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Changes in species richness with climate change in subalpine communities are dependent on regional environmental conditions and local functional composition

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Abstract

Questions: Climate change may have different effects on species richness depending on regional climates, soil types and the functional composition of local communities.

Location: Subalpine belt of the Grandes Rousses (Alps) and Sancy mountain ranges (the Massif Central), France.

Methods: We compared changes in species richness in response to recent climate change in communities from two mountain ranges subjected to contrasting environmental conditions, with a more continental climate and drier soils in the Alps than in the Massif Central. Vegetation composition of 189 and 157 plots was assessed in 1997 and 2017–2018 in the Alps and 1988–1989 and 2022 in the Massif Central, respectively. Five species traits (height, lateral spread, leaf area, specific leaf area and leaf dry matter content) were measured on 108 and 144 species, respectively. Changes in vegetation composition and species richness along spatial environmental gradients were analysed with correspondence analysis at the Sancy site and canonical correspondence analysis at the Alpe d'Huez site. Changes in functional composition across sites were analysed with principal components analysis. Changes in species richness with climate change were analysed with repeated-measure ANOVAs.

Results: In both mountain ranges summer temperatures increased and the hydric balance decreased over the past three decades, but snow cover duration decreased in the Alps only, whereas irradiance strongly increased in the Massif Central only. Functional composition was characterized by shorter and more conservative species in the Alps than in the Massif Central, which was dominated by tall exploitative species. Species richness overall decreased with climate change by ca 10% in the Alps but overall increased by ca 10% in the Massif Central. Species richness decreased in the Alps probably because of increasing competition induced by dwarf shrub encroachment due to decreasing snow cover duration, whereas species richness increased in the Massif Central probably due to increasing irradiance in a very nebulous climate.

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Conclusion: The opposite changes in species richness observed in the two mountain ranges with recent climate change were likely to be explained by their contrasting climate and soil conditions driving different functional compositions and diversity–environment relationships.

1 | INTRODUCTION

Climate change is considered to severely threaten overall earth biodiversity, both nowadays and in the near future. However, the evidence for sharp decreases in diversity has mainly been found in marine and freshwater systems and for animals (Bellwood et al., 2004; Wilson et al., 2005; Reid et al., 2019; Albert et al., 2021), but less so in terrestrial systems and for plant species which show a higher resistance to climate change than originally predicted (Thuiller et al., 2005; Bertrand et al., 2011; Cheaib et al., 2012; Lenoir, 2022).

Alpine plant communities are considered the most sensitive terrestrial system for biodiversity changes because of the steepness of ecological gradients and the isolation of most alpine summits (Körner, 2003; Anthelme & Lavergne, 2018). However, changes in species richness are highly dependent on the environmental context in terms of elevation, regional climates, soil types, snow cover duration and human pressure (Kammer et al., 2007; Scherrer & Körner, 2011; Rumpf et al., 2018; Nicklas et al., 2021). Pioneer resurvey studies have shown that species richness has increased at the high alpine and nival belts, probably due to climate warming (Grabherr et al., 1994; Gottfried et al., 2012; Pauli et al., 2012; Steinbauer et al., 2018), but the few studies conducted at the subalpine belt have rather observed decreases in species richness probably due to increasing competition with climate warming (Vittoz et al., 2009; Alexander et al., 2015; Nicklas et al., 2021; Michalet et al., 2024). Different regional climates may also trigger different community responses because competition is more likely to increase with warming in wet climates, whereas facilitation is expected to increase with increasing drought in drier climates, with opposite consequences for species richness (Choler et al., 2001; Callaway et al., 2002; Michalet et al., 2014). For example, comparing changes in alpine vegetation between the temperate climate of the Central Alps, the submediterranean climate of the Apennines and the drier Mediterranean climate of Crete, Steinbauer et al. (2022) found a thermophilization of the vegetation in the two northern wet mountains only, with a decline of cold-adapted cushion plants in the Alps. In addition, different mountain regions can further show dissimilar species pools, which is well recognized as a source of contingencies in community responses (Lessard et al., 2012).

Changes in species richness are also highly dependent on snow cover duration varying across space and time, that is, along mesotopography gradients and with climate change, respectively (Matteodo et al., 2016). Choler (2015, 2018) highlighted that the positive effect of an extended growing season due to decreasing snow cover can be counteracted by the detrimental effects of increasing the number of freezing days, with contrasting consequences for species' responses along mesotopographic gradients depending on species' functional strategies (see also Wipf et al., 2009). Sandvik and Odland (2014) assessed changes in Alpine snowbeds from Norway over a 30-year-long period and found an increase in species richness in both dry and wet snowbeds, mostly because of the invasion by shrubs, graminoids and herbs. However, drought-intolerant species were strongly reduced. Daniëls et al. (2011) found high changes in several snowbed communities from Greenland with an overall increase in species richness due to increasing drought. Carbognani et al. (2014) assessed vegetation changes in an alpine snowbed from the Italian Alps and found a high internal dynamic due to increased competition, but also an overall increase in species richness. In contrast, modeling the effects of changes in snow cover duration on arctic plant communities, Niittynen et al. (2018) found that a 20%–30% decrease in snow cover duration might fully compensate for the increase in species richness due to warming, potentially inducing important losses of vascular plants, lichens and bryophytes. Niittynen et al. (2020) also found with modeling that decreasing snow cover, together with warming temperatures, can substantially modify plant functional traits, with future plant communities projected to be occupied by taller plants with larger leaves and faster growth, and, thus, likely inducing an increase in competition and decrease in species richness.

