context. It differs from previous attempts to refine SDM predictions in alpine environments that used very high-resolution explanatory variables (Randin et al., 2009) or that took into account mechanistic processes such as the lag time associated with plant dispersal (Dullinger et al., 2012), although ideally these different approaches should be combined (Carlson et al., 2013). Our results support the conclusion that mountain plants could lose less range due to climate change than standard SDMs predict (Randin et al., 2009; Engler et al., 2011).

### Predicted land cover change in the Chamonix Valley

Linear mixed effects modelling of shifts in glacier and forest extent combined with a logistic model of plant succession in the wake of glacier retreat allowed for anticipation of land cover changes during the 2021–2080 prediction period considered in this study. The resulting dynamic land cover filters included two succession processes that were absent from the static (2008) land cover filter (for definitions of succession, refer to Connell & Slatyer, 1977). The first process consisted of a secondary succession dynamic in the form of forest expansion and upper tree line shift, which was particularly pronounced in agro-pastoral zones such as the mid-elevation (approximately 2100 m a.s.l.) Col de Balme sector (Fig. 4).

Although the use of time and topography as explanatory variables did not allow for disentanglement of climate and land use drivers in this study, evidence from elsewhere in the Alps points to land abandonment as the primary driver of forest expansion in subalpine areas below the potential physiological tree line (Gehrig-Fasel et al., 2007; Améztegui et al., 2010; Carlson et al., 2014). It appears likely that shifts in land use practices occurring in a climate warming context also contributed to the rapid increase in forest cover documented in the Chamonix Valley between 1952 and 2008, and to predicted forest expansion between 2021 and 2080. The second process imbedded in the dynamic land cover model consisted of simulating glacier retreat and ensuing primary succession dynamics. The predicted presence of forest and heath/meadow land cover classes in areas expected to become free of ice between 2008 and 2050 aligned both with observed historical changes in the study area (Fig. S2) and with observations of primary plant succession in glacier forelands from the Swiss Alps (Burga et al., 2010).

In the case of forest land cover modelling, our empirical approach aimed to capture information contained in aerial photos and to generate future scenarios of forest extent based on historical rates of change. While tree line position at the regional scale can be reliably predicted by temperature, variation at local scales is largely due to non-elevation specific drivers such as land use and geomorphic disturbance (Körner, 2007; Case & Duncan, 2014). Here, we did not attempt to disentangle the factors determining tree line position, but rather sought to quantify local trajectories of tree cover transitions.

### Table 2 Continued

<table>
<thead>
<tr>
<th>Static LC</th>
<th>Unfiltered</th>
</tr>
</thead>
<tbody>
<tr>
<td>Loss (ha)</td>
<td>Stable (ha)</td>
</tr>
<tr>
<td>3658</td>
<td>632</td>
</tr>
<tr>
<td>3377</td>
<td>340</td>
</tr>
<tr>
<td>2180</td>
<td>1745</td>
</tr>
<tr>
<td>2353</td>
<td>393</td>
</tr>
<tr>
<td>1066</td>
<td>1957</td>
</tr>
<tr>
<td>2539</td>
<td>674</td>
</tr>
<tr>
<td>2177</td>
<td>862</td>
</tr>
<tr>
<td>3256</td>
<td>205</td>
</tr>
<tr>
<td>2171</td>
<td>1257</td>
</tr>
<tr>
<td>3276</td>
<td>110</td>
</tr>
<tr>
<td>3330</td>
<td>153</td>
</tr>
<tr>
<td>1386</td>
<td>2023</td>
</tr>
<tr>
<td>1778</td>
<td>1814</td>
</tr>
</tbody>
</table>

SRC for most species in 2051–2080. For alpine plants in 2021–2050, SRC was negative in the unfiltered and static land cover scenarios, yet switched to being neutral when the dynamic filter was applied. Although alpine plants lost overall range in all three land cover scenarios for the 2051–2080 period (Fig. 5b), the least loss occurred when the dynamic filter was used to define suitable habitat (+13% relative to the unfiltered and +19% relative to the static scenarios; Table 1).
line shift ultimately resulting from the combined effects of climate, disturbance linked to land management and geomorphology, and biological constraints (competition and dispersal). For example, although climate is not addressed as an explicit driver of forest expansion, the land cover model was fit to observed shifts in tree line occurring in the context of 20th century climate change. Our goal was thus to estimate the overall extent of forest over time using the land cover model, and then to predict the distribution of tree species within this broader matrix based on climate suitability. We consider that combining the land cover model with SDM outputs provides complimentary information and that retaining the intersection of the two models adds fine-grained spatial heterogeneity to habitat suitability predictions that are otherwise largely based on temperature isotherms (Fig. 2).

