# Resurveying inner-alpine dry grasslands after 70 years calls for integrative conservation efforts

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A B S T R A C T

European inner-alpine dry grasslands face substantial threats within the increasingly human-altered landscape, endangering their persistence. To understand changes in dry grassland communities, we revisited historical vegetation plots of Josias Braun-Blanquet after 70 years in Val Venosta, Italy, hosting rare steppe-like grassland vegetation. By disentangling the key environmental factors encompassing climate, land use and human management, and ecological site preferences, we aimed at explaining changes in dry grassland communities with implications for future conservation.

By extending our analysis beyond conventional dissimilarity metrics and adopting a landscape-ecological perspective accounting for species-environment interactions, we assessed how environmental changes affect dissimilarity patterns among historical sites, recent non-protected sites, and recent protected sites with generalized additive modelling. Moreover, we examined ecologically significant species changes to evaluate their contribution to community variation within and between sites, discerning their consequences at the landscape scale.

Our results revealed significant changes in dry grassland sites, both on non-protected and protected sites. The encroachment of shrubs was associated with a significant increase in generalist species, including various woody species on sites where grazing had ceased. Furthermore, we observed a higher abundance of nutrient-demanding species on sites next to intensive agriculture. These trends were consistent regardless of the protection status, implying that current conservation measures may be insufficient to guarantee their future persistence. To ensure the long-term conservation of typical inner-alpine dry grasslands, interdisciplinary conservation efforts are essential to address adverse environmental impacts across the entire landscape.

## 1. Introduction

Biodiversity decline is a global issue affecting many ecosystems (Johnson et al., 2017), including semi-natural dry grasslands in Europe (Diekmann et al., 2019). This decline could reach critical levels across ecosystems if the current global environmental change continues at the present pace (Rinawati et al., 2013; Nunez et al., 2019). Predominantly human pressures have caused habitat transformations, which come along with the loss of highly specialized species (Hilpold et al., 2018; Magnes et al., 2020). Moreover, anthropogenic pressures are likely to be exacerbated by ongoing climate change (Warren et al., 2013). Unraveling the various environmental change drivers and understanding their complex consequences is crucial for effective habitat conservation, but it remains a significant research challenge (Meiners et al., 2015; Nori et al., 2023; Rinawati et al., 2013).

In this context, vegetation resurveys are particularly useful in detecting patterns of plant communities driven by global environmental change processes (Britton et al., 2017; Jandt et al., 2022; Hédl et al., 2017). Analyzing how species changes contribute to overall community variation over time can provide valuable insights into the underlying

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environmental mechanisms (Avolio et al., 2019; Baeten et al., 2014; Jandt et al., 2022). The most drastic vegetation changes in Europe likely occurred during the mid-20th century due to the expansion of the agro-industrial sector introducing management intensification (Leuschner and Ellenberg, 2017; Wesche et al., 2012). While most resurvey studies examine recent floristic changes due to a lack of long-term data, investigating the long-term past is essential for capturing the full magnitude of vegetation changes in response to environmental changes (Jandt et al., 2022; Hédl et al., 2017; Wesche et al., 2012).

The field documentations by Braun-Blanquet (1961) are such rarely available vegetation records and date back to the early and mid-20th century. His vegetation surveys comprise the first documentation of the continental steppe-like grassland communities in the major inner-alpine dry valleys, including the Val Venosta/Vinschgau (autonomous province of Bolzano, South Tyrol). These extra-zonal dry grassland communities harbor many rare steppe plant species that are genetically distinct from populations in the Eurasian continental core areas (Kirschner et al., 2020). As remnants of late glacial steppe vegetation, they are of significant conservation value and therefore designated as priority habitats in Europe (European Commission, 2013). Natura 2000 protected areas have been established with the aim of conserving species and creating a habitat network to ensure the connectivity of vital landscape elements, facilitating the dispersal and exchange of species (European Commission, 1992).

So far, the effectiveness of protection measures is largely unknown (EEA, 2020; Wesche et al., 2012). Furthermore, given the challenges of restoring habitats with specialized and rare plant species (Dostálek and Frantík, 2008), it is paramount to prioritize the preservation of existing remnants (e.g. by maintaining grazing regimes; Catorci et al., 2013). Up to now, it remains uncertain whether dry grassland species and communities can persist in Val Venosta in the face of ongoing environmental changes (Kindermann et al., 2023; Wilhalm, 2018). Identifying major threats is a precondition for the implementation of tailored conservation management strategies, such as the establishment of buffer zones to mitigate intense agriculture's impact or the reintroduction of suitable grazing systems to counteract shrub encroachment (Dostálek and Frantík, 2008; Napoleone et al., 2021).

In our resurvey, we aim to analyze the dry grassland communities in Val Venosta by integrating all available historical data with associated environmental conditions for disentangling patterns, causes, and consequences of biodiversity changes. Our main objectives are: (i) to analyze ecologically meaningful species gains and losses; (ii) to determine the major environmental drivers of change in dry grassland communities; and (iii) to assess the effectiveness of current protection measures. We anticipate that species gains and losses are primarily linked to human-induced changes such as abandonment and afforestation (Jandt et al., 2011; Lübben and Erschbamer, 2021; Prangel et al., 2023) but also eutrophication (Dengler et al., 2020; Wesche et al., 2012). We expected that the pronounced landscape transformation in the valley plays a predominant role in species changes (Kindermann et al., 2023), while climatic effects might not yet be visible (Török and Dengler, 2018). As dry grasslands occur inside and outside of protected areas, Val Venosta offers an ideal setting to investigate the effectiveness of protection measures. While many studies focus on individual drivers of species changes (Conradi and Kollmann, 2016; Titeux et al., 2016), our study aims to elucidate the relative importance of multiple environmental factors. By investigating the interface between landscape-level and species-level changes, our study enhances the understanding of species change from a landscape-ecological perspective.

Given the global relevance of human-driven biodiversity loss (Díaz et al., 2019; Gossner et al., 2016; Newbold et al., 2015), understanding the key drivers of change in dry grasslands can provide valuable guidance for conservation efforts (Nori et al., 2023). This knowledge may also be relevant to other inner-alpine dry grasslands facing similar environmental challenges (e.g. Magnes et al., 2020; Török and Dengler, 2018).

## 2. Materials and methods

### 2.1. Study area

The study area (Fig. 1), Val Venosta/Vinschgau (*Bolzano, South Tyrol, Italy*), is one of the few inner-alpine dry valleys that harbors extra-zonal steppe-like vegetation of the class *Festuco-Brometea* due to specific local climatic and topographic conditions (Braun-Blanquet, 1961). The suitability for highly specialized xerophytic species on the steep south-facing slopes of this valley results from a dry (partly below 500 mm $a^{-1}$ precipitation) and hot climate, which is amplified through the orographic seclusion provoked by the high mountains surrounding the valley (Wilhalm, 2018). The intra-montane location underscores the geographic island character of these steppe-like grassland communities (Leuschner and Ellenberg, 2017). Floristic studies recorded the presence of continental dry grassland species up to an elevation of approximately 1500 m a.s.l. (Braun-Blanquet, 1961; Lübben and Erschbamer, 2021; Schwabe and Kratochwil, 2004). The entire valley bottom, once dominated by subsistence farming, has undergone a transformation to intensively managed apple monoculture during the past decades (Hilpold et al., 2018; Tarmann, 2019; Wilhalm, 2018). In contrast, mountain slopes have experienced successional changes due to the abandonment of traditional grazing practices and afforestation (Kindermann et al., 2023).

To understand the current conservation status of these grasslands, we reassessed historical sampling sites across the valley (Braun-Blanquet, 1961). Some of the remaining dry grassland sites are in 5 protected areas of Val Venosta (Fig. 1), which were mostly established since 1981 (further details are provided in Suppl. Mat. 1 Table S2). This provides an opportunity to examine the effects of conservation efforts.