Plant community richness is known to be highly dependent on the functional composition of plant communities closely linked to biotic interactions, i.e., facilitation and competition (Grime, 1973; Michalet et al., 2006; Michalet et al., 2023; Munoz et al., 2023). Because functional composition also varies with environmental conditions, in particular climate and soil types (Díaz et al., 2016; Joswig et al., 2022), the effect of global change on diversity is likely to be mediated by changes in functional composition (Bjorkman et al., 2018; Niittynen et al., 2020; Bektas et al., 2023). Although it is not easy to separate the effects of local environmental conditions from those of functional composition, the latter can also influence changes in diversity with climate change due to differences in the relative frequency and abundance of functional strategies across mountain systems. For example, a high relative frequency of species intolerant to competition (i.e., short exploitative or short conservative species sensu Michalet et al., 2023) may enhance variation in species richness through changes in competitive responses with climate change. Alternatively, a high relative abundance of competitors (i.e., tall exploitative or tall conservative species sensu Michalet et al., 2023) may enhance variation in competitive effects of community dominants. Thus, since alpine systems with harsh physical conditions (e.g., continental and/or dry climates) are more likely to be dominated by short species intolerant to competition (Joswig et al., 2022; Michalet et al., 2023), we may expect strong decreases in diversity as environmental conditions improve with climate change in such mountain range due to the high local potential for competitive exclusion (i.e., due to the abundance of species intolerant to competition that could be excluded). Alternatively, in milder environmental conditions, the increase in competitive exclusion should be less pronounced due to the lack of species likely to be excluded. As a second alternative, in the case of pejoration of environmental conditions with climate change, increases in diversity are more likely to be the strongest in mild environmental conditions due to decreasing competitive effects there and even loss of species in the less favorable mountain range already subjected to harsh environmental conditions.

In this study we aim to compare changes in species richness with climate change in two contrasting mountainous areas, a dry continental mountain range from the southwestern Alps (Alpe d'Huez, French Alps) and a wet oceanic mountain range from the Massif Central (France). The higher physical stress of the former mountain range is strengthened by the occurrence of calcareous rocks (in addition to siliceous rocks), whereas the more favorable physical conditions of the latter are even improved by a homogenous volcanic substrate characterized by deeper soils with higher water availability than calcareous rocks (Michalet et al., 2002; Nemer et al., 2021). The two systems are very likely to also show contrasting functional compositions, due to the occurrence of dry short calcareous grasslands and tall siliceous heaths in the former and wet tall forb communities in the latter (Michalet & Philippe, 1993). Vegetation composition was assessed in 1997 and 2017–2018 in the Alps and 1988–1989 and 2022 in the Massif Central and functional composition was assessed through contemporary trait measurements in the two mountain ranges. We used multivariate analyses for quantifying correlations between changes in species richness, functional composition and environmental conditions in the two mountain ranges separately. We also quantified changes in climatic conditions and species richness between the ancient and recent vegetation surveys in each mountain range. We addressed four main questions: (i) did climate change similarly in the two mountain ranges, in terms of temperatures, water balance, snow cover duration and irradiance? (ii) What are the differences in functional composition between the two mountain ranges? (iii) What are the drivers of variation in species richness along spatial environmental gradients in the two mountain ranges? (iv) Did species richness show contrasting variations with climate change in the two mountain ranges?

2 | MATERIALS AND METHODS

2.1 | Study sites

The site in the Alps was located in the Grandes Rousses mountain range in the southwestern Alps close to the Alpe d'Huez ski resort (45°05′16″ N–6°05′08″ E, elevation 1860 m a.s.l.; Figure 1). The vegetation plots were located at the higher part of the subalpine belt, between 2100 and 2200 m. The Grandes Rousses mountain range has a semi-continental climate with a drier summer than most alpine sites

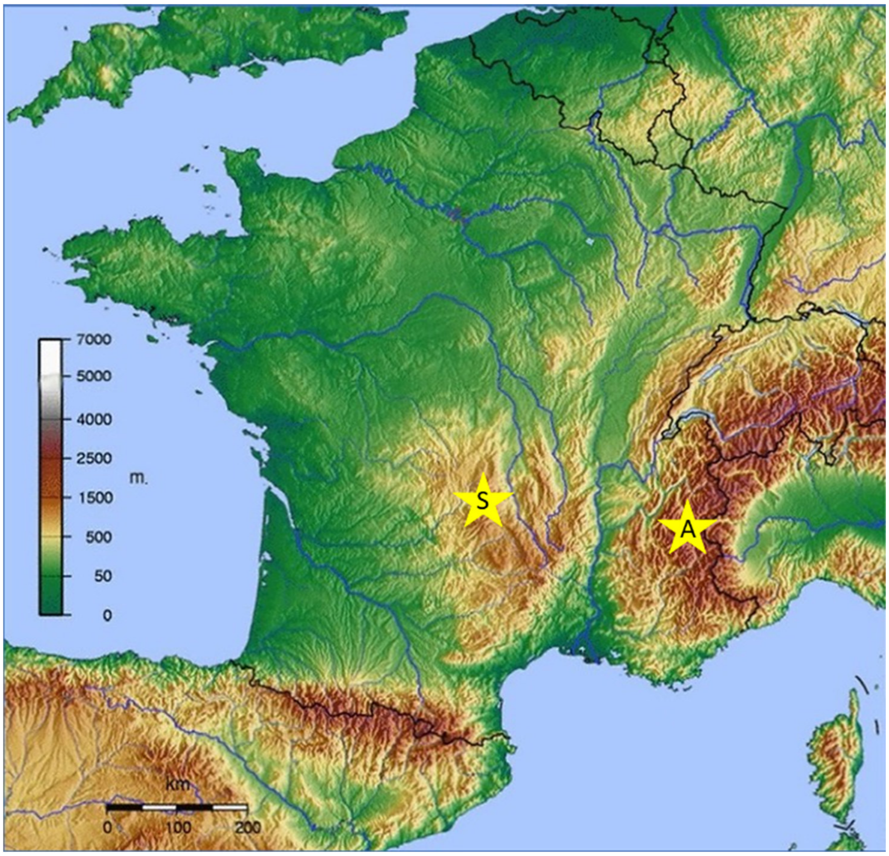

FIGURE 1 Localisation of the two sites in France. The Alpe d'Huez site (yellow star A) is located in the Alpine Chain in the east of France and the Sancy site (yellow star S) in the Massif Central more to the west of France.

revisited in the Alps due to its position in the southernwestern Alps (Ozenda, 1985; Michalet et al., 2002). Mean annual rainfall is 998 mm and the mean temperature is 9.0°C for the period 1990–2021 (Meteo France data for the Alpe d'Huez station; Appendix S1). The site has been moderately grazed by sheep for at least several decades, being located at the boundary of two pastoral units (approximately ten crossing of the site by a herd of 2000 animals each year). However, there was no documented change in grazing pressure between the two sampling dates (information given by local owners). We have no information on variation in grazing intensity by wild ungulates at this site during the study period.

