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RESEARCH ARTICLE

Widespread Shrubification on European Mountain Summits

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ABSTRACT

Shrubs are expanding across the cold ecosystems of our planet with potentially profound consequences for their biodiversity and functioning. However, evidence is still strongly biased towards the Arctic tundra, while a large-scale assessment of shrub expansion in alpine areas above the elevational treeline is missing so far. Here we quantified shrub cover changes over the past two decades in 576 permanent plots of 1 m^2 spread across the alpine vegetation belt of Europe's major mountain chains. Total shrub cover clearly increased in the plots with an average rate of about 2.6% per m^2 per decade (95% CI = 1.9%–3.4%), and this expansion was more pronounced for evergreen (2.0% per m^2 per decade, CI = 1.3%–2.7%) than for deciduous species (1.7% per m^2 per decade, CI = 0.9%–2.4%). The magnitude of individual species' cover shifts was positively associated with their plant height, but negatively with their leaf nitrogen content and light affinity. In sum, we show that shrub expansion is a widespread phenomenon also in the alpine zone of European mountains, with potentially far-reaching consequences for alpine plant dynamics, soil microclimates, snow patterns, carbon cycling, food chains and livelihoods.

1 | Introduction

Arctic and alpine environments are experiencing profound changes in biodiversity in response to contemporary climate change (Mekonnen et al. 2021; Pepin et al. 2022; Rantanen et al. 2022; González-Herrero et al. 2024; García Criado, Myers-Smith, et al. 2025), including the widespread expansion of shrubs across these cold and sparsely vegetated ecosystems. This phenomenon of shrub encroachment or *shrubification* is multifaceted, with shrub species experiencing local increases in height and cover (Forbes et al. 2010; Bjorkman et al. 2018a), locally filling in gaps between existing patches or expanding into new areas (Sturm et al. 2001; Chapin III et al. 2005; Myers-Smith et al. 2011). Paleo-ecological evidence indeed reveals shrub encroachment of the Arctic tundra during the Last Interglacial and Holocene post-glacial period, indicating that rising temperatures under climate change are likely the key driving factor of recent shrub expansion at higher latitudes (Birks 2008; Hallinger et al. 2010; Formica et al. 2014; Carlson et al. 2017; Crump et al. 2021). This conjecture is corroborated by an array of field experiments reporting a marked increase in shrub performance in artificially warmed plots across tundra ecosystems (Walker et al. 2006; Elmendorf et al. 2012; DeMarco, Mack, Bret-Harte, Burton, and Shaver 2014; Bjorkman et al. 2020). In addition to climatic changes, however, the progressive abandonment of century-old livestock grazing practices during the past

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few decades may have reinforced the encroachment by woody plants into sparsely vegetated Arctic environments (Améztegui et al. 2010).

In high-elevation areas, shrub encroachment as a result of warming temperatures and/or the abandonment of farming grounds and lifestock pastures has also been documented, for example, across the European Alps (Dullinger et al. 2003; Cannone et al. 2007, 2022; Malfasi and Cannone 2020), the Mediterranean Apennines (Palombo et al. 2013; Calabrese et al. 2018; De Toma et al. 2025) and the Scandes (e.g., Kullman 2004, 2010; Vowles et al. 2017; Vanneste et al. 2017) and the Scottish Highlands (e.g., Britton et al. 2009). The European Alps, in particular, have experienced intense greening above the tree line since the 1980s (Rumpf et al. 2022), a trend visible from space and which seems to be in tandem with increased shrub productivity and cover (Choler et al. 2021). Yet, considerable disparities exist among studies, species and regions, with shrub encroachment in the European Alps being chiefly driven by late-successional species (e.g., of the genera *Empetrum*, *Juniperus*, *Kalmia*, *Rhododendron*, *Vaccinium*) and in the Apennines mainly by*Juniperus communis* and *Pinus mugo*, while in the Scandes pioneer deciduous shrubs of the genera *Alnus*, *Betula* and *Salix* were found to expand. Besides deciduous shrubs, some studies (e.g., Klanderud and Birks 2003; Vuorinen et al. 2017; Maliniemi et al. 2018) have also reported vast increases of prostate evergreen shrub species such as *Empetrum nigrum* across high-latitude alpine sites. Most evidence is, however, still coming from smaller study areas calling for a more systematic, large-scale assessment of shrub expansion in alpine environments.

The potential ecological ramifications of shrub expansion above and beyond the treeline are manifold, but marked differences are found between tall deciduous and evergreen dwarf shrubs (Vowles and Björk 2019). The taller and denser deciduous shrub canopies reduce surface albedo, accelerating spring snowmelt (Sturm et al. 2005), but can also trap more snow during winter, which acts as insulation and locally increases soil temperatures (Myers-Smith and Hik 2013). The latter can, in turn, accelerate winter and summer nitrogen mineralisation rates, litter decomposition, and winter respiration (DeMarco et al. 2011, Vowles and Björk 2019), while the deciduous plant litter typically decomposes more easily, hence also speeding up carbon turnover rates (DeMarco, Mack, and Bret-Harte 2014). Furthermore, the taller canopies of deciduous shrubs can outcompete the smaller, light-demanding alpine specialist plants or other groundcover taxa such as lichens and bryophytes by shading (Vanneste et al. 2017), negatively impacting local species richness (Walker et al. 2006; Pajunen et al. 2011; García Criado, Myers-Smith, et al. 2025). Evergreen dwarf shrubs, on the other hand, tend to have more recalcitrant leaf litter, which decomposes slowly, thereby decelerating nutrient cycling and promoting the long-term build-up of soil carbon stocks (Sørensen et al. 2018). In order to understand the complex feedbacks related to shrub encroachment, as well as the consequences for alpine biodiversity and ecosystem functioning, we need a comprehensive overview of both deciduous and evergreen shrub cover changes using long-term observational data across large spatial scales.

Plant functional traits provide mechanistic insights into the relationships between species and their environment (Violle et al. 2007; Bruelheide et al. 2018). In particular, traits related to growth, resource acquisition and dispersal such as plant height at maturity, specific leaf area (SLA), seed mass and leaf stoichiometry (cf. Westoby 1998) have been widely used to study plant responses to changing climatic conditions (Díaz et al. 2022), as well as the variation in life-history strategies among species (Adler et al. 2013; Salguero-Gómez et al. 2016). These traits are generally also easy to measure and abundantly available in online databases such as TRY (Kattge et al. 2020) and the Tundra Trait Team (TTT) database (Bjorkman et al. 2018b). Since processes such as competition, survival, reproduction and dispersal determine a plant's performance and thus also the abundance it can attain in a certain environment, it is expected that temporal cover changes could relate to species' traits connected with these processes (Myers-Smith et al. 2019; Visakorpi et al. 2023). For instance, greater stature, SLA and leaf nitrogen (N) concentrations of plant species are typically associated with higher competitive ability and resource acquisition, while lighter seeds promote dispersal capacity and seed production (Hamilton et al. 2005; Bruelheide et al. 2018). Hence, shrub species with greater height, SLA and leaf N but lighter seeds could potentially have undergone greater cover increases under a warming climate (but see García Criado et al. 2023). Besides average trait values, trait variation within species (i.e., intraspecific trait variation; ITV) strongly matters, with greater ITV implying higher genetic differentiation and phenotypic plasticity and thus more opportunities for adaptation to changing environmental conditions (Albert et al. 2011; Jonsdottir et al. 2023). However, functional trait approaches have not yet been used to explain alpine shrub species' cover changes at a continental extent.

