universität wien

MASTERARBEIT / MASTER'S THESIS

Titel der Masterarbeit / Title of the Master's Thesis

Vegetation change in a pre-alpine landscape in the Northern Alps over 25 years

verfasst von / submitted by

Helena Kassandra Schwaiger BSc

angestrebter akademischer Grad / in partial fulfilment of the requirements for the degree of

Master of Science (MSc)

Wien, 2022 / Vienna, 2022

Studienkennzahl lt. Studienblatt / degree programme code as it appears on the student record sheet:	A 066 879
Studienrichtung lt. Studienblatt / degree programme as it appears on the student record sheet:	Masterstudium Naturschutz und Biodiversitätsmanagement
Betreut von / Supervisor:	Assoz.-Prof. Mag. Dr. Franz Essl

Table of contents

1. Abstract/ Zusammenfassung

1.1 Abstract

Both the abandonment and the ongoing intensification of land use lead to changes in vegetation composition, especially in nutrient-poor habitats such as extensively used grasslands. In my master thesis, I re-surveyed 151 relevés in the Jaidhaus basin in the Northern Alps of Upper Austria from the mid-1990s to assess how species richness and composition has changed, and to identify the underlying drivers. The focus was given on grasslands as grassland habitats are known to be particularly vulnerable to changes in land use, and many grasslands in Central Europe have been shown to loose species due to land use intensification or abandonment.

I found that the average species number in plots has not changed significantly over time, as both relevés with substantial species losses and gains have been recorded. However, there was a clear species turn over in the plots, with winners consisting mostly of species that prefer nutrient-rich conditions, while a substantial fraction of species of nutrient-poor sites declined. In particular, eutrophication was particularly conspicuous in vegetation types of nutrient-poor sites (Festuco-Brometea and Calluno-Ulicetea), and in wet habitats such as the Scheuchzerio-Caricetea fuscae. Wet habitats also showed clear signs of becoming more mesic. On average, thermophilic species increased in abundance across almost all vegetation types. Finally, alien species which were rare in the 1990s became considerably more abundant in the re-surveyed plots, with *Erigeron annuus* being the most common one. Still, the level of invasion is low.

Keywords: alien species, Ellenberg indicator values, grasslands, Jaidhaus basin, long-term vegetation change, plant species diversity, species loss

1.2 Zusammenfassung

Sowohl die Nutzungsauflassung als auch die Intensivierung der Landwirtschaft bringen Veränderungen in der Vegetation mit sich. Davon besonders betroffen sind Lebensräume nährstoffarmer Standorte. In meiner Masterarbeit habe ich 151 Vegetationsaufnahmen, welche bereits in 1990er Jahren im Jaidhaustal der oberösterreichischen Voralpen erhoben wurden, wiederholt. Ziel war es, die Veränderungen im Artenreichtum, aber auch die Veränderungen in der Artenzusammensetzung zu untersuchen und mögliche Ursachen dafür zu erfassen. Dabei wurde der Fokus auf Grünland- und Offenlandstandorte gelegt, da diese Lebensräume besonders von Landnutzungsänderungen betroffen sind. Außerdem verzeichnen zahlreiche Grünland-Lebensräume in Mitteleuropa starke Verluste in ihrem Artenreichtum durch Landnutzungsintensivierung und Nutzungsaufgabe.

Die Ergebnisse zeigen, dass sich die durchschnittlichen Artenzahlen der Aufnahmeflächen nicht signifikant von jenen der ersten Aufnahmen unterscheiden. Wobei sowohl Aufnahmen mit deutlichen Verlusten als auch welche mit starken Zunahmen an Arten zu verzeichnen sind. Deutliche Veränderungen zeigen sich jedoch in der Artenzusammensetzung: die Gewinnerarten gehören großteils Arten nährstoffreicher Standorte an, während zahlreiche, an nährstoffarme Bedingungen gebundene Arten starke Rückgänge erlitten haben. Besonders von der Eutrophierung betroffen sind Lebensräume nährstoffarmer Standorte wie die Klasse der Festuco-Brometea und Calluno-Ulicetea und feuchte Standorte wie die Klasse Scheuchzerio-Caricetea fuscae. Die vorkommenden Feuchtlebensräume zeigten zusätzliche eine deutliche Tendenz hin zu mesischen Bedingungen. In den meisten Vegetationsklassen ist außerdem ein Anstieg der Temperaturzahlen im Untersuchungszeitraum erkennbar. Neophytische Arten, die in den 1990er Jahren eine unbedeutende Rolle spielten, haben in den letzten 25 Jahren deutlich zugenommen, wobei *Erigeron annuus* die häufigste Art darstellt. Dennoch halten sich die Neophyten auf einem geringen Niveau.

2. Acknowledgements

I want to thank my supervisor Assoc.-Prof. Mag. Dr. Franz Essl for the great support and for providing the data from his diploma thesis. Further, a big thank to Bernd Lenzner, PhD, who supported the statistical analysis. I would also like to thank Michael Strauch, department for Nature protection (government of Upper Austria) and Mag. Christian Hatzenbichler (Bergwiesn-Verein) for providing photographs and information about land use and management measures in the protected area. Last but not least, a big thanks to Bettina Leitner, MSc, for the mental support and providing photographs. Thank you for your support.