The site in the Massif Central was located in the Sancy mountain range, which includes the highest summit of the volcanic chain of the French Massif Central (Puy de Sancy, 45°31′42″ N–2°48′50″ E, 1886 m a.s.l.). The vegetation plots were all located at the subalpine belt, between 1450 and 1880 m. Mean annual rainfall is 1600 mm and mean temperature is 6.0°C for the period 1990–2021 (Meteo France data for Chastreix station, 1385 m a.s.l.; Appendix S1). Thus, the Sancy mountain range has a very wet oceanic climate with more than twice the rainfall as in the Grande Rousses range at similar elevation and a much milder summer, explaining the location of the subalpine belt at lower elevation than the more continental Alpine site, although latitudinal positions are the same. Tree line elevation (and vegetation belts) is very dependent on oceanicity, with much lover vegetation belts in very oceanic climates (Ozenda, 1985). Additionally, there are no subalpine tree species in the Massif Central and the tree line is generally formed of dense thickets of *Salix* and *Sorbus* species. The site is only grazed by wild animals. Cows are grazing in some low parts of the mountain range that were not included in our sampling.

2.2 | Experimental design and plant communities

At the Alpe d'Huez site, 189 quadratic vegetation relevés of 0.5 m × 0.5 m were conducted in 1997 to sample the main communities occurring on soils from both calcareous and siliceous rocks and in different conditions of mesotopography and snow cover duration (Michalet et al., 2002). The quadrats were divided into 1-dm^2 sections providing 36 evenly spaced points for sampling species covers. We counted, for each species within a section, the number of points where it touched the circumference of a circle of 5 cm in diameter centered on each corner of the section. A species touched only once had a cover of 2.8%, while a cover of 1% was assigned to each species that was present in the quadrat but not touching any of the 36 contact points. The plots were tagged with wooden sticks that were precisely located in a 190 m × 85 m grid with a theodolite. We also measured in the field and in the laboratory 47 environmental and soil physical (including snow cover duration) and chemical variables for each of the 189 plots (see Michalet et al., 2002 for methods). Finally, a canonical correspondence analysis (CCA) was conducted on the vegetation composition of the 189 vegetation quadrats, 103 species and 20 environmental variables. We also conducted a correspondence analysis (CA) on the vegetation matrix alone and conducted a cluster analysis that distinguished 11 communities (Michalet et al., 2002). This additional CA was conducted in order to test the effect of the year of sampling on species composition (position of the scores of the communities, see subsection 2.5. Statistical analyses).

The CCA and CA results showed that the 11 communities were clearly separated into three groups: (i) calcareous ridges, on basic and dry unfertile soils; (ii) siliceous ridges, on acidic and rocky soils from convex slopes with a low snow cover duration; and (iii) mixed hollows, on acidic but deep fine-textured soils (from mixed mineral origin), in concave slopes with a long snow cover duration and high water and nutrient availability (Appendix S2). Water availability was the main ecological driver of CCA 1, since vegetation cover was highly correlated to this axis, and nutrient availability and temperature (related to snow cover duration) of axis 2, since nutrient availability was negatively correlated to this axis (Michalet et al., 2002).

At the Sancy site we selected 157 vegetation plots among approximately 700 relevés that were conducted in 1988–1989 with Braun-Blanquet's methodology by Michalet and Philippe (1993, 1995) in the reserves of Chastreix-Sancy and Chaudefour. Size of the plots was in general 10 m × 10 m. All plots were located at elevations between 1450 and 1880 m a.s.l. on volcanic soils within an area of 10 km × 5 km. The 157 plots were selected with multivariate analyses in order to sample enough replicates of all community types defined by Michalet and Philippe (1993, 1995) and in the different geographical and ecological conditions of the two reserves. Since vegetation relevés were only noted on a 1/25,000 map in the late eighties, we also selected only plots that could be precisely relocated in 2022. We then conducted a CA on the vegetation composition of the 157 plots followed by a cluster analysis in order to delimit 18 communities at the site. At the Sancy site, we could not conduct, as at the Alpe d'Huez site, a constrained analysis (CCA) to assess vegetation–environment relationships due to the lack of environmental measurements precisely recorded at each plot at the first sampling date. However, in order to characterize the environmental conditions of the 157 vegetation plots, we extracted a set of morphometric variables from a Light Detection and Ranging-derived digital elevation model with a resolution of 50 cm × z 50 cm. We considered the elevation, the slope and aspect of the plots and further computed the topographic wetness index (TWI, Boehner & Selige, 2006), the Diurnal Anisotropic Heating index (DAH, Boehner & Antonic, 2009) that reflects sun exposure and the length–slope factor (LS, Moore et al., 1991) that reflect potential soil erosivity. These variables were then correlated with the plot scores on the axes of the CA conducted on species composition.

The 18 cluster groups were gathered in three main groups corresponding to three trophic levels depending on their position along the first CA axis, oligotrophic communities (Ericaceae heathlands, *Nardus stricta* snowbeds and grasslands) on the left side, mesotrophic communities (*Patzkea paniculata* and *Calamagrostis arundinacea* meadows and *Luzula desvauxii* snowbeds) at intermediate position and eutrophic communities (Asteraceae megaphorbias, Michalet & Philippe, 1993) on the right side (Appendix S3). The first axis was explained by nutrient availability, increasing from negative to positive scores, whereas the second axis was explained by exposure and irradiance with decreasing irradiance from negative to positive scores.