### 2.2. Field sampling

#### 2.2.1. Historical site relocation

Locating historical sampling sites inevitably comes along with uncertainties that can only be minimized by narrowing down the study area with all ancillary historic site information (Kapfer et al., 2017). The historic field documentations by Braun-Blanquet (1961) comprise detailed site information about elevation, aspect, slope, percentage cover, plot size and a site description (Braun-Blanquet, 1961, compare Suppl. Mat. 1, Table S1). To filter potential field sites, we compared all provided terrain information with a DEM at 1 m resolution (Rumpf et al., 2019) and cross-checked the presence of (dry) grasslands with historical aerial photographs from 1945 and a recent high-resolution orthophoto (an example is displayed in Suppl. Mat. 2). This allowed us to curtail the possible field sites to one or two specific slopes. We considered a site as no longer present, if no dry grassland was present at the identified slope due to land use change (e.g. only shrubs/forest or agriculture matched the sampling location), or if the given site description itself was not traceable, e.g. named as "home pasture" (Braun-Blanquet, 1961, p. 220, translated by the authors).

Of the 78 historical sites, we relocated 51 and excluded 27 sites, of which 21 sites today are subject to succession (shrub and forest communities) or agricultural intensification (apple orchards, vineyards), while 6 sites could not be traced. Another 6 sites were excluded at a later stage due to inconsistent data availability of the necessary environmental variables such as land cover information, leaving a total of 45 sites for the analyses.

We aimed at determining the least possible change within the dry grassland communities compared to the historical reference survey (Diekmann et al., 2019), i.e. we only sampled the defined field areas if dry grassland was still present (Wesche et al., 2012). Once the presence of dry grasslands (even in marginal areas) could be confirmed with the orthophoto, we considered the area comparable to the reference period. Thus, we assumed that the presence of other plant communities in close vicinity of the selected grassland sites reflects a successional trend that
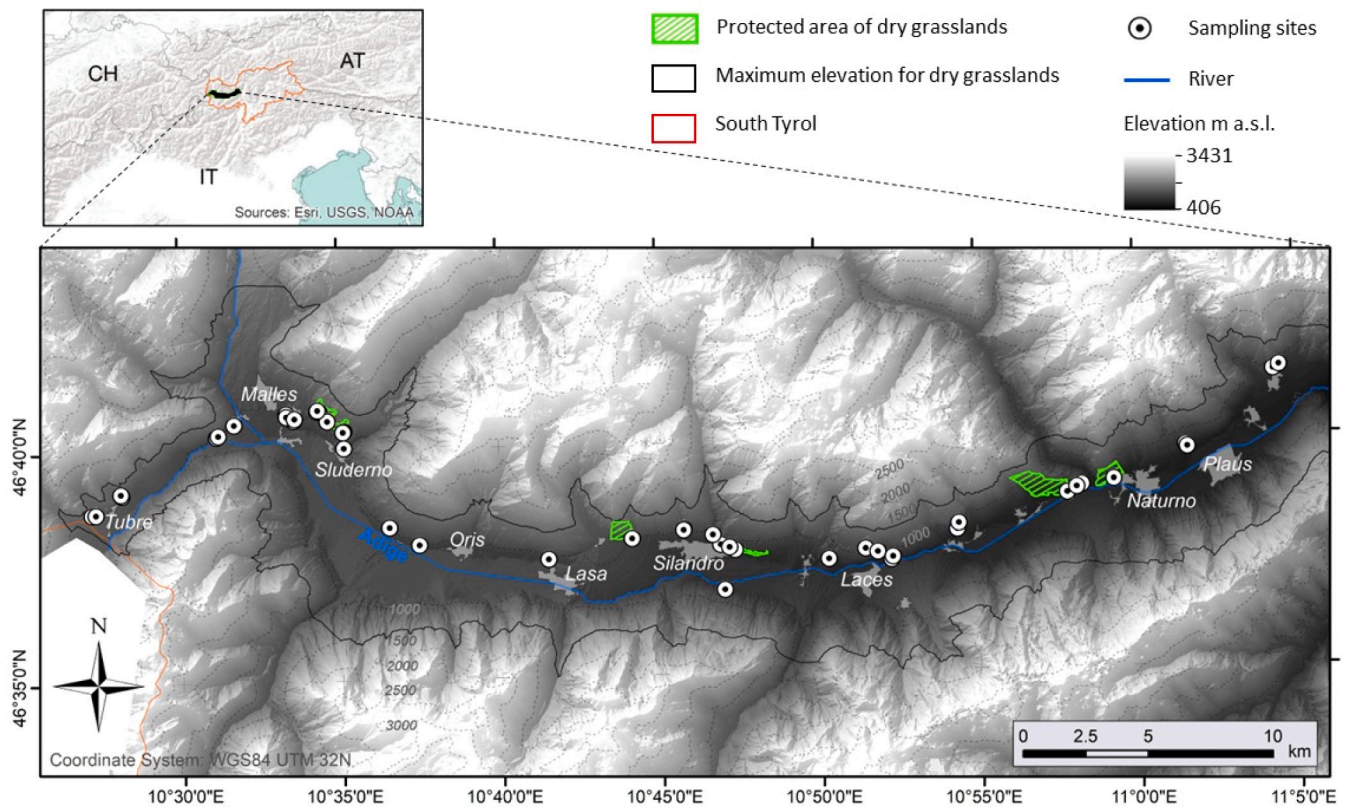
**Fig. 1.** Map of the study area, Val Venosta/Vinschgau, Bolzano, South Tyrol, Italy. Exact geo-location and additional site information can be consulted in Suppl. Mat. 1, Table S1. GIS-data: catalogue of the Autonomous Province of Bolzano (https://geokatalog.buergernetz.bz.it/geokatalog).

may represent a transition state of the historical grassland if no other grassland area matching the sampling criteria (as exemplified in Suppl. Mat. 2) existed.

### 2.2.2. Vegetation resurvey

Once we confirmed the presence of dry grassland vegetation by in-situ inspection (Becker-Scarpitta et al., 2019), we resurveyed the site matching the size of the historical relevé (majority of plots were 50 m$^2$), revisiting the sites twice in the vegetation optimum periods of 2020 and 2021. We estimated the cover of all occurring vascular plant species present within rectangular 5 m × 10 m plots (Suppl. Mat. 3) corresponding to the historical documentations by the classical scale of Braun-Blanquet (1964) and converted the historical and recent cover values to mean class percentages for further analyses as follows: $r = 0.1$ %, + = 0.5 %, 1 = 2.5 %, 2 = 15 %, 3 = 37.5 %, 4 = 62.5 %, 5 = 87.5 % cover (Tüxen and Ellenberg, 1929-1936). To allow for comparison in species abundance between past and today, the syntaxonomy was aligned with the EuroVegChecklist (Mucina et al., 2016), nomenclature with the Austrian checklist, which includes South Tyrol (Fischer et al., 2008) and with the checklist of South Tyrol (Wilhalm et al., 2006). Additionally, we recorded the proportion of herbs, grasses and the grazing regime (grazed vs. non-grazed, naturally vs. managed and animal species, if apparent, Suppl. Mat. 1 Table S2).

### 2.3. Environmental data

To examine changes in community composition of dry grasslands, we selected various environmental variables representing known drivers of change (Suppl. Mat. 4, Török and Dengler, 2018). To account for climatic changes between both surveys, we obtained 20 bioclimatic variables in 1 km resolution for each site using the ClimateEU v. 4.62 software (Marchi et al., 2020). Since historical data was collected across several years (1936–1961), we derived climate normals for each data set

(past: 1931–1960, present: 1981–2010) to best approximate climatic conditions. Changes in land use and other human influences were assessed by calculating landscape metrics based on a spatial land cover map available for both reference periods derived via automated classification of historical aerial photography and a recent orthophoto (further details on generation of the land cover map are provided in Kindermann et al., 2023). To account for the landscape composition and spatial configuration surrounding the sampling sites, two buffers were applied aggregating elements in immediate vicinity ($r = 25$ m) and the wider surrounding ($r = 500$ m) of a certain land cover class (such as the percentage of agriculture or encroachment in vicinity to the sampled sites; compare Table 1). We focused on describing main aspects of the structural landscape pattern (area, edge, proximity and spatial configuration; Haines-Young and Chopping, 1996). We discarded highly correlated variables ($r_s > 0.8$), based on Spearman's rank correlation coefficient due to the partial non-normally distributed variables to avoid redundant variables for all following analyses (Suppl. Mat. 4, Figs. S2 and S3) leaving 11 environmental variables (Table 1). Finally, we used species indicator values for describing habitat preferences as these can be considered a reasonable approximation of environmental conditions in the absence of direct measurements (Diekmann, 2003). We derived mean species indicator values based on species presence-absence data per site for light (L), temperature (T), continentality (C), soil reaction (R), humidity (U) and nitrogen (N) based on Guarino and La Rosa (2019). In this work, classical Ellenberg indicator values have been adjusted for the Italian flora. Specifically, the range of L and T has been increased (i.e. 1–12 instead of 1–9 in the original Ellenberg classification) to account for their high intensity in Italy (Guarino and La Rosa, 2019; Schwabe et al., 2007). Indicators were subsequently used to capture co-occurring species preference for habitat conditions between the surveys and protection status.