3. Introduction

Human activity has a large impact on global biodiversity loss (Mihoub et al., 2017; Finderup Nielsen et al., 2019) due to land use changes, pollution, climate change, direct exploitation, and the introduction of invasive alien species (IPBES, 2019). However, on smaller spatial scales studies disagree in terms of reported changes in species richness and show divergent results. While many surveys revealed a decline in plant diversity (Eichenberg et al., 2021; Jansen et al.,2019; Hülber et al., 2017; Wesche et al., 2012), as well no net-changes in species richness have been recorded (e.g., Vellend et al. 2013; Diekmann et al., 2014; Ridding et al., 2021) or species richness has even increased in some cases (e.g., Finderup Nielsen et al., 2019; Mitchell et al., 2017; McCune et al., 2013; Bühler et al., 2011). Both rare and common plant species decline is associated with different anthropogenic drivers. Increasing eutrophication via fertilization and airborne nitrogen deposition is one important driver of biodiversity loss (e.g. Bobbink et al. 2015). The fragmentation of habitats increases isolation of remaining habitat patches with detrimental impacts on diversity (Jansen et al., 2019). In Europe, rare und threatened species experienced severe losses in recent decades (Zehm et al., 2020; Kempel et al., 2020); however, in some cases conservation efforts have halted or reversed these declines (Bruelheide et al., 2020). Species which are not in the focus of monitoring projects are often overlooked and their decline occurs unnoticed as was recently shown for moderately common species (Jansen et al., 2019; Bruelheide et al., 2020).

Those plant species that have increased in abundance are mostly those that grow well under high nutrient inputs such as nutrient-indifferent species (Peppler-Lisbach et al., 2020) or species restricted to nutrient rich conditions (Hülber et al., 2017). Further, gains and losses differ between native and non-native species (Cardinale 2018), and accordingly, the invasion of new, alien species can (partly) compensate for the loss of native species. As a result, plant communities often become more homogeneous (Bühler & Roth, 2011; Finderup Nielsen et al., 2019).

European grasslands have been created over thousands of years by extensive land use (grazing, mowing) on a wide range of different sites (Tälle et al., 2016); consequently, grasslands are highly diverse and a wide range of different grassland habitats have

developed (Habel et al., 2013, Batáry et al., 2015, Janssen et al., 2016) These grasslands are important contributors to biodiversity (Habel et al., 2013). For grasslands in Europe, the intensification of land use is one of the major drivers of plant biodiversity loss with cascading effects on other taxonomic groups such as arthropods (Gossner et al., 2016). In addition, the opposing process, i.e. the abandonment of marginal, yet often species rich extensively used grasslands, is another ongoing process with substantial negative impacts on grassland biodiversity (Halada et al., 2017). Thus, low-intensity farming is crucial for the conservation of a large fraction of European grassland biodiversity (Sutcliffe et al., 2015). The abandonment of these biodiversity rich habitats changes their ecosystem functions and structure (Halada et al., 2017) which underlines the importance of persisting land use. The traditional forms of sustainable land use serve not only a natural but also a cultural heritage (Tälle et al., 2016). Although numerous grassland habitats are protected by the European Habitas Directive (European Commission, 2007), grassland habitats severely decreased in area of extent and occurrence in the last decades (Hülber et al., 2017). Since these nutrient-poor grasslands are not ecomnomically profitable any more, they have mostly been abandoned or fertilized followed by high-intensity mowing or grazing. Both intensification and abandonment of land use cause a loss of grassland species (Diekmann et al., 2014).

Another facet of the human impacts on plant diversity is the spread of alien species. In particular, European lowlands and warm areas are increasingly invaded by alien species (Chyrtrý et al., 2009). Various drivers cause the spread of these non-native species, like climate change (Marini et al., 2009), human disturbance (Medvecká et al., 2013), nutrient availability (Medvecká et al., 2013) and transport along train and road networks (Kueffer, 2011). Due to climate change, a further spread of aliens into higher altitudes is expected (Kueffer, 2011). While the level of invasion of aliens into grasslands is still relatively low in Europe, it is increasing (Axmanová et al. 2021).

In this thesis, I assessed the changes in the grassland vegetation of a pre-alpine landscape in Upper Austria – the Jaidhaus basin – over 25 years by re-surveying 151 plots sampled in 1995. In particular, the following research questions were addressed: 1) How did species richness and community composition (e.g. by using Ellenberg Indicator Values) change over the last 25 years? 2) What are the impacts of land use, land use changes and of the

recent establishment of a protected area on observed changes in species richness and community composition? 3) Did the distribution of aliens increase during the last 25 years?

4. Methods

4.1 Study area

The study area is located in the pre-Alps near the village of Molln in southeastern Upper Austria. It consists of a grassland-dominated landscape in a basin with the name “Jaidhaus” situated at the Krumme Steyrling, a tributary of the Steyr-river. The Jaidhaus basin covers an area of about 5 km^2 (Figure 3).

In the north, the study area is delineated by the mountain-peaks Kienberg and Hirschkogel. The southern part of the study area is encircled by the Tanzkogel and the Großer Buchberg in the west and the Raiblmaissspitz in the east. All surrounding mountains reach an altitude of around 1000 m above sea level (BEV, 2021), whereas the study area is located between 510 to 720 meters above sea level. The river Krumme Steyrling is a braided river that is running through the study area from south to the north. At the forester's lodge Jaidhaus, another small valley opens to the east, called “In den Sanden”, which is drained by a brook that seeps away in summer (Figure 3).

