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RESEARCH ARTICLE

# Recent vegetation shifts in the French Alps with winners outnumbering losers

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## Abstract

1. Quantifying the impact of global change on biodiversity is a central focus of ecological research, essential for guiding policy decisions and conservation management strategies. Mountain ecosystems, recognized as early indicators of climate change impacts and centres of exceptional biodiversity, can provide critical insights into these biodiversity shifts. However, accurately assessing biodiversity changes remains challenging due to limitations in data quality, particularly regarding coverage over adequate temporal scales and fuzzy sampling strategies.
2. Here, we analysed more than 11 million expert-verified occurrence records of 4250 plant species from the French Alps collected over the past 30 years. Using a robust detection framework to statistically correct spatiotemporal biases, we quantified changes in species distributions, identifying winners (species expanding their range) and losers (species contracting their range).
3. Our results indicate that approximately one-third of alpine plant species have significantly expanded their distribution, while about 13% experienced range declines since the '90s. Although species responses did not strongly correlate with their floristic characteristics or IUCN status, expanding species were typically characterized by high colonization ability (ruderal), rapid growth (acquisitive strategies) and tolerance to higher temperatures (thermophilic). Despite a weak overall phylogenetic signal, winners or losers were disproportionately represented in some families and genera.
4. *Synthesis*. This study advances our understanding of recent biodiversity changes in mountain ecosystems, laying the groundwork for identifying underlying drivers and supporting targeted future conservation initiatives.

KEYWORDS
detection, French Alps, functional traits, mountain ecosystem, plant range shift, temporal change

## 1 | INTRODUCTION

Maintaining the integrity and biodiversity of natural ecosystems is a growing global concern, as reflected in initiatives such as the European Green Deal, the EU Biodiversity Strategy for 2030, the Sustainable Development Goals, and the Kunming-Montreal Global Biodiversity Framework (GBF). Protecting terrestrial ecosystems, preserving their biodiversity and restoring degraded ecosystems are essential for sustaining their contributions to people (e.g. carbon sequestration, food supply, timber production and flood protection). Despite these efforts, terrestrial biodiversity has continued to decline substantially over recent decades (IPBES, 2019). Achieving the GBF targets, that is, stabilize biodiversity loss by 2030 and foster the recovery of natural ecosystems in the subsequent two decades, requires a robust framework for identifying declining and expanding species, quantifying range shifts and understanding the associated functional and evolutionary consequences (Cardinale et al., 2018; Dornelas et al., 2019). Regional-scale studies are increasingly recognized as pivotal in advancing progress towards these targets Gonzalez et al. (2023).

Mountain ecosystems are critical sentinels of global change Guisan et al. (2019), making them essential for studying biodiversity dynamics. These ecosystems are characterized by pronounced plant stratification along elevational gradients, historically shaped by a combination of temperature and humidity. Over the past ~10,000 years, this stratification has also been influenced by human activities, including cycles of settlement and land abandonment (Gehrig-Fasel et al., 2007; MacDonald et al., 2000). The stratification of vegetation along these gradients significantly impacts other components of the local biodiversity, influencing both above-ground communities Martinez-Almoyna et al. (2024) and below-ground systems (Calderón-Sanou et al., 2024). Together, these components provide essential services for human well-being in mountainous regions, such as carbon sequestration, timber production and pastures (Bardgett & van der Putten, 2014; Delgado-Baquerizo et al., 2020).

Due to their unique environmental contexts, mountain ecosystems world-wide host exceptionally high levels of plant biodiversity (Rahbek et al., 2019), with many endemic species and a diverse array of life forms. Higher alpine belts, for instance, are dominated by a few plant families that have evolved traits to tolerate low temperatures (Qian et al., 2021), which could make them particularly susceptible to ongoing climate change (Chen et al., 2011; Lenoir et al., 2008). Extreme environmental conditions have historically protected mountain ecosystems from biological invasions. However, growing human appropriation of landscapes and climate change are now driving shifts in plant distributions. While an increase in plant richness on high latitude (Myers-Smith et al., 2011) and high elevation is well-documented (Lamprecht et al., 2018; Pauli et al., 2012; Steinbauer et al., 2018), extinctions at lower elevations are progressing more slowly (Alexander et al., 2018). Despite evidence of upward shifts for certain species, a comprehensive assessment of distribution changes across all species remains lacking.

The detection of species change forms a cornerstone of the detection-attribution framework advocated by GEO-BON Gonzalez et al. (2023). Detection of vegetation change is usually assessed via changes in species coverage or frequency (Klinkovská et al., 2024). Robust estimates require large historical datasets with high spatial resolution. For instance, Jandt et al. (2022) used data from long-term repeated vegetation-plot records to report more losses than gains in the German flora over the last century, which corroborates the findings of Timmermann et al. (2015) in the Danish flora. These analyses also offer a means to assess the current conservation of declining species. Klinkovská et al. (2024) used data on the Czech flora, collected over the past six decades, to determine whether expanding species are invasive or opportunistic colonizers responding to climate change (Eichenberg et al., 2021; Jandt et al., 2022). These insights are vital for strengthening biodiversity protection and restoration, particularly at regional scales where conservation efforts are most effective.

Beyond identifying species that lost or gained territory over the past decades, the ability to profile which species are expanding or contracting their ranges but also whether some clades show distinct shifting patterns may provide a deeper understanding of the underlying mechanisms behind observed changes and may allow better prediction of future changes (Lavergne et al., 2010). Trait-based and phylogenetic approaches offer a particularly valuable framework for this. Functional traits—morphological and physiological characteristics of plants that affect their fitness (Violle et al., 2007)—can be used to better understand species' functional strategies and their variation along environmental gradients (Garnier et al., 2015). For instance, traits provide insights into a species' tolerance for temperature extremes, humidity fluctuations or resource conservation strategies (Lavorel & Garnier, 2002). Revealing that winner species exhibit specific combinations of traits, such as those adapted to warmer conditions or frequent disturbances, can help elucidate the mechanisms behind biodiversity changes. For example, Guo et al. (2018) linked colonizing species to ruderal strategies, that is, species with a rapid completion of the life cycle and benefiting from disturbances (Grime, 1977), while Henn et al. (2024) associated winners with acquisitive trait strategies, which are species with faster growth but lower stress tolerance (Reich et al., 1997). However, the relationship between functional traits and species temporal trends may vary depending on life forms (Delalandre et al., 2023). Nevertheless, some traits seem to be key to better understand plant responses to warmer temperature such as plant height (Bjorkman et al., 2018; Maes et al., 2020; Timmermann et al., 2015) or specific leaf area (Guittar et al., 2016; Venn et al., 2011) as those traits reflect both competitive ability and resource capture and retention trade-offs (Reich, 2014). While conceptually it makes sense that functional traits should be able to predict winners and losers under climate change, empirical evidence is mixed. Some studies found support for a relationship between the trends of species and their functional traits (Kühn et al., 2021; Pinho et al., 2025; Soudzilovskaia et al., 2013), while others did not (García Criado et al., 2023). Wiens et al. (2010) suggested that traits shaping species' ecological niches are often phylogenetically conserved, which implies that responses to climate change could be too (Burns & Strauss, 2011). While bird population declines have shown strong phylogenetic signals (Davis et al., 2010; Lavergne et al., 2013), evidence for plants remains sparse. Building models that predict winner and loser species from their functional traits and phylogeny can become important tools for management to anticipate future changes.

