Are different facets of plant diversity well protected against climate and land cover changes? A test study in the French Alps

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Climate and land cover changes are important drivers of the plant species distributions and diversity patterns in mountainous regions. Although the need for a multifaceted view of diversity based on taxonomic, functional and phylogenetic dimensions is now commonly recognized, there are no complete risk assessments concerning their expected changes. In this paper, we used a range of species distribution models in an ensemble-forecasting framework together with regional climate and land cover projections by 2080 to analyze the potential threat for more than 2500 plant species at high resolution (2.5 × 2.5 km) in the French Alps. We also decomposed taxonomic, functional and phylogenetic diversity facets into α and β components and analyzed their expected changes by 2080. Overall, plant species threats from climate and land cover changes in the French Alps were expected to vary depending on the species' preferred altitudinal vegetation zone, rarity, and conservation status. Indeed, rare species and species of conservation concern were the ones projected to experience less severe change, and also the ones being the most efficiently preserved by the current network of protected areas. Conversely, the three facets of plant diversity were also projected to experience drastic spatial re-shuffling by 2080. In general, the mean α-diversity of the three facets was projected to increase to the detriment of regional β-diversity, although the latter was projected to remain high at the montane-alpine transition zones. Our results show that, due to a high-altitude distribution, the current protection network is efficient for rare species, and species predicted to migrate upward. Although our modeling framework may not capture all possible mechanisms of species range shifts, our work illustrates that a comprehensive risk assessment on an entire floristic region combined with functional and phylogenetic information can help delimitate future scenarios of biodiversity and better design its protection.

Changes in climate, notably a warming climate, are expected to strongly impact biodiversity in mountain environments (Pauli et al. 2012). Species are expected to migrate upward to keep pace with suitable climates, which should lead to an increase of diversity in higher altitudes in the near term (Walther et al. 2005). In return, it should ultimately lead to a decline in the number of species specialized for high alpine conditions, outcompeted by more competitive species from low-lands (Pauli et al. 2012). Earlier modeling studies that projected and analyzed future trends in mountain floras have shown dramatic decline of alpine species and strong spatial turnover (Thuiller et al. 2005). However, those studies carried out at European scales and coarse spatial resolution were not able to correctly account for mountain peculiarities such as topographic micro-heterogeneity and meso-scale refuges (Randin et al. 2009, Carlson et al. 2013). Recent studies have instead shown that when models were applied to high resolution, specifically over mountains, results were less pessimistic,

indicating that mountain floras could still persist in some specific areas (Engler et al. 2011, Dullinger et al. 2012).

In addition to the threat from an altering climate, land cover is expected to change in the coming century in response to both, climate and socio-economic changes, the latter driven by demographic growth and changes in agricultural practices. Although land cover change is known to be one of the strongest drivers of biodiversity change (Sala et al. 2000), most risk assessments have only considered climate change (but see Barbet-Massin et al. 2012). The combination of both climate and land cover changes could however favor some particular species to the detriment of others. For instance, extension of forest cover due to land abandonment and an increased demand in wood products is an important driver of change in sub-alpine ecosystems. To date, no risk assessment has been carried out to evaluate the dual effects of climate and land cover change on the entire flora of a biogeographic region like the French Alps.

In addition to climate and land cover change threats to species ranges, it is also important to forecast the dual effects of these changes on the various facets of biodiversity. Despite few exceptions (Thuiller et al. 2011, Buisson et al. 2013), most of published biodiversity scenarios so far have only considered species richness and taxonomic turnover and their future protection status over a continent (Araújo et al. 2011). Although it is obviously of interest to examine the consequences of climate and land cover changes on species richness, this approach implies that all species are independent phylogenetic and functional units. An alternative view is to account for the shared evolutionary history of species and assess how phylogenetic diversity might be influenced by environmental change (Thuiller et al. 2011, Faith and Richards 2012). In addition, such a complementary view also considers that species share more or less similar functions based on their trait values (Violle et al. 2007) and that environmental change affects the distribution of trait diversity across space and time in a different manner than sole species richness (Thuiller et al. 2006, Buisson et al. 2013). The spatial patterns of these other facets of biodiversity are increasingly investigated at global (Safi et al. 2011) and regional scales (Devictor et al. 2010, Pio et al. 2011), but no study has investigated, so far, the projected re-arrangement of different biodiversity facets in response to environmental change in a region for a complete group of species such as plants. In a mountain environment such as the French Alps, we expect higher spatial variation in taxonomic diversity than in both functional and phylogenetic diversity since several species belong to the same functional groups or lineages. More particularly, we expect that in extreme environments (e.g. cold temperature), the current functional diversity will likely increase in response to climate warming due to the upward migration of lowland species. Concerning phylogenetic diversity, we expect to see less spatial variation of phylogenetic diversity than species or functional diversity under both current and future conditions since few large lineages dominate the entire region. Spatial re-shuffling of species within those lineages should not drastically change this pattern. This obviously represents a contrast between taxonomic, functional and phylogenetic diversity that leads to important patterns of changes. An additional advantage of looking at different facets of biodiversity in response to environmental change is the possibility to decompose diversity into spatial components, namely α, β and γ diversity. This allows measuring whether environmental changes result in local changes (α-diversity) or rather influence the spatial turnover between sites (β-diversity). Conservation actions to protect species and diversity should ultimately account for those different facets, but there exist only few studies looking at whether the current protected area networks are able to jointly protect species and biodiversity facets in the context of expected environmental changes.

In this paper, we take these challenges by assessing the response of the entire flora of the French Alps at high spatial resolution (i.e. 250 m) to both regional climate and land cover changes. We address here three main questions: 1) what are the potential consequences of climate and land cover changes on plant species distributions and associated trait characteristics in the French Alps? 2) Will the spatial re-arrangement of species influence the spatial distribution of taxonomic, phylogenetic and functional diversity patterns? 3) Is the current protected area network sufficient to protect both threatened species and the different facets of biodiversity in a warmer world? To address these questions, we modeled the spatial distribution of the whole flora of the French Alps at high resolution using bedrock, climate and land cover variables in an ensemble-forecasting framework (Araújo and New 2007). Using downscaled regional climate models and a range of land cover change scenarios, we then investigated whether plant species would likely loose or gain suitable environmental space. We tested whether differential responses occurred between rare and common species, life forms or IUCN species threat categories. At the assemblage level, we then used a framework based on Hill's numbers (Hill 1973, Chao et al. 2010) that allowed us to decompose α-diversity and β-diversity into meaningful numbers (i.e. equivalent number, Jost et al. 2010) for taxonomic, phylogenetic and functional diversity (Leinster and Cobbold 2012). We finally built an innovative gap analysis to measure the ability of the current protected area network to protect both species and the different facets of biodiversity for the horizon 2080.

