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

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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

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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; Harsch *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 km^2 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 km^2). 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 Forestrière* (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

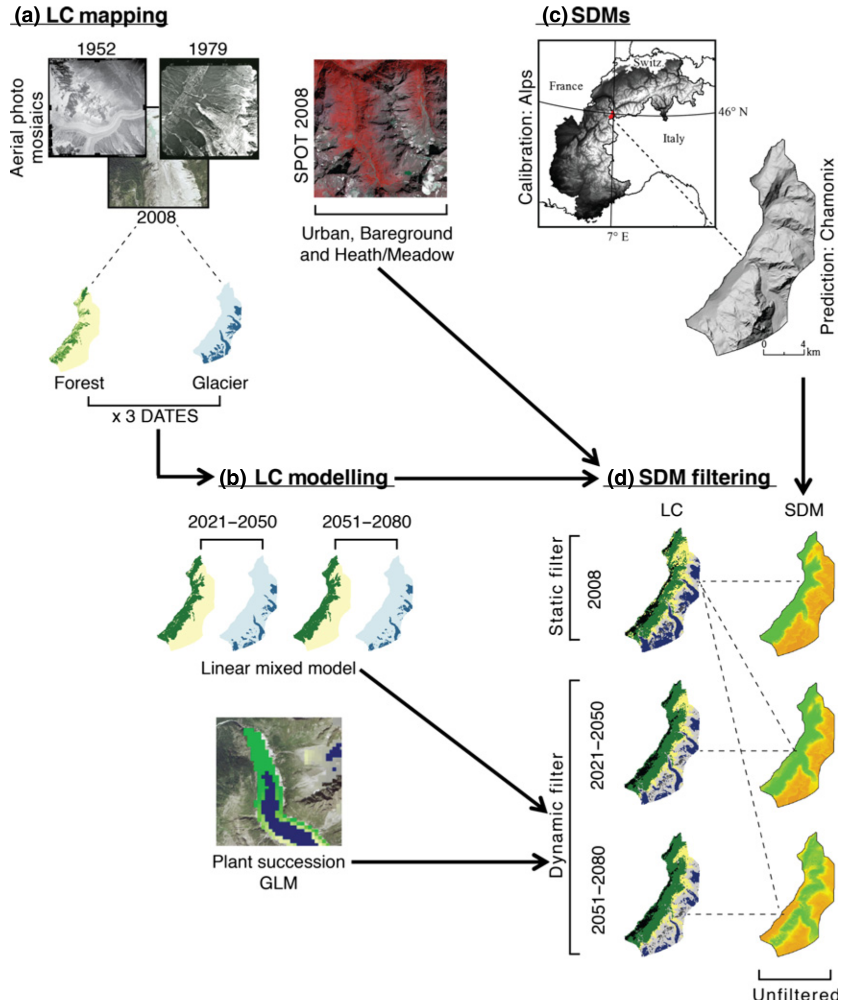

Figure 1 Overview of the methodological approach utilised. Dashed lines represent data manipulation within a step, while solid arrows represent transitions between steps. LC = land cover; SDMs = species distribution models.