**Table 1**

Final set of variables used for the change analyses. Species indicator values are used to capture co-occuring species trends to the environmental variables.

| Category | Variable (abbreviation) | Specification | Source |
|---|---|---|---|
| Climatic conditions | Mean annual temperature ($T_{annual\ mean}$) | Long-term average temperature data for the historical (1931–1960) and recent survey (1981–2010) | Marchi et al. (2020) |
| | Mean annual precipitation ($P_{annual\ mean}$) | Long-term average precipitation data for the historical (1931–1960) and recent survey (1981–2010) | |
| | Summer heat: moisture index (SHM) | Ratio between mean warmest month temperature and precipitation of the mean growing season from May to September divided by 1000 | |
| Human management and land use | Grazing | Grazing type on the site, if any | Documented in-situ during field sampling |
| | %-encroachment, r = 25 m | Areal share (in percent) of encroachment (i.e. shrubs) in immediate vicinity of the sampled site at a radius of 25 m | Kindermann et al. (2023), McGarigal et al. (2023) |
| | Edge:area ratio | Ratio of edge length to total area of the grassland patch where the sampled site is located | |
| | Fractal dimension | Defines the compactness of the grassland patch (spread diffusely or comprehensive area of grassland) of the sampled site | |
| | %-woody land cover, r = 500 m | Areal share (in percent) of woody land cover classes in the wider surrounding of the sampled site at a radius of 500 m | |
| | %-agriculture, r = 500 m | Areal share (in percent) of intensive agriculture in the wider surrounding of the sampled site at a radius of 500 m | |
| | Nearest anthropogenic infrastructure, m | Closest anthropogenic infrastructure (any human built structure) measured in meter | |
| | Core area, ha | Total inner area of the patch where the sampled site is located, considering a distance of 3 m to the edge | Kindermann et al. (2023), Labadessa et al. (2017), McGarigal et al. (2023) |
| Species indicator values for the Italian flora | Light (L) | Preferred light conditions averaged for all species per site, range: 1 (shadow) - 12 (light) | Guarino and La Rosa (2019) |

**Table 1** (*continued*)

| Category | Variable (abbreviation) | Specification | Source |
|---|---|---|---|
| | Temperature (T) | Preferred temperatures averaged for all species per site, range: 1 (cold) - 12 (hot) | |
| | Continentality (C) | Preference for continental conditions averaged for all species per site, range: 1 (oceanic) - 9 (continental) | |
| | Humidity (U) | Preferred humidity averaged for all species per site, range: 1 (dry) -9 (humid) | |
| | Reaction (R) | Preferred soil conditions averaged for all species per site, range: 1 (acid) - 9 (alkaline) | |
| | Nitrogen (N) | Preferred nitrogen level averaged for all species per site, range: 1 (nutrient-poor) - 9 (nutrient-rich) | |

### 2.4. Data analysis

To test for differences in species composition between the historical and recent sites, we calculated multivariate dispersion within and among the sites based on Bray-Curtis dissimilarity implementing permutational analysis of variance. Since there is evidence that an active protection status could foster the conservation of dry grasslands in the valley (Kindermann et al., 2023), we defined our groups based on recent protected (22) versus non-protected sites (23, compare Suppl. Mat. 1 Table S2). Between-group variation confirmed highly significant differences (F = 5.96, $p$ = 0.001) between all groups (historic, recent protected, recent non-protected). Within-group variation was not significantly different (F = 0.78, $p$ = 0.51), which confirmed the suitability of the designated groups. Thus, we appointed the following groups for the subsequent analysis: (i) recent non-protected sites, (ii) recent protected sites and (iii) the respective historical sites. For calculations we used the statistical programming language R (R Core Team, 2023) using the package *vegan* (Oksanen et al., 2022).

### 2.4.1. Changes of environmental variables over time

To identify general temporal patterns of change in environmental variables, which reflect shifts in species indicator values for habitat conditions and changes in management-related and climatic variables (as detailed in Table 1), we employed the mean response ratios (RR) as our effect size estimate. The RR represents the natural-log proportional change of mean variable values (Xi) between historic and resurveyed plots [RR = ln(Xi_resurvey/Xi_historic)]. This analysis enabled us to distinguish between protected and non-protected sites, allowing us to identify variations in proportional changes of environmental variables over time. Positive RR values indicate an increase in the respective variable, while negative RR values indicate a decrease, with zero suggesting no change. Significance was established when the 95 % confidence interval (CI) did not overlap with zero. To perform these RR calculations, we used the "escalc" function from the *metafor* package (Viechtbauer, 2010). We applied the ROMC measure to account for potential correlations between observations arising from the paired and longitudinal nature of our data (Lajeunesse, 2011).

### 2.4.2. Changes in communities and relation to environmental variables

To understand species changes and relevant environmental drivers, we performed the following analyses:

(i) We assessed differences in species composition by applying non-metric multidimensional scaling (NMDS) as an ordination method based on Bray-Curtis dissimilarity (k = 3 dimensions, stress value = 0.17). Followingly, we used generalized additive modelling (GAM) to analyze the relationship between community composition and environmental variables. To avoid under$-$/overdispersion, we optimized the selected model parameters by iterative assessment of various diagnostic tests (residual quantile-quantile plots, residual histograms, *p*-values for the parametric coefficients and the basis dimension (k = 4) of the model's function, provided in Suppl. Mat. 5). We best approximated the original probability distribution family within the model (tweedy, Gaussian, or negative binomial) to account for non-normally distributed data (Wood et al., 2016). To understand the statistical significance and effect size, we calculated average marginal effects (AME) of ordination scores for each environmental variable based on the NMDS axes (Arel-Bundock, 2023). We did not assess the effect size of indicator values because they are directly linked to species composition (Zelený and Schaffers, 2012). In a next step, we determined the impact of each environmental variable in explaining dissimilarity patterns between the groups through pairwise comparison of estimated marginal means (Arel-Bundock, 2023). This approach allowed us to draw nuanced inferences about the impact of the environmental variables on each group (magnitude). Finally, we visualized results of the GAM by fitting smoothed surfaces of the environmental variables onto the NMDS ordination, using the function "ordisurf" (Wood, 2011).

(ii) We assessed the compositional heterogeneity in relation to changes in the presence or absence of species. Therefore, we calculated binomial deviance ($\Delta D_i$) of recent species in comparison to the historical frequency of species occurrence by following the approach outlined in Baeten et al. (2014). This analysis allowed us to identify key species changes that significantly have influenced community composition, indicating either divergence (more heterogeneus composition) or convergence (more homogeneous composition) over time. Qualitatively, we focused on species that best describe overall community variation and trends. Specifically, we considered species that had a significant impact on the (dis)similarity between sampling sites (NMDS, function "envfit"), were characteristic for dry grasslands (following Braun-Blanquet, 1964, Delarze et al., 2015, Leuschner and Ellenberg, 2017) or had a significant $\Delta D_i$ in frequency of occurrence ($p \leq 0.05$, based on $n = 2000$ permutations). Species with $\Delta D_i < 0$ were considered as indicators of community convergence, i.e. rare species that became rarer or omnipresent species that became even more common. Contrastingly, species with values $\Delta D_i > 0$ were considered as indicators of community divergence, i.e. rare species that became more frequent or omnipresent species that became less frequent (Baeten et al., 2014).

Finally, we performed chi-squared tests (or Fisher's exact tests in the case of small count data) to test for significant ($p \leq 0.05$) shifts in species habitat preferences, life strategy, and life forms based on species presence/absence (i.e. count data) between groups. The significance levels were adjusted using Bonferroni correction for multiple testing.