In addition to functional traits, ecological indicators reflecting plant niche requirements can help to explain species-specific responses to a changing environment (Diekmann 2003). These indicators have been developed to describe a species' niche optimum or niche width along gradients of major environmental conditions such as soil moisture, pH, and nitrogen as well as light availability and thermal regime, and are thoroughly supported by empirical measurements (Ellenberg et al. 1974; Dengler et al. 2023). These environmental conditions are subject to change under a warming climate in alpine systems, including changing soil temperature regimes (Marta et al. 2023), alterations in edaphic conditions owing to eutrophication or acidification (Lieb et al. 2011), transformation of snow patterns (Dedieu et al. 2014; Blau et al. 2024), and shifting hydrological and nutrient cycling rates (Pepin et al. 2022). As a result, species with, for instance, a preference for higher temperatures may have shifted their cover more than species adapted to colder temperatures (Gottfried et al. 2012). The explanatory power of ecological indicators for shrub species' cover changes under a changing climate has, however, not been evaluated so far.

Here we quantified shrub cover changes, both at plot and species level, over the past two decades in 576 permanent plots spread across the alpine zone of Europe's major mountain chains. These plots are part of GLORIA (Global Observational Research Initiative in Alpine Environments; https://gloria.ac.at), which is the largest monitoring network of mountaintop floras worldwide. All plots were surveyed at least twice between 2001 and 2022. Species-specific trait values related to plant structure and resource economics as well as ecological indicators for major plant niche dimensions were compiled and related to the plot-level abundance shifts. Besides average trait values and niche optima, we also included ITV and niche widths in our analyses. Specifically, we addressed the following questions:

1. Has shrub cover, both deciduous and evergreen, increased on European mountaintops over the past two decades?
2. Is this increase in cover over time uniform across shrub species?
3. Can plant traits or niche optima explain the species-level differences in cover changes over time?
4. Does higher trait variation or niche width of a species imply a higher increase in its cover over time?

2 | Methods

2.1 | Shrub Cover Data

Data on percentage cover of individual shrub species were gathered from a broad set of permanent plots across Europe's major mountain chains. These plots are part of the GLORIA network, a global and long-term monitoring program devoted to studying the impact of climate change on our planet's alpine flora. We used a subset of the European GLORIA dataset including the 18 mountain sites distributed across the Boreal, Temperate and Mediterranean biomes with resurveys spanning at least 20 years (Figure 1a). Each mountain site consists of four summits spread across an elevational gradient from subalpine grasslands near the treeline up to the uppermost vegetation zone available. A standardized setup of permanent plots is used on the mountain summits, following the protocol of Pauli et al. (2015). Each summit contains 16 plots of 1 m^2, arranged in four quadrat clusters of 3 m × 3 m, of which the outer quadrats were surveyed. The quadrat clusters are positioned in the major cardinal directions (North, East, South, West) at the 5-m contour line below the highest summit point (Figure 1b). Here, we focused on the two lowest summits in each site only, given that the ecosystems near the treeline are most strongly affected by shrub cover dynamics. This resulted in a dataset of 36 mountain summits with 576 permanent plots in total (see Table S1 for a complete list of summits).

Species-level data on the occurrence and abundance (i.e., visual estimation of plant cover relative to the plot area) of all vascular plants were gathered from these plots at least twice over the past two decades (average sampling interval between baseline survey and last resurvey = 20.5 ± 0.9 years). Our analysis here focused exclusively on shrub species. In total, 66 different shrub species were distinguished based on the classification by Plants of the World Online (POWO; https://powo.science.kew.org, including both categories 'shrub' and 'subshrub'), which were subsequently subdivided into deciduous (22 species) and evergreen shrubs (44 species; see Table S2 for a complete shrub species list). The total shrub cover, as well as the deciduous and evergreen shrub cover, was calculated per plot as the sum of covers of all individual species within the respective groups. We excluded all shrub species with a total number of occurrences lower than 29 across the full dataset (i.e., less than 5% of the total plot count) to avoid biases in the species cover shift calculations caused by rare species, hence only retaining 31 shrub species of which 8 are deciduous and 23 evergreen (Table S2).

For each group (all shrubs combined, deciduous shrubs and evergreen shrubs) and for each species separately, the cover shift over time was quantified as the plot-level log-response ratio of percentage cover values in the baseline survey and the last resurvey (Equation 1).

$$lnRR = \frac{ln\frac{C_{last\ resurvey}}{C_{baseline}}}{\Delta t} \qquad (1)$$

With $lnRR$ representing the log-response ratio, $C_{last\ resurvey}$ the plot-level percentage shrub cover in the final resurvey, $C_{baseline}$ the plot-level percentage shrub cover in the baseline survey, and Δt the time difference (in years) between the baseline and final resurvey. Notably, species absent from a plot in both surveys (i.e., species × plot combinations with zero abundances at both timepoints) were removed. Colonisations (i.e., species with zero abundance in a plot at the baseline survey and X% abundance with $X > 0$% in the last resurvey) were handled as a full cover increase (+X%). For computational reasons, 0.001% cover was then added to the nominator. Extinctions (i.e., species present in a plot with Y% abundance at the baseline survey but absent at the last resurvey) were treated similarly.

2.2 | Trait Data

Species-specific trait values were compiled by combining records from the TRY 6.0 database (Kattge et al. 2020) with the Tundra Trait Team database (TTT; Bjorkman et al. 2018a, 2018b). Data comprised only publicly available trait records. We focused on four fundamental functional traits associated with different key aspects of plant ecology: plant height at maturity, specific leaf area (SLA; leaf area per dry mass), seed mass, and leaf nitrogen (N) content per unit dry mass. Plant height is strongly associated with competitive ability, with taller plants shading out shorter competitors (Díaz et al. 2022). SLA reflects the trade-off between carbon investment in the leaf structure and light capture for photosynthesis, with high-SLA plants typically obtaining their nutrients more easily (Wright et al. 2004). Seed mass is linked to dispersal and colonisation capacity, with smaller seeds generally dispersing over longer distances but larger seeds entailing a higher germination rate and seedling survival (Westoby and Wright 2006). Leaf N content is a good indicator for plant growth rates and nutritional status, with greater leaf N contents typically indicating faster plant growth rates (Niklas 2006). At larger scales, this trait is even related to ecosystem nutrient cycling and ecosystem stability (Xu et al. 2020).