2.3 | Vegetation composition resurvey, morphological trait measurements

In July 2017–2018 and July 2022, we resurveyed with the same sampling methodologies the 189 plots of Alpe d'Huez and the 157 plots of Sancy, respectively. In July 2021 and 2022, we conducted morphological trait measurements on the 108 most frequent species of the plots of Alpe d'Huez and of the 144 most frequent species of the Sancy plots, respectively. At both sites, measurements were conducted on at least five mature and healthy individuals of each species. Five traits were measured following standardized protocol (Cornelissen et al., 2003): extended maximum plant height (cm), plant width (cm), leaf area (LA, cm^2), specific leaf area (SLA, cm^2/g) and leaf dry matter content (LDMC). At least one mature and healthy leaf per individual was selected to measure LA (software *Winfolia*, Regents Instruments, Quebec, Canada). Leaf dry weight was measured after drying samples for three days at 80°C. Trait values of the five individuals were averaged per species before analyses.

2.4 | Climate

In order to assess changes in climate conditions that occurred between the two vegetation surveys at the two sites, we used the records of the Meteo France climatic stations of Alpe d'Huez (1860 m a.s.l., Alpine site) and Chastreix (1385 m a.s.l., Sancy site) for both temperatures (T_{mean}, T_{max}, i.e., day temperatures, and T_{min}, i.e., night temperatures) and P (rainfall). We also used data obtained from the S2M (SAFRAN–SURFEX/ISBA–Crocus– MEPRA) reanalysis for snow cover duration and nebulosity for the Alpe d'Huez site (Vernay et al., 2022) and the SAFRAN (*Système d'Analyse Fournissant des Renseignements Adaptés à la Nivologie*) data for snow cover duration and global radiations in the Sancy site (Durand et al., 1993). For both data types and at both sites we used daily records for the 1990–2020 period and then calculated summer hydric balance, summer mean of maximum temperatures and snow cover duration (annual number of days with snow covering the ground at the 5–10-cm threshold).

2.5 | Statistical analyses

In order to assess changes in climate conditions, we correlated at both sites summer hydric balance, summer mean of maximum temperatures, summer mean nebulosity, summer sum of global radiation and snow cover with time, for the period 1990–2020.

In order to assess differences in functional composition between the two sites, we conducted a principal components analysis (PCA) on a matrix of 252 species (108 species for the Alpe d'Huez site and 144 species for the Sancy site) and five species traits. Then, we used one-way ANOVA for testing the effect of the site on the scores of the species on the first two axes of the PCA.

We tested, separately at each site, a year effect on the plot scores along the CA axes and on the species richness with repeated-measure ANOVAs, where the year of sampling was considered as a within-subject factor. Finally, we tested whether year effects were statistically different between the vegetation clusters identified for each site. To do so, we computed two different mixed ANOVAs, one per site, where time was considered as a within-subject factor and the clusters as between-subject factors.

All multivariate analyses were conducted with ADE-4 software (Thioulouse et al., 1997) and ANOVAs and regressions were performed within the R environment (R Core Team, 2021). All ANOVAs were followed by post hoc tests when necessary.

3 | RESULTS

At both sites during the 1990–2020 period, summer hydric balance significantly decreased ($r = -0.39$ and -0.55, $p = 0.03$ and 0.001, for the Alpe d'Huez and Sancy sites, respectively, Figure 2a,b) and summer mean of maximum temperatures significantly increased ($r = 0.56$ and 0.43, $p = 0.001$ and 0.015, for the Alpe d'Huez and Sancy sites, respectively, Figure 2c,d). Summer sum of global irradiance only significantly increased at the Sancy site ($r = 0.39$, $p = 0.03$, Figure 2f), whereas summer mean nebulosity did not significantly vary at the Alpe d'Huez site ($p = 0.38$, Figure 2e). In contrast, snow cover duration significantly decreased at the Alpe d'Huez site ($r = -0.53$, $p = 0.002$, Figure 2g), but did not significantly vary at the Sancy site ($p = 0.45$, Figure 2h).

The PCA conducted on the traits of the species of both sites showed two main axes of functional variation: the first axis correlated to the size traits (height, lateral spread and leaf area) and the second axis correlated to growth traits (SLA and LDMC). Thus, four main functional syndromes may be observed, tall conservative species at the upper right of the diagram (e.g., *Rhododendron ferrugineum*, only present at the Alpe d'Huez site, mostly on wet oligotrophic siliceous soils), tall exploitative species at the lower right of the diagram (e.g., *Heracleum sphondylium*, only present at the Sancy site, mostly in tall megaphorbias on wet eutrophic soils), short conservative species at the upper left of the diagram (e.g., *Globularia cordifolia*, only present at the Alpe d'Huez site, mostly on dry calcareous ridges) and short exploitative species at the lower left of the diagram (e.g., *Potentilla aurea*, present at both sites, mostly in short wet grasslands from snowbeds) (Figure 3). Species from both sites had very different overall positions in the diagram, with primarily much taller species at the Sancy than Alpe d'Huez site (highly significant site effect on the PCA 1 axis; $F = 43.1$, $p < 0.001$). Species from the Sancy site were also more exploitative than species from the Alpe d'Huez site (highly significant site effect on the PCA 2 axis; $F = 19.1$, $p < 0.001$).