Material and methods

Study area

This study was conducted over the French Alps region (Fig. 1), which covers 26 000 km² and presents a wide range of environmental conditions due to mixed continental, oceanic and Mediterranean climate influences and steep altitudinal gradients.

We used a vegetation database from the National Alpine Botanical Conservatory (CBNA, Fig. 1, dark grey shading in the national map), including more than 164 500 sampling plots recorded between 1980 and the present at a resolution greater than or equal to 250 m. Two sampling methods were used: 31 569 of these plots corresponded to comprehensive phytosociological relevés (i.e. phytosociological method hereafter) and thus provided both presence and absence data, whereas the rest of the plots consist of presence-only data (i.e. single occurrence method hereafter). We started with the 3250 plant species present in the CBNA database, based on a standardized species taxonomic nomenclature (Kergélen 1993).

To complement these data, we also gathered additional 4000 occurrence data points from the National Mediterranean Botanical Conservatory (CBMED) for 1000 species from the previous list that also occur in the extreme south of French Alps (Fig. 1, light grey shading in the national map). This additional information from the Mediterranean area allowed us to be confident that the warm portion of species niches was adequately captured (Fig. 1). All presence and absence information were overlaid to the 250 m analysis grid. When at least one presence was recorded for a given species over a 250 m pixel, it was noted as presence. This procedure has the advantage of smoothing the sampling bias in highly sampled sub-regions.

We then removed species occurring in less than 20 pixels to make sure enough information was provided to the models
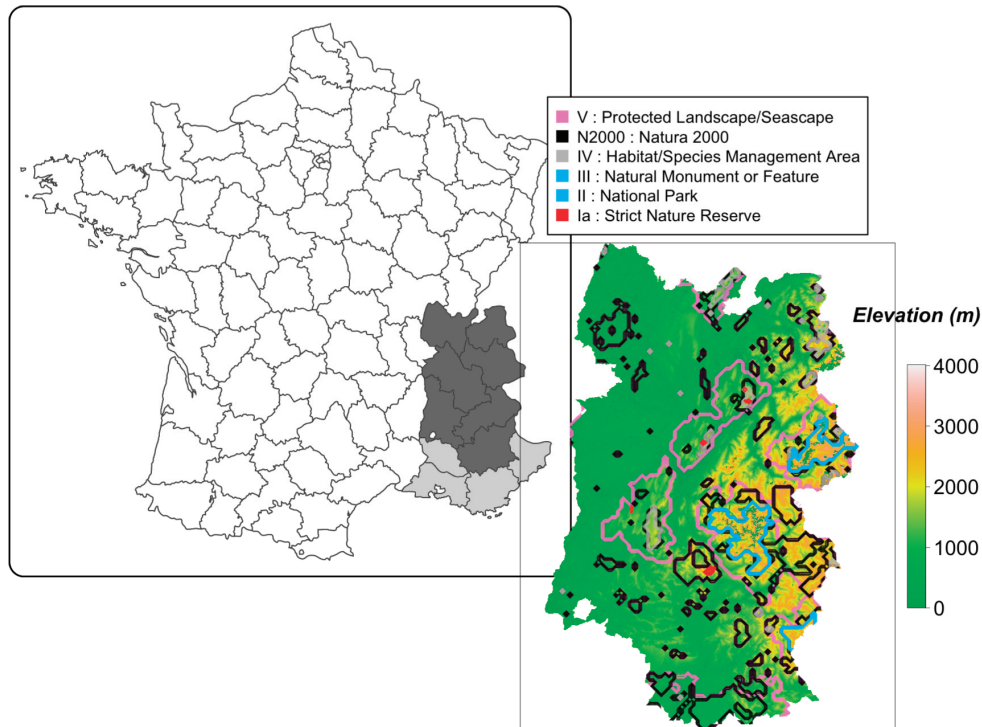
Figure 1. Representation of the study area. Dark grey shades represent the study area where the risk assessment was conducted (CBNA zone). Light grey shades represent the area where additional presence–absence information was gathered for calibrating the models (CBNMED zone). The zoom represents the current protected area network in the French Alps (CBNA zone) with the different labeling corresponding to the official classification (WDPA 2005).

for fitting meaningful relationships. We thus retained 2857 species for our modelling analysis over the French Alps.

Chorological information

Rarity classification – we used a measure of regional rarity that classifies the species from our study area based on a protocol from the CBNA (Supplementary material Appendix 2, Table A1). It is based on the 250 m analysis grid we used for our study area. R = 100 – [100 × T/C], where C is the total number of 250 m pixels in the study area and T is the number of 250 m pixels where the species was recorded as present.

Red list classification – in order to classify the threat status of all plant species of the region, we used the National and Regional Red Lists. When a species was present in the national red list I, it was considered as 'priority species'; when present in the national list II, it was considered as 'strictly protected'; and finally, when a species was only present in the regional list of the French Alps, it was considered 'locally protected'. Remaining species were classified as 'unprotected'.

Each of our study species was further classified into altitudinal vegetation life zones. To do so, we followed Engler et al.'s (2011) approach by dividing our study area into four vegetation belts (Theurillat 1991). Alpine: life zone with a vegetation period lasting ~50–100 d yr⁻¹ (i.e. mean annual temperature < 3°C) and encompassing exclusively vegetation above the upper limit of the natural treeline. Only grasslands or low shrublands dominated by low chamephytes such as dwarf *Salix* sp. are found in this vegetation belt. Subalpine: life zone with a vegetation period lasting ~100–200 d yr⁻¹ (i.e. mean annual temperature between 3 and 6°C) and located between the closed montane forest and the uppermost limit of small individuals of tree species. This zone represents the transition zone between fully-grown forest and Alpine grasslands. Deciduous trees are mostly absent from this vegetation belt, which is dominated by conifers. Montane: life zone with a vegetation period of ~200–250 d yr⁻¹ (i.e. mean annual temperature between 6 and 10°C) where the native vegetation is mainly composed of fully grown coniferous forest, or mixed forests with deciduous trees such as *Fagus sylvatica*. Colline: lowest and warmest life zone with a vegetation period of more than 250 d yr⁻¹ (i.e. mean annual temperature > 10°C) and where the native vegetation is mainly composed of deciduous tree species such as *Quercus* sp., *Fraxinus* sp. or *Acer* sp.

Trait information

For the functional diversity analyses, we focused on three key functional traits: the specific leaf area (SLA, light-capturing area deployed per unit of leaf dry mass), the height of plant's canopy at maturity and the seed mass, that are well known components of the leaf-height-seed (LHS) syndrome of plant traits (Westoby 1998). Seed mass relates to dispersal distance and establishment success, height is considered as a surrogate of species' ability to intercept light, while SLA strongly relates to species relative growth rate (Westoby et al. 2002). In addition, we added life form information to reflect integrated strategies and longevity. All trait diversity analyses

were conducted with these four traits that we log-transformed (for SLA, height and seed mass) prior to the analyses.