In this paper, we address the challenge of identifying, quantifying, characterizing winning, stable and losing plant species over the last 30 years across the French Alps. To achieve this, we leveraged an extensive semi-structured plant dataset encompassing approximately 4250 species sampled over the past 30 years by expert botanists. This dataset represents about 60% of the total plant diversity in France and captures the entire plant diversity of the French Alps. To correct for temporal and spatial sampling biases, we employed the Frescalo method (Hill, 2012) to generate unbiased time series at the species level, while accounting for associated uncertainties. Using a Bayesian framework, we then quantified temporal trends and then classified species as winners, losers or stable. We expected more species to gain distribution area than to lose area (Finderup Nielsen et al., 2019; Jandt et al., 2022), given that the climate becomes overall more favourable for plants in the French Alps (i.e. warmer temperatures) and grazing pressure decreases in some areas (i.e. land abandonment). Additionally, we examined the distribution of these species across families to identify those that are disproportionately losing area and, potentially, species in the long term. Using a molecular species-level phylogeny of the European Alps, we further tested whether loser and winner species show specific phylogenetic patterns, which could jeopardize or benefit entire clades. After identifying taxonomically and phylogenetically area-gaining and losing species, we characterized the biogeographic status of these species. We expected species with high IUCN conservation status to be over-represented in the group of species losing distribution area, and invasive species to be over-represented in the group of winner species. We also tested Grime's strategies (Grime, 1977), with the expectation that ruderal species colonizing newly disturbed areas would be more likely to be winner species (Klinkovská et al., 2024). Finally, we employed a trait-based modelling approach based on machine learning to assess whether the observed species trends can be predicted based on functional traits. We hypothesized that species exhibiting rapid growth and higher tolerance to elevated temperatures (thermophilous species; De Frenne et al., 2015) would show increasing trends. Through this integrative framework, our study provides critical insights into temporal plant dynamics, offering a robust foundation for understanding and predicting biodiversity changes in mountain ecosystems.

## 2 | METHOD

### 2.1 | Data compilation

#### 2.1.1 | Study area

This study was carried out in the French Alps and its surroundings (Figure S1), a region spanning 61,000 km$^2$ and characterized by diverse environmental conditions due to the interplay of continental, oceanic and Mediterranean climate influences, coupled with steep altitudinal gradients. Elevation ranges from sea level up to 4810 m a.s.l., and mean elevation is approximately 848 m a.s.l. For the purpose of this study, we gridded the area by 2728 pixels of 5 × 5 km and used botanical and environmental data at this resolution.

#### 2.1.2 | Plant distribution data

Our research questions focused on the vascular plant species of the French Alps (Alpine convention), but we wanted to account for their wider distribution, especially towards Mediterranean ecosystems. We thus chose a two-step approach. We first selected the 4250 species well-represented in the recently compiled and cleaned vegetation databases of the National Alpine Botanical Conservatory (CBNA), which contains nearly 7,080,000 plant data points collected in the French Alps between 1992 and 2022 (http://simethis.eu/). We then combined the CBNA database with the database of the National Mediterranean Botanical Conservatory (CBNMed) covering the region between the Alps and the Mediterranean for the selected mountain species. These two databases integrate three types of data including (occurrence records, plant relevés and archival records), with the first two information sources accounting for 97% of the information. Plant occurrence data and plant relevés were collected by CBNA and CBNMed botanists across a grid composed of 5 × 5 km$^2$ cells. The sampling was designed to systematically cover as many different habitats as possible within each grid cell, ensuring a representative capture of species diversity and distribution. The 5,960,000 occurrence records entering the database contain information on the presence of species in a specific location and year (see Figure S1 for spatiotemporal distribution of data points; 4,010,000 occurrences from CBNA and 1,950,000 occurrences from CBNMed). The 3,550,000 plant community relevés were sampled in homogenous plots with smaller plots of only 10 m$^2$ in heterogeneous habitats and larger forest plots of up to 1000 m$^2$ and contain information on exhaustive species lists in a specific location and year (see Figure S1; 3,060,000 relevés from CBNA and 490,000 relevés from CBNMed). Finally, additional archival sources, including herbarium records, bibliographic sources, and manuscript notes, provide supplementary historical information. Overall, our combined dataset contains information on 4250 mountain plant species, following the standardized taxonomic nomenclature of TAXREF (2025), and 9,510,000 observations throughout the French Alps extending to the Mediterranean (see Figure S1). The dataset underwent rigorous validation through expert consultations with taxonomists and field biologists.

#### 2.1.3 | Plant characteristics

To better profile winning and losing species, we first classified them based on large-scale geographic distribution such as floristic and conservation status, followed by plant strategies such as Grime's

CSR strategies (Grime, 1977), Landolt indices (Landolt, 1977; Landolt et al., 2010), and specific functional traits. Therefore, for our 2043 focal species (which correspond to the species for which we get all trait values), we extracted the Raunkiaer's life-form classification (i.e. herb, graminoid, shrub and tree; Raunkiaer, 1934) from the TRY database (Kattge et al., 2020), the most critical IUCN regional conservation status (i.e. least concerned, near-threatened, vulnerable, endangered, critically endangered; IUCN, 2022), and floristic status (i.e. natives, archaeophytes (introduced before 1492), and neophytes (introduced after 1492)) from the simethis database (http://simethis.eu/). We also measured plant commonness as the sum of the number of sites where the species was recorded at least once. We also used functional trait measurements conducted across the French Alps, available from (Brun et al., 2022), complemented by the TRY database (Kattge et al., 2020) for a few missing data points (see Deschamps et al., 2023). We selected six traits to represent the global spectrum of plant form and function (Díaz et al., 2016): height (H), stem-specific density (SSD, only considered for shrub and tree species), leaf area (LA), specific leaf area (SLA), leaf nitrogen content per area (Nmass) and seed mass (SM). Plant height is associated with the ability to capture light resources and disperse diaspores (Díaz et al., 2016). SSD indicates a trade-off between growth potential and the risk of mortality from biomechanical or hydraulic failure (Díaz et al., 2016). LA has strong implications for leaf energy and water balance (Wright et al., 2017), while SLA reflects a trade-off between carbon gain and longevity (Wright et al., 2004). Nmass concentrations serve as indicators of plant photosynthetic capacity and resource use strategy (Wright et al., 2004). Finally, seed mass reflects a trade-off between seedling survival and colonization ability in space and time (Moles & Westoby, 2006). Importantly, these traits are not independent from each other but correlate along axes of plant ecological strategies. For example, the H–SM dimension could be seen as reflecting the r (colonization) versus K (exploitation) continuum (Salguero-Gómez, 2017), while the leaf mass per area (LMA; inverse of SLA)–Nmass dimension reflects the acquisitive–conservative continuum (Grime et al., 1997; Wright et al., 2004). The interpretation of these functions based on functional traits may vary considerably across plant life forms (i.e. trees, shrubs, herbs, graminoids), particularly given the substantial trait variability within each life form group (Wright et al., 2004). Thus, all traits were log-transformed and rescaled within each life form. Using three functional traits such as leaf area, leaf dry matter content and specific leaf area, we estimated the proportion of C, S, and R strategies (i.e. competitive, ruderal, stress-tolerant or mixed, sensu Grime, 1977) of each species, following the algorithm of Pierce et al. (2017). We ensured that the algorithm produced consistent results by comparing the CSR proportions with qualitative information on CSR from the Androsace database (https://androsace.osug.fr/home). Additionally, we included four Landolt indices (Landolt, 1977; Landolt et al., 2010). These indices classify species based on their light tolerance (light), temperature preference (temp), soil moisture (moisture) and soil nutrient preference (nutrient). Each index is scored on a five-point scale, where 1 represents low and 5 high preferences. These indices were analysed as numeric variables within our model. To analyse the distribution of winner and loser species along the phylogenetic tree of life, we used the recent molecular species-level phylogeny of the European Alps, sourced from the PhyloAlps project (http://phyloalps.org/, see Appendix S1).

## 2.2 | Statistical analyses

The aim of our statistical analyses was threefold: First, we aimed at removing spatiotemporal biases from our semi-structured plant database caused by heterogeneous sampling in space and time. Second, we used the corrected temporal trends to identify species gaining (i.e. winning trends) or losing in the distribution area over time (i.e. losing trends), while propagating uncertainties from the first step. Third, we linked the identified winning and losing trends to species' characteristics, traits, and taxonomy and phylogeny.