For glacier modelling, predictive scenarios of glacier retreat generated during this study were simplified (two-dimensional) and did not explicitly address processes known to drive glacier retreat dynamics, such as climate (air temperature and snow fall), the extent and elevation of upper accumulation zones, ice flow dynamics and topography (Haeberli & Beniston, 1998). While our approach was useful for generating future scenarios of glacier extent based on historical trends, other studies predicting the accelerated loss of ice over the next decades indicate that we likely under-estimated 21st century glacier retreat in our study area (Jouvet et al., 2009; Huss et al., 2010). Finally, the correlative approach
between dynamic and static land cover scenarios were greatest proportional differences in species range gain in the 31 mountain plants considered. Among tree species, the puts led to contrasting predictions of habitat suitability for Combining 21st century land cover change with SDM out-
distributions Effects of land cover filtering on predicting species
approach, unless strong breaks in climate and land use
past multiple decades suggest that our projected land cover
observed for both forest and glacier cover change over the
and glacier extent. However, the comparable linear trends
observed for both forest and glacier cover change over the
the past multiple decades suggest that our projected land cover
trends may not differ much from a more mechanistic
approach, unless strong breaks in climate and land use
trends occur in the near future.

**Effects of land cover filtering on predicting species distributions**

Combining 21st century land cover change with SDM out-
puts led to contrasting predictions of habitat suitability for
the 31 mountain plants considered. Among tree species, the
greatest proportional differences in species range gain
between dynamic and static land cover scenarios were
obtained by tree line species such as Pinus cembra and Picea
abies (Table 1). Accounting for forest expansion in the
dynamic land cover filter allowed tree line species to track
climate changes by moving upward, as opposed to being lim-
ited by the fixed tree line barrier imposed by the static land
cover filter. In both static and dynamic land cover scenarios,
however, strict habitat filtering based on forest land cover
excluded tree co-occurrence with meadow or heath com-
munities, or in favourable microsites known to enable the instal-
lion of pioneer tree individuals above tree line (e.g. Batllori
et al., 2009). We used tree line to define the upper limit of
tree suitable habitat, considering that the abundance and
biomass of isolated trees located above tree line was minimal.
Furthermore, the underlying land cover model accounted for
tree succession into areas of meadow/heath and bare ground.
When the dynamic filter was applied to trees such as Fagus
sylvatica and Acer pseudoplatanus, higher amounts of gain
in suitable habitat relative to other land cover scenarios
could be attributed to below tree line forest densification
and colonization dynamics (Table 1).

Consideration of overall species range change (SRC)
allowed for comparison of the effects of the three different
land cover scenarios (Fig. 5b). When the dynamic filter
was applied, the greater predicted habitat gain and SRC for
trees in 2021–2050 suggested that modelled forest expan-
sion in the dynamic filter outpaced habitat gain due to
predicted climate change alone. In 2051–2080, however,
greater SRC among trees for the unfiltered SDM showed
that climate-induced range change surpassed forest expan-
sion predicted by the land cover model. Such findings align
with a recent study conducted in the French Alps, which
showed that the expansion of tree species responded rap-
idly to land use change, but exhibited prolonged lag times
in response to climate change (Boulangeat et al., 2014).
Also, given the reliance of our land cover model on extrapol-
ating observed historical changes, our predictions are
likely to be less pertinent for the more distant 2051–2080
time period.

Heath species posed a particular challenge in this land
cover filtering exercise, as their thermal limits do not align
with either tree line or alpine-nival ecotone boundaries, and
their biogeography spans a broad range of intermediate
mountain habitats. Additionally, the present-day distribution
of heath communities is difficult to detect using remote sens-
ing, due to the frequent occurrence of heath as forest under-
storey species and also their similar spectral signal relative to
grasslands. Given that we were unable to quantify historical
changes in the distribution of heath species, and the broad
range of habitat types in which they occur, we decided to
not to restrict favourable habitat for this group except by
glacier cover. Even so, the neutral to negative trend in SRC
predicted in the dynamic scenario likely underestimates the
future prevalence of heath species in the study area. Contrary
to our model predictions, recent observation of heath expan-
sion and invasion of alpine zones in the Chamonix Valley
would suggest that heath species are likely to be beneficiaries
of warming mountain zones during the 21st century
(A. Delestrade, personal observation).