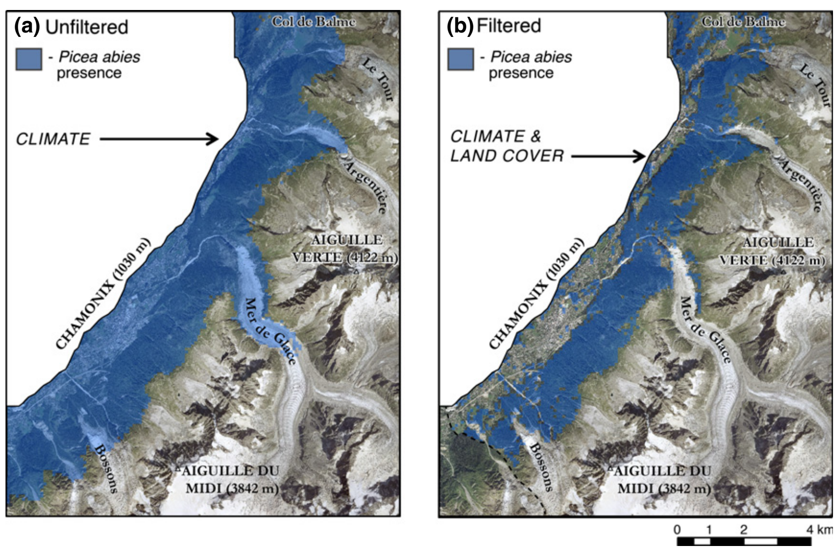

Figure 2 Example of using land cover to filter species distribution model predictions for the present-day period in the Chamonix Valley. (a) Predicted presence of *Picea abies* representing the unfiltered species distribution model output. (b) Predicted presence of *Picea abies* representing the species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

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.

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 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):

$$FI_{ij} = (F_{ij} - NF_{ij})/(F_{ij} + NF_{ij}) \quad (1)$$

$$GI_{ij} = (G_{ij} - NG_{ij})/(G_{ij} + NG_{ij}) \quad (2)$$

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):

$$FI_{ij} = a_i + b_{01}SLOPE_i + b_{02}ELEV_i + b_{03}YEAR_{ij} + b_{04}ELEV_i * YEAR_{ij} + \upsilon_{0i} + \upsilon_{1i}YEAR_{ij} + \varepsilon_{ij} \quad (3)$$

$$GI_{ij} = a_i + b_{01}SLOPE_i + b_{02}ELEV_i + b_{03}YEAR_{ij} + b_{04}ELEV_i * YEAR_{ij} + \upsilon_{0i} + \upsilon_{1i}YEAR_{ij} + \varepsilon_{ij} \quad (4)$$

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, υ are random effects and ε 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

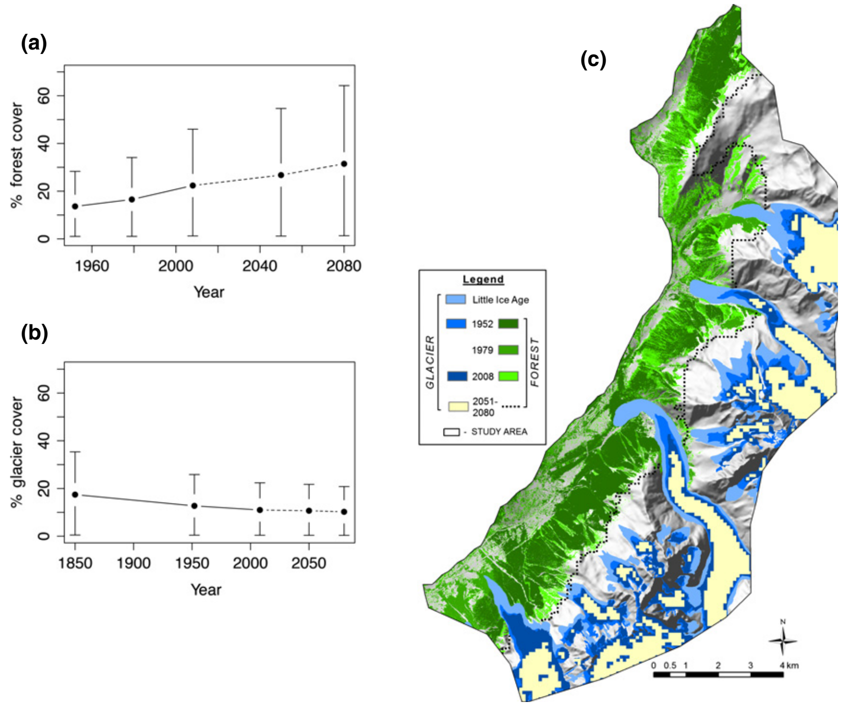

Figure 3 Percentage of forest (a) and glacier (b) cover averaged among 1 ha grid cells (N = 12,242) across the study area for the three historical dates considered (1952, 1979 and 2008 for forest and 1850, 1952 and 2008 for glacier), showing 95% confidence intervals. Solid lines represent historical land cover data, while dashed lines represent predicted land cover. (c) Juxtaposition of historical land cover data with predicted tree line and glacier position for 2051–2080.