First, to correct for spatiotemporal biases in the plant distribution data, we applied the local frequency scaling approach of the Frescalo algorithm (Hill, 2012), which provides, as far as possible, an unbiased estimation of temporal species trends. Frescalo comprises two main steps: a first step to correct for spatial sampling biases and a second step to correct for temporal sampling biases (Hill, 2012) and has been successfully used in previous studies of vegetation change (e.g. Auffret & Svenning, 2022; Eichenberg et al., 2021; Fox et al., 2014; Montràs-Janer et al., 2024). For the correction of spatial biases, each 5 × 5 km pixel is assigned a neighbourhood defined as the 100 most ecologically similar sites selected from the 200 geographically closest sites. Ecological similarity was assessed in terms of climatic, edaphic and geologic similarities (see Appendix S2). This correction adjusts rank-frequency curves across the neighbourhood to standardize sampling intensity. To correct for temporal biases in sampling intensity, we aggregated the data into six 5-year periods spanning from 1992 to 2022. Frescalo then estimates the relative frequency of each species across the entire study area for each time period based on a chosen set of reference species. Ultimately, the approach provides an estimate of species frequency for each time period together with an estimation of the uncertainty around these estimates (see Appendix S2 for full details of the methods and parameter values).

Second, we estimated species trends and identified winning and losing species from the Frescalo time series. In order to propagate the uncertainties from the Frescalo estimates, we used Bayesian generalized linear multilevel models (*brms* R package, Bürkner, 2021). Specifically, we included estimates of species frequencies as the response and year as a continuous predictor and added the standard error of the species frequency from Frescalo as a measurement error. In a first step, species were classified into three categories based on temporal trends: winners, losers and non-significant change. Species were considered winners if their estimated slope was positive and both bounds of the 95% confidence interval were greater than zero. Conversely, species were defined as losers when the slope was negative and the entire 95% confidence interval fell below zero. Species whose 95% confidence interval overlapped zero were categorized as showing non-significant change. This latter group includes both species with genuinely flat trends and those with strong but uncertain trends due to high variability. To distinguish between these two cases, a second model was applied specifically to the species initially classified as showing non-significant change. To do so, we compared two models for each species: Y~1 (stable) and Y~Year (non-significant change; where Y corresponded to the species frequency). The models were compared using the WAIC index, and the one with the lowest AIC was selected. If the Y~year model was selected and the slope was significant, the species was classified as a winner (significant positive slope) or loser (significant negative slope); otherwise, the species was classified as showing non-significant changes. If the Y~1 model was retained, the species was classified as stable. Finally, 6% of species only had a single frequency estimate value above zero in the Frescalo series and were thus classified as data deficient. Therefore, we finally got five groups of species such as 'winners', 'losers', 'stable', 'non-significant changes' and 'data deficient'. Hereafter, we focused only on winners, losers and stable species. Non-significant change species (30% of species), while showing some of the steepest slopes, were excluded from the trait-based analyses because these slopes were either due to outlier data or idiosyncratic responses over time. Additionally, we calculated an error corresponding to the width of the confidence interval around each slope, where wider intervals indicated greater uncertainty in the trend estimate.

As a visualization of our winner, loser and stable species, their temporal trends and their spatial distribution, we provided summary atlases and a web application (https://frescalo.osug.fr/) for stakeholders. The experts verified whether the trends identified by our model aligned with their field observations and expectations. For over a 100 species randomly selected, botanical experts completed a table indicating whether the trends we observed were consistent with their knowledge. Overall, this validation confirmed that the model was reliable for most species. However, the feedback also revealed limitations of the model for certain species groups. For example, vernal species, for which sampling efforts have significantly declined in recent years, were less accurately modelled. Similarly, species under heavy grazing pressure, which experts anticipated to decline, were not always effectively captured by the model, potentially due to lag effects. This exchange with experts was maintained throughout the study and was key to better interpret results of the model.

Third, we aimed to profile the winning and losing species to see whether certain commonly measured characteristics would provide some understanding of the temporal dynamics. Due to the greater uncertainty in slope estimation for data-deficient and non-significant change species, we focused only on winners, losers and stable species with available trait information ($n = 1366$). This approach ensured that our interpretation was more representative of the observed temporal changes. We first investigated the effects of plant commonness using a linear model, and the protection (IUCN), biogeographic status and the Grime's strategies (i.e. CSR, Grime, 1977) using chi-squared tests. Then, we tested whether winning and losing species could be predicted based on species' traits and Landolt indices using random forest models with the estimated trend as the response variable (caret package, Kuhn, 2008). Random forests are well suited for this analysis because they make minimal assumptions about the shape of the relationships between species' trends and their traits and can also account for collinearity between predictor variables. As the number of species was unevenly distributed across life forms and to better disentangle the trait effects for each life form, we ran separate random forest models for each life form (tree, shrub, herb and graminoid). To assess the predictive performance of these models, we used a fivefold cross-validation. We randomly split data into five equally sized sets. A model was trained on 80% (i.e. fourfold over 5) of the data (training set) and used to predict species' trends in the remaining 20% (test set). This process was repeated five times for each partition. The predictions from the five test sets were combined to assess model performance. Performance was evaluated using both the $R^2$ metric and the Spearman correlation coefficient between predicted and hold-out observed values. The $R^2$ allows us to assess the proportion of variation in the predicted values that is explained by the observed values, while the Spearman correlation allows us to test whether the model predicts well the ranks of species temporal trends. Finally, we extracted variable importance scores and generated partial dependence plots (iml package, Molnar et al., 2018). In addition to the statistical tests of the random forest models, we also performed a principal component analysis (PCA) on all traits and Landolt indicators for all species. In this analysis, we considered all species together because we wanted to map the functional shifts both between life form and between winner and loser species of each life form. Unlike the random forest model, PCA assumes that each trait corresponds to a single multivariate normal distribution with equal variance across niches. We used R version 4.4.1 for all analysis.

## 3 | RESULTS

Of the 4250 plant species studied, about a third (1299 species) significantly increased ('winners' hereafter), and 13% (563 species) significantly decreased their distribution over the past 30 years ('losers' hereafter; Figure 1). The remaining species showed no change over time (860 species), non-significant trends (1256 species), or we did not have sufficient data for any robust conclusions (272 species). Moreover, winning trends tended to be stronger (median = 0.009, interquartile range = 0.007) than losing trends (median = −0.007, interquartile range = 0.005). All species trends are available within an online app (https://frescalo.osug.fr/).

We found no relationship between winning and losing trends and overall species' commonness (Figure 1c). Also, winning and stable species were evenly distributed across different conservation statuses ($X^2$, $p < 0.01$). Yet, somewhat unexpectedly, losing species were more frequently found among those with lower conservation status (i.e. least concern and near-threatened vs. vulnerable, endangered, critically