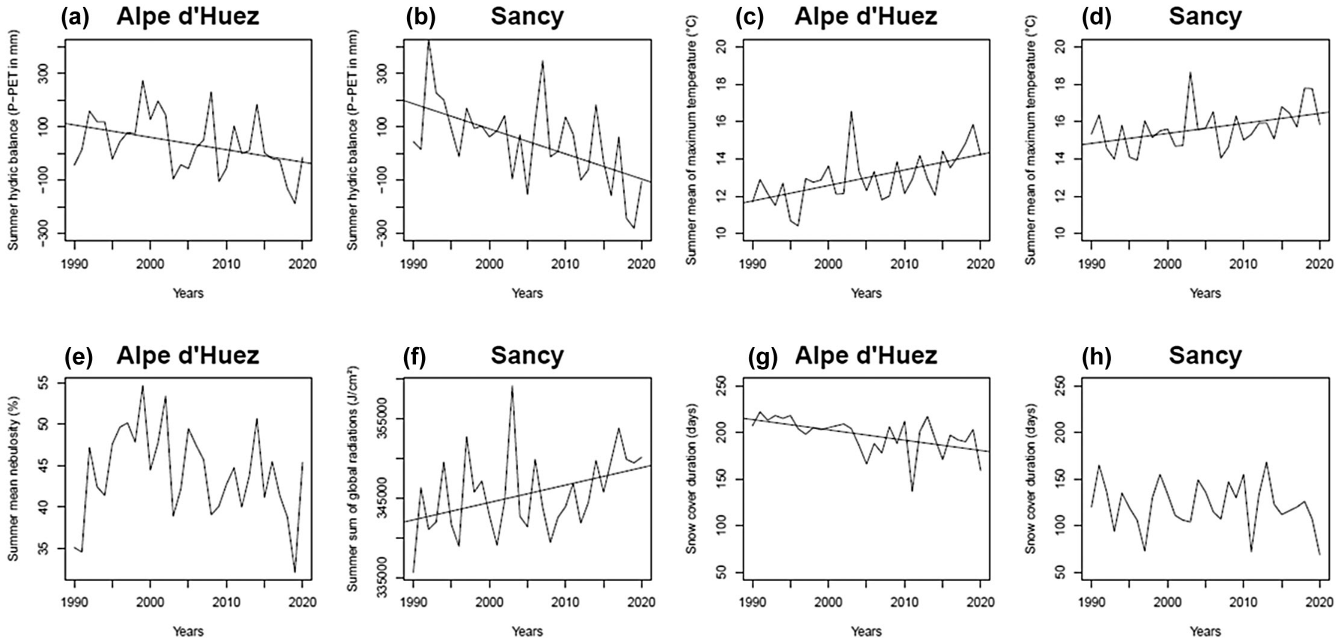

FIGURE 2 Changes in (a,b) summer hydric balance; (c,d) summer mean of maximum temperature; (e,f) summer mean nebulosity or summer sum of global radiation; (g,h) annual snow cover duration at the Alpe d'Huez and Sancy sites during the 1990–2020 period, respectively. Only significant trends are drawn.

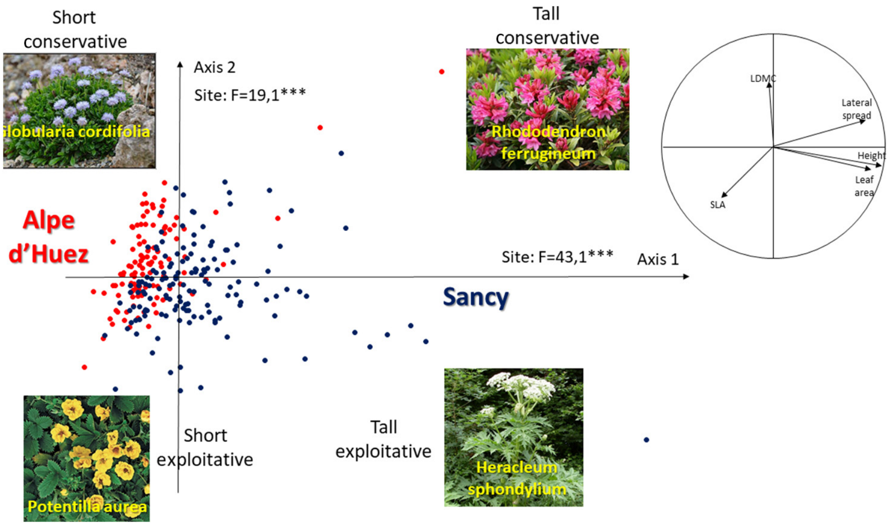

FIGURE 3 Diagram of components 1–2 of the PCA conducted on the plant traits of the species of the two sites, with in red species from Alpe d'Huez et in blue species from Sancy. One example of each of the four primary plant strategies is shown at the four extremes of the two primary axes of functional differentiation following Díaz et al. (2016) and Michalet et al. (2023). The circle at the top right of the graph shows correlations of the five measured plant traits with the two axes (size traits for the horizontal axis and growth traits for the vertical axis).

At the Alpe d'Huez, there was, for both years of sampling, a highly significant unimodal relationship between species richness and the position of the plots on the first axis of the CA conducted on vegetation composition (Figure 4 and see Appendix S2 showing that plot positions on the first axis of the CCA [and CA, as both diagrams were highly similar] were primarily correlated to water availability and vegetation cover). This means that, for both years of sampling, species richness was the highest at intermediate position along the first CA axis in plant communities of intermediate cover and biomass, i.e., mesic calcareous grasslands dominated by *Carex sempervirens*, but lower in short dry calcareous grasslands dominated by *Globularia cordifolia* and the lowest in the wettest communities on siliceous rocks with the highest cover and biomass (heathlands dominated by ericaceous shrubs). There was no statistically significant difference in plot scores on the first CA axis between the two years of sampling ($F_{1,188} = 1.06$, $p = 0.305$; Figure 4). There was a statistically significant difference in species richness between the two years of sampling ($F_{1,188} = 99.18$, $p < 0.001$), with on average a 10% decrease from 1997 to 2017–2018. Finally, we found a statistically significant interaction between time and clusters ($F_{11,177} = 2.46$, $p = 0.008$; Figure 5a). Considering Bonferroni-adjusted *p*-values, the changes in species richness between the two years of sampling were significant only for calcareous short grasslands, calcareous *Juniper* heathlands, *Vaccinium* heathlands from hollows, and siliceous short grasslands.