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 with projected land cover maps for the respective time periods 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 into areas that were glaciated in 2008 (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

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).

	Year	Observed 1850	1952	1979	2008	Predicted 2021–2050	2051–2080
Forest	% Cover		17	20	26	36	37
	Area (km^2)	–	20.59	24.23	32.16	43.48	45.5
Glacier	% Cover	30	22	–	19	14	10
	Area (km^2)	36.87	26.71	–	22.96	16.61	11.73

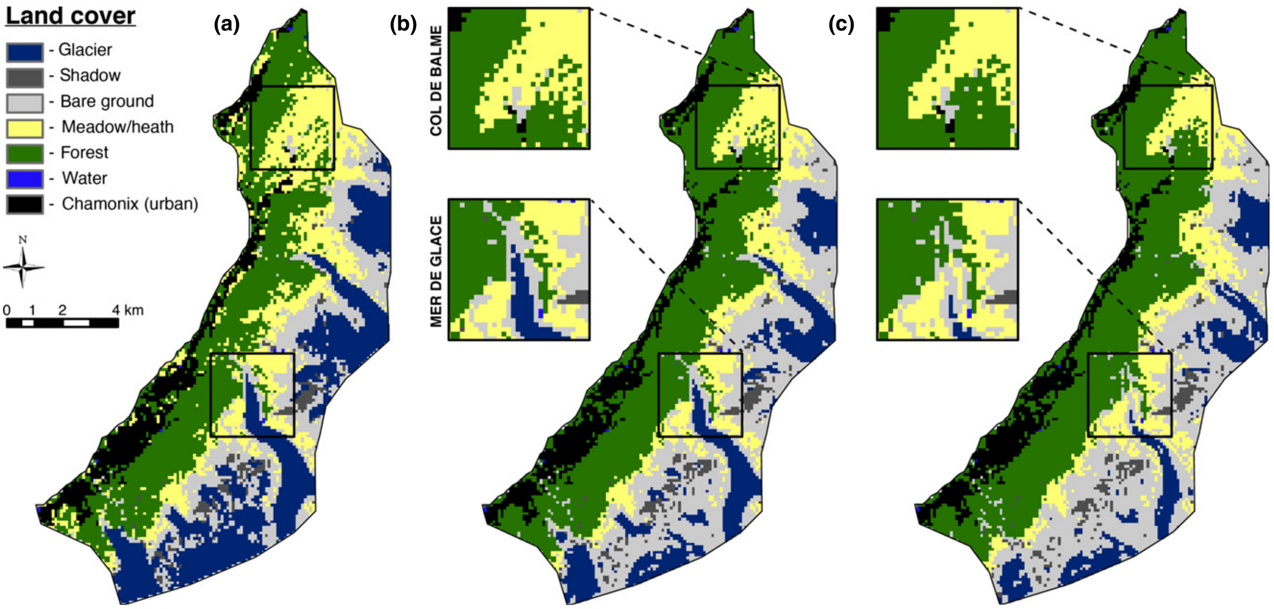

Figure 4 Land cover filters used to define areas of favourable habitat for the 36 plant species considered: (a) 2008 (b) 2021–2050 and (c) 2051–2080. Inset maps represent modelled plant succession dynamics on the foreland of the Mer de Glace Glacier and in the Col de Balme agro-pastoral area.