These traits were extracted from the trait database ANDROSACE (Thuiller et al. unpubl.). The database includes trait information for Alpine plants from individual projects and freely available databases such as LEDA (Knevel et al. 2003), BioFlor (Kühn et al. 2004), Ecoflora (Fitter and Peat 1994) and CATMINAT (Julve 1998). We excluded 102 species for which we had less than two traits for the LHS syndrome, which left us with 2755 species for analyses.

Phylogenetic information

We reconstructed a genus-level phylogeny based on DNA sequences available in GenBank, using the procedure proposed in Roquet et al. (2013). We used the following DNA regions: three conserved chloroplastic regions (rbcL, matK and ndhf) and 8 regions for certain families or orders (atpB, ITS, psbA-trnH, rpl16, rps4, rps4-trnS, rps16, trnL-F). Global or taxonomically local alignments were performed with several algorithms (implemented in MAFFT, (Katoh et al. 2002); MUSCLE, (Edgar 2004); and Kalign, (Lassmann and Sonnhammer 2005) and then compared with the program MUMSA to select the best alignment (Lassmann and Sonnhammer 2005). Alignments were then cleaned with TrimAl (Capella-Gutierrez et al. 2009) to remove ambiguously aligned regions before performing a phylogenetic inference analysis with RAxML (Stamatakis 2006). The phylogenetic inference was performed while constraining deep nodes based on a family level angiosperm supertree (based on Davies et al. 2004, Moore et al. 2010). We extracted from the phylogenetic inference a set of 100 trees closes to the maximum likelihood score. Because there was little difference in topology and likelihood between those trees and the best one (i.e. the tree with the highest log-likelihood), all subsequent analyses were only conducted with the best ML tree. This tree was dated using penalized likelihood as implemented in r8s (Sanderson and Driskell 2003) with 25 fossil constraints (extracted from Schuettpelz and Pryer 2009, Smith et al. 2009, Bell et al. 2010). Finally, we randomly resolved terminal polytomies by applying a birth-death (Yule) bifurcation process within each genus. We only used one randomly resolved tree here, while ideally, it should have been done 100 times. The main issue was that the overall analysis was impossible to run over 100 trees due to computational limitations. Using a similar approach for Europe plants, Thuiller et al. (2011) showed that the general patterns of phylogenetic diversity over Europe were relatively stable with respect to random resolution of polytomies.

Environmental data

We used a set of environmental variables that are known to be strong drivers of plant species distribution over the French Alps.

Variables included a soil map representing the percentage of carbon in the bedrock, derived from the harmonized geological map of the Alps (Bd-Charm 50 – BRGM; < www.geocatalogue.fr/Detail.do?id = 4156#>).

Current climate was mapped as a 250 m raster, downscaled from 1 km Worldclim climate grids (Hijmans et al. 2005). We first downscaled the monthly climate normals (1950–2000) to a spatial resolution of 250 m, to better represent the topographic variation of climate in our study area using a mowing window regression approach. In a second step we used these downscaled temperature and precipitation grids to derive maps of five bioclimatic variables, which 1) have an obvious impact on plant life in mountain environments; and 2) showed some independent variation across the study area ($r < 0.75$): isothermality (mean diurnal range/temperature annual range; bio3), temperature seasonality (bio4), temperature annual range (bio7), mean temperature of coldest quarter (bio11) and annual sum of precipitations (bio12). We refer to Dullinger et al. (2012) and its supplementary materials for more details on the downscaling procedure.

Future climate by 2050 and 2080 (2021–2050 and 2051–2080) was represented by a set of regional climate model (RCM) runs driven by two emission scenarios (A1B and A2), originating from the ENSEMBLES EU project, which has physically downscaled global circulation model (GCM) data generated for the 4th assessment report of the IPCC (2007). All RCM scenarios were statistically downscaled to the same 250 m spatial resolution using the change factor method (Anandhi et al. 2011). To further check the sensitivity of our results to RCM calculations, we have used 3 different RCMs, namely HadRM3, RCA3 and CLM (Jones et al. 2004a, b, Collins et al. 2006, Meijgaard et al. 2008) fed by three different GCMs (HadCM3, CCSM3 and ECHAM5, respectively) resulting in 3RCM/GCM combinations. We only made these estimates for A1B while for A2 we considered the combination RCA3 × CCSM3. The output from the three RCMs differ in the degree of projected warming by 2100, with the HadRM3, the CLM and RCA3 models generating average summer temperatures increases around 5.0°C, 3.8°C and 2.3°C, respectively. The relative changes in summer precipitation projected by 2100 by the RCMs HadRM3, CLM, and RCA3 amount to −10, −12 and −15%, respectively. This variability in projected climate trends for the A1B scenario represents well the variability assembled by the whole suite of model projections generated in the EU project ENSEMBLES.

Current land cover for the whole French Alps was represented by CORINE Land cover 2006 at 250 m resolution by using the level 1 classification (i.e. built-up areas, arable lands, permanent crops, grasslands, forests and others). However, to tease apart the effects of glacier and sparsely vegetated areas, we re-classified the class 'other' class into 7 classes (glacier, water, saline waters, bare rocks, sclerophyllous vegetation, sparsely vegetated areas, wetlands and others, by assigning level 2 classification values here) leading to a total of 12 classes.

Future land cover at 250 m was taken from the EU projects ALARM and ECOCHANGE (Dendoncker et al. 2006, 2008, Rounsevell et al. 2006) that we re-classified to meet the 12 classes of the current land cover maps, spanning the period 2006–2080. We then retained the period 2021–2050 and 2051–2080 to be consistent with the climatic data. We used two socio-economic storylines that are consistent with the climate change scenarios.

GRAS – growth applied strategy: deregulation, free trade, growth and globalisation will be policy objectives actively pursued by governments in this storyline. Environmental policies will focus on damage repair and limited prevention based on cost benefit-calculations. This scenario is considered equivalent to A1b. BAMBU – business-as-might-be-usual: policy decisions already made in the EU are implemented and enforced in this storyline. At the national level, deregulation and privatization continue except in 'strategic areas'. Internationally, there is free trade. Environmental policy is perceived as another technological challenge. This scenario is considered equivalent to A2.

We further used maps representing the current protected area network, which we extracted from the World Database on Protected areas (IUCN and UNEP 2009). It distinguishes seven categories ranging from 'strict natural reserve' (Ia) to 'protected area with sustainable use of natural resources' (VI) (Fig. 1). The category of Natura 2000 (N2000), which is not available within the IUCN framework, was additionally downloaded from the European environment agency (<www.eea.europa.eu/data-and-maps/data/natura-2000-eunis-database>). We then calculated zonal statistics using these two datasets to estimate the percentage of each 250 m cell of the study area covered by the N2000 and the seven IUCN categories.