This pre-alpine landscape is characterised by meadow and pasture farming, due to the reforestation of abandoned grasslands, forestry has increased in importance during the last decades (Land OÖ, 2010). The valley floor is characterized by meadows, pastures as well as narrow floodplain-forests and a few wet meadows along the Krumme Steyrling. Most of the steep slopes rising from the valley floor are currently used for forestry, and to a lesser extent for grazing. Due to the steepness of the terrain, many meadows and pastures were abandoned and became afforested (Priller, 2014) (Figure 1).

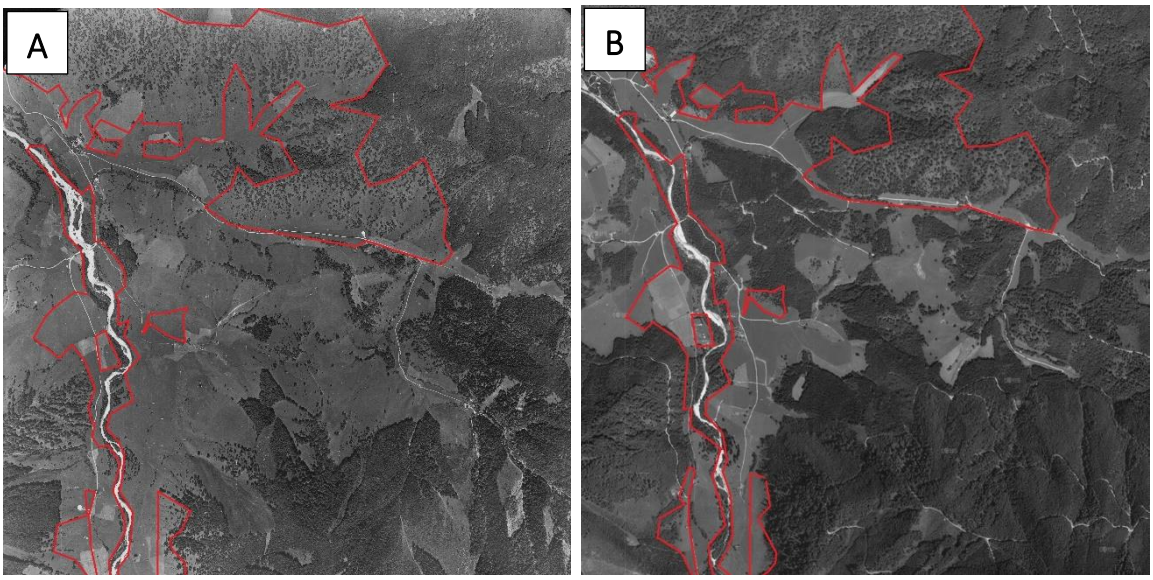

Figure 1: Aerial photographs of the study area and the conservation area (red) A) taken in 1953, Source: Bundesamt für Eich- und Vermessungswesen. flight title: 1953002. Picture 8060 edited by Christian Hatzenbichler; B) taken in 2013, Source: http://www.doris.at/Karten/karten.aspx edited by Christian Hatzenbichler.

On account of the commitment of the association Bergwiesn Verein, some of these abandoned steep former grasslands have been put again into use in recent years (Bergwiesn Kulturlandschaftspflegeverein, 2021). The two aerial photographs above (Figure 1) and the photographs below (Figure 2) show how re-afforestation and succession have changed the landscape during the last decades.

Except for a few weekend houses, a forester's lodge and a fish farm at the northern entry of the basin, there are no houses. There is one public road that leads to the National Park Kalkalpen, a few kilometers further south.

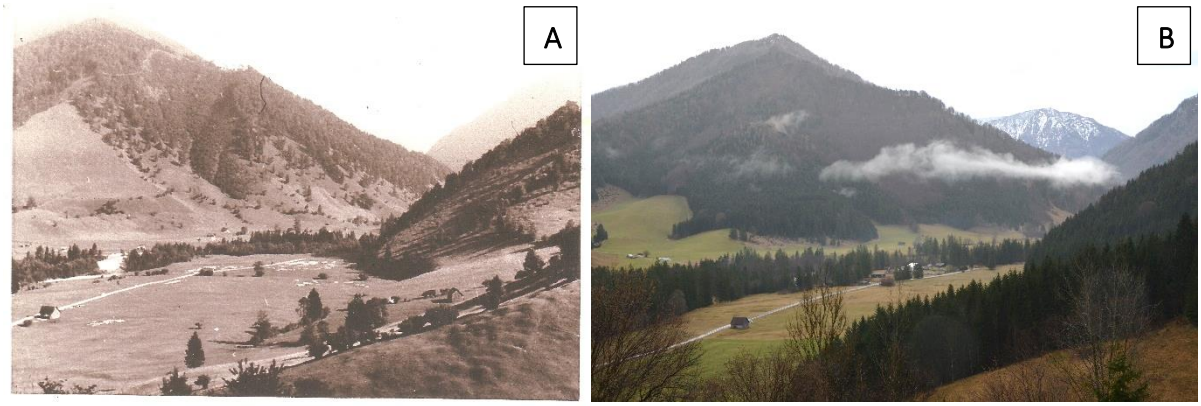

Figure 2: (A) Photography from the 1950ies showing the "Buckelwiesen" in the Jaidhaus basin, view to southeast with Rablmaiß-Spitz in the background, Source: Christian Hatzenbichler; (B) same view in 2021, Source: Bettina Leitner

4.1.1 Geology and climate

The study area belongs to the Northern Calcareous Alps (Oberösterreichische Voralpen), and is characterized mostly by alkaline soil conditions. Limestone and dolomite form the bedrock, and the Krumme Steyrling deposited calcareous gravel in the valley floor and re-shaped the geomorphology there. The "Buckelwiesen", i.e. grasslands with a mosaic of shallow depressions and small mounds, which are unique for the area, were formed by the dynamics of the river and, on account of their small-scale relief heterogeneity, offer a broad spectrum of micro-habitats (Haseke, 1995).