(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 plants 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 (Table 1). 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 1). 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 2 Predicted range change in 2051–2080 relative to current distributions for dynamic, static and unfiltered land cover scenarios by species and vegetation group

		Dynamic LC						Static LC						Unfiltered					
	Species	Loss (ha)	Stable (ha)	Gain (ha)	% Loss	% Gain	SRC	Loss (ha)	Stable (ha)	Gain (ha)	% Loss	% Gain	SRC	Loss (ha)	Stable (ha)	Gain (ha)	% Loss	% Gain	SRC
Tree	*Populus tremula*	27	1659	1196	1.60	70.94	69.34	27	1659	627	1.60	37.19	35.59	183	2958	985	5.83	31.36	25.53
	Betula pendula	854	1193	216	41.72	10.55	−31.17	854	1193	128	41.72	6.25	−35.47	2250	1373	162	62.10	4.47	−57.63
	Betula alba	1696	332	506	83.63	24.95	−58.68	1696	332	413	83.63	20.37	−63.26	2341	380	2036	86.04	74.83	−11.21
	Alnus incana	0	442	1528	0.00	345.70	345.70	0	442	1234	0.00	279.19	279.19	96	1078	1959	8.18	166.87	158.69
	Acer pseudoplantanus	490	2073	1799	19.12	70.19	51.07	490	2073	1062	19.12	41.44	22.32	1507	2859	4919	34.52	112.67	78.15
	Larix decidua	407	1608	728	20.20	36.13	15.93	407	1608	363	20.20	18.02	−2.18	568	2253	4410	20.14	156.33	136.19
	Picea abies	517	2836	1009	15.42	30.09	14.67	517	2836	272	15.42	8.11	−7.31	1545	4373	2799	26.11	47.30	21.19
	Pinus cembra	1692	574	101	74.67	4.46	−70.21	1692	574	10	74.67	0.44	−74.23	2893	1626	3466	64.02	76.70	12.68
	Pinus uncinata	1306	822	1029	61.37	48.36	−13.02	1306	822	693	61.37	32.57	−28.81	1827	1259	4636	59.20	150.23	91.02
	Fagus sylvatica	237	1332	2756	15.11	175.65	160.55	237	1332	1967	15.11	125.37	110.26	966	2046	3572	32.07	118.59	86.52
Heath	*Salix caprea*	197	3530	2318	5.286	62.195	56.909	197	3530	2115	5.286	56.748	51.462	673	4444	3485	13.15	68.11	54.95
	Arctostaphylos uvaursi	2491	766	1560	76.481	47.897	−28.585	2491	766	1490	76.481	45.748	−30.734	3018	978	3080	75.53	77.08	1.55
	Calluna vulgaris	363	10	22	97.319	5.898	−91.421	363	10	22	97.319	5.898	−91.421	506	10	24	98.06	4.65	−93.41
	Rhododendrum ferrugineum	2224	2268	328	49.51	7.302	−42.208	2221	2271	231	49.443	5.142	−44.301	2592	3826	2715	40.39	42.30	1.92
	Vaccinium myrtillus	2239	3260	683	40.716	12.42	−28.296	2238	3261	496	40.698	9.02	−31.678	3100	4328	2466	41.73	33.20	−8.54
	Vaccinum uliginosum	3433	5	40	99.855	1.163	−98.691	3432	6	38	99.825	1.105	−98.72	5328	51	669	99.05	12.44	−86.62
	Vaccinium vitisidaea	2412	3294	179	42.271	3.137	−39.134	2409	3297	19	42.219	0.333	−41.886	2974	6194	1209	32.44	13.19	−19.25
	Empetrum nigrum	3661	629	34	85.338	0.793	−84.545												
	Sorbus chamaemespilus	3377	340	1375	90.853	36.992	−53.861												
	Juniperus sibirica	2181	1744	555	55.567	14.14	−41.427												
Alpine	*Ranunculus glacialis*	2353	393	956	85.69	34.81	−50.87												
	Dryas octopetala	1115	1908	1873	36.88	61.96	25.07												
	Salix herbacea	2539	674	1081	79.02	33.65	−45.38												
	Linaria alpina	2177	862	1094	71.64	36.00	−35.64												
	Carex curvula	3256	205	706	94.08	20.40	−73.68												
	Silene acaulis	2172	1256	1311	63.36	38.24	−25.12												
	Festuca halleri	3276	110	669	96.75	19.76	−76.99												
	Sedum alpestre	3330	153	621	95.61	17.83	−77.78												
	Trifolium alpinum	1399	2010	797	41.04	23.38	−17.66												
	Gentiana acaulis	1784	1808	823	49.67	22.91	−26.75												
	Saxifraga oppositifolia	3592	14	9	99.61	0.25	−99.36												
	Mean	1832.16	1229.35	900.06	57.72	42.52	−15.20												