Only records reported as single measurements or individual means in the respective online databases were retained. Likewise, only control and ambient values were used, whereas experimental treatments or herbarium specimens were not considered given that our interest was in trait records from unmanipulated wild specimens. Outliers were removed following the rule that values greater than three standard deviations from a

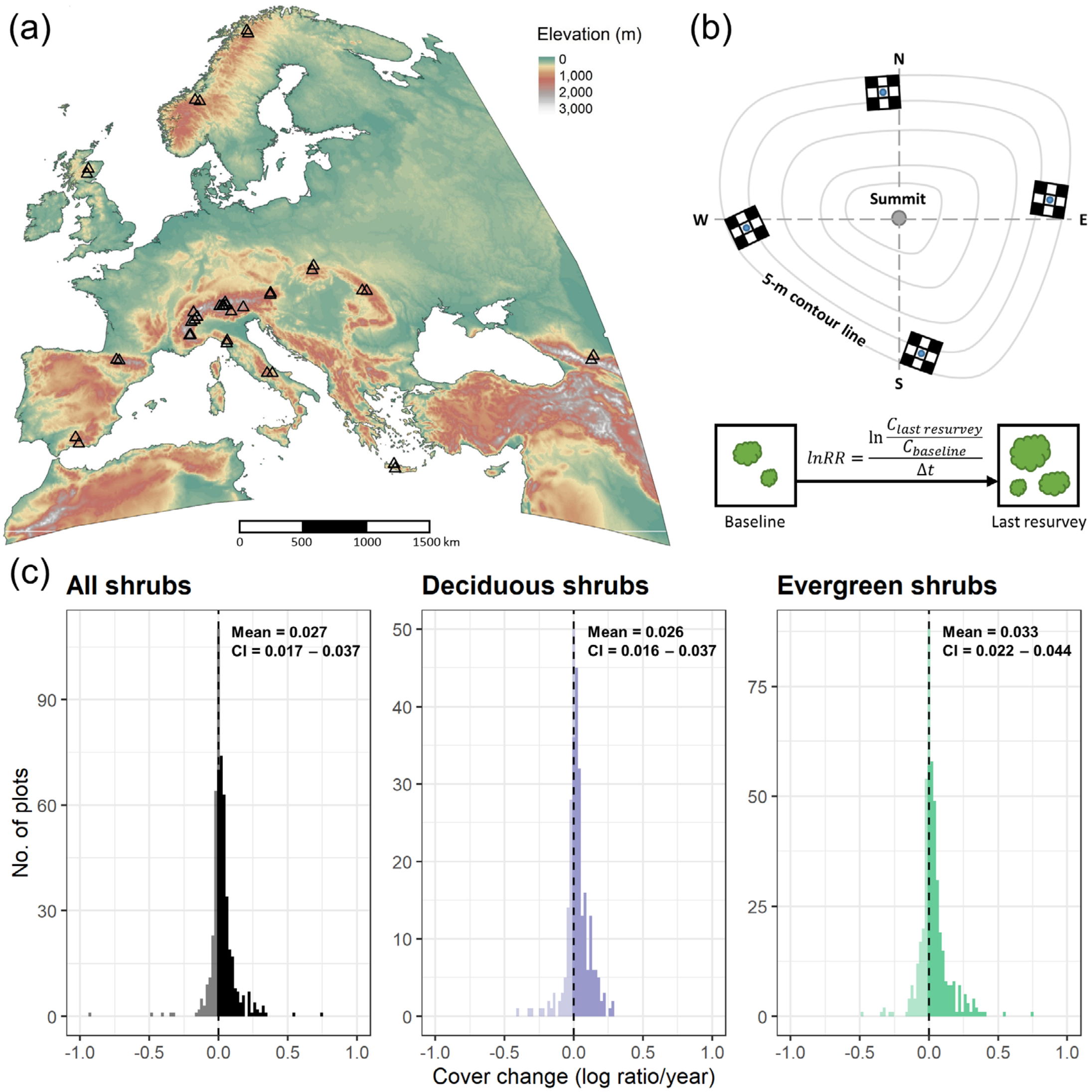

FIGURE 1 | (a) Map of the 18 GLORIA-Europe sites spread across Europe's major mountain ranges. Each site consists of four summits, of which only the ones in the alpine vegetation belt were selected (36 mountain summits with 576 1-m^2 permanent plots in total). (b) Setup of 1-m^2 plots arranged in four quadrat clusters positioned at the 5-m contour line below the summit in every cardinal direction. Only the outer quadrats (black squares) were surveyed at regular time intervals (median interval = 7 years) between 2001 and 2022. For each plot and survey, the total, deciduous and evergreen shrub cover was calculated by summing the percentage covers of individual shrub species. The abundance shift over time was then quantified as the log-response ratio (lnRR) between the cover in the baseline survey and final resurvey. (c) Distribution of cover shifts over time across plots for all shrubs combined, deciduous shrubs and evergreen shrubs. Darker and shaded bars indicate plots with positive (i.e., cover increase) and negative cover shifts over time (i.e., cover decrease), respectively. Mean cover shifts and 95% confidence intervals (CI) are indicated in the top right corner of each panel.

species' mean should be omitted (cf. García Criado et al. 2023). In total, 15,359 trait records were retained with an average of 549 records per species. Trait values were available for 82%, 84%, 78% and 72% of species for plant height, SLA, seed mass and leaf N content, respectively. For each of these species, we then calculated the mean trait values, which were assumed to represent mature and healthy plants grown under natural conditions within the species distribution range (see Díaz et al. 2022). Deciduous shrub species were, on average taller, had greater SLA, lower seed mass and higher leaf N content than evergreens (Figure S1). In addition to the mean trait values, intraspecific trait variation (ITV) was computed as the coefficient of variation (CV, that is, the ratio between the standard deviation and the mean) of all trait values per species (see Table S3). We specifically opted for the CV to represent ITV owing to its independence from the mean trait values and because it puts the ITV of all traits on the same scale making cross-trait comparison possible.

2.3 | Niche Optimum and Width

Besides structural and resource economics traits, plant niche requirements can help to explain the variation in cover shifts among species. To this end, ecological indicators were directly extracted from the Ecological Indicator Values for Europe (EIVE) 1.0

database (in supplementary 8 from Dengler et al. 2023) for the five main plant niche dimensions: soil moisture (M), soil nutrients (N), soil reaction (R), light (L) and temperature (T). For each species and environmental gradient, we extracted both the niche optimum and niche width value (i.e., 5 gradients ×2 values = 10 ecological indicators per species). Niche optima are quantified as the centre (i.e., mean) of a species' realized niche along the respective environmental gradients, while niche widths describe the amplitude and variability in niches within a species across its distribution range (see Dengler et al. 2023 for details on the workflow and calculation procedure). The empirical indicators for niche optima and niche widths are based on a broad series of regional datasets across Europe, which were rescaled into one value and vary on a standardized ordinal scale between 0 and 10, with 0 and 10 representing the lowest and highest possible value of the respective environmental variable across these European datasets, respectively (see Table S4). To illustrate, species with a low niche optimum for light tend to prefer shadier conditions, while species with high values typically grow in open, light-rich conditions. Similarly, low and high niche width values for light are applicable to species that tolerate a narrow and broad range of light regimes, respectively.