The Jaidhaus basin is characterized by a temperate sub-oceanic montane climate with high precipitation. The weather station at 600 m altitude in Windischgarsten (ZAMG) which is located c. 20 km to the south reported an annual precipitation sum of 1473 mm in 2020 (1443 mm in the reference period 1990-2010); annual mean precipitation for the last decade (2011-2020) were 1419 mm, i.e. an change of 24 mm compared to the previous twenty years. The annual mean temperatures for the same year was 8.9°C compared to 7.4°C for the reference period (1990-2010); in general, annual mean temperatures for this weather station for the last decade (2011-2020) were 8.9 °C, i.e. an increase of 1.5 °C compared to the previous twenty years (ZAMG, 2020).

4.1.2 Protected area

Already in the 1990s, plans to establish a protected area in the Jaidhaus basin were developed, but did not realize (Essl, 1999). Finally, in 2014, a nature conservation reserve including 35 hectares of meadows and pastures and 284 hectares of forests (including open forests with interspersed abandoned grasslands) was decreed (Priller, 2019). It contains many habitats of high nature conservation value, of which extensively used, nutrient poor meadows and pastures are of particular importance (Essl, 1999). They provide habitat for many species that have become rare in Upper Austria (Hohla et al., 2009), for instance *Aster amellus* (Italian Aster), *Anacamptis morio* (Green-winged Orchid),

and *Anacamptis pyramidalis* (Pyramidal Orchid) (Aeschimann et al., 2004; Fischer et al., 2008).