Table 2 Continued

Static LC						Unfiltered					
Loss (ha)	Stable (ha)	Gain (ha)	% Loss	% Gain	SRC	Loss (ha)	Stable (ha)	Gain (ha)	% Loss	% Gain	SRC
3658	632	10	85.268	0.233	−85.035	5399	2982	329	64.42	3.93	−60.49
3377	340	1331	90.853	35.808	−55.044	3964	418	4363	90.46	99.57	9.11
2180	1745	488	55.541	12.433	−43.108	2540	2509	2542	50.31	50.35	0.04
2353	393	216	85.69	7.87	−77.82	3686	1396	891	72.53	17.53	−55.00
1066	1957	945	35.26	31.26	−4.00	3161	2764	2526	53.35	42.63	−10.72
2539	674	214	79.02	6.66	−72.36	3827	1972	879	65.99	15.16	−50.84
2177	862	216	71.64	7.11	−64.53	4122	2107	891	66.17	14.30	−51.87
3256	205	190	94.08	5.49	−88.59	5541	720	814	88.50	13.00	−75.50
2171	1257	250	63.33	7.29	−56.04	3711	2808	1028	56.93	15.77	−41.16
3276	110	204	96.75	6.03	−90.73	5861	413	836	93.42	13.33	−80.09
3330	153	184	95.61	5.28	−90.32	6517	483	681	93.10	9.73	−83.37
1386	2023	302	40.66	8.86	−31.80	3594	2906	593	55.29	9.12	−46.17
1778	1814	247	49.50	6.88	−42.62	4227	2724	665	60.81	9.57	−51.24
3592	14	1	99.61	0.03	−99.58	6964	38	4	99.46	0.06	−99.40
1829.55	1231.97	515.42	57.64	26.91	−30.73	3080.03	2073.42	1923.68	58.36	48.53	−9.84

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).