For the eleven alpine plant species considered, the shift
from positive SRC in 2021–2050 to net negative SRC in
2051–2080 when the dynamic land cover filter was used
(Fig. 5b) aligns with the hypothesis that alpine plant range
loss will occur gradually (Dullinger et al., 2012). Although
we considered the 'full dispersal' scenario here, it has been
shown that dispersal limitation causes alpine plants to lag
behind climate shifts and to persist in marginal conditions
before reaching a critical extinction threshold (Dullinger
et al., 2012). Such findings suggest that the consequences of
climate change may require multiple decades to become fully
apparent in alpine plant communities. In our results, the
observed tipping point for alpine plants from SRC gain in
2021–2050 to loss in 2051–2080 could be due to upward
shifts in suitable habitat in the context of conically shaped
mountain summits (Körner et al., 2011). When alpine plants
move upward in elevation to track favourable climate condi-
tions, inevitably they lose ground due to the decreasing
amount of available surface area. Despite the predicted loss
of suitable alpine habitat due to 21st century regional climate
warming (Engler et al., 2011), it has been suggested that
alpine plants will be able to persist locally by means of topo-
graphically defined micro-refugia (Randin et al., 2009; Scher-
rer & Körner, 2011). Our findings contribute to the
hypothesis that climate-driven SDMs might over-predict
alpine plant habitat loss by pointing out that the loss of alpine plant habitat could be further mitigated by new habitat made available by glacier retreat.

CONCLUSION

The results of this study point to the rich potential of combining trajectories of land cover change with species distribution modelling methods as a means of better understanding the response of mountain ecosystems to 21st century climate change. We show that remote sensing-derived land cover information can refine both current and future predictions of habitat suitability for plant species. We further demonstrate that when rates of glacier loss, primary succession and forest expansion are taken into account in addition to traditional climate drivers, high-elevation plants are predicted to lose less overall range than when mountain land cover is held constant. Although in this study we combined land cover modelling with species distribution models, the approach used here could readily be applied to filter the predictions of more complex, process-based biodiversity models applied to mountainous regions.

ACKNOWLEDGEMENTS

The research leading to this paper received funding from the European Research Council under the European Community’s Seven Framework Programme FP7/2007–2013 Grant Agreement no. 281422 (TEEMBIO). Collaboration and data sharing was facilitated by the Mont Blanc Atlas project (http://atlas-montblanc.org), initiated by the Centre de Recherche sur les Ecosystèmes d’Altitude (CREA). Most of the computations presented in this paper were performed using the CIMENT infrastructure (https://ciment.ujf-grenoble.fr), which is supported by the Rhône-Alpes region (GRANT CPER07_13 CIRA: http://www.ci-ra.org) and France-Grille (http://www.france-grilles.fr). We thank the SO/SOERE GLACIOCLIM (CNRS/Univ. Grenoble Alpes/IRD) and the LabEx OSUG@2020 (funded by the ‘Programme d’Investissements d’Avenir’ from the French government implemented by the ANR), for the funding of the orthorectification, georeferencing and mosaicing of 1952 aerial photographs.

REFERENCES


and retrogradation (green wave effect) of natural vegetation. NASA/GSFC, Final Report. Greenbelt, MD, 1 137.

SUPPORTING INFORMATION
Additional Supporting Information may be found in the online version of this article:
Appendix S1 SPOT satellite imagery.
Appendix S2 Species distribution modelling.
Appendix S3 Land cover model selection.

Figure S1 Model performance, estimated by the true skill statistic (TSS), by vegetation group.
Figure S2 Glacier retreat and plant succession on the Mer de Glace Glacier between 1952 and 2008.
Table S1 Model evaluation parameters for forest and glacier linear mixed models relative to grid cell resolution. Akaike’s information criteria (AIC), log likelihood and random effects residuals were used to assess the ability of fixed effects to explain between grid cell variation in FI and GI. Resolutions that appear in bold were retained for forest index (FI) and glacier index (GI) modelling.
Table S2 Range change metrics for predicted forest cover in 2021–2050 and in 2051–2080 for different grid cell resolutions. The 300 m resolution is in bold as this was the grid cell size that was retained and integrated into the dynamic land cover filter.

BIOSKETCH
Bradley Z. Carlson is currently a PhD student working on the EMABIO team at the Laboratory of Alpine Ecology (LECA) in Grenoble, France. His project is focused on integrating remote sensing data into models of plant distribution in high-elevation landscapes.

Author contributions: W.T., P.C., A.D. and B.Z.C. conceived the ideas; N.Z., C.F.R. and D.G. collected data and built species distribution models; J.R. carried out habitat mapping using satellite imagery; A.R. provided historical glacier extent data and expertise; B.Z.C. performed the majority of data analysis, including land cover modelling, and led the writing.

Editor: Mathieu Rouget