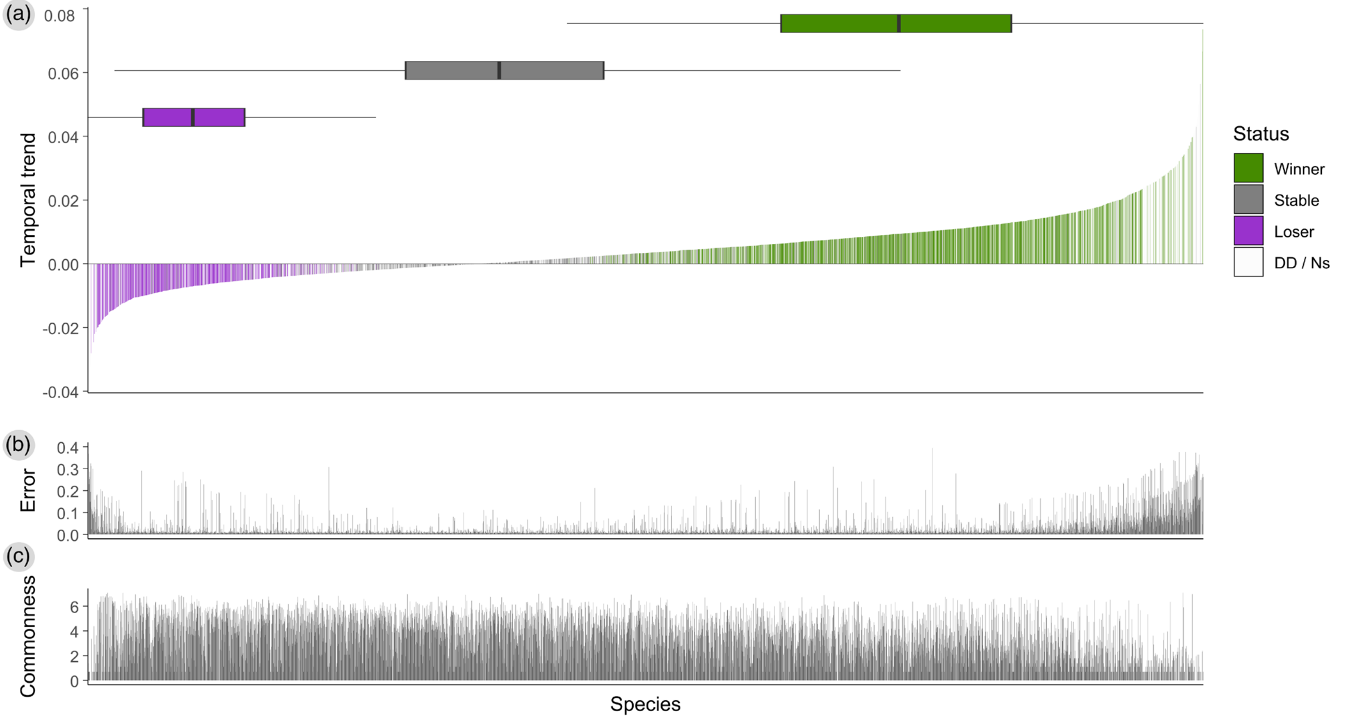


**FIGURE 1** Estimated temporal trends in species frequency over the last 30 years (1992–2022) for 4250 species (a), error in trend estimates (b) and species' commonness (c) plotted against species identities. Errors are estimates of the width of the trend confidence interval and represent a measure of uncertainty. Significant winners are shown in green, stable species in grey, and losers in purple. The boxplots illustrate the range of winning, losing and stable species. Species with missing data or no significant change are displayed in white for clarity (see Figure S2 for a figure with all species). Species change over time can be explored in detail at https://frescalo.osug.fr/.

endangered; $X^2$, $p<0.001$, Figure S3b). Furthermore, losing species were predominantly found among native species and much less among neophytes and archaeophytes (Figure S3c), but note that non-native species accounted for only 3% of all studied species (126 species).

There was no phylogenetic signal of past winning and losing trends across the entire phylogeny ($\lambda=0.07$, see Appendix S1). However, some families were dominated by winners, for example, *Orchidaceae*, *Papaveraceae* (69% and 56%, respectively), while others were dominated by losers, for example, *Caprifoliaceae* and *Saliaceae* families (61% and 52%, respectively). This was also true at the genus level, with the *Orobanche* (79%), *Trifolium* (62%), *Vicia* (59%), *Medicago* (57%) and the *Poa* (56%) genera mostly dominated by winner species, and the *Salix* and *Epilobium* genera mostly dominated by loser species (72% and 53%, respectively; Figure 2).

We then investigated whether species with winning versus losing trends differ in their functional strategies, starting with the Grime strategies. We found that winners and losers were not equally distributed among Grime's functional strategies ($X^2$, $p<0.001$). From loser over stable to winning species, the proportion of ruderal strategies (R) increased, while competitive (C) and stress-tolerant strategies (S) decreased (Figure 3). In the next step, we used plant functional strategies and Landolt preference indices to predict species temporal trends. The regression models predicted species trends moderately well. Graminoid species were the best-predicted group ($R^2=0.31$; Figure 4a), whereas shrubs had the lowest prediction accuracy ($R^2=0.14$; Figure 4a). Herbaceous and tree species fell in between, with $R^2$ values of 0.16 and 0.17, respectively (Figure 4a). While the shrub model tended to underpredict winner species (see Figure S4), the herb and graminoid models tended to overpredict loser species (see Figure S4). When focussing on the rank order of species trends, and not trend value quantifications, graminoid species were best predicted ($\rho=0.59$), followed by herbs ($\rho=0.44$), trees ($\rho=0.43$) and shrubs ($\rho=0.34$).

The most important functional traits for predicting species temporal trends differed between the four growth forms. Landolt's temperature preference was a key trait for trees, graminoids and, to a lesser degree, for herbs (Figure 4b). For these species, increasing temperature preferences were associated with positive past temporal trends. Specific leaf area was particularly important for shrubs and herbs (Figure 4b). For herbs, SLA seemed positively related to species trends although this trend is weak. Similarly, for shrubs, high SLA values were associated with more positive changes in species frequency, but the relationship was non-linear, with the most declining species having intermediate SLA values (Figure 4c). However, for both shrubs and herbs, the relative responses of SLA remained weak. Furthermore, temporal changes for trees and herbs were influenced by plant height (Figure 4c). However, while taller trees were winners, taller herbs were losers. Temporal trends of shrubs were negatively influenced by SSD and positively influenced by LA (Figure 4c). Finally, herbs with lower seed mass were stronger winners (Figure 4c).

We finally mapped and explored the positions of winner and loser species in multifunctional trait space (Figure 5; Figure S5). We did this for the four life forms together as the main purpose was to visualize the

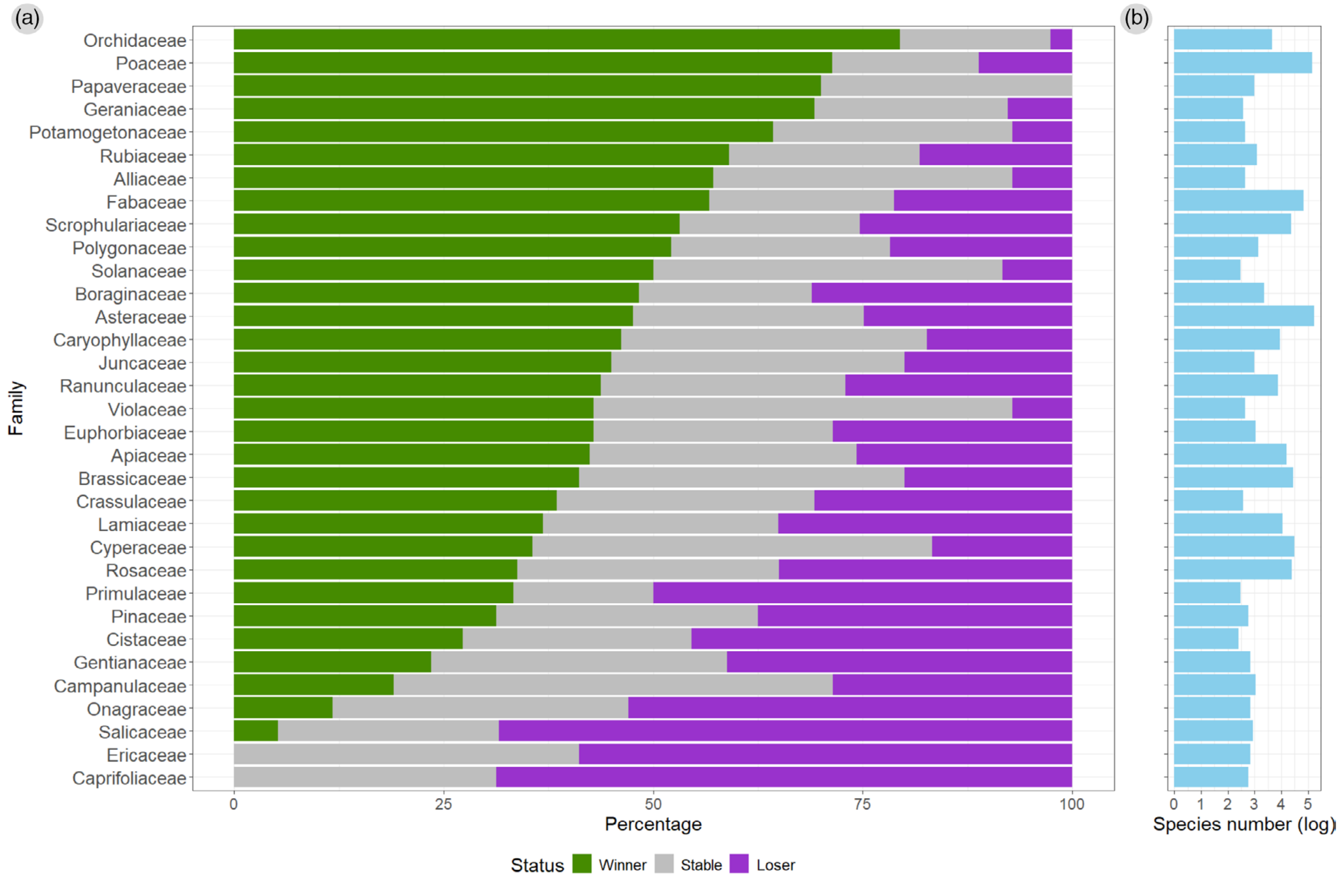


**FIGURE 2** Proportion of winner, loser and stable species within each family (a). The *y*-axis shows the family ranked by the proportion of winner, loser and stable species (*x*-axis) associated with the number of species (log, b) within each family. Winners are shown in green, stable and losing species in grey and purple respectively. For presentation purposes, we presented families that included at least 10 species. See Figure S6 for the entire dataset.