For our analysis, we utilized R packages *vegan* (Oksanen et al., 2022), *rstatix* (Kassambara, 2022), *mgcv* (Wood, 2011), *gratia* (Simpson, 2022), *marginaleffects* (Arel-Bundock, 2023) and the function "dDEV" (Baeten et al., 2014).

## 3. Results

### 3.1. Changing environmental patterns

We observed significant differences in climatic variables ($T_{annual\ mean}$, $P_{annual\ mean}$, SHM) across all sites between the reference periods 1931–1960 and 1981–2010, with an increase in mean annual temperatures (+1.2 °C), higher precipitation levels (+5.8 %), and marginal increases in the SHM (+1 %, Fig. 2).

Patterns of temporal change in environmental variables, related to land use, were evident. Non-protected sites exhibited a significantly higher proportion of encroachment (RR = 0.35 [0.1, 0.60]) that increased by 43 % towards their edges. They also had a higher edge:area ratio, a closer distance to anthropogenic infrastructure, and a marginally greater fractal dimension compared to historical site means.

Protected sites, on the other hand, also had a higher edge:area ratio. They also showed a substantial change in the share of intensive agriculture amounting to an 88 % increase in their surroundings and a simultaneous decrease of woody land covers. For the other variables, no consistent trends were observed due to high standard deviations and variation among sites.

Species indicator values exhibited similar temporal trends across all sites, with L, T, and C marginally decreasing, and N increasing significantly at both non-protected and protected sites.

### 3.2. Impact of environmental variables on a changing species composition

Average marginal effects of the environmental variables (Fig. 3) indicate that an increase in dissimilarity between sites is significantly related to an increase in encroachment rate, fractal dimension, edge:area ratio, nearest anthropogenic infrastructure and all climatic variables. These effects vary across the ordination axes, with only the fractal dimension, mean annual temperature and nearest anthropogenic infrastructure consistently significant for both axes. A negative effect size is observed for mean annual precipitation in the second NMDS axis. The variables %-woody land cover and %-agriculture within a 500 m radius and core area show no significant relationship with both axis.

To address variations in the significance of environmental variables across groups, pairwise marginal means were computed (Table 2). Each variable is significant in at least one group comparison.

The model results confirm that non-protected sites differ significantly from historic sites in their response to environmental conditions (Table 2a). Community dissimilarity is significantly influenced by a higher share of encroachment and woody land cover on recent non-protected sites, along with a smaller mean core area compared to historical sites.

The most substantial factor contributing to the dissimilarity between historic and recent protected sites (Table 2b) was the share of agriculture, which has notably increased in the vicinity of protected sites. Community dissimilarity is further reflected in a rise in nutrient-demanding species, as well as changes in climatic variables and related lower species indicator values (i.e., T, L).

Table 2c identifies the key environmental variables driving community dissimilarity between protected and non-protected sites. Land use variables, particularly those associated with successional processes, have a more pronounced effect on the ordination patterns of non-protected areas, while intensified agriculture significantly influences the group of protected areas.

Fig. 4 displays the community dissimilarity between the groups with the smoothed surfaces (contour lines) of key environmental variables fitted to the NMDS ordination axes (see also Suppl. Mat. 6). The general dissimilarity patterns unveiled a gradual shift in community composition from the historical to the recent survey even though overall species numbers per site remained constant (historical: 27, recent protected: 26, recent non-protected: 31). Non-grazed sites exhibited the greatest dissimilarity, irrespective of their protection status.
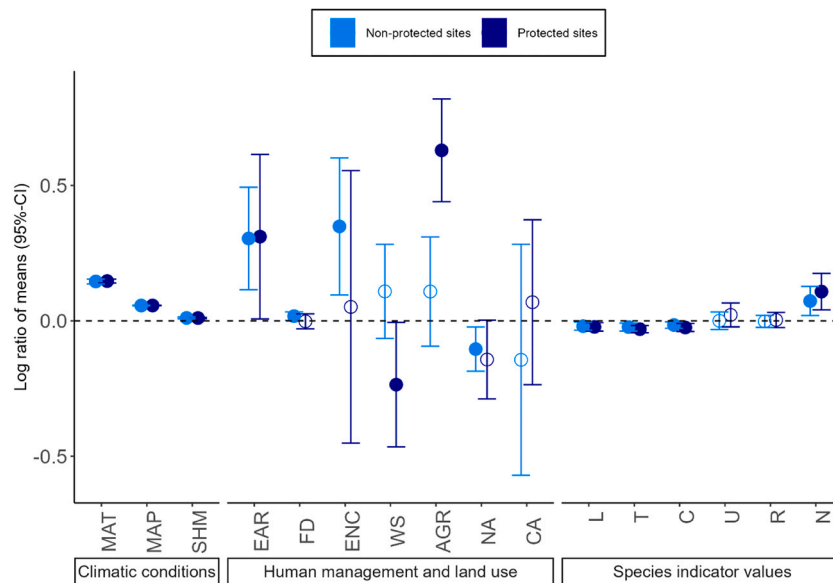
**Fig. 2.** Changes over time on protected (*N* = 22) and non-protected (*N* = 23) sites in environmental variables characterizing climatic conditions (MAT - mean annual temperature, MAP - mean annual precipitation, SHM - summer heat:moisture index), human management and land use (EAR - edge:area ratio, FD - fractal dimension, ENC - areal share of encroachment at a radius of 25 m, WS - areal share of woody land cover at a radius of 500 m, AGR - areal share of agriculture at a radius of 500 m, NA - nearest anthropogenic infrastructure, CA - core area), and mean species indicator values (L - light, T - temperature, C - continentality, U - humidity, R - reactivity, *N* - nitrogen). Changes are presented as mean proportional changes (response ratios), which are calculated as the natural logarithm of the ratio of means, along with a 95 % confidence interval (CI). We categorized sites into two groups based on their protection status: protected (*N* = 22) and non-protected (*N* = 23). A fully colored dot indicates a significant change in a variable over time, meaning the confidence interval does not overlap with zero. In contrast, hollow dots represent the absence of a significant change. When the values are positive, it suggests an increase in the variable, while negative values indicate a decrease.
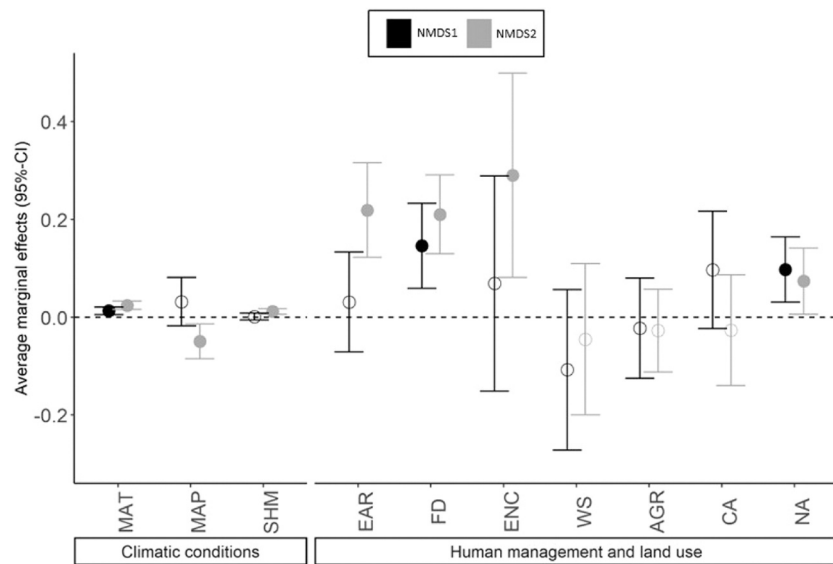


**Fig. 3.** Average marginal effects for all environmental variables as explaining variables for the dissimilarity patterns in the NMDS. Marginal effects are reported as proportional change of the variable with a 95 % confidence interval (CI). Each variable is represented for the two corresponding NMDS axes of the ordination. A fully colored dot indicates a significant effect of the variable, meaning the confidence interval does not overlap with zero. In contrast, no significant effect is illustrated by hollow dots. Variable abbreviations are: MAT - mean annual temperature, MAP - mean annual precipitation, SHM - summer heat:moisture index, EAR - edge:area ratio, FD - fractal dimension, ENC - areal share of encroachment at a radius of 25 m, WS - areal share of woody land cover at a radius of 500 m, AGR - areal share of agriculture at a radius of 500 m, NA - nearest anthropogenic infrastructure, CA - core area.