At the Sancy site, there was, in both years of sampling, a highly significant linear decrease in species richness along the second axis of the CA conducted on vegetation composition (Figure 6 and see Appendixes S3 and S4B showing that plot position on the second axis of the CA was primarily correlated to the radiation index, i.e., global radiation, and, thus, exposure). This means that, in both years of sampling, the highest species richness was found in communities with a southern exposure where irradiance was the highest, that is, tall mesotrophic meadows dominated by *Patzkea paniculata* or *Calamagrostis arundinacea*, and the lowest species richness was found in communities with a northern exposure where irradiance was the lowest, i.e., tall eutrophic megaphorbias and short grasslands from snowbeds dominated by *Nardus stricta*. There was a statistically significant difference in plot scores along the CA axis 2 between the two years of sampling ($F1{,}156 = 12.35$, $p < 0.001$; Figure 6). This means that, with climate change, the relative importance of species with a southern exposure increased, whereas the importance of species with a northern exposure decreased. There was a statistically significant difference in species richness between the two years of sampling ($F_{1,156} = 21.464$, $p < 0.001$, Figure 6), with an overall increase of 10% from 1988–1989 to 2022. Finally, we found no statistically significant interaction between time and clusters ($F_{12,144} = 1.74$, $p = 0.065$, Figure 5b). However, the analysis confirms a clear cluster effect on species richness $F_{12,144} = 15.78$, $p < 0.001$ and of the year of sampling $F_{1,144} = 16.01$, $p < 0.001$. In contrast, there was no relationship between species richness and the first CA axis (data not shown), that was significantly explained by the erosivity index (i.e., LS, see section 2. Materials and Methods) controlling soil fertility and nutrient availability (Appendix S4A).

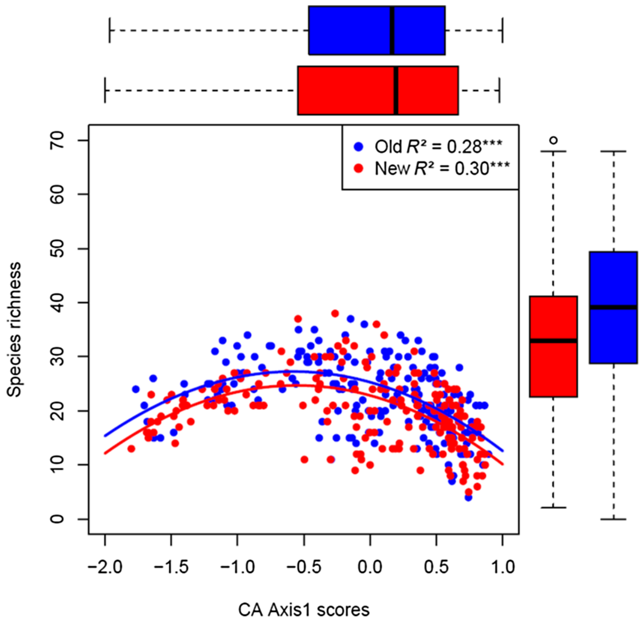

FIGURE 4 Changes in species richness with increasing plot scores on axis 1 (related to increasing vegetation biomass) of the correspondence analysis conducted on the vegetation composition of the 378 plots of the Alpe d'Huez site (1997 plots and curve are in blue and 2017–2018 ones in red). Regression coefficients and significances of the polynomial curves are indicated on the top right of the graph (***, $p < 0.001$).

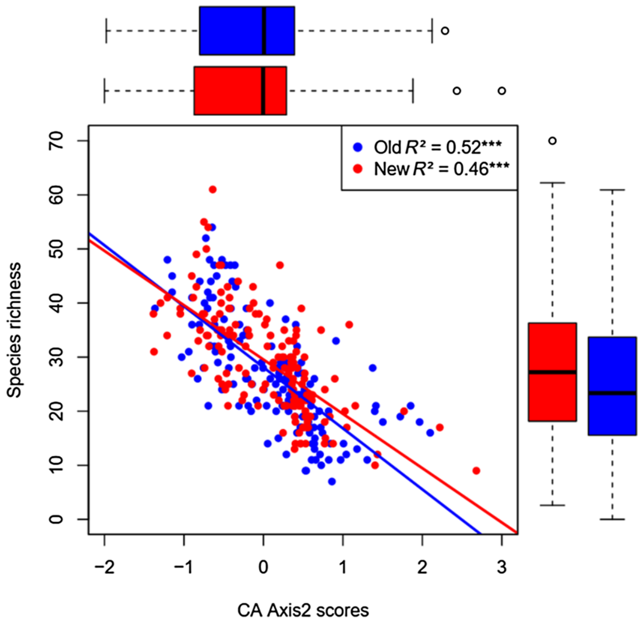

FIGURE 6 Changes in species richness with increasing plot scores on axis 2 (related to decreasing irradiance) of the correspondence analysis conducted on the vegetation composition of the 314 plots of the Sancy site (1988–1989 plots and curve are in blue and 2022 ones in red). Regression coefficients and significances of the linear curves are indicated on the top right of the graph (***, $p < 0.001$).