overall shifts (Figure 5; Figure S5). The first three axes of the trait space accounted for 55% of the total variation, with the first axis explaining 23% of the variation and being dominated by plant height and seed mass, the second axis explaining 20% and driven by SLA and moisture, and the third axis explaining 12% and being primarily influenced by temperature (Figure 5c). We observed that the functional space was clustered by life form, with the exception of graminoids, which covered a broader central area (Figure 5). The functional space of winning and losing trees (and partly shrubs) was well-separated along the first axis, with winners being taller (Figure 5a), while winners and losers of shrubs, graminoids and herbs were differentiated along the second axis, with winners having higher SLA (Figure S5). We also observed a clear distinction in temperature tolerance between the functional spaces of winner and loser herb species (Figure S5C), with species having higher temperature tolerance being more likely to be winners.

## 4 | DISCUSSION

The French Alps host a remarkably diverse and unique pool of plant species. Understanding how their frequencies have changed over the past three decades is crucial for assessing biodiversity dynamics. Leveraging a unique dataset and correcting for biases with statistical methods, our study found that 56% of the 4250 species showed no clear trend, including 20% with stable frequencies, 30% with idiosyncratic responses, and only 6% with insufficient data. Of the remaining species, three-quarters were winners and one-quarter were losers, 31% and 13% of the total, respectively. Importantly, even though the tendency of species to gain or lose in their frequencies over the French Alps was not simply explained by one or two key plant features, it could still be moderately well modelled by the combination of the different information we have on these species. Notably, ruderal species were more likely to be winners while species' commonness, invasion status and protection status were not linked to winning tendencies. Declining species were more likely to display Grime's competitive strategies, to be native and of low conservation concern, while commonness was not important. However, these broad classifications do not capture finer trait-based strategies. By incorporating functional traits, we identified general patterns: winning species tended to be taller, tolerate higher temperatures, exhibit more exploitative leaf strategies and display greater drought resistance. While certain plant families and genera contained clusters of winners or losers, phylogeny as a whole was not a strong predictor of temporal trends.

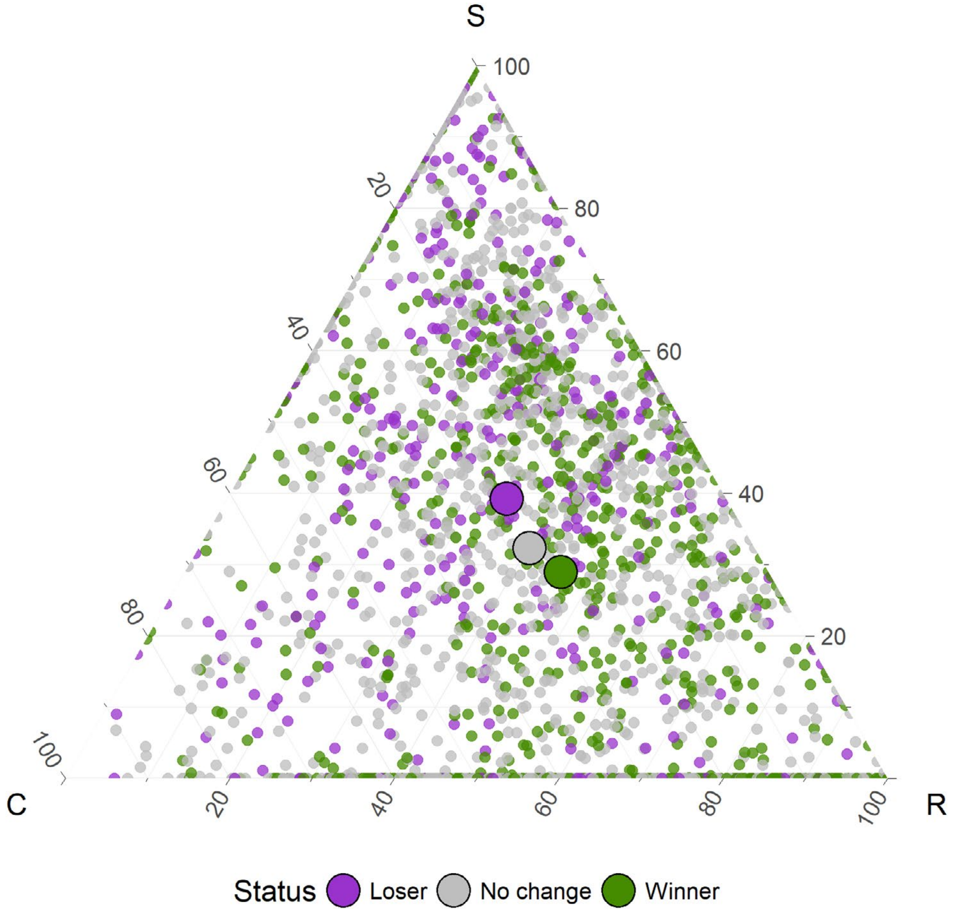
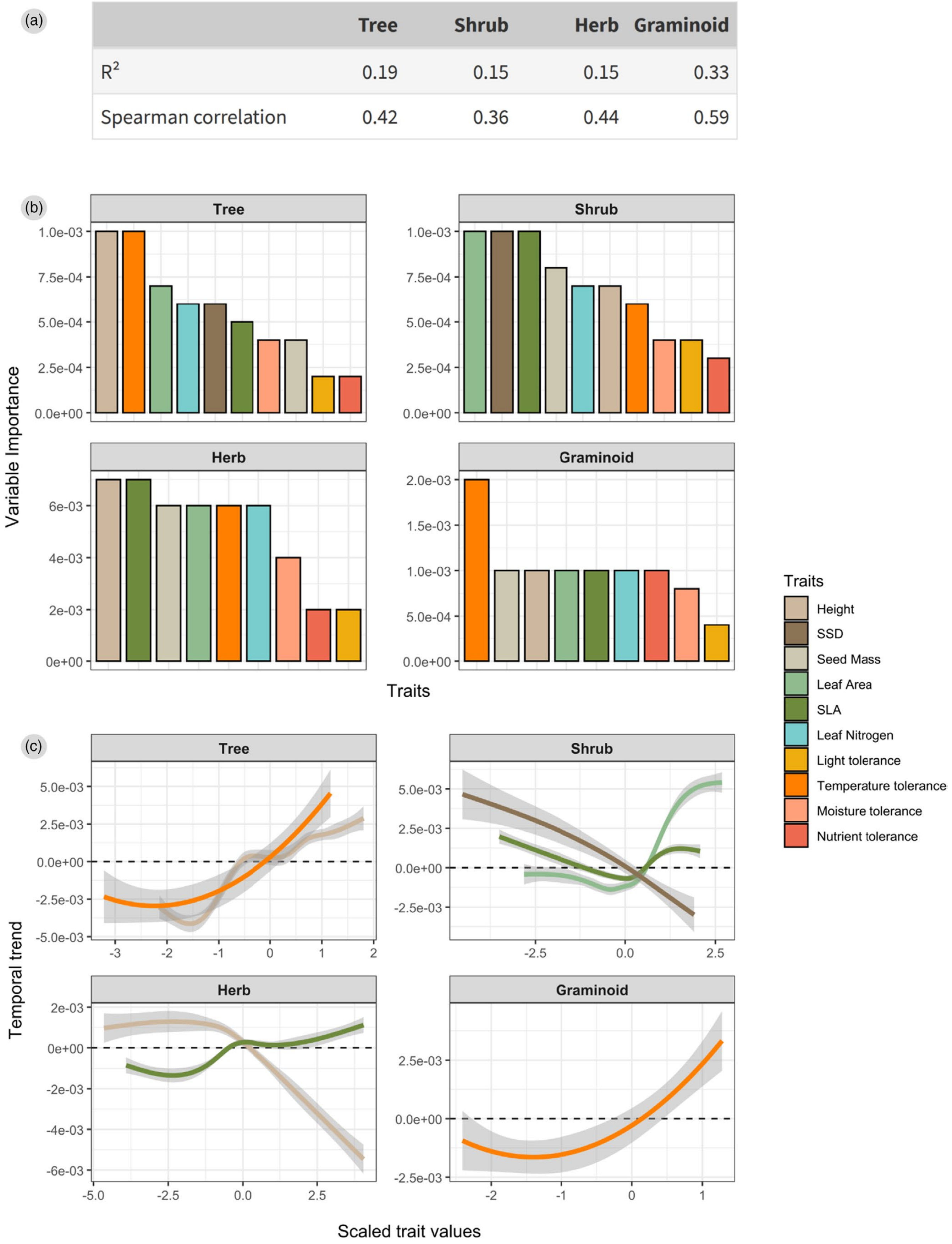