**Table 2**

Pairwise marginal means are calculated to identify differences in the impact of environmental variables on the community dissimilarity between groups. We computed three group-specific comparisons to precisely quantify the magnitude and significance of the environmental variables between: a) historic to recent non-protected sites b) historic to recent protected sites c) recent non-protected to protected sites. Significant differences are highlighted in bold and significance scores are coded as follows *: significant at $p \leq 0.05$, **: significant at $p \leq 0.01$, ***: significant at $p \leq 0.001$ and ns: not significant. A negative prefix of the pairwise marginal mean corresponds to a decrease. For example: both, encroachment and core area significantly explain the dissimilarity patterns between historical and recent non-protected sites (column a). While the encroachment has increased, the mean core area has decreased on recent non-protected sites.

| Environmental variable | a) Non protected - historic sites | | b) Protected - historic sites | | c) Protected - non protected sites | |
|---|---|---|---|---|---|---|
| | Pairwise marginal mean [CI] | z | Pairwise marginal mean [CI] | z | Pairwise marginal mean [CI] | z |
| $T_{annual\ mean}$ (C°) | 0.01 [−1.27, 1.29] | $0.01^{ns}$ | 0.9 [0.08, 1.72] | $\mathbf{2.16}^{*}$ | 0.9 [−0.34, 2.13] | $1.42^{ns}$ |
| $P_{annual\ mean}$ (mm) | 45.8 [−4.84, 96.40] | $1.77^{ns}$ | 99.8 [49.3, 150.3] | $\mathbf{3.87}^{***}$ | 54.0 [5.35, 102.6] | $\mathbf{2.18}^{*}$ |
| Summer heat:moisture index | 6.27 [−2.46, 15.0] | $1.41^{ns}$ | 10.79 [2.61, 19.0] | $\mathbf{2.58}^{**}$ | 4.52 [−3.05, 12.1] | $3.86^{ns}$ |
| Edge:area ratio | 0.18 [0.01, 0.35] | $\mathbf{2.12}^{*}$ | −0.08 [−0.19, 0.04] | $−1.35^{ns}$ | −0.26 [−0.42, −0.09] | $\mathbf{−3.04}^{**}$ |
| Fractal dimension | 0.02 [−0.09, 0.13] | $0.36^{ns}$ | −0.16 [−0.26, −0.06] | $\mathbf{−3.19}^{***}$ | −0.18 [−0.29, −0.07] | $\mathbf{−3.12}^{**}$ |
| %-encroachment ($r = 25$ m) | 47.60 [10.2, 85.1] | $\mathbf{2.49}^{*}$ | −15.2 [−40.5, 10.0] | $−1.18^{ns}$ | −62.9 [−98.3, −27.4] | $\mathbf{−3.47}^{***}$ |
| %-woody land cover ($r = 500$ m) | 37.1 [10.8, 63.46] | $\mathbf{2.77}^{**}$ | −10.1 [−26.5, 6.25] | $−1.21^{ns}$ | −47.3 [−72.9, −21.63] | $\mathbf{−3.61}^{***}$ |
| %-agriculture ($r = 500$ m) | −3.59 [−19.7, 12.5] | $−0.44^{ns}$ | 23.67 [10.8, 36.5] | $\mathbf{3.61}^{***}$ | 27.25 [15.2, 39.3] | $\mathbf{4.42}^{***}$ |
| Nearest anthropogenic infrastructure (m) | −1.31 [−2.29, −0.33] | $\mathbf{−2.63}^{**}$ | −0.89 [−1.62, −0.15] | $\mathbf{−2.36}^{*}$ | 0.43 [−0.48, 1.34] | $0.92^{ns}$ |
| Core area (ha) | −25.5 [−46.5, −4.55] | $\mathbf{−2.38}^{*}$ | −12.5 [−29.4, 4.28] | $−1.46^{ns}$ | 13.0 [−3.9, 29.89] | $1.51^{ns}$ |
| L | −0.03 [−0.23, 0.23] | $−0.23^{ns}$ | −0.39 [−0.61, −0.17] | $\mathbf{−3.45}^{***}$ | −0.36 [−0.61, 0.1] | $−0.36^{ns}$ |
| T | −0.29 [−0.55, −0.03] | $\mathbf{−2.17}^{*}$ | −0.23 [−0.41, −0.05] | $\mathbf{−2.46}^{**}$ | 0.06 [−0.2, 0.32] | $0.45^{ns}$ |
| C | −0.03 [−0.17, 0.11] | $−0.43^{ns}$ | −0.15 [−0.26, −0.04] | $\mathbf{−2.72}^{**}$ | −0.12 [−0.26, 0.02] | $−1.71^{ns}$ |
| U | 0.3 [−0.12, 0.17] | $0.34^{ns}$ | 0.2 [−0.11, 0.15] | $0.33^{ns}$ | 0.01 [−0.15, 0.14] | $0.05^{ns}$ |
| R | 0.09 [−0.23, 0.40] | $0.53^{ns}$ | −0.07 [−0.33, 0.19] | $−0.51^{ns}$ | −0.16 [−0.46, 0.15] | $−0.98^{ns}$ |
| N | 0.3 [−0.01, 0.61] | $1.89^{ns}$ | 0.33 [0.08, 0.58] | $\mathbf{2.59}^{**}$ | 0.03 [−0.32, 0.38] | $0.16^{ns}$ |

The contour lines further illustrate that particularly non-grazed sites are characterized by increasing encroachment rates (see Fig. 4a) and less compact patch areas, as indicated by an increasing fractal dimension (Fig. 4b). Moreover, sites with a high percentage of intensive agriculture in proximity (Fig. 4c) are associated with species that are adapted to high nutrient levels (Fig. 4e). Although climatic conditions indicate higher mean annual temperature values on recent sites (Fig. 4d), this is so far not reflected by species favoring high temperature values ($T_{Indicator\ values}$, Fig. 4f). Overall, the fitted surfaces reflect the results presented earlier (Fig. 3 and Table 2).

### 3.3. Species contribution to community variation

To understand the environmental impact on community composition, we displayed the key changes in species composition ($\Delta D_i$) and their changes in frequency (in brackets) in Fig. 5. Most species exhibited a positive relationship between groups and contributed to either increased or decreased community heterogeneity (quarters b and c). For example: *Achillea tomentosa* had a negative $\Delta D_i$, indicating increased homogeneity across sites due to its rarity and decline in frequency.

Fewer species exhibited a negative relationship (quarters a and d), indicating differing $\Delta D_i$ values between protected (x-axis) and non-protected sites (y-axis). Notably, certain species significantly contributed to greater community variation in non-protected sites, among them *Quercus pubescens* (tree), *Crataegus monogyna* (shrub) and *Senecio inaequidens* (invasive alien herb). These species did not show a significant trend on protected sites. Character species were evenly distributed across all quarters and did not show a significant trend. At the same time, mesophytic generalist species that are not typical of dry grassland were promoting heterogeneity, such as *Daucus carota* or *Trifolium campestre*. Moreover, those species were associated with sites that are surrounded by a high share of agriculture that significantly influenced the community variation (details on all species scores of the NMDS are provided in Suppl. Mat. 7).

Species indicative of historical sites in the NMDS were typical dry grassland species such as *Petrorhagia saxifraga, Carex supina* and *Potentilla pusilla*. Protected and non-protected sites without a grazing regime exhibited various species trends: On protected sites, typical dry grassland species such as *Lactuca perennis* and *Festuca rupicola* were characteristic species in NMDS, whereas on non-protected sites, less specialized and more mesophytic forbs such as *Hypericum perforatum* and *Vincetoxicum hirundinaria*, and invasive tree species such as *Robinia pseudoacacia* increased significantly.