2.4 | Statistical Analyses

First, linear mixed-effect models (LMMs) were used to test whether the mean cover shift for all shrub species combined, deciduous shrubs and evergreen shrubs differed significantly from zero. These models included a fixed intercept as well as a random intercept term of aspect nested within summit and summit nested within mountain site to account for the hierarchical structure of the dataset and potential spatial autocorrelation effects between shrub communities in plots of the same aspect, summit, and site (Equation 2).

$$lnRR_{group} \sim 1 + (1|\,site\,/\,summit\,/\,aspect) \tag{2}$$

With $lnRR_{group}$ the log-response ratio of cover changes over time in each group per plot (all shrubs combined, deciduous shrubs and evergreen shrubs) and $(1|\,site\,/\,summit\,/\,aspect)$ the nested random intercept term. A similar model as in Equation (2) was used to test whether the log-response ratio of cover changes over time for each species separately differed significantly from zero.

Next, to test whether plant traits could explain the species-level abundance shifts, another LMM was built with the log-response ratio of cover changes as the response variable, the four mean trait values as fixed effects, and aspect nested within summit and summit nested within mountain site as random intercept. Another random intercept term of genus nested within plant family was added to the model to account for phylogenetic relatedness among species in our dataset (Equation 3, but see Table S5 for alternative models with species as random intercept instead of the phylogenetic structure to account for baseline species-specific differences not captured by traits). All mean trait values were z-transformed to facilitate model interpretation and parameter coefficient comparisons. Similar LMMs were built with ITVs, niche positions or niche widths as sets of predictors. Some predictors (mean plant height, mean seed mass, ITV of SLA, and ITV of seed mass) were log-transformed before the analyses to meet model assumptions. Multicollinearity among predictors was checked for all models using variance inflation factors (VIF), but no issues were detected (VIFs < 3).

$$\begin{aligned} lnRR_{species} &\sim MTV_{Height} + MTV_{SLA} + MTV_{Seed\ mass} \\ &+ MTV_{Leaf\ N} + (1|\,site/summit/aspect) + (family/genus) \end{aligned} \tag{3}$$

With $lnRR_{species}$ the log-response ratio of cover changes over time for each shrub species per plot, MTV_{Trait} the z-transformed mean trait values per species, and $(1|\,site\,/\,summit\,/\,aspect)$ and $(1|\,family\,/\,genus)$ the random intercept terms. Owing to the multivariate nature of our models, missing trait or EIVE indicator values meant that the respective species was omitted from the analyses (i.e., for 35% of shrub species in the trait models and 6% of species in the niche indicator models).

To check for additional sources of variation in plot-level shrub cover changes, an alternative series of models was run using modified versions of Equations (2) and (3). Regional differences in the total shrub cover change per plot, for instance, Equation (2) but with site as response variable and aspect nested within summit as random intercept. Among-species differences in cover change were evaluated using a modified version of Equation (3) substituting traits by species identity as fixed effect. Additionally, to check how the plot-level shrub cover changes related to the change in total vegetation cover per plot (i.e., greening trend) as well as the cover of other plant types, Equation (2) was run but with the total cover of all species combined as well as the cover of forbs and graminoids, instead of shrubs, as response variables. Finally, to account for the fact that trait effects may vary depending on the geographic positioning of a summit or mountain site in the species' climatic niche, an alternative series of univariate models was run including the separate mean trait values as fixed effect, but adding a random slope factor on the traits (Equation 4).

$$lnRR_{species} \sim MTV_{Trait} + \left(MTV_{Trait}|\,site\,/\,summit\,/\,aspect\right) + (1|\,family\,/\,genus) \tag{4}$$

All analyses were performed in the statistical programming software R version 4.4.1 (R Core Team 2021), using the packages *dplyr* (Wickham et al. 2023) for data manipulation, *lme4* (Bates et al. 2015) and *broom.mixed* (Bolker and Robinson 2022) for model building, and *ggplot2* (Wickham 2016) and *patchwork* (Pedersen 2024) for visualisation. Relationships were interpreted as statistically significant when the 95% confidence intervals (CI) of model estimates did not overlap with zero.

3 | Results

The average log-response ratio of total plot-level shrub cover was significantly different from zero (mean = 0.027, CI = 0.017–0.037), indicating that shrub abundance clearly increased over the past two decades on the studied mountaintops. Similarly, the average deciduous (mean = 0.026, CI = 0.016–0.037) and evergreen (mean = 0.033, CI = 0.022–0.044) shrub cover per plot was also significantly different from zero, with the mean increase being slightly greater for evergreen than for deciduous shrubs (Figure 1c). Translated to absolute percentage cover, the increases in total cover in the 1-m^2 plots corresponded to an average of 2.64% (CI = 1.87%–3.40%), 1.66% (CI = 0.92%–2.41%) and 1.96%