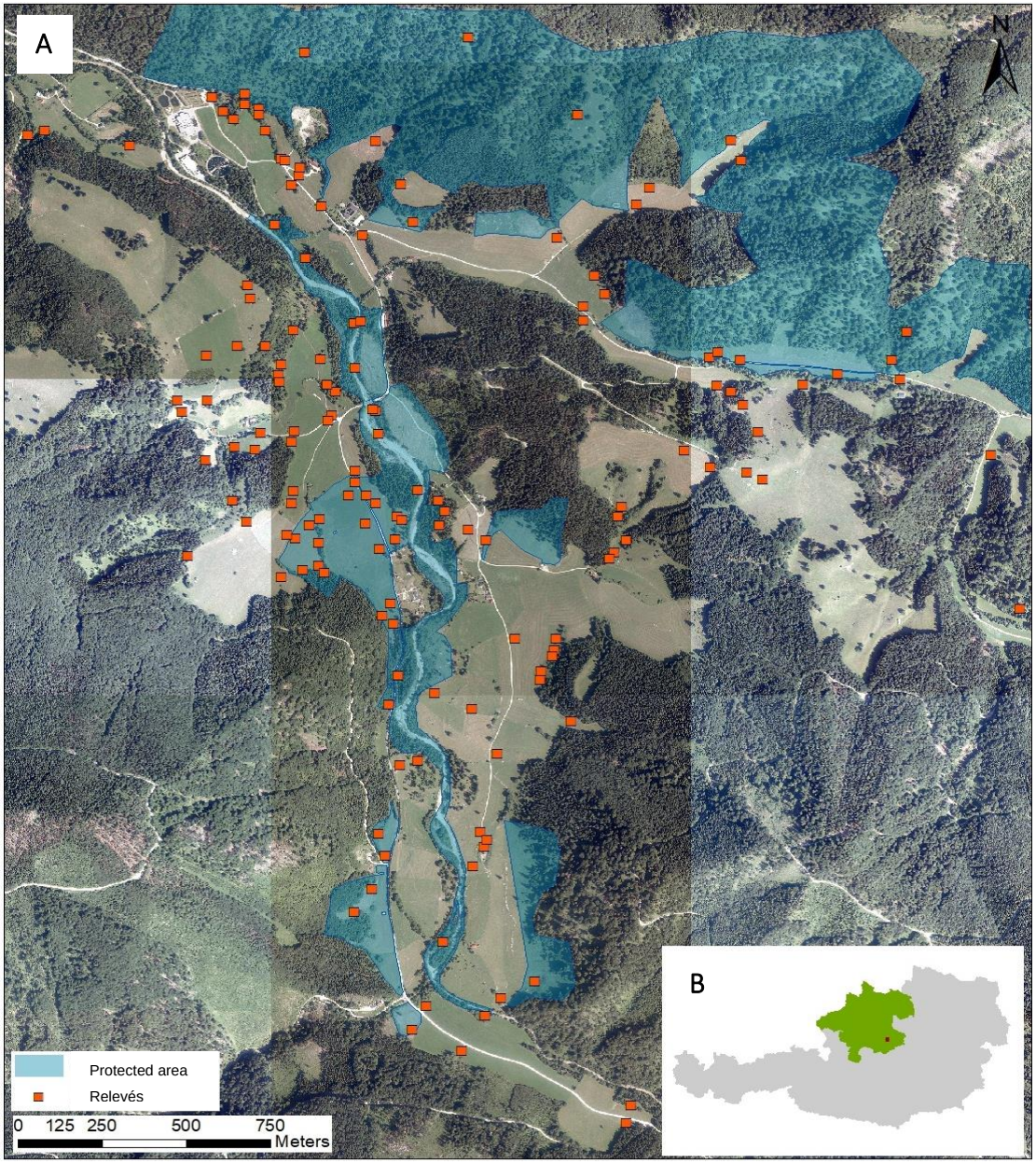

Figure 3: (A) Overview of the study area Jaidhaus basin including the protected area (blue area) and the sampling plots (orange dots). (B) Location of the study area (red box) in Austria (grey) and Upper Austria (green) Source: Open Government Data (Land Oberösterreich)

In addition to regular mowing times and restrictions on fertilizer application, further conservation measures have been implemented in the protected area. Some afforested areas with a total size of 14 ha have been cleared and some of them were sown with a broad range of species by transplanting hay from adjoining areas. The cleared

"Buckelwiesen" east of the bridge Seebachbrücke are now grazed with white donkeys, in order to restore the former nutrient poor pastures (Priller, 2019).

4.2 Sampling design

About 250 relevés were established in the Jaidhaus basin by Essl (1998) in 1995 and 1996. These include many different vegetation types such as grasslands, rocks, forests, and river gravel (Essl, 1998). As my study focuses on grasslands, relevés from other vegetation types were excluded – as it was argued that vegetation changes in non-used (e.g. river gravel) or less-intensively used (i.e. forests) likely were moderate. For relocating the relevés, field maps, old notations, and verbal descriptions of the plots in Essl (1998) were used. In the second survey period, I used a GPS to locate the exact position (geographic uncertainty: 3 m) of the plots (Table S 1: GPS coordinates of the resurveyed plots. Coordinate system: WGS84Table S 1).

Data collection

Although the historical data was collected according to the Braun-Blanquet method (Braun-Blanquet, 1984), the resurvey was done using species cover estimates in percent as this method is more appropriate for quantifying vegetation changes. For most of the relevés, such as meadows, pastures and fallows, plot size of 40 m^2 (mostly squares of 5 x 8 meters depending on the terrain) was chosen, replicating the plot size of the first sampling period. For some vegetation types, however, smaller plots of 5 or 8 m^2 (squares of 1 x 5 and 2 x 4 meters) were established, e.g. in ruderal sites, trampled grasslands or rock habitats (Essl, 1998). In addition to the basic header data of the relevé, a complete species list was collected, subdivided into three layers: herb layer, shrub layer (height of woody plants > 1 m), and tree layer (> 5 m); the proportion of the plot covered by each species was estimated in percent for each layer.

Sampling took place between early May and end of August 2020. The sampling date was set close to the sampling date of the initial survey to ensure compatibility among surveys.

4.3 Analysis

For evaluation and analysis, I transformed the historical data from Braun-Blanquet to percentage values acoording to Tüxen & Ellenberg (1937) and van der Maarel (1979).

For each species, I retrieved the Ellenberg Indicator Values (EIV) from (Ellenberg & Leuschner, 2010). EIVs characterize species ecological preferences in relationship to environmental factors, i.e. nutrient availability, light, water availability, temperature, climatic continentality, soil reaction and soil salinity (Ellenberg & Leuschner, 2010). They are based on expert opinion and are given in nine categories. EIVs are widely used for ecological analyses (Ellenberg, 1992). Here, I used EIVs to calculate weighted community values for each relevé. The percentage of each species was divided by the sum of all cover percentages of all occurring species with known EIV per relevé, and finally multiplied by the EIVs for the species. Summing up these values gives the community values of relevés for a certain environmental factor. Species with unknown EIV and species which behave indifferently regarding a certain EIV are not considered in this analysis. Community indices describe the ecological preferences of communities in relationship to certain environmental variables; here, I analysed how community indices of paired relevés have changed over time.

To test for changes in species number among vegetation classes and land use types between the two sets of relevés, I did a test for normal distribution and afterwards a mean value comparison (Wilcoxon-Test, for matched samples). This was also done for the comparison of the weighted community values (nutrients, moisture, and temperature). Furthermore, I tested for differences in the community values between the two survey periods, grouped according to the vegetation classes. Therefore, I used a pairwise, non-parametric test (Wilcoxon). Land use changes among the two survey periods were visualized with a Sankey diagram. To investigate the effect of land-use transitions between the two sampling periods on species richness I ran linear models with a Gaussian error distribution. As response variable I used the change in species richness of a site between the sampling in 2020 and 1995 ($\Delta SR_{2020-1995}$). As response variable I used the interaction

term between the land use classification in 2020 and 1995. Model assumptions were checked visually using diagnostic plots.

I used IBS SPSS Statistic version 27 and the R software (R Core Team 2019) for statistical analysis.