Species distribution modeling

An ensemble of forecasts of species distributions models (SDM, Thuiller 2004, Araújo and New 2007, Marmion et al. 2009) was obtained for each of the 2755 species considered. The ensemble included projections from five statistical models, namely generalised linear models (GLM), generalised additive models (GAM), boosted regression trees (BRT), mixture discriminant analysis (MDA) and Random Forest (RF). Models were calibrated for the baseline period using a 70% random sample of the initial data and evaluated against the remaining 30% data, using both the area under the curve (ROC, Swets 1988), and the true skill statistic (TSS, Allouche et al. 2006). This analysis was repeated 2 times, thus providing a 2-fold internal cross validation of the models. All calibrated models were then projected under current and future conditions at a 250 m resolution over the whole French Alps (CBNA delimitation, Fig. 1). To summarise all projections into a meaningful integrated projection per species we used the weighted mean probability procedure, which gives the sum of all projections from all models and cross-validations weighted by their respective predictive performance estimated using the TSS (Marmion et al. 2009). However, we only included the models that reached both a TSS and ROC > 0.3 and > 0.8, respectively. The ensemble forecast was transformed into binary presence–absence maps using the threshold that maximises TSS. Models were calibrated from data from both CBNA and CBNMED regions (dark and light grey shading in Fig. 1) and were projected onto the CBNA region (French Alps) only (Fig. 1; dark grey shading). Models and the ensemble forecasting procedure were performed within the BIOMOD package (Thuiller 2003, Thuiller et al. 2009) in R.

Optimizing the spatial resolution of the analysis to get meaningful estimates of diversity metrics

One principal critique towards a SDM is that it neither accounts for dispersal limitation nor for biotic interactions (Elith and Leathwick 2009, Carlson et al. 2013). In other words, when single SDMs are stacked together for estimates of species richness or associated diversity metrics, they likely overestimate the observed diversity (Pottier et al. 2013). By assumption that dispersal and biotic interactions do influence the observed species richness and diversity at a finer resolution than does environmental filtering (Boulangeat et al. 2012), we therefore expect that stacked SDMs provide more meaningful predictions of species diversity when aggregating the data at lower resolution (i.e. reducing the pervasive effects of dispersal, biotic interactions and stochastic processes). We thus tested at which resolution our stacked SDMs were most accurate at predicting the observed species diversity starting from the original resolution at which species were modeled (250 m) to lower resolutions. To do so, we aggregated all modeled presence–absence species distribution under current conditions at different incremental spatial resolutions ranging from the original 250 m to 5 km. We did the same with the observed data. For both modeled and observed distributions, we considered a species present in one larger pixel when there was at least one presence at the consecutive higher resolution. We then compared the observed species richness with the projected one (stacked SDMs) across the whole French Alps at varying resolutions using Spearman rank correlations (Supplementary material Appendix 2, Fig. A1). We accounted for bias in sampling effort and the two sampling methods (see details in Supplementary material Appendix 1).

As expected, the correlation increased with coarser resolution. We selected the 2.5 km resolution as the best trade-off between high-resolution projections and appropriateness of the biodiversity estimates (Supplementary material Appendix 2, Fig. A1). All subsequent results and analyses have been performed at the 2.5×2.5 km resolution.

Measures of species' sensitivity

Each ensemble of binary species projections under current and future conditions was converted into two metrics of species' sensitivity.

The first metric gives the relative change in habitat suitability (CHS, or species range change) by measuring to what degree the future suitable area is larger or smaller than the current suitable area:

$$\text{CHS} = ([\text{Future suitable area} - \text{Current suitable area}] / \text{Current suitable area}) \times 100 \qquad (1)$$

The second metric quantifies the proportion of the current range that will become unsuitable under future conditions, namely loss of suitable habitat:

$$\text{LSH} = 100 - [(\text{Overlap(Future,Current)} / \text{Current}) \times 100] \qquad (2)$$

This metric allows to measure the risk of local extinction as it does not consider dispersal into new areas. A species losing

100% of its current suitable habitats is at high risk of extinction even if it is projected to gain new suitable habitats.

Diversity decomposition

The last few years have seen an upsurge of diversity metrics that can be used for measuring taxonomic, phylogenetic and trait diversity in a consistent way (Pavoine and Bonsall 2011, Tucker and Cadotte 2013). Here we used Leinster and Cobbold's (2012) framework that builds on a generalization of Hill's numbers (Hill 1973) to compute diversity metrics incorporating species differences (such as phylogenetic divergence of functional dissimilarity).

We used this framework to estimate both α and β-diversity for three biodiversity facets, namely taxonomic, phylogenetic and functional diversity under current and future conditions. α-diversity was estimated as the local diversity within each pixel for each of the three facets (following Eq. 3). The spatial turnover, β-diversity, was estimated using a moving window around each focal pixel. This moving window consisted of the 8 pixels contiguous to the focal pixel. γ-diversity was the total diversity of this window. The γ, α and resulting β components were then estimated for this window. The β value was then reported to the focal pixel and mapped. The general formula calculates the diversity D for a relative abundance vector p = {pi} of the S species present in the pixel, and a matrix Z containing the similarities Z_{ij} between species i and j:

$$D(p) = \left(\sum_{i=1}^{S} p_i \left(\sum_{i=1}^{S} z_{ij} p_j \right) \right) \tag{3}$$

The α-diversity of each pixel was calculated from the vector of species presences–absences per pixel, while the γ-diversity was calculated per window from the vector of species mean probability of presence over the moving 3×3 pixel window. The number of pixels to calculate β-diversity was chosen to ensure enough variability while keeping the setting around the focal pixel homogenous enough to be meaningful in term of species assemblages and meta-community structure (here 2.5 square kilometers).

The mean α-diversity of a window $\bar{\alpha}$ was calculated as the mean of the diversities of its constituent $N = 9$ pixels of α-diversity (inline) (Tuomisto 2010a, b). Finally the β-diversity of the window was calculated as the ratio of the γ-diversity and the mean α-diversity of a window. Z, the similarity matrix, was calculated as 1 minus the cophenetic distance between species for phylogenetic diversity and the Gower distance for the four selected traits (SLA, height, seed mass and life form) for trait diversity, divided by the maximum respective distance to have Z bounded by 0 and 1.

The advantage of using a multiplicative framework of α, β, and γ decomposition with Leinster and Cobbold's (2012) diversity index is that it allows the β of a window to be independent of α, and ranging from 1 (if pixels are identical) to the size of the window, 9 (if pixels are fully dissimilar). Therefore the β values of windows with contrasting mean α-diversity values are still comparable (i.e. equivalent numbers, Jost 2007).

Efficiency of the current protected area network

We finally tested the efficiency of the current protected area network to safeguard species and diversity facets under current and future conditions. Analyses were performed at two protection levels: 'truly protected' areas ([Ia, II, III, IV and Natura2000]); and protected areas with sustainable use of natural resources (V) plus the truly protected areas.