**FIGURE 3** Relative proportion (%) of C, S and R strategies per species. Little dots represent individual species and the large dots surrounded by black represent centroids of the winner (green), loser (violet) and stable (grey) species.

We identified more winners than losers in the French Alps, a pattern that contrasts with findings from Eichenberg et al. (2021), Jandt et al. (2022) and Jansen et al. (2019), who reported widespread declines in German flora, as well as Timmermann et al. (2015), who observed similar trends in Denmark. However, our results align with those of Finderup Nielsen et al. (2019) and Klinkovská et al. (2024), who found that species losses in Czech and Danish flora, respectively, were offset by significant species gains. These discrepancies highlight that plant responses to environmental changes vary considerably across Europe, with particularly pronounced shifts in mountainous regions (Thuiller et al., 2005). Mountain regions have been widely documented as areas of rapid floristic change, with many species shifting their ranges to higher elevations (Lenoir et al., 2008; Pauli et al., 2012; Steinbauer et al., 2018; Vitasse et al., 2021; Vittoz et al., 2008), especially to track isotherm shifts (Chan et al., 2024). However, plant responses to climate change are also often delayed (Alexander et al., 2018; Bertrand et al., 2011; Svenning & Sandel, 2013), with longevity and long-term indirect competitive interactions fostering extinction lags and dispersal limitations hindering leading range edge expansions (Alexander et al., 2018). Moreover, Dullinger et al. (2012) suggested that delayed Holocene recolonization still shapes alpine plant distributions. While many species in mountain ecosystems are expanding their ranges at the leading edges (i.e. winners; Alexander et al., 2018), relatively few are already being replaced (i.e. losers), apart from a few high-elevation species that lack the possibility of further upslope expansion (Alexander et al., 2015; Finderup Nielsen et al., 2019). Consequently, the observed dominance of winner species in our study may be explained by plant upslope shifts that are more rapid than population extinctions at the trailing edge.

Our study revealed that one-third of the plant species analysed exhibited non-significant changes over time. While most studies

**FIGURE 4** Prediction of trends in species frequency by functional traits and Landolt preference indices for each growth form. Random forest power (a) using the linear correlation coefficient ($R^2$) and the Spearman rank correlation test between predicted and observed values (see Figure S4) for each life form (i.e. tree, shrub, herb and graminoid). Variable importance for each trait and growth form (b). The *y*-axis represents the importance of each trait, ranked from most to least important (*x*-axis). Partial response plot for the most important variable for each growth form (c). While the *x*-axis shows the scaled trait values, the *y*-axis corresponds to the temporal trend slope (positive values correspond to winner species). Regression lines show the predictions of generalized additive models (GAMs).



|  | Tree | Shrub | Herb | Graminoid |
|---|---|---|---|---|
| $R^2$ | 0.19 | 0.15 | 0.15 | 0.33 |
| Spearman correlation | 0.42 | 0.36 | 0.44 | 0.59 |

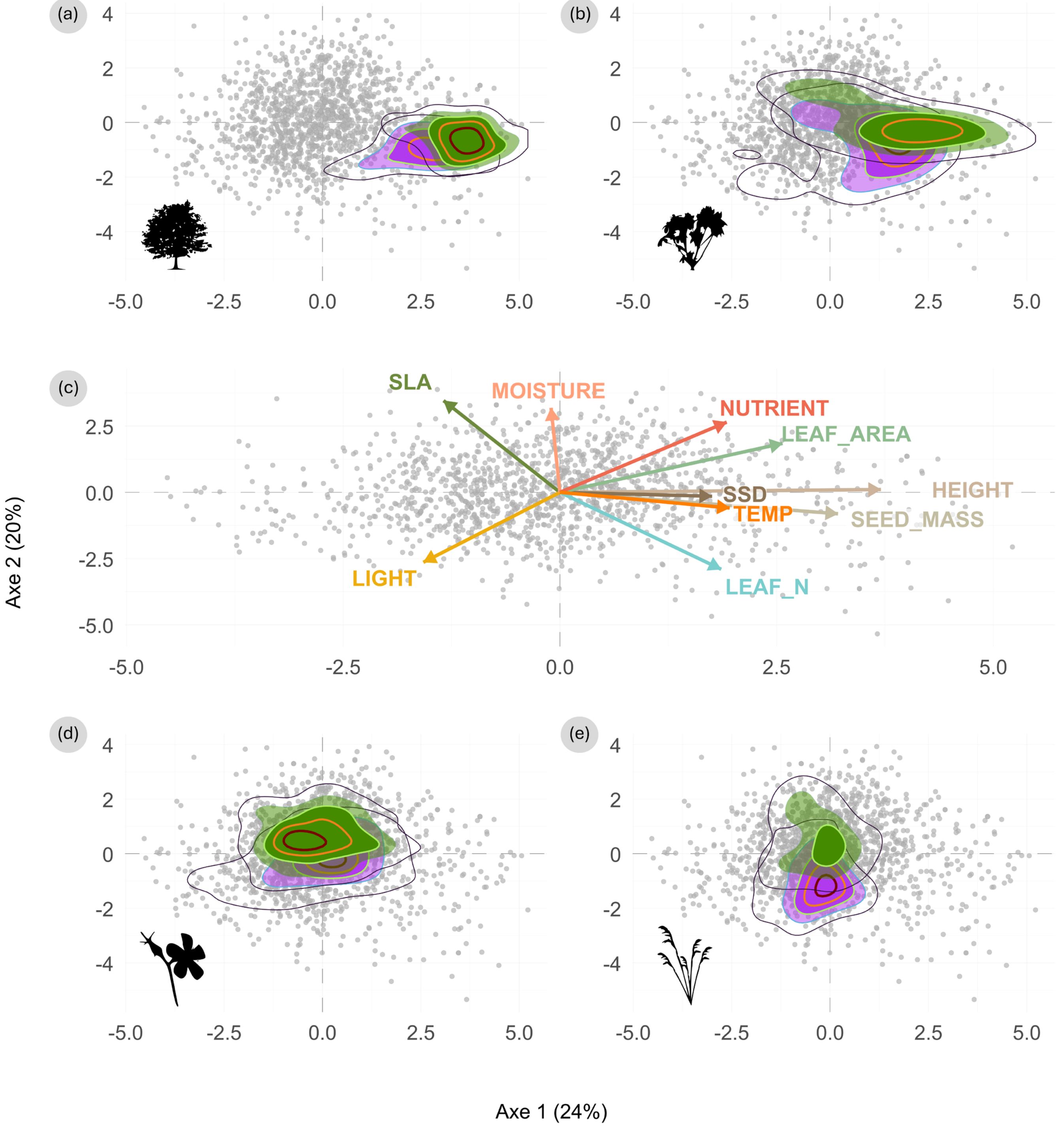


FIGURE 5 Partitioning of plant trait space across tree (a), shrub (b), herb (d) and graminoid (e) species. The first dimension (*x*-axis) captures plant height and seed mass with a total of 24% of the variation, while the second dimension (*y*-axis) captures SLA and light tolerance with a total of 20% of the variation (c). The purple contour corresponds to the loser species, while the green contour shows the winner species.