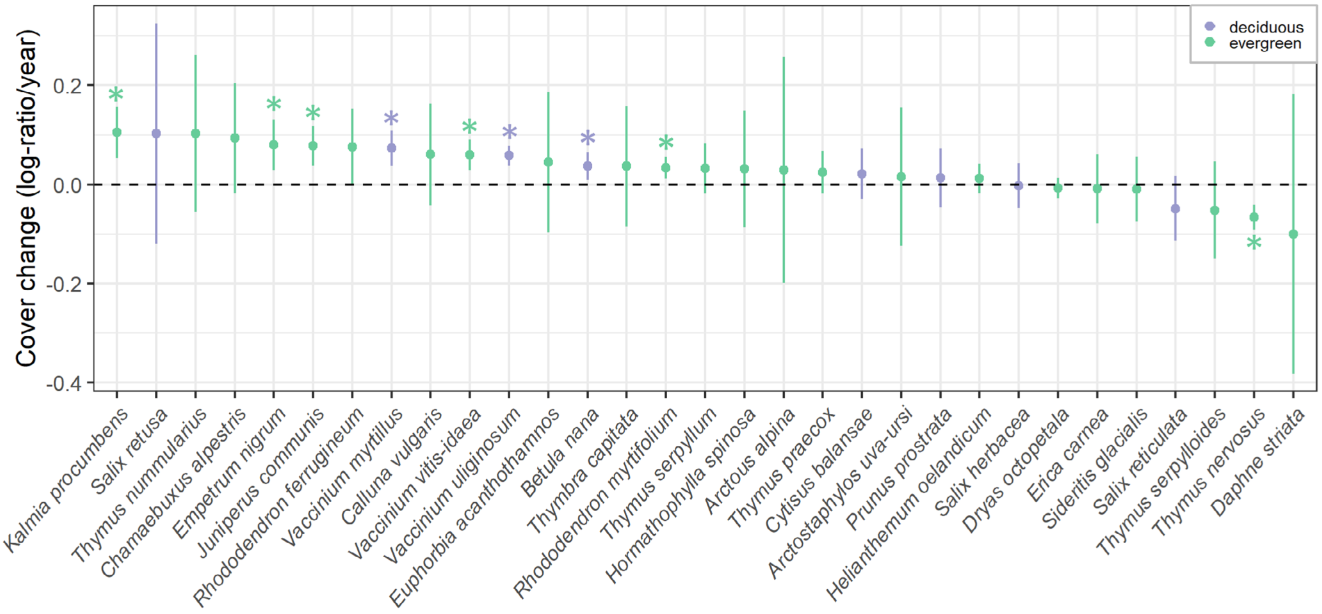

FIGURE 2 | Cover shift, quantified as the plot-level log-response ratio of percentage cover values in the baseline survey and the last resurvey, of the 31 studied shrub species. Dots and error bars represent mean and 95% confidence intervals (CI) of the species' cover shifts across all plots. Species are ordered in descending mean change value and coloured according to their functional group (i.e., deciduous vs. evergreen). The dashed black line depicts zero cover change. Species' mean cover changes are considered significant over time if the 95% CI does not overlap with zero: Nine species showed a significant increase in cover over time (*Kalmia procumbens, Empetrum nigrum, Juniperus communis, Rhododendron ferrugineum, Vaccinium myrtillus, V. vitis-idaea, V. uliginosum, Betula nana* and *R. kotschyi*) and only one species a significant decrease (*Thymus nervosus*); indicated by (*).

(CI = 1.26%–2.67%) per decade for the total, deciduous and evergreen shrub cover, respectively. Little among-region differences in the amount of shrub cover change per plot could be detected, implying that shrubification of alpine summits is likely a widespread and uniform phenomenon across Europe (Table S6). Moreover, the rate of change in total vegetation cover per plot was highly similar to that of shrubs (i.e., an average increase of 2.46% per m^2 per decade). Forb and graminoid cover, however, remained virtually stable over time (Figure S2), illustrating that shrubification is the primary driver of greening on our mountain summits.

Out of the 31 studied shrub species, nine showed a significant increase in cover over time (*Kalmia procumbens, Empetrum nigrum, Juniperus communis, Rhododendron ferrugineum, Vaccinium myrtillus, V. vitis-idaea, V. uliginosum, Betula nana*, and *R. kotschyi*) and only one species a significant decrease (*Thymus nervosus*). Among the shrub species with increasing cover, six were evergreen and three deciduous (Figure 2).

Looking at the relationship between functional traits and the shrub species' cover shifts over time, only mean plant height showed a positive effect on the log-response ratio of shrub species cover (slope = 0.019, CI = 0.005–0.034; Figures 3, 4, S3, Table S7). This relationship confirms our hypothesis and was mainly driven by taller evergreens of the genera *Juniperus*, *Rhododendron*, *Erica* and *Calluna*. Contrastingly, the mean leaf N content was negatively associated with the shrub species' cover changes (slope = −0.030, CI = −0.048 to −0.010; Figures 3, 4, S3, Table S7), which did not match our initial expectations. The absence of significant effects in the separate set of univariate trait models showed that there were no trade-offs in the trait effects among sites or mountain summits (Table S8, Figure S4). Concerning the niche position and niche width indicators, we only found a significant negative effect of the species' indicator for light (L) on the log-response ratio of shrub cover (slope = −0.021, CI = −0.037 to −0.002; Figures 3, 4, S5, Table S7), which also contrasted with our hypothesis. Overall, the variation explained by the models' fixed effects (i.e., marginal R^2) was relatively low ($R^2 < 0.1$; Table S7). Among-species differences, however, only accounted for 11% of variation in shrub cover change, which in turn represents the upper limit of variation that could possibly be explained by species characteristics (Table S9).

4 | Discussion

Our study provides the first continent-wide and multidecadal assessment of shrub encroachment in the alpine zone. Using vegetation resurvey data from 576 permanent plots located on alpine summits across Europe's major mountain chains, we show that plot-level shrub cover clearly increased over the past two decades and that the cover increase was slightly higher for evergreen than for deciduous species. Looking at the species-level cover changes, we found that species with greater height increased their cover more, while higher leaf N concentrations and light affinity were associated with smaller cover changes. Overall, the explanatory power of the models was low, and species trait variation or niche widths did not appear to affect shrub cover changes over time. While ongoing shrub cover changes may have far-reaching consequences for the functioning of alpine ecosystems, predicting this may not be straightforward given that species' cover dynamics poorly relate to their occupied trait spaces and niche requirements.

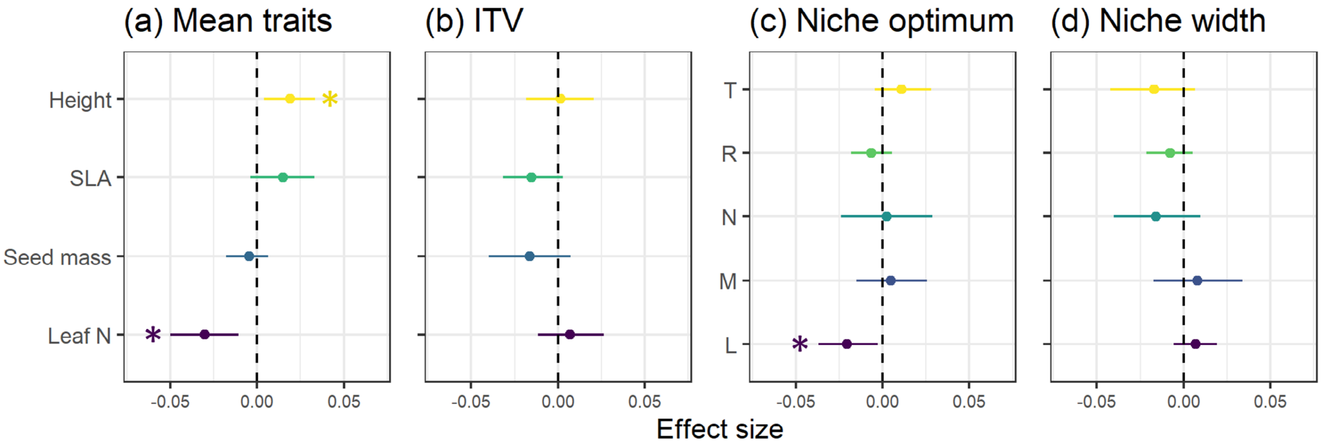

FIGURE 3 | Effect of mean trait value (a), intraspecific trait variation (ITV; b), niche optimum (c) and niche width (d) on the shrub species' cover shifts (quantified per species as the plot-level log-response ratio of percentage cover values in the baseline survey and the last resurvey). Functional traits included are plant height (m), specific leaf area (mm^2/mg), seed mass (mg) and leaf nitrogen content (mg/g), while plant niches are quantified by the Ecological Indicator Values for Europe (EIVE; *sensu* Dengler et al. 2023) for temperature (T), soil reaction (R), nutrients (N), moisture (M) and light (L). Dots and error bars depict mean estimates and 95% confidence intervals (CI) from linear mixed-effect models with the species' cover shifts as response variable, the mean traits, intraspecific trait variations (ITV), niche positions or niche widths as predictors, and species and aspect nested within summits nested within region as random intercepts. The dashed black line represents the zero line. Effects are considered statistically significant when 95% CIs do not contain zero.