With regards to species, we first estimated to which percentage each species of the study area was protected with regards to its conservation status. In other words, for each 2.5 km pixel we extracted the percentage of area protected, and then calculated the percentage of protected area for each species under current and future conditions (Alagador et al. 2011).

With regards to diversity, a gap analysis was conducted with a complementarity perspective (Faith et al. 2003). More specifically, we up-scaled the protected area network to 2.5 km choosing an arbitrary threshold of 50% (i.e. if a 2.5 km pixel contained ≥ 50% protected area, we considered it as protected). Then, we compared α-diversity in- and outside of the protected area network and calculated the β-diversity between the two areas to investigate the complementarity between the two areas. If the current protected area network were successful in protecting the different diversity facets, then in and outside protected areas would have a similar α-diversity and a β-diversity equals to 1, which is the minimum in the Leinster and Cobbold's (2012) framework. This calculation was carried out under both current and future conditions.

Results

Performance of species distribution models

Overall, the performance of SDMs was high with an average TSS and ROC of about 0.48 and 0.98 respectively (Supplementary material Appendix 2, Fig. A2). Interestingly, rare alpine species were extremely well-predicted according to both measures of performance (median TSS of 0.6 and ROC close to 1). There was no other general trend in performance except that alpine species were usually better predicted than those from lower altitudes. We removed 213 species from the following analyses due to TSS and ROC being below 0.3 and 0.8, respectively. Thus, 2542 species were examined below.

Species' sensitivity to climate and land cover change

In general, species' sensitivity to both climate and land cover changes differed between altitudinal vegetation belts and in respect to species' conservation and rarity status, but irrespective of regional climate models, climatic scenarios, or land cover scenarios (Fig. 2 for the A1B – GRASS scenario, Fig. A3, A4 and A5 in the Supplementary material Appendix 2 for the remaining RCMs and scenarios). Colline species were always predicted to experience an increase in suitable habitats due to a strong increase in suitable climate at higher altitudes, while lower altitude bands remain suitable. Species from the other altitudinal vegetation belts were generally
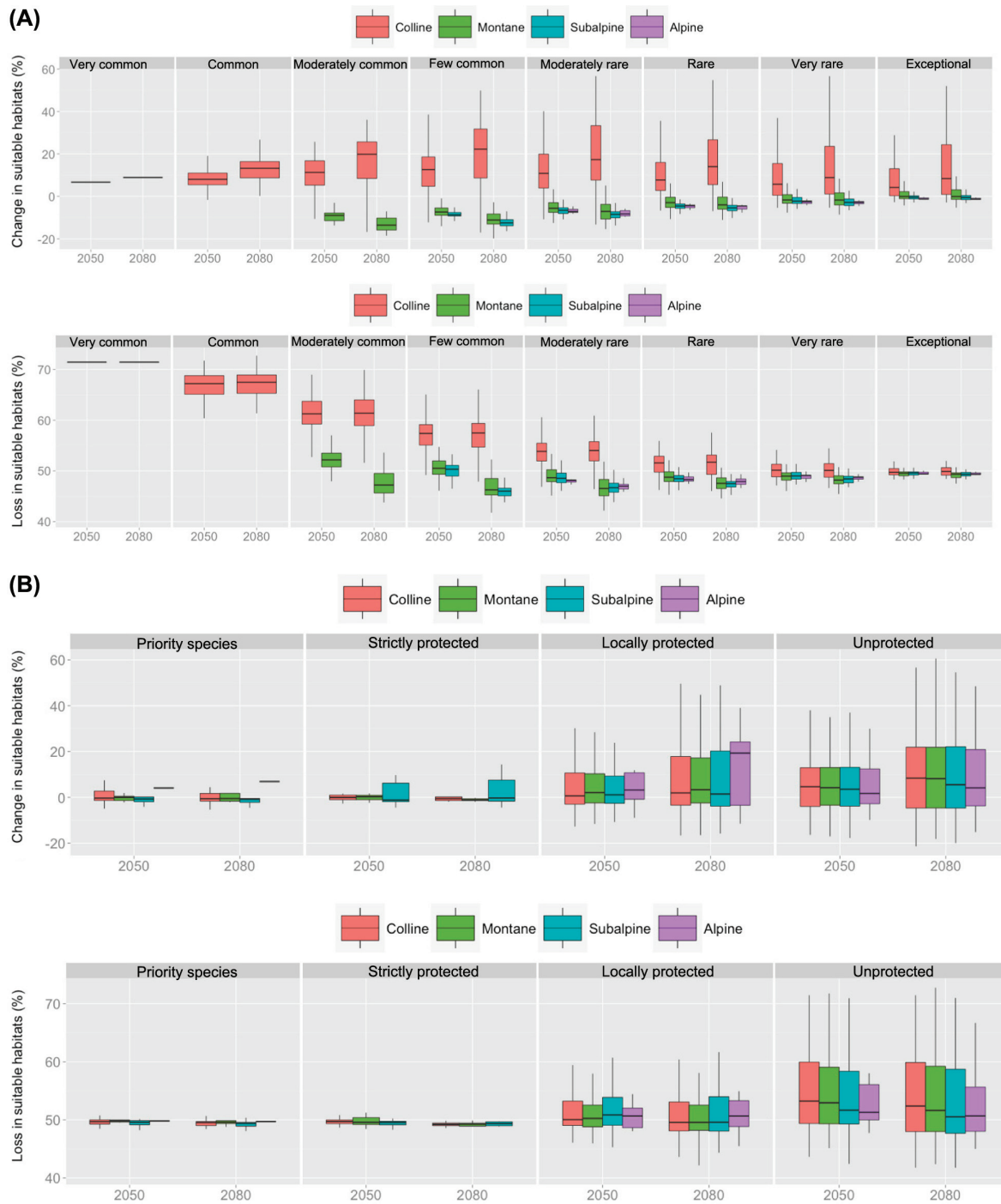
Figure 2. Species sensitivity to climate and land cover change by 2080 with respect to their rarity-commonness value (A) and their conservation status in the study area (B). Results are ordered by altitudinal belts to which the species belong. Up and lower panels differ in the measure of sensitivity. Up panels represent change in suitable habitats (CHS), while lower panel represents loss in suitable habitats (LHS) by 2080 (HadCM3/HadRM3 driven by the A1b scenario and the GRASS storyline).

predicted to have moderate change in suitable conditions (CHS, Fig 2A – top panel) although they were, in general, predicted to loose a fair amount of currently suitable areas (LSH, Fig. 2A – lower panel, 48% on average), which is likely due to the general decrease in area with increasing altitude. If those species are not able to migrate toward more favorable conditions, they will be under strong threat. Interestingly, when going from moderately rare to exceptionally rare species, the

predicted loss in environmental suitability decreased (LSH, Fig. 2A – lower panel). In other words, extremely rare species are not predicted to experience a drastic loss in suitable conditions.