5. Results

5.1 Change in Species

A total of 424 species were recorded in 2020 in the 151 relevés, compared to 421 species in 1995. The median species number across all relevés was 46 in the first survey period, and 45 in the second one (Figure 4). Species numbers vary greatly among relevés, even more so in the second survey period (Figure 4). In the most species-rich relevé, 101 species were recorded in a plot of 40 m^2 size. The relevés with highest species richness are located on sites managed for conservation purposes (i.e. restored nutrient-poor grasslands that had formerly been afforested or abandoned) within the protected area. In these relevés, species of forests and forest fringes were abundant and contributed to very high species numbers.

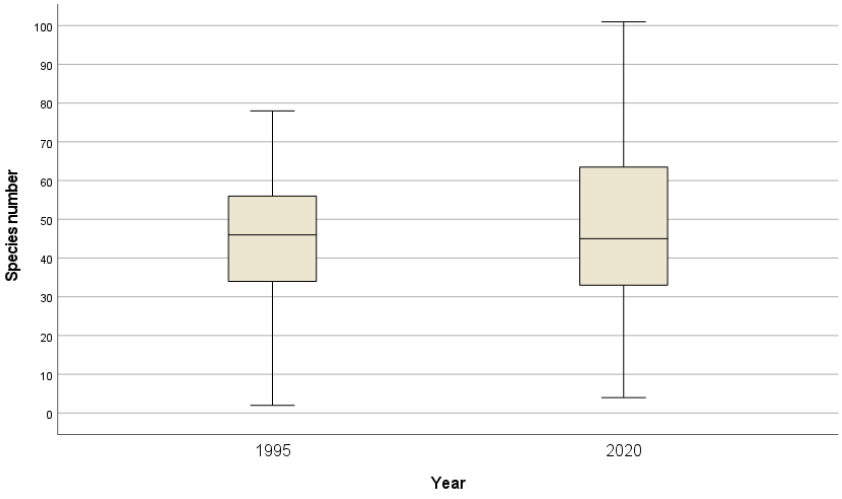

Figure 4: Mean number of vascular plant species per relevé and survey period. Relevés from 1995 (N = 151) and replicated relevés in 2020 (N=151)

Despite that mean species numbers per relevés did scarcely change between both survey periods, and there were pronounced changes in the frequency of occurrence on the species-level (Table 1). The ten species that lost the most occurrences between both survey periods represent species of nutrient poor meadows and pastures (Oberndorfer, 2001), like *Carlina acaulis* (Silver thistle) on the very top that disappeared from 38 plots.

While most of these species are not particularly rare species, some are listed in the Red List of Upper Austria (Hohla et al., 2009) in near threatened category. On the other hand, mainly species of nutrient-rich habitats and ruderal sites belong to the winners. Grasses of nutrient-rich grasslands like *Poa pratensis* (Common meadow-grass) and *Lolium perenne* (Perennial ryegrass) show a strong increase.

Table 1: Top 10 loser and winner plant species based to their increase of decrease in the plots between the two sampling periods.

Loser species	decrease	Winner species	increase
Carlina acaulis	- 38	*Poa pratensis*	+ 34
Centaurea jacea	- 31	*Fragaria vesca*	+ 24
Euphrasia officinalis ssp. *rostkoviana*	- 31	*Lolium perenne*	+ 21
Centaurea scabiosa	- 24	*Hypericum perforatum*	+ 21
Campanula rotundifolia	- 23	*Senecio ovatus*	+ 20
Gymnadenia conopsea	- 23	*Prunella vulgaris*	+ 20
Briza media	- 22	*Mentha longifolia*	+ 20
Potentilla erecta	- 22	*Festuca rupicola*	+ 20
Buphthalmum salicifolium	- 21	*Arenaria serpyllifolia*	+ 20
Tragopogon orientalis	- 20	*Galium aparine*	+ 19

While many moderately common species of nutrient-poor grasslands declined, 55 species disappeared completely (Table S 2). Unsurprisingly, most of the disappeared species were found only in a few plots in 1995, for example: *Aster amellus* (Italian aster), *Crocus albiflorus* (Spring crocus) and *Eleocharis quinqueflora* (Fewflower spikerush). Clearly, the loss of a species in the relevés does not necessarily imply that the respective species has gone extinct in the study area. At the same time 58 species were newly recorded in the second survey period. Apart from 11 newly recorded alien species (Figure 12, several common species of forests like *Carex sylvatica* (European woodland sedge), *Galeobdolon montanum* (Yellow archangel) or *Viola reichenbachiana* (Pale wood violet) were recorded for the first time. Other new arrivals show a preference for nutrient-rich sites such as *Galium aparine* (Catchweed) and *Clematis vitalba* (Traveller's Joy).

5.2 Changes in weighted community values in vegetation types over time

Overall, the numbers of relevés per vegetation class changed between both survey periods (Figure 5): the vegetation class with most relevés were semi-dry grasslands of the Festuco-Brometea (1995: 64 relevés, 2020: 54 relevés), followed by nutrient rich mesic grasslands of the Molino-Arrhenatheretea (1995: 48 relevés, 2020: 49 relevés). Overall, the number of relevés declined in all vegetation classes of nutrient-poor sites, while it increased in classes of nutrient-rich sites.