Chi-Square tests (Table 3) confirmed the statistical significance ($p = 0.006$) of the occurrence of species not typical of dry grassland habitats between the two surveys and between both recent groups (Table 3ab, Suppl. Mat. 8). The presence of (nano)-phanerophytes increased significantly, particularly at non-protected sites ($p < 0.001$). Furthermore, the results indicate that species associated with specific life forms and ecological strategies have benefited from changing environmental conditions. On recent sites stress-tolerant ($p_{protected} = 0.036$, $p_{non-protected} = 0.006$, Table 3) and competitive species increased ($p = 0.028$, each). Overall, only the changes between the historical and recent records are significantly different (Table 3ab).
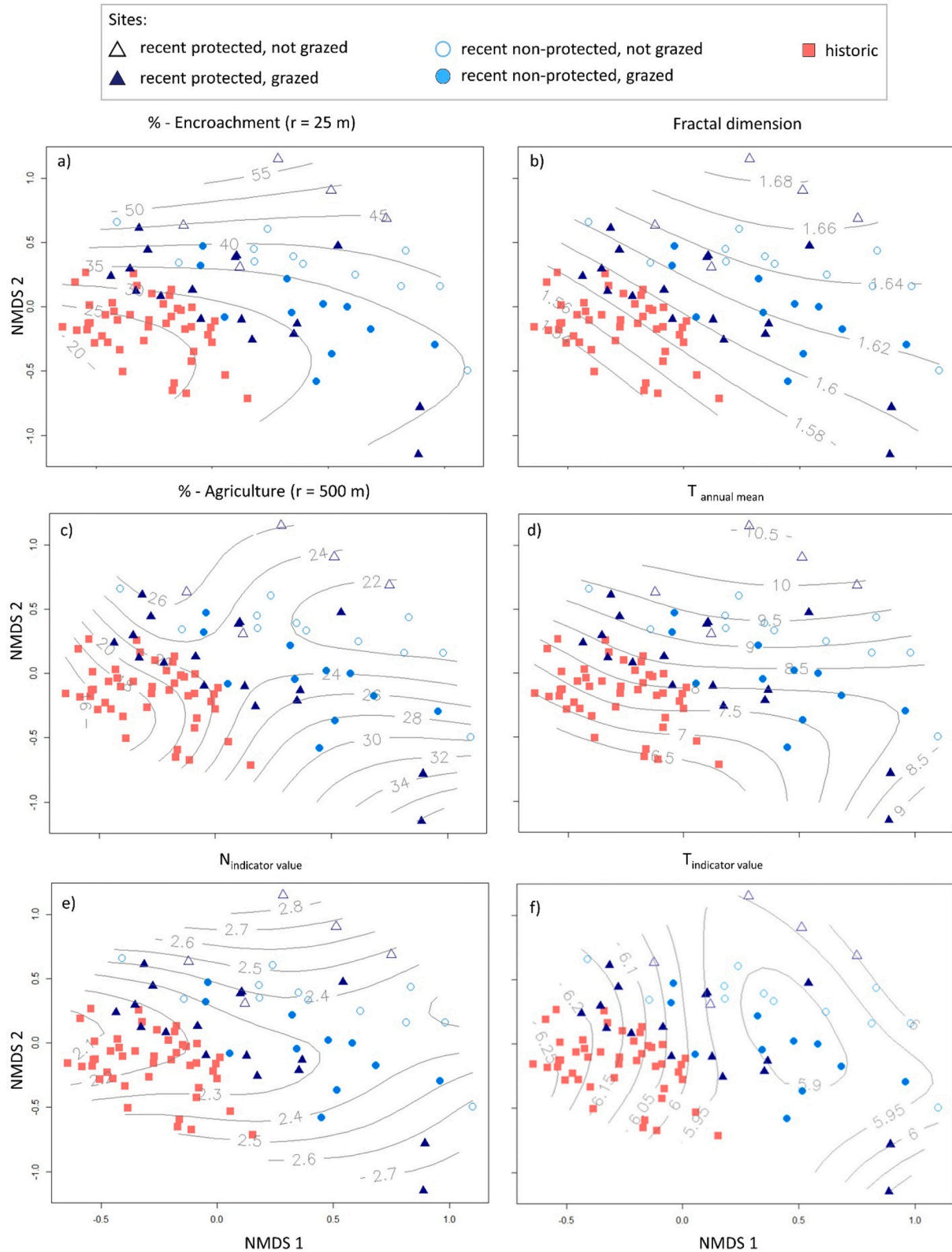
**Fig. 4.** Non-metric multidimensional scaling (NMDS) ordination based on past and present dry grassland species composition of all sites (equal for a–f). Additionally, a selection of significant environmental variables resulting from generalized additive modelling to the ordination axes are visualized as contour lines for: a) %-encroachment ($r = 25$ m), b) fractal dimension, c) %-agriculture ($r = 500$ m) and d) $T_{annual\ mean}$, e) $N_{Indicator\ valuesi}$ and f) $T_{Indicator\ values}$. Groups for the resampled recent sites are further divided into protected + grazed, protected + non-grazed, non-protected + grazed and non-protected + non-grazed sites to highlight diverging developments between varying management strategies.
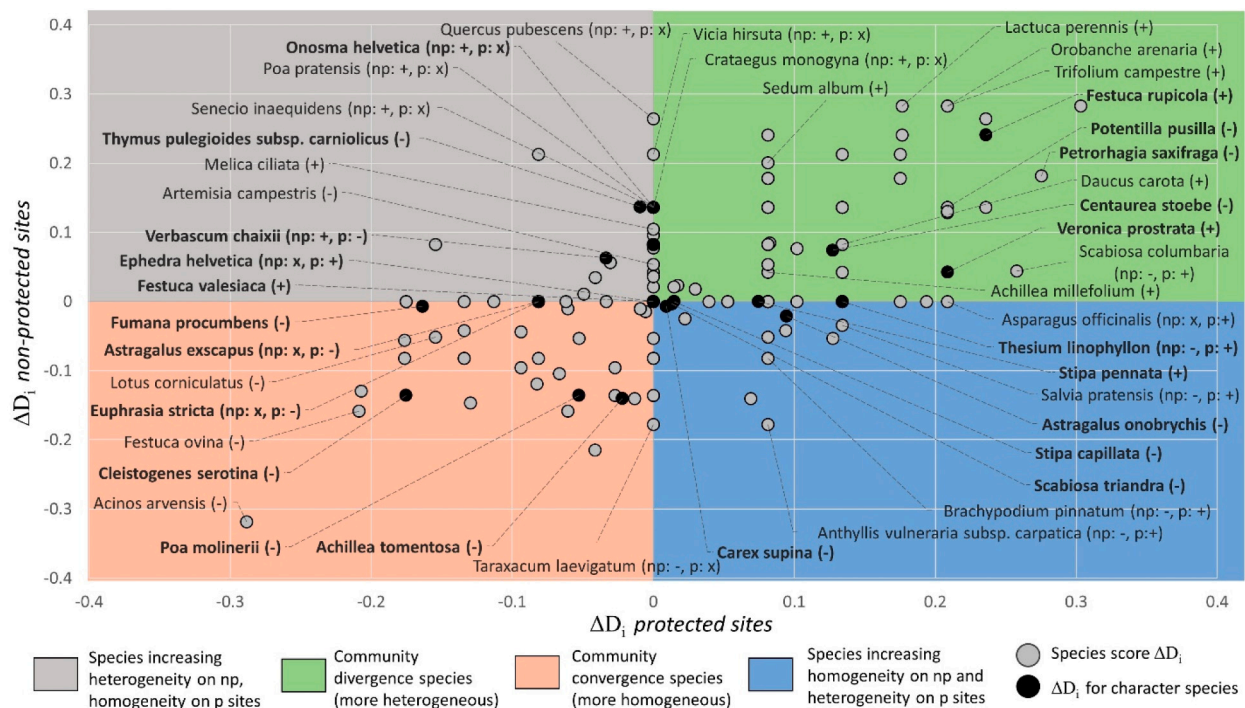
**Fig. 5.** Species that contribute to an increasing (values > 0) or decreasing (values < 0) community variation between recent non-protected (y-axis) and protected (x-axis) sites compared to the historical survey. A more homogeneous composition (values < 0) is represented by either rare species that became rarer or frequently present species that became more frequent (quarter b). The opposite quarter (c) accounts for a more heterogeneous composition (values > 0) between the sites. Quarter a and d show diverging trends between protected and non-protected sites. Changes in species frequency are indicated in brackets after the species names (np: non-protected and p: protected) as follows: + for increasing species frequency, − for decreasing frequency, x for species that were not present in one of the surveys for the respective group. Full species names as well as scores for all species can be consulted in Suppl. Mat. 7.