categorized species into three groups—winners, losers and stable (e.g. Finderup Nielsen et al., 2019), or only into winners and losers (e.g. Eichenberg et al., 2021; Jandt et al., 2022; Klinkovská et al., 2024; Timmermann et al., 2015), we proposed to add the new category of 'non-significant change species' in order to appropriately consider uncertainty and error propagation from the underlying long-term but biased data. Uncertainty is often under-considered, which can lead to misinterpretation of the observed trends. In our study, species classified as showing non-significant changes were often those with the most extreme trends when using classical regression slopes. Without accounting for uncertainty, these species would have been misidentified as the strongest winners or losers in our dataset. Upon closer examination, these species were typically either rare, and thus subject to higher uncertainty, or species displaying non-linear temporal trends or idiosyncratic trajectories over time. Consequently, we argue that incorporating trend uncertainty into the detection process (Dornelas et al., 2013; Johnson et al., 2024) is crucial for accurately communicating the 'real' trends of the species (see Johnson et al., 2024; Pescott et al., 2022 for methodological suggestions). This approach is fundamental to improving the reliability of biodiversity trend assessments. Moreover, our study area encompasses a vast region influenced by numerous factors, both climatic (e.g. temperature, drought) and anthropogenic (e.g. land use). However, these factors often exert highly localized and heterogeneous effects. For instance, a watershed that has been entirely abandoned from a pastoral perspective experiences a significant reduction in grazing pressure, leading to ecological dynamics that may diverge sharply from those observed in the rest of the territory. This spatial variability applies to all drivers, resulting in contrasting trajectories within the same region. Such heterogeneity inevitably increases uncertainty in ecological trends estimation at large spatial scales, making it crucial to consider this uncertainty as valuable information in itself. Despite these strong spatial variations, it is particularly encouraging to note that for approximately 65% of the species studied—whether declining, increasing and stable—trends can be determined with a high degree of confidence. This robustness of conclusions, despite territorial disparities, highlights the relevance of the approach used to analyse large-scale ecological dynamics.

Past research shows that plant responses to environmental changes can be idiosyncratic (Alexander et al., 2018; Lenoir et al., 2008), making it challenging to draw a comprehensive picture of winning and declining species. As mentioned earlier, some species exhibit non-directional changes, others remain stable over time, while some show clear positive or negative temporal trends. Essentially, the variety of species corresponds to a diversity of temporal responses. This variability underscores the need to first better profile species in order to understand their observed responses and, ultimately, to determine whether winner and loser species are over or underrepresented in some relevant groupings of plant species. In this context, we sought to characterize winning, losing and stable species based on their IUCN status and biogeographic profiles. Interestingly, our findings show that threatened species (classified as vulnerable, endangered or critically endangered) did not exhibit a clear trend of decline. This contrasts with the results of Klinkovská et al. (2024), who reported that threatened species were among those declining. In our study, we defined winner and loser species based on temporal trends over a 30-year period and across the entire French Alps, whereas IUCN status may reflect changes at more localized spatial and reduced temporal scales. For instance, a species might be considered threatened due to a sharp decline within a specific valley, which may not accurately represent its overall trend across the broader French Alps region. This discrepancy highlights that regional temporal trends and species' protection status are not necessarily comparable, a point also raised by Eichenberg et al. (2021). An alternative explanation could be that conservation measures have been effective. For example, a species once designated as highly protected might have experienced a reversal of its initial decline, leading it to no longer be classified as a loser. We also found that loser species were predominantly native, while winners were more often non-native (i.e. neophytes and archaeophytes). These results align with previous studies documenting a spread of exotic species and a decline in native species (Eichenberg et al., 2021; Finderup Nielsen et al., 2019). Furthermore, Iseli et al. (2023) reported an expansion of non-native species towards higher elevations, consistent with findings by Guo et al. (2018), Haider et al. (2010) and Pyšek et al. (2011), who observed a peak in non-native species richness from lowlands to mid-elevation. Moreover, Alexander et al. (2016) explored the factors driving the spread of non-native species along elevational gradients, highlighting their strong dispersal abilities, adaptation to disturbed areas and high phenotypic plasticity. Our findings reinforce the idea that environmental change reshapes plant communities not only through species losses but also by favouring opportunistic species with traits suited to new conditions.

Plant traits have long been used to investigate ecological plant strategies (Garnier et al., 2015; Grime, 1977; Westoby et al., 2002) and have recently been applied to better understand plant responses to global changes (Henn et al., 2024; Pacifici et al., 2017). Past research on the link of plant characteristics to their winning and losing strength gives contradictory results with some studies showing support for significant links (Kühn et al., 2021; Pinho et al., 2025; Soudzilovskaia et al., 2013) while others find no relationship (Beissinger & Riddell, 2021; García Criado et al., 2023). Here we add to this research question with an impressive dataset of over 4000 species over the French Alps. Our initial findings indicate that winner species are predominantly associated with ruderal strategies, while loser species are mainly characterized by competitive or stress-tolerant strategies. These results align partially with Klinkovská et al. (2024), who reported a decline in stress-tolerant species but observed no significant trends for ruderal species. In contrast, Timmermann et al. (2015) identified winner species as being associated with competitive strategies, while ruderal and stress-tolerant strategies were linked to losers. Ruderal species, which thrive in conditions of low stress and high disturbance, are often annuals (Grime, 1977) and are particularly common among alien species, unlike stress-tolerant species (Alexander et al., 2016; Dainese et al., 2017; Pyšek et al., 2011). Their strong colonization and naturalization abilities (Guo et al., 2018) may explain why we found that winner species are predominantly ruderal. Conversely, species with competitive or stress-tolerant strategies tend to have low colonization capabilities (Guo et al., 2018), which may explain why these species are associated with losers, as their capabilities to colonize new areas is very low, and thus, cannot escape their current threatened habitat, conversely to winner species. Furthermore, (Grime, 1977) suggested a direct link between CSR strategies and plant functional traits. As our findings suggest that CSR strategies help differentiate between winning and losing species, we aimed to investigate in more detail the underlying traits linked with the temporal species changes.

While functional traits have been extensively used to study community responses to environmental changes (Funk et al., 2017; Lavorel & Garnier, 2002), Green et al. (2022) noted that relatively few studies focus on predicting the ecological effects of global change using traits (but see García Criado et al., 2023). Indeed, LES (Leaf Economics Spectrum) traits have proven crucial in trait-based approaches for capturing ecological processes (Funk et al., 2017) and plant responses to global warming (Kühn et al., 2021). In our models, we found that functional traits and Landolt indicators explained one-fifth of the overall variation in species past distributional gains and losses. These results, consistent with our findings on CSR strategies, confirm that traits significantly account for the variation associated with species' temporal trends. Specifically, we observed a clear pattern for functional traits and Landolt indices, that is, species with acquisitive functional trait strategies were predominantly winners across different life forms. These findings align with Henn et al. (2024), who reported that alpine plants showing positive distributional trends were primarily associated with acquisitive strategies. However, García Criado et al. (2023) found that tundra shrub winners and losers were poorly predicted by functional traits, although species with greater plasticity in seed mass and specific leaf area exhibited larger projected range shifts.