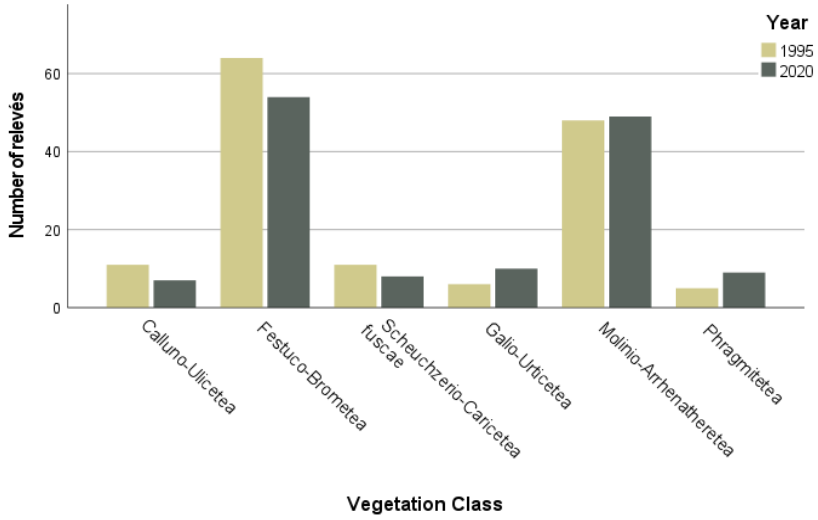

Figure 5: Frequency of vegetation classes according to the two sets of relevés. The figure only shows a selection of the most frequent vegetation classes.

Regarding the weighted community values for nutrients, a trend towards eutrophication over all vegetation classes is evident. The nutrient-poor vegetation classes (i.e. Festuco-Brometea, Calluno-Ulicetea Scheuchzerio-Caricetea fuscae) show significant differences. Weighted community values for nutrients in the mentioned classes increased between both surveys. This was not the case for nutrient-rich vegetation classes (Figure 6).

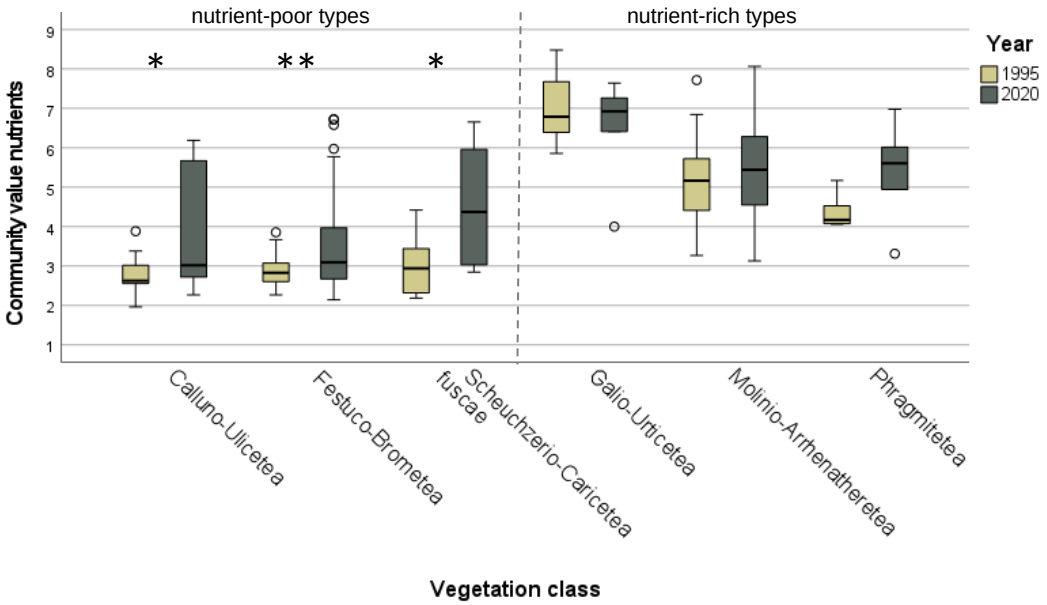

*Figure 6: Weighted community values for nutrients grouped into the most frequently recorded vegetation classes. Both the old and the new relevés belong to the vegetation classes corresponding to the data of 1995. Calluno-Ulicetea (N=11), Festuco-Brometea (N=64), Galio-Urticetea (N=6), Molinio-Arrhenatheretea (N=48), Phragmitetea (N=5), Scheuchzerio-Caricetea fuscae (N=11). Outliers marked with a circle/star are located 1.5 times respectively 3 times above the interquartile distance. Significant differences in marked classes: * < 0.05; ** < 0.01 (Wilcoxon-Test, p-value: 0.05)*