## 4. Discussion

### 4.1. Non-specialized species cause heterogeneous communities

Our resurvey, spanning over 70 years, uncovers the cause-effect relationship between vegetation dynamics and key environmental drivers that have shaped inner-alpine dry grasslands since then. We revisited historical sites surveyed as early as 1936 by Braun-Blanquet (1961), which allowed capturing the full magnitude of changes of these dry grassland communities. Our study revealed substantial deficits in the effectiveness of protected areas for preserving dry grasslands in a human-dominated landscape. Repeated field sampling confirmed substantial floristic changes of dry grassland sites in Val Venosta, in agreement with previous studies (Lübben and Erschbamer, 2021; Schwabe and Kratochwil, 2004). Particularly, the analysis of species gains and losses facilitated the identification of the relationship between species changes and environmental drivers in the dry grassland communities (Jandt et al., 2022).

By quantifying the effect size and magnitude of each environmental variable, we could demonstrate their impact on the species composition of all recent sites in comparison to the reference data. The profound landscape changes in the valley significantly impacted species composition, resulting in a degradation of the species composition across all recent sites (protected and non-protected). On non-grazed sites, the influences of surrounding woody habitats (%-encroachment in a radius of 25 m) provoked distinct species changes. The sites are characterized by an increasing presence of shrubs and trees, as well as higher frequency of species not typical of dry grassland habitats, which was also found by Lübben and Erschbamer (2021). This underpins the importance of grazing to counteract the effects of abandonment through litter reduction and curtailing encroachment (Dostálek and Frantík, 2008; Elias et al., 2018; Prangel et al., 2023).

Where no grazing regime is present, sampled sites were characterized by less compact and more heterogeneous patch structures (increasing fractional dimension and edge:area ratio) with proportionally larger fringe areas (Kindermann et al., 2023). This makes the grassland patches susceptible to the introduction of species from adjacent habitats (Diekmann et al., 2014). This was also evident on non-grazed protected sites. Hence, the overall increase in community variation and heterogeneity does not demonstrate successful conservation of dry grasslands, but rather indicates that the fragments are subject to progressive habitat shifts (Diacon-Bolli et al., 2012). Increased species richness at grassland edges is driven by ecotone conditions (Burst et al., 2017; Hilpold et al., 2018; Magnes et al., 2020), favoring strong competitors. This is indicated by the increase of tall-growing, long-lived species with rather low light requirements (Landolt et al., 2010), which was also found in German dry grasslands (Diekmann et al., 2014). Similarly, indicator values indicated a decline in thermophilic species typical of full light conditions.

Recent studies have highlighted that agricultural intensification currently exerts the greatest pressure on biodiversity in grassland ecosystems (Boch et al., 2018; Gossner et al., 2016; Hilpold et al., 2018). Our results showed that species composition significantly changed towards more nutrient-demanding species at sites surrounded by intensive agriculture ($r$ = 500 m), which was also found by Wesche et al. (2012). This trend was particularly strong on protected sites where the share of agriculture in the vicinity increased most. This indicates the predominant role of eutrophication as a human-induced pressure (Dengler et al., 2020; Török and Dengler, 2018), regardless of the protection status. While altered grazing intensity could directly contribute to nutrient increase, indirect mechanics refer to strong local winds in the valley (Wilhalm, 2018) that may contribute to the transport of nutrients (e.g., mineral fertilizer, gaseous nitrogen compounds) or sprayed insecticides (Tarmann, 2019) upslope into sensitive ecosystems, even in protected sites that are less impacted by successional processes.

The spatial pattern of dry grassland in the valley has changed

**Table 3**

We tested for significant differences between the two surveys (historic and recent) for the three functional groups: species' life strategy, form and habitat preferences. We tested for significant changes of historical sites to recent non-protected sites (a) and historical sites to recent protected sites (b). It was further tested if today protected and non-protected sites differed significantly between each other (c). Changes in species counts (#) in the functional groups are given as: + for increasing, − for decreasing and = for equal presence. Significant differences are highlighted in bold and coded as follows: *: significant at $p \leq 0.05$, **: significant at $p \leq 0.01$, ***: significant at $p \leq 0.001$ and ns: not significant. $P$-value and test statistics are based on a chi-square test or a Fisher's exact test (indicated as Fi) for groups with small count data.

| | | Test for significant differences of functional characteristics between historic and recent sites | | | | Equivalent analysis between recent site groups | |
| --- | --- | --- | --- | --- | --- | --- | --- |
| | | a) Change on non-protected sites | | b) Change on protected sites | | c) Protected vs. non-protected | |
| Functional group | | Trend | $\chi^2$ | Trend | $\chi^2$ | Trend | $\chi^2$ |
| Category | Subcategory | # | | # | | # | |
| Life strategy | Mixed strategy (csr) | + ns | 6.21 | + ** | 0.15 | + ns | 14.1 |
| | Competitive (c) | + * | 10.8 | + * | 1.03 | + ns | 9.16 |
| | Stress tolerators (s) | + ** | 18.2 | + * | 1.09 | + ns | 8.71 |
| | Ruderal | + ns | 0.25 | + ns | 0.06 | + ns | 0.55 |
| Life form | Geophyte | + ns | Fi | + ns | Fi | = ns | Fi |
| | Chamaephyte | + ns | 4.06 | + ns | 0.36 | - ns | 7.84 |
| | Hemicryptophyte | + ns | 7.73 | + * | 1.5 | + ns | 13.2 |
| | Therophyte | + ns | 1.71 | + ns | 0.07 | - ns | 0.07 |
| | (Nano)phanerophyte | + *** | Fi | + * | Fi | + ns | Fi |
| Community type | No typical dry grassland habitat | + ** | 27.9 | + ** | 2.83 | + ns | 22.4 |
| | *Convolvulo arvensis-Agropyrion repentis* | + ns | Fi | + ns | Fi | - ns | Fi |
| | *Sedo-Scleranthetalia* | = ns | 0 | + ns | 0 | = ns | 0.49 |
| | *Bromion erecti* | + ns | Fi | + ns | Fi | + ns | Fi |
| | *Xerobromion erecti* | + ns | Fi | + ns | Fi | - ns | Fi |
| | *Cirsio-Brachypodion pinnati* | + ns | 0.19 | + ns | 0 | = ns | 2.4 |
| | *Festucion valesiacae* | + ns | Fi | + ns | Fi | = ns | Fi |
| | *Stipo-Poion xerophilae* | + ns | 0.66 | + ns | 0 | = ns | 0 |

considerably (Kindermann et al., 2023). This became evident in the high proportion of dry grassland sites that were not traceable during our re-visitation of Braun-Blanquet's original sites (Braun-Blanquet, 1961). Even though the total areal transformation cannot be quantified based on our data, we could clearly show that losses in area are related to successional processes such as encroachment especially at those recent sites without grazing management. The strong anthropogenic landscape transformation is caused by agricultural intensification (Kindermann et al., 2023). In this regard, it has been found that the intensification towards apple monoculture in the valley had severe environmental impacts on the biota of upslope dry grassland and has partly led to an extinction of species belonging to the Zygaenidae family (Tarmann, 2019) and a wide-spread degradation of butterfly communities (Huemer and Tarmann, 2001). Consequently, biotic losses and homogenization seem inevitable in the long-term (Boch et al., 2018; Hilpold et al., 2018; Hodgson et al., 2005; Wilhalm, 2018), unless these adverse effects will be mitigated or fully controlled, e.g. though buffer zones or a reduction in pesticide use.

### 4.2. Future conservation of dry grasslands at a tipping point

Even though overall community variation has increased up to now, the clear trend towards generalist species immigration reveals the serious transformative status of the dry grasslands. Further environmental pressures, such as changing precipitation patterns with more pronounced weather extremes and overall temperature increases (IPCC, 2022) are expected to significantly alter vegetation structure in the future (Dibari et al., 2021; Midolo et al., 2021). The trend towards a deficit in water availability during summer heat, as indicated by the summer heat:moisture index, potentially comes along with an increase of drought/heat-stress tolerant species, extinction risks for less adaptive species, and the possibility of invasion by alien species (Hasanuzzaman, 2020).