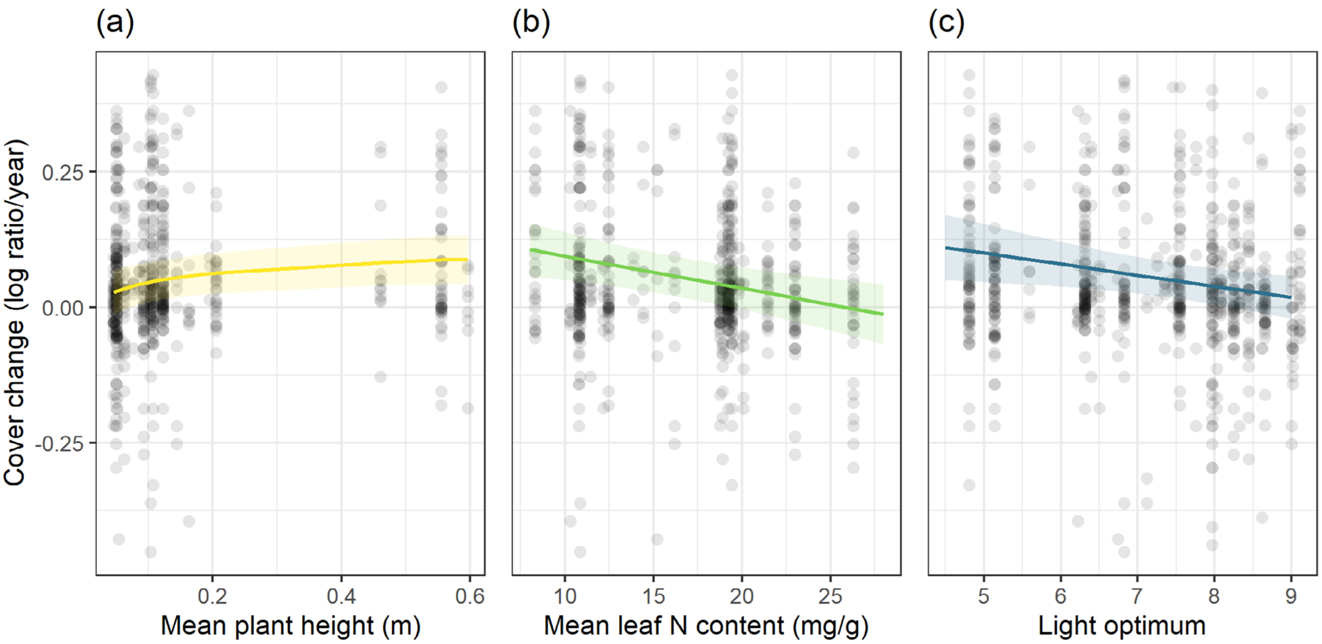

FIGURE 4 | Scatterplots depicting significant relationships between mean plant height (a), mean leaf nitrogen (N) content (b) and optimum for light (c), on the one hand, and shrub species' cover shifts, on the other hand. The abundance shift was quantified per species as the plot-level log-response ratio of percentage cover values in the baseline survey and the last resurvey. The shrub species' optimum for light was based on the Ecological Indicator Values for Europe (EIVE; *sensu* Dengler et al. 2023), and varies along an ordinal scale from 0 (low light affinity, typical for shaded habitats) to 10 (high light affinity, typical for open habitats). Lines and shaded ribbons depict model predictions and 95% confidence intervals (CI) for linear mixed-effect models, while black dots with fading to avoid overlap show the actual data points. The *x*-axes are back-transformed from log-scale to linear scale to facilitate interpretation of the graphs.

4.1 | Cover Changes Differ Among Evergreen and Deciduous Shrub Species

Unexpectedly, evergreen shrubs showed a slightly higher expansion rate than deciduous species, contrasting with a plethora of studies from the Arctic tundra where mostly increases in the cover of tall deciduous shrubs of the genera *Alnus*, *Betula*, and *Salix* have been observed (Tape et al. 2006; Myers-Smith et al. 2011). These shrubs are strong competitors for resources with the potential to outcompete prostrate or low-growing vegetation via shading through their tall canopy architecture as well as efficient nutrient acquisition through benevolent mycorrhizal associations (Martin et al. 2017; Schore et al. 2023). This is further corroborated by Dobbert et al. (2021) suggesting positive growth responses of deciduous shrubs to future warming, possibly dominating over evergreen competitors at the same sites. For instance, while the deciduous *Betula nana* benefited from a prolonged growing season and winter warming in Arctic-alpine environments, the evergreen *Empetrum hermaphroditum* exhibited strong negative sensitivity to late-frost exposure following earlier melt-out dates. Freezing events early in spring have been shown to affect other evergreen shrub species as well (see Venn and Green 2018), which was attributed to the fact that they have not yet become frost-hardened after snowmelt.

Contrarily, in the European Alps, prominent advances of late-successional shrubs of the genera *Rhododendron*, *Juniperus*, *Vaccinium* and *Empetrum* have been reported, many of which are evergreens (Cannone et al. 2007, Cannone and Pignatti 2014, Malfasi and Cannone 2020). In a study by Wilson and Nilsson (2009) on a Swedish mountainside, the greatest cover increase was observed for the evergreen shrub *E. hermaphroditum* over a 30-year period, but primarily at intermediate elevations. Malfasi and Cannone (2020) observed a clear negative influence of decreasing snow cover under global warming on the recruitment of the evergreen species *Rhododendron ferrugineum*, and attributed this to the lower water supply as well as increased probability of freezing damage. Yet, a shift in the species' reproductive strategy from sexual reproduction to vegetative propagation at the recruitment stabilizing phase could have prevented a subsequent reduction in cover, and in some cases even promoted local expansion through additional layering and vegetative growth. An alternative explanation for the higher increase in evergreen shrub cover could be that many tall deciduous shrub species are prone to grazing due to their highly palatable, nutrient-rich leaves (e.g., *Salix glauca* in the Scandes), which could have inhibited their expansion to some extent. Livestock grazing by, for example, sheep or reindeer has a millennia-old tradition in the alpine zone of Europe (see Pajunen et al. 2012; Mayer and Erschbamer 2017), halting the encroachment of alpine meadows by deciduous shrubs while most evergreen dwarf shrubs seem to be unaffected (Vowles et al. 2017). On top of that, foliar damage and reduced productivity has been noted for several deciduous shrub species owing to recent severe insect outbreaks under warmer winter conditions (Finger-Higgens et al. 2021). Finally, it is not unlikely that recent summer droughts, especially on the Mediterranean summits and in the Alps, adversely affected shrub expansion, particularly in deciduous species, whereas evergreens tend to be more resistant to low soil moisture conditions (Dobbert et al. 2022).