This was mirrored when considering the protection status of species (Fig. 2B). Most unprotected species were predicted to expand their suitable area (CHS, Fig. 2B – top panel, e.g. usually common species from the lowlands) whereas species
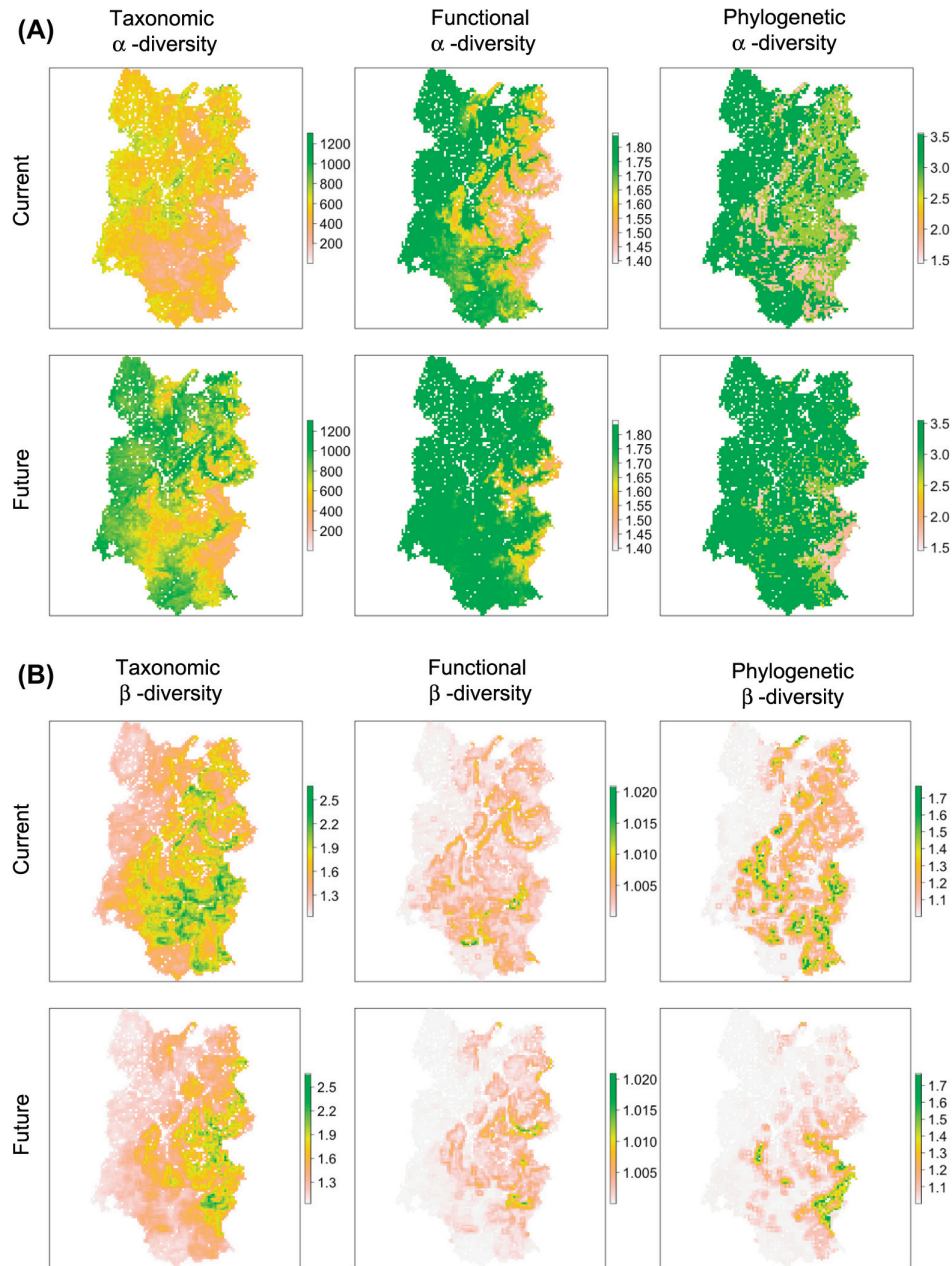
Figure 3. Spatial patterns in α-diversity (A) and β-diversity (B) with parameter *q* equals to zero (presence–absence) for the three facets of plant diversity and under current and future conditions by 2080 (HadCM3 × HadRM3 driven by the A1b scenario and the GRASS storyline).

with strict and top priority protection were not predicted to be strongly affected by the modeled climate and land cover changes (Fig. 2B) top and lower panels).

Mapping of taxonomic, phylogenetic and trait diversity across space and time

Patterns of α- and β-diversity differed spatially and in response to climate and land cover changes by 2080 (Fig. 3 and Supplementary material Appendix 2, Fig. A6, A7 and A8). Under current conditions, there was a less pronounced variation in taxonomic α-diversity across the French Alps than in phylogenetic and functional diversity, whereas this patterns was reversed for β-diversity. Interestingly, even if they are somehow correlated to taxonomic diversity, both phylogenetic and functional α-diversity were relatively high in the low-lands (western French Alps) and only decreased in the high mountain areas where national parks are located (Fig. 1). Functional α-diversity showed a more marked spatial pattern than did phylogenetic α-diversity, which did not vary strongly throughout the French Alps, certainly because most of the main angiosperm clades are occurring throughout the study region. However, phylogenetic β-diversity showed a more marked pattern than did functional β-diversity, with high turnover in ecotones between low land and high mountains zones (Fig. 3B).

Under climate and land cover changes (here using the HadCM3/HadRM3 models driven by the A1b emission scenario and GRASS storyline), the spatial patterns tended to change more drastically for taxonomic than for both functional and phylogenetic α-diversity. Taxonomic α-diversity was predicted to increase almost everywhere while still decreasing from lowlands to high mountains. For the other two facets, we observed a strong increase in α-diversity at high altitudes. On the contrary, β-diversity was projected to severely decrease for the three facets. In other words, there is a general tendency toward diversity homogenization, except in the very high mountain tops and transition zones between montane and alpine belts. Given the general trends in CSH and LSH, this reflects a migration of species from the lowlands to higher elevations, which tended to increase the functional and phylogenetic α-diversity of the mountaintops. Interestingly, for a same scenario A1B-GRASS, projections diverged in functions of the combinations of GCM × RCM used (Fig. 3, Supplementary material Appendix 2, Fig. A6, Fig. A7). For instance, while change in α- and β-diversity were relatively similar between HadCM3/HadRM3 (Fig. 3) and CLM/ECHAM5 (Supplementary material Appendix 2, Fig. A6), the combination RCA3/CCSM3 led to less severe changes, with overall the same patterns as with the other two climate models, but lower in terms of absolute values. This last combination under the A2 emission scenario and BAMBU storyline when modeled with the RCA3/CCSM3 climatic model gave more drastic changes than under the A1b × GRASS scenarios.