Although the climatic conditions exhibited higher mean annual temperature values, this was not reflected in a higher abundance of species favoring high temperature values (i.e. species indicator values). These results are consistent with previous findings (e.g. Dengler et al.,

2014; Wesche et al., 2012), indicating that effects of climate change are not yet the primary cause of changes in floristic diversity. Even though future projections predict a loss of habitat suitability for montane species of up to 80 % by 2070–2100 (Engler et al., 2011), climatic trends may not necessarily lead to a decline in the rather well-adapted dry grassland species. On the contrary, we found that on recent sites fewer species adapted to a hot climate are present. Thus, species changes did not follow the same pattern as climatic conditions, but rather exhibited complex and divergent trends that were likely caused by multiple environmental interactions. The decline of species that prefer high temperatures ($T_{\text{Indicator values}}$), despite the divergent climatic trends, could be explained by the increasing woody cover. Shadowing effects could evoke a change in micro-climatic habitat conditions towards cooling (Bieringer et al., 2013; Labadessa et al., 2017; Thompson et al., 2017). Such combined environmental effects may become more problematic in the future. To fully understand the resilience of the dry grasslands to climate change impacts, further research is needed to determine the adaptive capacity of dry grassland species, as for example expressed in functional trait variation (Midolo et al., 2021; Wellstein et al., 2013).

Species composition close to the historical survey seem to depend on a rather low percentage of intensive agriculture in the surrounding area. Species associated with high adaptability to nutrient enrichment (e.g. *Brachypodium pinnatum*; Leuschner and Ellenberg, 2017) clearly increased in frequency in direct proximity to areas with intensive agriculture. Further, compactness and edge structure of the grassland patches were negatively associated with the absence of grazing, regardless of the protection status. Only actively grazed sites without intensive agriculture in the immediate vicinity maintained a similar spatial extent and community composition compared to the historical references.

Our results show that the designation of protected areas alone does not necessarily foster the preservation of dry grasslands as the surrounding landscape significantly influences their quality. Direct and indirect land-cover changes, such as succession, pose the most immediate threat to the extent and species composition of dry grasslands. This underpins the importance of integrating land use information into

climate change impact assessments to gain a comprehensive under-
standing of all consequences for biodiversity (Titeux et al., 2016). Since
intensive agriculture is not expected to decline in the valley, the future
conservation of dry grasslands remains questionable under both pres-
sures, with consequences for all species that depend on dry grassland
habitats (e.g. Tarmann, 2019; Wesche et al., 2012).

*4.3. Practical implications and recommendations*

Dry grasslands represent a heritage of the European cultural land-
scape (Hejcman et al., 2013). While active protection measures, such as
shrub removal, are successful tools for maintaining the habitat extent,
the overall trends on both protected and non-protected sites revealed
that current conservation efforts might not be sufficient for the
comprehensive preservation of these inner-alpine dry grasslands. Pre-
serving dry grasslands remains challenging within a cultural landscape
that is dominated by intensive agriculture and the cessation of tradi-
tional management such as grazing. Such processes are equally preva-
lent in other inner-alpine dry valleys (e.g. Boch et al., 2019; Magnes
et al., 2020). The alerting results call for more in-depth and prompt
conservation efforts (García-Roselló et al., 2023), particularly when
considering the significant contribution of dry grasslands to the overall
biodiversity of inner-alpine dry valleys (Kirschner et al., 2020; Wilhalm,
2018). Successful conservation requires increasing societal awareness
and responsibility (Ramos et al., 2016). In this context, especially
transdisciplinary and integrative approaches are needed to reinforce
joint efforts of conservation at landscape-scale (Nguyen et al., 2021;
Rinawati et al., 2013). As outlined by Bennett (2016), such approaches
can greatly strengthen the stakeholders' connection to the traditional
landscape, ensuring that the efforts undertaken have a lasting impact
(Valkó et al., 2018). A shift towards more sustainable management
systems that account for landscape-level interactions seems inevitable to
preserve the remaining dry grassland fragments in coexistence with
culturally evolved agricultural land use.

*4.4. Remaining uncertainty in the resampling approach*

Resurvey studies potentially are biased due to the imprecise reloca-
tion of the historical sampling sites. While we cannot completely dismiss
a potential observer bias and potential relocation error (Kapfer et al.,
2017), adherence to the strict protocol (by incorporating all available
historical site information) allowed us to assume quasi-permanent plots.
Uncertainties about sampling parameters, including timing and species
identification expertise, were best mitigated through repeated site visits
and consultation with experienced botanists familiar with critical taxa in
the flora in South Tyrol. Even though the findings must be interpreted
with care, identified species changes in our study generally confirm
previous findings in Val Venosta (Lübben and Erschbamer, 2021). Our
results also corroborate that the remaining uncertainty manifests as
statistical noise rather than systematic error in our long-term vegetation
change analysis (Kopecký and Macek, 2015). Moreover, our study pro-
vided a direct link between potential drivers and observed changes in
species composition, which proved consistent with expected pressures
on dry grasslands (Dengler et al., 2014; Diekmann et al., 2014; Török
and Dengler, 2018). Although we cannot rule out the possibility that
individual rare species remained undetected, resurvey studies still offer
the best strategy for documenting changes in vegetation from past to
present under the premise of careful interpretation (Chytrý et al., 2014).
Since the most dramatic floristic changes likely occurred in the mid-20th
century due to the expansion of the agro-industrial sector entailing
management intensification (Leuschner and Ellenberg, 2017; Wesche
et al., 2012), our study is of particular value despite some inherent
uncertainties.

## 5. Conclusion

Today's continental steppe-like dry grassland sites are embedded in
an increasingly inhospitable landscape matrix for the preservation of
such highly specialized habitats. Dry grassland species composition has
changed markedly, even within protected areas. The most imminent
drivers of change are related to alterations in land use. While there is
more variation within and between sites compared to the historical
survey, the increasing heterogeneity can be attributed to immigration of
non-specialized species from the surrounding habitats. Our results imply
that the original dry grassland sites are changing towards increasing
dominance of shrubs and more nutrient demanding species in proximity
to highly intensive farmland, such as apple orchards. We documented
this trend regardless of the current protection status, which highlights
that current protection efforts might not be sufficient to secure the long-
term preservation of the remaining dry grassland sites. While the overall
extent of dry grassland in protected areas remained relatively contin-
uous, plant communities did not necessarily indicate habitat integrity.
Instead, they exhibited similarly pronounced changes in species
composition compared to non-protected sites depending on the land-
scape context (i.e. on non-grazed sites and next to intensive agriculture).

In our study of dry grassland communities, we successfully identified
the causes and consequences associated with relevant environmental
change drivers. Our approach goes beyond conventional dissimilarity
metrics, adopting a landscape-ecological perspective that accounts for
species-environment interactions. Our findings underpin the need for
increased conservation efforts to effectively mitigate the evident envi-
ronmental impacts. The most straightforward solution might present a
combination of active shrub removal and the reintroduction of suitable
grazing regimes to counteract adverse successional processes. However,
it is crucial to think beyond individual actions and address landscape-
scale processes too, such as the drift of nutrients and pesticides from
intensive agriculture, which have emerged as additional and highly
relevant factors of degradation. To effectively address environmental
impacts and ensure the long-term preservation of the remaining dry
grasslands, a holistic conservation approach involving interdisciplinary
collaboration and engagement with diverse stakeholders across the
entire landscape context will be essential.

**CRediT authorship contribution statement**

EK, NH and CW conceptualised the study. EK, GB, ME and CW
collected field data. EK developed the methodology. EK carried out data
curation, with assistance of GB. EK performed the data analysis, with
assistance of ME. EK prepared the original draft of the manuscript. CW
and NH supervised the study. All authors reviewed and edited the
manuscript.

**Declaration of competing interest**

The authors have no relevant financial or non-financial interests to
disclose.

**Data availability**

All data that was generated during this study (i.e. field data) is shared
in the supplementary material. Historical reference data can be con-
sulted in the monograph of Josias Braun-Blanquet, published in 1961.

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## Appendix A. Supplementary data

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