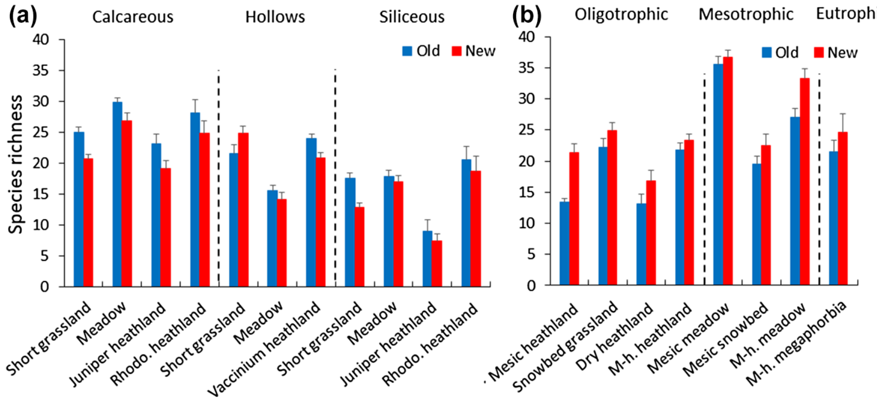

FIGURE 5 Changes in species richness (means ± SE) of communities from the Alpe d'Huez (a) and Sancy (b) sites. Rhod.: Rhododendron. M.-h.: Meso-hygric. A detailed presentation of the communities can be found in Appendix S2 for the Alpe d'Huez site and in Appendix S3 for the Sancy site.

4 | DISCUSSION

In response to our first question, climate change induced a similar increase in summer temperature and decrease in water balance in the two subalpine systems, but snow cover duration decreased only in the dry semi-continental Alpe d'Huez site, whereas summer global radiations increased in the wet oceanic Sancy site only. In response to our second question, there were strong differences in functional composition between the two sites with taller and more exploitative species in the Sancy site than in the Alpe d'Huez site. In response to our third question, spatial variation in species richness was driven by different ecological processes at the two sites. In the Alps, species richness showed a unimodal relationship along a physical stress/community biomass gradient, whereas, in the Massif Central, species richness increased with increasing global radiation from north to south exposure. Finally, in response to our fourth question, there were significant changes in species richness with climate change at both sites, but in opposite directions, with a negative effect of climate change in the Alps but a positive effect in the Massif Central. These results suggest that variation in species richness with climate change in these two subalpine systems was highly dependent on the regional context.

4.1 | Climate change in the two mountain ranges

Consistent with previous studies, in both mountain ranges, we found an increase in maximum temperature and a decrease in water balance during the summer period (Gobiet et al., 2014; Nicklas et al., 2021), a physical change known to have induced a “thermophilization” of alpine communities in many places across the world (Gottfried et al., 2012). Snow cover duration has also been shown to be strongly reduced in several mountain ranges and in particular in the Alps. For example, Carrer et al. (2023) have shown using ring-width records that the duration of current snowpack cover in the southern Italian Alps was 36 days shorter than the long-term mean, a decline that is unprecedented over the last six centuries. Climate change has been predicted to decrease snow cover duration the most in low-alpine and arctic environments. Indeed, Larternser and Schneebeli (2003) have found only slight changes at high altitudes for the Swiss Alps (2003) and more pronounced decreases at mid and low altitudes at the end of the last century (see also Beaumet et al., 2021). The Alpe d'Huez site was located at the subalpine belt and, consistently, we found a significant decrease in snow cover duration. However, there were no significant changes in snow cover duration in the Massif Central, although it was also located at the subalpine belt.

In contrast, the summer sum of global radiations significantly increased at the Sancy site while summer nebulosity did not significantly vary at the Alpe d'Huez site. Solar irradiance has shown complex temporal variations at the earth's scale during the last century with opposite trends depending on the continents and primarily variation in aerosols emissions (Ohmura, 2006). However, we are not aware of available information at lower scale within continents (but see Stanhill & Cohen, 2005 for the USA), which limits our understanding of the different trends that we found in this study between the two studied mountain ranges.

4.2 | Differences in functional composition between both mountain ranges

The PCA analysis conducted on five morphological traits of the 252 species sampled at the two sites showed the occurrence of two main independent functional syndromes structuring the functional composition of these subalpine communities, a size traits syndrome opposing tall to short species and a growth traits syndrome opposing conservative to exploitative species. This result is highly consistent with the global study conducted by the TRY network (Díaz et al., 2016) and recent more local studies (Michalet et al., 2023), and stressed that the subalpine habitats assessed in our two studies were sufficiently different to encompass the primary gradients of functional diversification of herbaceous and shrub species.

There were strong differences in functional composition between the two sites, which can easily be explained by their differences in climate and soil conditions. The most important difference was found for size traits with taller species at the wet oceanic Sancy site than at the more continental and drier Alpe d'Huez site. This is consistent with the study of Joswig et al. (2022) conducted on the TRY database that showed that size traits were highly correlated with climate conditions, with taller species in warm and wet climates and shorter species in colder and drier ones. However, it is very likely that differences in bedrock types also contributed to driving these functional patterns, since the Alpe d'Huez site included both calcareous and siliceous rocks whereas the Sancy site only included volcanic rocks. A number of studies have shown that grassland habitats are drier on calcareous than siliceous (and volcanic) rocks, because of the higher levels of water infiltration occurring on calcareous than siliceous rocks (Michalet et al., 2002; Nemer et al., 2021). There were also significant differences in growth traits, with more exploitative species at the Sancy than the Alpe d'Huez site that could be explained by the interaction between climate and soil conditions, consistent with Joswig et al. (2022). Calcareous soils are less fertile than siliceous soils in grassland ecosystems from stressed climates, due to the higher drought stress limiting soil organic matter decomposition and, thus, nutrient availability (Michalet et al., 2002). Additionally, water and nutrient fluxes are higher on concave slopes of oceanic volcanic mountain ranges, such as the Sancy site, than on convex slopes of calcareous and siliceous bedrocks of more continental sites, such as the Alpe d'Huez site.

To summarize, there was a higher relative abundance of short conservative species at the Alpe d'Huez site and of tall exploitative species at the Sancy site, because of the occurrence of higher drought and nutrient stresses at the former than at the latter site, related to both differences in climate and soil conditions.