4.2 | Winner Shrub Species Have Greater Stature but Lower Leaf Nitrogen and Light Affinity

Our analyses showed that shrub species with greater plant height at maturity and lower leaf N contents also tended to have larger cover increases over time. Greater stature may indeed confer a competitive advantage over other species in a warming alpine biome (see Gaudet and Keddy 1988). However, similar positive responses could be expected from species with higher SLA or leaf nutrient concentration indicating more efficient resource acquisition, but this was not confirmed by our analyses (see also Bjorkman et al. 2018a, 2018b). For SLA, the continent-wide effect could have been masked by regional trade-offs in plant strategies, for instance, caused by high SLA being beneficial with warming at higher latitudes but low SLA being associated with better resistance against droughts in the Mediterranean mountain ranges. However, our separate set of univariate models accounting for such regional variation in trait effects could not confirm this conjecture. Higher leaf N, on the other hand, is sometimes linked to increased plant palatability (Schädler et al. 2003), which could explain why shrub species with lower leaf N increased their cover more over time on our summits, being less susceptible to herbivory.

Contrary to our expectations, however, no significant effects of trait variation (i.e., ITV) on the magnitude of species-level cover shifts could be detected, implying that higher trait plasticity is not likely to support increased opportunities for alpine shrub species to expand their covers under a warming climate. One possible explanation could be that, for many alpine shrubs, genetic variation, and thus adaptability under a changing environment, mainly emanates from differentiation among, and not within, populations. Indeed, genetic differentiation can be comparatively high among the spatially isolated populations of alpine plants as a result of limited gene flow, random genetic drift or selection in topographically heterogeneous mountainous landscapes (Reisch and Rosbakh 2021). Hence, it is likely that the isolated populations of a certain shrub species on our mountain summits will not profit from the species' regional gene pool for adaptation, regardless of its size (Ægisdóttir et al. 2009). Alternatively, because trait records were collected from multiple databases to maximise coverage across (sometimes rare) shrub species, the geographical range of sampling may differ considerably across species and not necessarily reflect the species' full distribution range, introducing a potential bias in the ITV calculations. Also unexpectedly, ecological indicators for plant niche optimum and niche width, reflecting species environmental preferences, proved to be poor predictors of shrub species' cover changes, apart from the significant negative influence of the niche optimum for light. In other words, shrub species preferring shadier habitats increased their cover more over time than high light-affinity species. Albeit counterintuitive at first, it is possible that several forest and treeline shrubs such as *Vaccinium myrtillus* and *V. vitis-idaea* have taken advantage of the warming temperatures in the alpine zone, and hence expanded their cover, equivalent to the widespread *borealisation* trend observed in plant communities across the Arctic tundra (García Criado, Barrio, et al. 2025).

4.3 | Critical Viewpoints and Avenues for Future Research

Overall, the explanatory power of our models was low (marginal $R^2 < 0.1$ only including the fixed effects), supporting the idea that most alpine shrub species do not only show trait responses to a changing climate but that species responses are more likely to be complex, individualistic and highly heterogeneous, and potentially further complicated by concurrent changes in land-use within the alpine zone such as changes in herbivore densities and grazing pressure. When including the random structure (i.e., nested design of the sampling with different aspects, summits and sites), the models' explanatory power increased to about 0.3 (conditional R^2), which is common in continental-scale ecological studies. Still, interspecific differences in our shrub species pool, and thus the maximum amount of variability that can be attributed to species traits or environmental preferences, could only account for 11% of variation in cover changes. The latter corroborates García Criado et al. (2023) showing that range shifts and abundance changes in common tundra shrubs do not necessarily result in directional turnover of shrub trait composition. Furthermore, it should be noted that the shrub species included in our dataset are highly heterogenous in, among others, growth form (including both tall shrubs and erect or prostrate dwarf shrubs) and habitat preference (with, e.g., *Rhododendron* species typically growing within alpine snowbeds and *Kalmia procumbens* preferring exposed ridges). This could have further contributed to the idiosyncratic responses observed here, and advocates for more detailed species- or group-level approaches rather than including all species together into a holistic model.

Alternatively, including additional morphological or physiological traits in our models related to, for example, clonality, wood density, frost hardening, water-use efficiency, stomata density, rooting depth or mycorrhizal associations and plant palatability, could improve the explanatory power, particularly when there is a more direct relationship to a species' climatic responsiveness (cf. Kühn et al. 2021). Still, data on these traits are relatively scarce or highly heterogeneous, especially for many of the less frequent alpine shrub species in our dataset. Moving beyond traits, it is possible that demographic processes such as inter- and intraspecific competition, growth, survival, fecundity, germination and establishment exert a more pronounced influence on shrub species cover dynamics (García Criado et al. 2023). This could be particularly true for alpine environments where steep changes in aspect, slope and exposure can cause large variation in climatic conditions over small spatial scales (Körner 2003). These fine-scale climatic gradients are known to have a strong impact on the demographic rates of alpine plants (Forbis 2003). Together, the complex relationships between demography and interwoven climatic gradients continue to shape population growth rates and abundance dynamics of alpine plant species in heterogeneous mountain terrains (Oldfather and Ackerly 2019). Individual-based models (IDMs) offer a powerful tool to simulate demographic rates and population dynamics in a changing world, and have previously been applied to alpine plants (see Cotto et al. 2017). Particularly interesting is that these IDMs incorporate information on eco-evolutionary dynamics, which is highly relevant in the context of long-lived alpine species with limited potential for adaptive evolution in a rapidly changing environment. However, the demographic data necessary to parameterise and validate such models remains to date limited, and further research is required to what extent demographic rates and evolutionary processes can steer the response of alpine shrub species to climate change.