Among LES traits, plant height was most important for trees and herbs, specific leaf area for shrubs and herbs, leaf area and stem-specific density for shrubs and seed mass for herbs. These findings highlight the role of both the colonization/exploitation and acquisitive/conservative continua (Díaz et al., 2016; Wright et al., 2004) in plant responses to temporal changes. Beyond LES traits, temperature tolerance was key for trees and graminoids, while other Landolt indices were less significant. This suggests that, alongside acquisitive strategies, winner species also exhibit higher temperature tolerance. Empirical studies confirm that warming and increased light drive plant community shifts across temporal and spatial scales (Borderieux et al., 2024; Bowler et al., 2017; De Frenne et al., 2015; Govaert et al., 2021; Griffin-Nolan et al., 2019; Martin et al., 2019; Zhu et al., 2024), often leading to biodiversity loss (Hautier et al., 2018) and functional trait shifts such as increased plant height (Bjorkman et al., 2018; Blondeel et al., 2020; Maes et al., 2020). Our results support the thermophilization hypothesis (Borderieux et al., 2024), linking warming to more acquisitive strategies (De Frenne et al., 2015). Winner species among trees were taller, consistent with colonization strategies benefiting from warming and increased light (Díaz et al., 2016; Westoby et al., 2002). Shrub winners were associated with higher LA and lower SSD, reinforcing their expansion in alpine ecosystems (Choler et al., 2021; Myers-Smith et al., 2011). Herb winners exhibited higher SLA and lower SM, favouring acquisitive strategies and enhanced dispersal ability (Leishman et al., 1995; Römermann et al., 2008). Meanwhile, graminoid winners were primarily linked to temperature tolerance, aligning with findings that grassland communities shift more rapidly towards species adapted to warmer, drier conditions (Zhu et al., 2024).

Community trait values have closely evolved with climate in recent decades (Hudson et al., 2011), with plant height increasing in response to warming (Bjorkman et al., 2018; Elmendorf et al., 2012; Guittar et al., 2016). Capturing these shifts requires annual trait measurements; however, studies based on species-specific traits may blur the true patterns (Hollister et al., 2005), as these studies do not explicitly consider the interspecific plasticity. Despite this, our study, which encompasses a broad range of species, allowed us to identify overarching trends. An additional consideration, highlighted by (Körner, 2003), is the high variability of microclimates within a species' distribution. This has important implications for plant strategies, as species may not necessarily need to shift their range or trait values if they can find microclimatic refugia within their original range. This hypothesis suggests that minor abiotic variations may not directly force species changes but that small-scale shifts to nearby refugia may be sufficient. Interestingly, our large-scale study revealed that both species distributions (i.e. coverage) and trait values shift in response to abiotic changes. While this does not negate the role of microclimates, it suggests that broader-scale processes may be driving these changes. For instance, minor abiotic variations may initially cause only small shifts in species distributions. However, these shifts could intensify competition, ultimately favouring species that are better adapted—often those with greater thermophilic abilities.

We also tested whether winning and losing strength of species was linked to their phylogenetic relatedness but found no support for this hypothesis at the level of the entire phylogenetic tree. In the literature, bird population declines have shown strong phylogenetic signals (Davis et al., 2010; Lavergne et al., 2013), while evidence for plants is less conclusive. Apart from the phylogenetic signal in flowering time tracking (Davis et al., 2010; Pau et al., 2011), no studies have highlighted a clear phylogenetic signal in plant species' response to climate change. Nonetheless, we found some signal in certain families and genera. For instance, the *Orchidaceae* family and the *Orobanche* genus were predominantly characterized by winning species, particularly thermophilic species such as *Orobanche lutea*, *Orobanche alba*, *Orobanche alsatica* and *Orobanche teucrii*.

Finally, given the semi-structured nature of our data, we adopted a specific approach to rigorously integrate uncertainty throughout our analysis. Continuous feedback from botanists ensured that empirical impressions were statistically transcribed as accurately as possible. To address biases, we applied multiple frameworks—including data debiasing, trend analysis and statistical modelling—while explicitly acknowledging uncertainty by introducing additional species categories beyond simple 'winners' and 'losers'. However, some biases remain. For instance, *Larix decidua Mill., 1768* appears to be expanding in the Southern Alps (Choler et al., 2021), yet our dataset includes human-planted stands in the Northern Alps, where conditions are less favourable. This leads to a greater observed decline in the Northern Alps than the increase in the South, incorrectly classifying the species as a 'loser'. Similarly, for the *Orchidaceae* family, the number of records doubled in the last 2 years of our dataset. Since this abrupt increase is concentrated in a single period, it is not fully accounted for by our debiasing method, resulting in most species in this family being classified as 'winners'. Aware of these limitations, we employed a Bayesian approach and a cautious classification strategy to place significant weight on uncertainty. While this may have led to an overestimation of species with inconclusive trends, it ensures a more transparent and reliable interpretation of biodiversity changes.

In conclusion, our study reveals that non-responding species are the most prevalent, followed by winners and some losers. However, alongside evidence of the uphill movement of many mountain plant species, our findings suggest that plants in these ecosystems lag behind their shifting niches. Range shifts appear to be slow, with potentially trailing edges retreating more gradually than leading edges advance, contributing to a concerning temporal extinction lag. Notably, despite the diverse and sometimes opposing global change drivers across different regions of the French Alps, we identified shared characteristics and trait strategies among both winning and losing species. Overall, we argued that accurately conveying species' temporal changes remains complex, and there are numerous biases that need to be effectively communicated. However, beyond species characterization and description, predicting responses through traits and phylogeny may significantly enhance our understanding of the ongoing changes. Lastly, our study provides a digital tool for stakeholders, enabling them to visualize spatial and temporal trends for each species, so that they can better understand current changes and act accordingly.

## AUTHOR CONTRIBUTIONS

**Romain Goury:** Conceptualisation, formal analysis, methodology, writing—original draft, visualisation. **Wilfried Thuiller:** conceptualisation, funding acquisition, methodology, project administration, supervision, writing—review and editing. **Sylvain Abdulhak:** Data curation, investigation, methodology. **Gilles Pache:** Data curation, investigation, methodology. **Jérémie Van Es:** Data curation, investigation, methodology. **Diana E. Bowler:** Supervision, methodology, writing—review and editing. **Julien Renaud:** Software, methodology, visualisation. **Cyrille Violle:** Methodology, validation, writing—review and editing. **Tamara Münkemüller:** Conceptualisation, funding acquisition, methodology, project administration, supervision, writing—review and editing.

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## CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.70159.

## DATA AVAILABILITY STATEMENT

The data used to produce the main results and figures can be found on Zenodo: https://zenodo.org/records/15705680 (Goury et al., 2025).

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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.** Phylogenetical analysis of species trends.

**Figure S1.** Plant sampling design. Spatial coverage of the number of occurrences over the entire study area (a). Temporal number of occurrences (b) and species (c) observed each year.

**Figure S2.** Temporal change of species over the last 30 years. The *y*-axis shows the slope of the species from the Bayesian model, while the *x*-axis corresponds to the species. Species have been removed for clarity. Winners are shown in green, while stable and losing species are shown in grey and purple respectively. Species with missing data and no significant change are shown in red and yellow respectively. For details of species change over time, see https://frescalo.osug.fr/.

**Figure S3.** Characterisation of winners and losers. Temporal trend of species as a function of their commonness (i.e., number of pixels where a species has at least one occurrence), (a). Each pixel corresponds to one species. The proportion of species according to their (b) regional Red List category and their (c) biogeographic status. Winners are shown in green, stable and declining species in grey and purple respectively. Species with missing data and no significant change are shown in red and yellow respectively.

**Figure S4.** Prediction of temporal trend (slope) using traits for species and each life form. The *x*-axis shows the observed values, while the *y*-axis shows the predicted values. Each point corresponds to a species, and winners are shown in green, while stable and losing species are shown in grey and purple respectively. The red line corresponds to the 1:1 line, which represents well predicted values. The top-left panel corresponds to tree species, the top-right represents shrubs, while the bottom left and right panels represent herb and graminoid species.

**Figure S5.** Partitioning of plant trait space across tree (a), shrub (b), herb (d) and graminoid (e) species. The first dimension (*x*-axis) captures plant height and seed mass with a total of 24% of the variation, while the second dimension (*y*-axis) captures temperature tolerance with a total of 13% of the variation (c). The purple contour corresponds to the loser species, while the green contour shows the winner species.

**Figure S6.** Proportion of winner, loser and stable species within each family (a). The *y*-axis shows the family ranked by the proportion of winner, loser and stable species (*x*-axis) associated with the number of species (log, b) within each family. Winners are shown in green, stable and losing species in grey and purple respectively.

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