4.3 | Contrasting changes in species richness in the two mountain ranges

Interestingly, with climate change species richness decreased by 10% at Alpe d'Huez but increased by 10% at Sancy. There are a number of known limitations in resurveys of vegetation plots that may produce biased results, among them the uncertainty in plot location, differences in plot size and observer or seasonal bias (Kapfer et al., 2017). Our results are very unlikely to have been confounded by any of those potential biases for the following reasons: (i) the uncertainty in plot location was null at the Alpe d'Huez site because plots were marked with permanent sticks and quite low at the Sancy site as they were precisely indicated on a 1/25,000 map (plots that were not easily found using habitats conditions and map location were excluded from the analysis); (ii) at the Alpe d'Huez site we used a similar plot size with a quadrat at the two dates while we applied the same phytosociological method of air minima at the Sancy site; (iii) the first author was present at the two sites and at both periods during vegetation sampling; and (iv) plots at both sites were revisited in the same season during the two periods. Climate change effects are also not easily separated from the effects of land use change. For example, grazing abandonment has increased in some mountain areas (Tasser & Tappeiner, 2002; Kammer et al., 2007) and this modulates the effects of climate change on the trajectories of vegetation composition and diversity at local scale (Steinbauer et al., 2018). However, different changes in grazing pressure at the two sites are very unlikely to explain the contrasting changes in species richness observed in our study because grazing by domestic animals was low and did not significantly change at both sites.

To detect the ecological processes that might have driven the opposite changes in species richness with climate change in the two mountain ranges it is worth assessing the local drivers of changes in species richness along spatial gradients at both sites. At the Alpe d'Huez site, Michalet et al. (2002) have shown that there was a unimodal relationship between species richness, and vegetation cover, and environmental conditions, in particular water availability in relation to substrate types (as observed along the first axis of the CCA conducted on species composition and environmental factors, see Figure 4), consistent with Grime's (1973) model. Additionally, Michalet et al. (2024) have shown that the primary driver of changes in taxonomic and functional composition that occurred at this site with climate change was the decrease in snow cover duration (as observed by significant composition changes observed along axis 2 of the CCA, see Appendix S2), with taller (or larger) species and, thus, higher community biomass in 2017–2018 than in 1997. Thus, we argue that the overall decrease in species richness that was detected at this site was very likely induced by the overall increase in community biomass (and, thus, competition) due to decreasing snow cover duration. This would be consistent with the results of a number of studies that have shown the primary role of variation in snow cover duration for driving changes in composition and species richness with climate change, in particular at arctic sites currently subjected to high shrub encroachment (e.g., Niittynen et al., 2018, 2020).

At the Sancy site, we showed that variation in species richness along spatial gradients was rather driven by the level of global radiations (as observed along the second axis of the CA conducted on species composition, see Figure 6), in relation with exposure and slope degree (see Appendixes S3 and S4). Thus, in contrast to the Alpe d'Huez site, species richness was not dependent on community biomass, likely because the Massif Central is so wet (see Appendix S1 showing that there is twice more annual rainfall in the Massif Central than at Alpe d'Huez at similar elevation) that community biomass is always high in almost all habitats. Instead, species richness likely increases with global radiation in the Massif Central, from approximatively 20 species in the northern concave more shady habitats to approximatively 60 species in the southern convex more exposed ones. Thus, considering that summer global radiations strongly increased in the Massif Central with global change, we argue that species richness increased with global change probably due to increasing global radiations (as shown by the significant shift of all vegetation plots through time along the second axis of the CA), such as shade-intolerant species from the sunniest habitats being able to colonize less exposed habitats in a shinier mountain range (Figure 6). Such interpretation may find additional support in future studies where the spatial variability of changes in global radiation over the last decades is assessed within the Sancy massif.

5 | CONCLUSION

Our results suggest that changes in species richness with recent climate change of subalpine communities from two mountain ranges having contrasting climatic (and bedrock) conditions depend on the interplay between the level of physical stress in each mountain range, their functional composition and different drivers of variation in species richness along spatial ecological gradients between the two mountain ranges, together with the specific climatic variations induced by climate change in each range. In the dry and semi-continental site of Alpe d'Huez dominated by short conservative species, climate change induced a decrease in species richness likely because spatial variation in species richness was primarily driven by variation in community biomass and because climate change occurred mostly at this site through a strong decrease in snow cover duration that increased community biomass and, thus, likely the competitive exclusion of short species. In contrast, in the wet oceanic Sancy site dominated by tall exploitative species, climate change induced an increase in species richness because variation in species richness is primarily driven by variation in global radiation that significantly increased with climate change, thus, inducing a positive light and warming effect for short species, in particular short exploitative species.

AUTHOR CONTRIBUTIONS

Richard Michalet did the sampling in 1997 and Richard Michalet and Blaise Touzard the sampling in 2017–2018 at the Alpe d'Huez site. Richard Michalet did the sampling in 1988–1989 and Richard Michalet, Blaise Touzard, Ida Delpy and Colin Hostein sampled vegetation composition in 2022. Auriane Eisenberg, Julien Pottier and Nicolas Gross sampled functional traits in 2022 at the Sancy site. Richard Michalet, Julien Pottier and Nicolas Gross ran the statistical analyses. Richard Michalet wrote the first draft of the manuscript and all authors contributed to editing it.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data that support the findings of this study are available at https://datadryad.org/stash/dataset/doi:10.5061/dryad.wpzgmsbw8

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Climatic diagrams of the two sites.
Appendix S2. Presentation of the Alpine study system.
Appendix S3. Presentation of the Massif Central study system: distribution of the 157 plots (1988–1989 sampling) in 18 cluster groups positioned in the 1–2 diagram of a correspondence analysis.
Appendix S4. Relationship between the scores of the plots on the two first axes of the correspondence analysis (CA) conducted in the Massif Central and environmental variables, (A) CA axis 1 scores and erosivity index (length–slope factor; LS) with p-value <0.001 and $R^2=0.27$, and (B) CA axis 2 scores and radiation index (Diurnal Anisotropic Heating; DAH) with p-value<0.001 and $R^2=0.21$.

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