Finally, we acknowledge that our models do not account for the strong spatial heterogeneity in microclimates, topography, soil moisture, nutrient availability and snow dynamics, which is typical for alpine terrains and allows species to reside and thrive in microrefugia even though the surrounding environment is not optimal (Graae et al. 2018). Such microvariability in environmental conditions is typically not captured by generic ecological indicator values. To illustrate, while the thermal niche of plants is generally estimated in relation to ambient air temperatures that are measured in weather stations at 2 m height (i.e., macroclimate), small-statured or prostrate alpine shrubs are more likely to respond to microclimate, that is, fine-scale temperature variation near the ground (see Graae et al. 2012). Developing microclimate-based thermal niche indicators, similar to the endeavours by Lenoir et al. (2013) and Haesen et al. (2023), could be an interesting way forward here, as these might have more explanatory power. Of course, this requires long-term microclimate monitoring efforts paired with vegetation data across the alpine biome, which is currently being realized by global networks such as the Microclimate Ecology & Biogeography Network (https://meb-network.com; Lembrechts et al. 2020) and MIREN (Haider et al. 2022).

5 | Conclusion

5.1 | Implications for Alpine Biodiversity and Ecosystem Functioning

Both deciduous and evergreen shrub cover has clearly increased across Europe's alpine vegetation belt over the past 20 years. This shrub expansion could have far-reaching implications for mountain biodiversity and ecosystem functioning. Dense shrub growth could decrease many of the native specialist plants through competition for light and nutrients, leading to homogenization of the alpine vegetation. Shrubs can also alter the surface energy balance by reducing the albedo, and change the soil thermal regime through shading in summer and additional snow trapping in winter. Higher soil temperatures, in tandem with altered litter inputs, may eventually also alter decomposition and carbon turnover rates, with possibly global consequences through complex feedback processes (Wookey et al. 2009, Vowles and Björk 2019). However, the more pronounced increase in evergreen compared to deciduous shrubs observed in our pan-European study, could imply that many of these ecosystem-wide effects are dampened given that some evergreen shrubs with lower stature are far less likely to influence snow cover and, in turn, soil microclimates. Moreover, the input of more recalcitrant litter from evergreen dwarf shrubs can slow nutrient cycling and amplify ecosystem carbon storage, thereby partly offsetting the negative feedback loop caused by albedo changes (reviewed by Vowles and Björk 2019). Including shrub dynamics and their complex interactions with the environment into mechanistic climate models (e.g., General Circulation Models used by the IPCC) could thus be of paramount importance to more accurately predict these feedbacks between alpine vegetation changes and the global climate system.

Second, our analyses made clear that increasing shrub cover is poorly associated with a specific combination of trait values or variation, nor to individual species' niche requirements. Future endeavours could therefore investigate the role of other morpho-physiological traits with more direct relationships to species' environmental change responses as well as the explanatory power of alternative niche indicator values that capture the fine-scale, in situ measured variation in environmental conditions experienced by alpine plants. Additionally, accounting for demographic rates and evolutionary processes could further deepen our understanding of the complex nature of alpine shrub abundance dynamics in a changing world. To date, however, the availability and reliability of such data are still highly deficient. While our study provides foundational insights into the intricate mechanisms driving shrub cover dynamics on mountaintops at unprecedented biogeographical scales, we emphasize the need for more complete and comprehensive databases of alpine plant trait and environmental conditions based on widespread, in situ sampling efforts paving the way towards deeper mechanistic understanding.

Finally, further research is needed to identify whether the observed trend of increasing shrub cover on European mountaintops will continue in the future, especially because more and more studies point towards shrub *browning* as a result of foliar frost damage following advancement in snowmelt dates caused by warm-winter spells or in early spring (albeit at the moment particularly in Arctic regions; see Myers-Smith et al. 2020, Bokhorst et al. 2022). Continued monitoring of shrub cover changes across space and time, whether greening or browning, is thus of the utmost importance and should be a priority on the future research agenda of mountain environments.

Author Contributions

T.V. conceived and designed the study, in close collaboration with P.D.F., K.V., B.J.G., S.D., and H.P. T.V. and H.B. performed the data analyses. T.V. wrote the manuscript. All authors contributed to the data collection and provided extensive feedback during the writing of the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The raw data used in this study is available upon request at the GLORIA coordination office (gloria.office@boku.ac.at), while a derivative of the data including plot-level and species-level shrub cover shifts as well as all code necessary to reproduce the analyses and figures is available on Github (https://github.com/to-vanneste/GLORIA-shrubification.git) and Figshare with unique identifier (DOI) 10.6084/m9.figshare.31398462.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Boxplots showing the difference in plant height (log-transformed; (a), SLA (b), seed mass (log-transformed); (c) and leaf nitrogen content (d) between deciduous and evergreen shrub species. **Figure S2:** Distribution of cover shifts over time across plots for all species combined (i.e., greening), forbs and graminoids. **Figure S3:** Model estimates (mean ± 95% CI) for the shrub species' cover changes over time (calculated as long-response ratios) as function of the mean trait values for plant height, specific leaf area (SLA), seed mass and leaf nitrogen (N) content. Shrub species are ordered (top to bottom) according to decreasing modelled cover changes (a), plant height (b) and leaf N content (c). **Figure S4:** Scatterplots for the alterative series of univariate models with the mean trait values as random slope terms to account for the fact that trait effects of shrub species' cover changes may vary depending on the region. **Figure S5:** Model estimates (mean ± 95% CI) for the shrub species' cover changes over time (calculated as long-response ratios) as function of the niche optima for moisture, soil reaction, nutrient levels, light and temperature (EIVE indicator values). **Table S1:** List of GLORIA mountain sites and summits located in the alpine vegetation belt. **Table S2:** List of shrub species in the GLORIA database. Species were classified as shrubs accodring the Plants of the World Online (POWO), including both 'shrubs' and 'subshrubs'. **Table S3:** Mean trait values and intra-specific trait variation (quantified as coeficient of variation; CV) for the shrub species' plant height at maturity (m), specific leag area (SLA; mm^2/mg), seed mass (mg) and leaf nitrogen (N) content (mg/g). **Table S4:** Niche optimum and width for the shub species' ecological indicator values for soil moisture (M), soil nutrient status (N), soil acidity (R), light (L) and temperature (T). **Table S5:** Mean parameter estimates (±SD or 95% CI) for alternative linear mixed-effect models relating shrub species cover shifts over time to mean trait values (model 1), intra-specific trait variation (model 2), niche optima (model 3) and niche widths (model 4), but with species as random intercept term instead of the phylogenetic structure. **Table S6:** Mean parameter estimates (±SD or 95% CI) for the effect of region on the plot-level total shrub cover. **Table S7:** Mean parameter estimates (±SD or 95% CI) for linear mixed-effect models relating shrub species cover shifts over time to mean trait values (model 1), intra-specific trait variation (model 2), niche optima (model 3) and niche widths (model 4). **Table S8:** Mean parameter estimates (±SD or 95% CI) for alternative series of univariate trait models with added random slope on mean trait values. **Table S9:** Mean parameter estimates (±SD or 95% CI) for the effect of among-species differences on plot-level shrub cover changes.