Protected area network in the face of environmental change

When focusing on the existing truly protected network (categories I, II, III, IV and Natura2000), the level of protection clearly met the conservation status of the species (Fig. 4). Priority species were best protected on average (42%) under current conditions, followed by species strictly protected (38%). Despite this high average protection, 13 of the 48 priority species and 10 of the 39 strictly protected species have less than 25% of their range protected. Species locally protected or without any conservation status were, on average, not very well covered (23 and 18% respectively) by the network, possibly due to their generally larger ranges. The same trends were predicted under future conditions (Fig. 4). Interestingly, priority species were predicted to even increase the proportion of their protected range under future conditions despite the comparably high variability among RCMs and scenarios. The pattern was somehow consistent for strictly protected species (except under two A1b RCMs scenarios, Fig. 4). Species locally protected or unprotected were not predicted to have any significant change in their level of protection. Patterns were similar when considering all protected areas in the French Alps ([Ia, II, III, IV, V and Natura2000]; Supplementary material Appendix 2, Fig. A9).

When considering the overall protection of the different diversity patterns we observed no turnover between the three facets' diversities in- and outside of the protected areas, under both current and future conditions (results not shown as β-diversity was always equal to 1 when comparing the three

diversity facets in and out of the protected area network). In other words, the spatial distribution of the protected area network in the French Alps generally protects the three facets of diversity well and seems well positioned to keep doing so in a near future. The fact that a quite large number of species have less than 25% of their range protected tempers this positive result and highlights that protecting diversity as a whole does not necessarily mean that individual species are well protected.

Discussion

Summary of the main findings

Here we demonstrated the promise of generating biodiversity scenarios for several facets of biodiversity together within the same modelling framework. Such an approach is needed to complying with different conservation options, that put more emphasis on species richness, the functioning of ecosystems, or the evolutionary history of biota, and that are able to contrast these options across geographic space and a protection network. By doing so, future conservation actions can be designed to better fit some of these conservation options and better compensate projected alteration of ecosystem functioning or projected loss of particular phylogenetic lineages.

In this paper, we asked whether projected climate and land cover change would strongly influence the potential suitable habitats of plant species and the spatial patterns of diversity facets in the French Alps, and ultimately whether current reserve network would adequately protect biodiversity given projected changes. The short answer is yes, but not necessarily as expected. Indeed, although the currently suitable climate and land cover is going to shrink for a large portion of species, new suitable areas still seem to be available for many of them. Obviously, these newly suitable habitats, generally available at higher altitudes, would have to be reached and this will heavily depend on the capacity of species to migrate fast enough to keep track with their preferred conditions (Dullinger et al. 2012). Reciprocally, the supposedly 'lost' conditions should not be interpreted as 'immediate local extinction' as it will depend on plant longevity, their tolerance to climate variability (Zimmermann et al. 2009, Dullinger et al. 2012) and competition from immigrating species (Svenning et al. 2014).

Nevertheless, species from different altitudinal-vegetation belts show opposing patterns. Species from the montane vegetation belt are projected to have a decrease in suitable area. This result certainly has to do with mountains topography as migrating up-ward necessarily means reducing range areas. However, why do species from subalpine and alpine belts not show the same pattern? Indeed, those species, generally rare, are projected to be much less affected by climate and land cover changes than others. We hypothesize here that calibrating the species models at very high spatial resolution allowed us to capture the fine-scale relationships between plant species from high altitude and their meso-scale environment (Randin et al. 2009) and that high alpine species may potentially tolerate wider climatic fluctuations than previously thought (but see Beaumont et al. 2011).
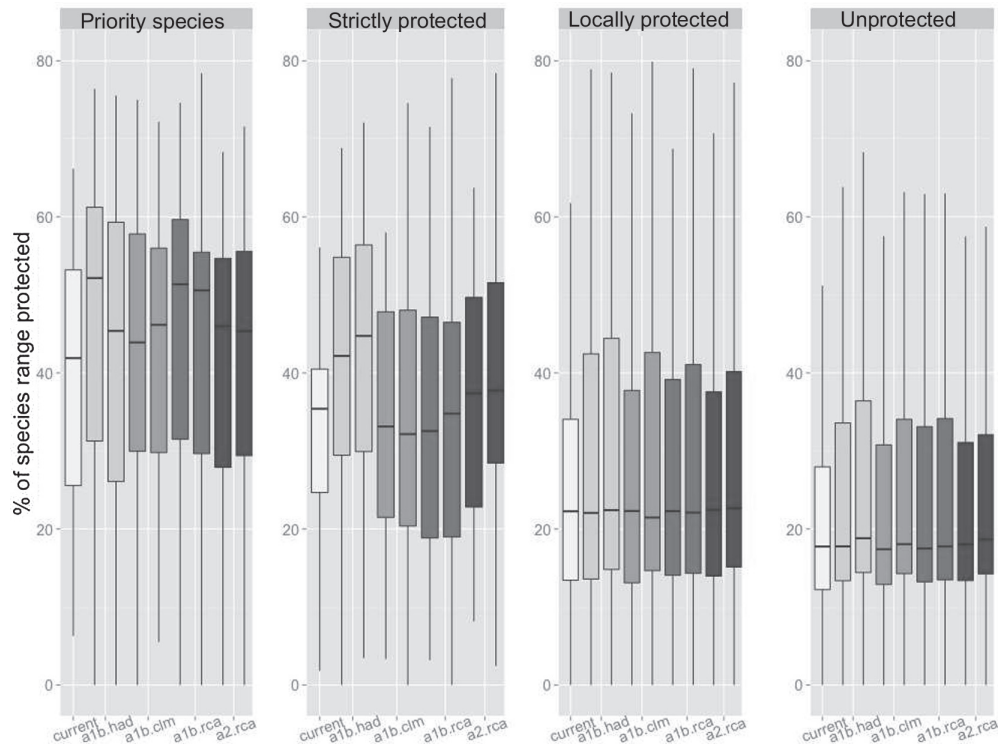
Figure 4. Level of species protection over the French Alps under current and future conditions by 2050 and 2080 with respect to species conservation status. Y-axis represents the percentage of species ranges that are protected, over all species from a given conservation status (i.e. priority species, strictly protected, locally protected, unprotected). The x-axis represents the current and future conditions. For each future condition (i.e. a given color for a given name), there are two bars, one for 2050 and one for 2080 (from left to right). Abbr.: A1b. had: HadCM3/HadRM3 climate model driven by the A1b scenario and the GRASS storyline. A1b.clm: ECHAM5/CLM driven by the A1b scenario and GRASS storyline. A1b.rca and A2.rca: CCSM3/RCA3 climate model driven by the A1b and A2 scenarios and the GRASS and BAMBU storylines, respectively. The protected area network corresponds here to truly protected' areas (Ia, II, III, IV and Natura2000).