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

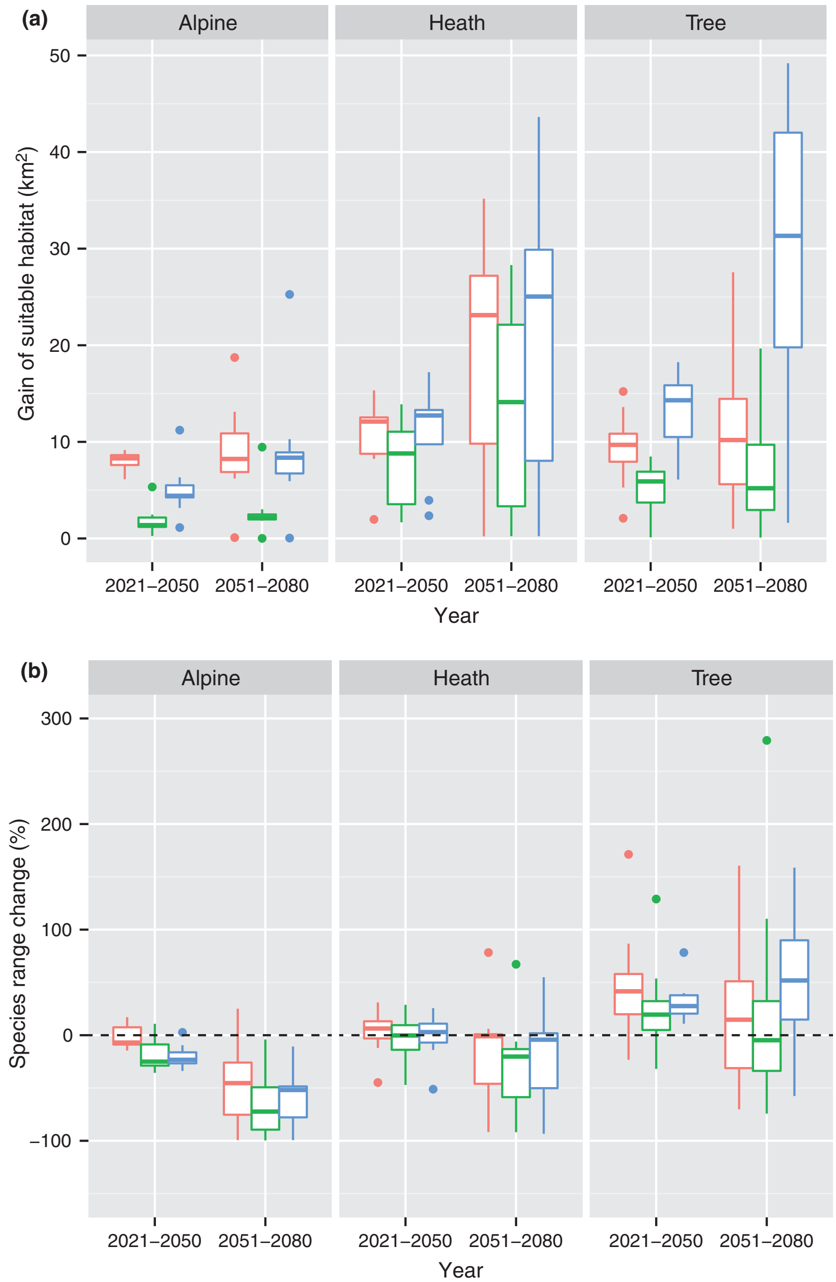

Figure 5 (a) Predicted gain in suitable habitat (km^2) for 2021–2050 and for 2051–2080 for the three plants groups and the three land cover scenarios considered. (b) Predicted species range change (%) for 2021–2050 and for 2051–2080 for the three plants groups and the three land cover scenarios considered. Red boxplots correspond to the dynamic land cover scenario, green box plots to the static land cover scenario, and blue boxplots to the unfiltered SDM output.

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 used here to model plant succession dynamics in deglaciated areas did not account for factors such as seed dispersal, substrate, or soil moisture, nutrient and mineral content, all of which are known to influence the rate and location of primary succession in glacier forelands (Chapin *et al.*, 1994; Fastie, 1995; Rydgren *et al.*, 2014).

Future studies that integrate glacier retreat with biodiversity forecasting should combine mechanistic models of tree line (e.g. Lischke *et al.*, 2006) and glacier retreat (e.g. Jouvet *et al.*, 2009) with innovative, process-based tools for modelling primary plant succession in glacier forelands. In this study, incorporating nonlinear, transformative change in the land cover model was not statistically feasible due to the limited number of historical observations (three dates) of forest and glacier extent. However, the comparable linear trends observed for both forest and glacier cover change over 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 outputs 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 limited 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 communities, or in favourable microsites known to enable the installation 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 pseudoplantanus*, 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 expansion 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 expansion 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 rapidly 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 extrapolating 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 sensing, due to the frequent occurrence of heath as forest understorey 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 expansion and invasion of alpine zones in the Chamonix Valley would suggest that heath species are likely to be beneficiaries of warming mountain habitats 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 conditions, 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 topographically defined micro-refugia (Randin *et al.*, 2009; Scherrer & 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 remotesensing-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.

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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.

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