The protected area network seems very efficient to protect extant plant diversity under current conditions in the French Alps. Our modeling analyses also suggest that it will continue to do so in the future, and likely even protects more species and more diversity under changed environmental conditions. This result is in contradiction to previous studies at large spatial scales from mostly lower altitudes, where large areas are covered by similar vegetation. For instance, Araújo et al. (2011) suggested that around 58% of European plant and terrestrial vertebrate species could lose suitable climate in protected areas, whereas losses affected 63% of the species of European concern occurring in Natura 2000 areas. Our analysis on the French Alps does not corroborate those general European findings, suggesting: a) that multi-scale assessments are of interest to contrast regional vs continental situations, and b) that higher altitudes with a rich habitat diversity might be less affected by environmental change than are lowlands. In the French Alps, most of the protected areas are located in remote, high altitude areas and span a large elevation gradient. The three main National Parks have 81% of their area above 2000 m a.s.l. These high altitude areas are also the ones projected to provide suitable climate and land cover to more species in the future, with an upward migration of species from lowlands. Obviously, the extinction debts of species due to long-term dynamics, biotic interactions and limited dispersal might modify this pattern (Van der Putten et al. 2010, Dullinger et al. 2012) but it

is reasonable to assume that high altitudinal protected areas will gain species and diversity under these changing conditions. Glacial retreats are already providing more space for high altitude species (Burga et al. 2010), and will thus probably buffer the negative impacts of competition from immigrating species from lowlands (Carlson et al. 2013).

Our multi-facets framework allowed us to forecast that the spatial distribution of taxonomic, functional and phylogenetic diversity in the French Alps will probably change drastically. Indeed, although the α-diversity should in general increase in most of the area (invading plant species from lowlands) and should also be well protected, the β-diversity is expected to strongly decrease for all three diversity measures. Interestingly, the general patterns generally fit our expectations. Changes in species diversity in response to future scenarios were much more pronounced than for the other two diversity facets. As also expected, the current spatial pattern of phylogenetic diversity was already quite homogenous under current conditions, and this homogenization was predicted to increase in the future. Similarly, functional diversity at moderate to high altitude was also predicted to increase in the future due to the arrival of migrants from lower altitudes with new sets of traits. On the one hand, this is a rather positive output as, for instance, an increase of functional diversity ultimately leads to an increase of ecosystem productivity and resilience (Loreau 2000, Cadotte et al. 2011). This is especially true in our case where we selected

four traits known to have strong relationships with ecosystem functioning. For instance, Garnier et al. (2004) showed that specific leaf area was a strong marker of primary productivity and litter decomposition rate. More generally, it also means that, with climate and land cover change, we can expect to see a higher diversity of plants in terms of the leaf-height-seed plant ecological strategy scheme, thus encompassing a wide range of functions. The same conclusion holds for plant phylogenetic α-diversity that has been shown to be a robust predictor of productivity and stability (Cadotte et al. 2012). On the other hand, at regional scale, the projected decrease in β-diversity implies a general trend towards homogenization in diversity across the landscape, with few exceptions at highest elevations.

Uncertainties and perspectives

Although we have tried to incorporate modeling uncertainty through ensemble forecasting of species distributions and through the use of a range of RCMs and emission scenarios, our projections are still subject to various sources of possible errors and should not be interpreted as true forecasts, but rather as a projection of general trends instead. We have used correlative species distribution models that account for dispersal and biotic interactions in a very indirect way (Guisan and Thuiller 2005). The non-explicit inclusion of these important processes on range dynamics causes uncertainties when modeling species ranges at high spatial resolution under environmental changes (Van der Putten et al. 2010, Thuiller et al. 2013). Recent metacommunity models suggest that local species extinction in changing environments are strongly enhanced by negative biotic interactions (Norberg et al. 2012), and that overlooking biotic interactions would cause models to over-predict future species prevalence. Nevertheless, biotic interactions have been shown to mostly influence the spatial variation in species' abundance rather than occurrence in the French Alps (Boulangeat et al. 2012). Because of these potential sources of errors, we did not interpret our results at the resolution at which we gathered and calibrated the models. Instead, we optimized the spatial resolution at which the pervasive effects of dispersal, history and biotic interactions were less influential on projected biodiversity distribution patterns (Supplementary material Appendix 2, Fig. A1). This is especially true for topographically very heterogeneous regions such as the French Alps, and may not be sufficient to overcome these problems for large flat lowland areas. By comparing observed and modeled species richness from simple stacking of individual species projections, we found that correlative SDMs did also well in projecting species richness when degrading the resolution to 2.5 or 5 km. We are thus relatively confident that the detected patterns are robust with respect to the underlying hypotheses of correlative SDMs. However, the development of distribution models for alpine plant species incorporating a number of fine scale ecological processes is definitely an important task (Carlson et al. 2013).

An additional issue of our analysis concerns the relatively static view of biodiversity. Indeed, we considered effects of environmental change on plant diversity in the French Alps. In an era of environmental change, species from the

Mediterranean area will obviously migrate and invade the southern French Alps, while more temperate species from the west of France will most likely immigrate into the Alps. This does not influence the analyses of species ranges but it could certainly influence the resulting patterns of biodiversity facets. For instance, changes in taxonomic α-diversity at the edge of our study area are certainly misleading and an influx of species not yet present in the French Alps would certainly increase species richness and decrease the predicted homogenization (Fig. 3). Obviously, the migration of exotic species from abroad or species from very different clades would have an influence of the overall patterns but the effect will be rather minor given that a high number of major plant clades are already present; for instance, in the French alpine flora there are representatives of 150 plant families (compared to 415 families in the world according to APG III). Indeed, when considered at regional scale, naturalized exotic species tend to belong to the same families or lineages as the ones already occurring in the recipient region (Thuiller et al. 2010).

Conclusion

Climate and land cover changes are projected to modify the spatial distribution of plant species and plant diversity in the French Alps. Although the most common species are projected to experience drastic changes in their suitable habitats, rare species seem to be much less affected by projected environmental changes, mostly because they occupy specific meso-scale environmental conditions at very high altitude that remain to be present in the future. Most importantly, those species should be equally well protected under environmental change as they are now. Our gap analysis demonstrates that threatened species or species of conservation interest are well-protected under current conditions, and remain to be so in the future. Our models indicate that the spatial patterns of plant diversity of the three facets (taxonomic, phylogenetic and functional) will be severely modified. Overall, although the patterns of change are not necessarily overlapping across the three types of diversity, local α-diversity is generally predicted to increase at the cost of β-diversity. Most of the changes are projected to occur at the mid-altitudinal vegetation belts, which represent the ecotone between lowland and high altitude vegetation strategies. To the best of our knowledge, this is the first complete risk assessment carried out over a comprehensive region, combining up-to-date climate, land cover and species distribution models, together with a multi-facet view of plant diversity. More regional risk assessments are needed to effectively test the efficiency of current protected area networks in this era of drastic changes.

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