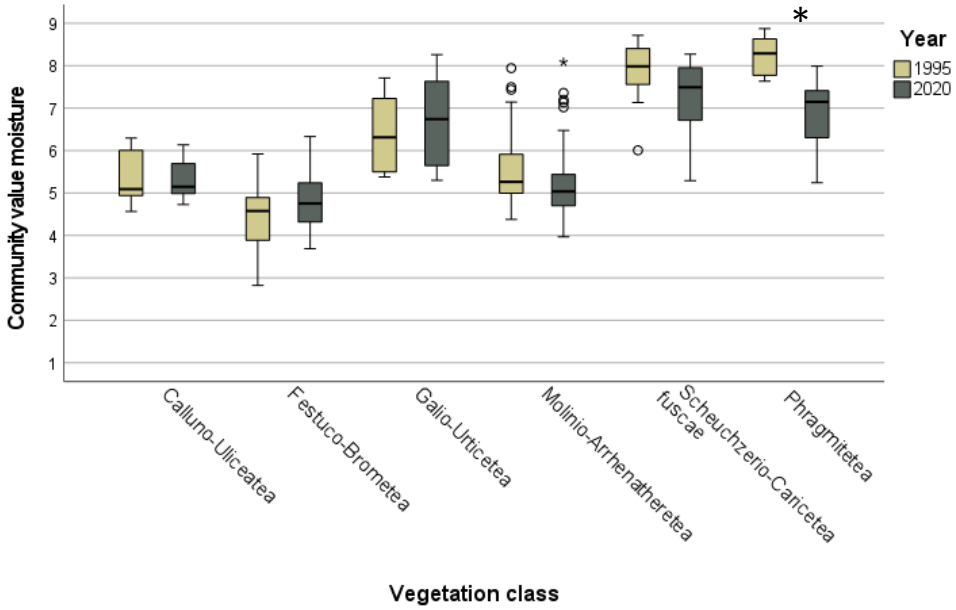

*Figure 7: Weighted community values for moisture grouped into the most frequent vegetation classes. Both the old and the new relevés belong to the vegetation classes corresponding to the data of 1995. Calluno-Ulicetea (N=11), Festuco-Brometea (N=64), Galio-urticetea (N=6), Molinio-Arrhenatheretea (N=48), Phragmitetea (N=5), Scheuchzerio-Caricetea fuscae (N=11). Outliers marked with a circle/star are located 1.5 times respectively 3 times above the interquartile distance. Significant differences in marked classes: * < 0.05 (Wilcoxon-Test, p-value: 0.05)*

Similarly, there was a substantial change in weighted community values based on EIVs. For moisture, I found that community indices shifted towards more mesic conditions in vegetation classes of wet sites (i.e. Phragmitetea and Scheuchzerio-Caricetea fuscae). However, I only detect a significant change for Phragmitetea (Figure 7).

Regarding the weighted community values for temperature, there is a trend across all vegetation classes towards more thermophilic species composition over time. This trend is significant for several classes, i.e. the Festuco-Brometea, Scheuchzerio-Caricetea fuscae and Calluno-Ulicetea (Figure 8).

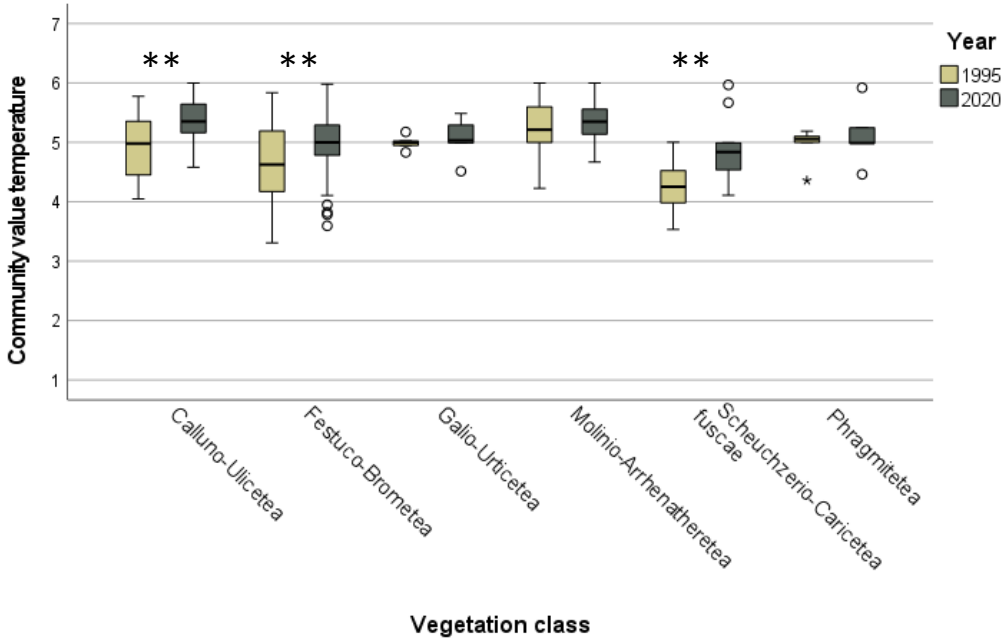

*Figure 8: Weighted community values for temperature of the most frequently recorded vegetation classes. Data are grouped according to the vegetation class the plot of the first survey was belonging to. Calluno-Ulicetea (N=11), Festuco-Brometea (N=64), Galio-Urticetea (N=6), Molinio-Arrhenatheretea (N=48), Phragmitetea (N=5), Scheuchzerio-Caricetea fuscae (N=11). Outliers marked with a circle/star are located 1.5 times respectively 3 times above the interquartile distance. Significant differences in marked classes: * < 0.05; ** < 0.01 (Wilcoxon-Test, p-value: 0.05)*

5.3 Changes in land use and impact of the protected area

Most resurveyed sites did not change in terms of their land use category, but some changes occurred (Figure 9). Many of the fallows of the first survey (n = 19) were put into use again and most of these sites are now used as meadows or pastures. Considerable fewer plots (n = 6) were abandoned between both survey periods. Only a few sites, mostly already abandoned ones or used meadows in the first survey period, were afforested (two and two, respectively).

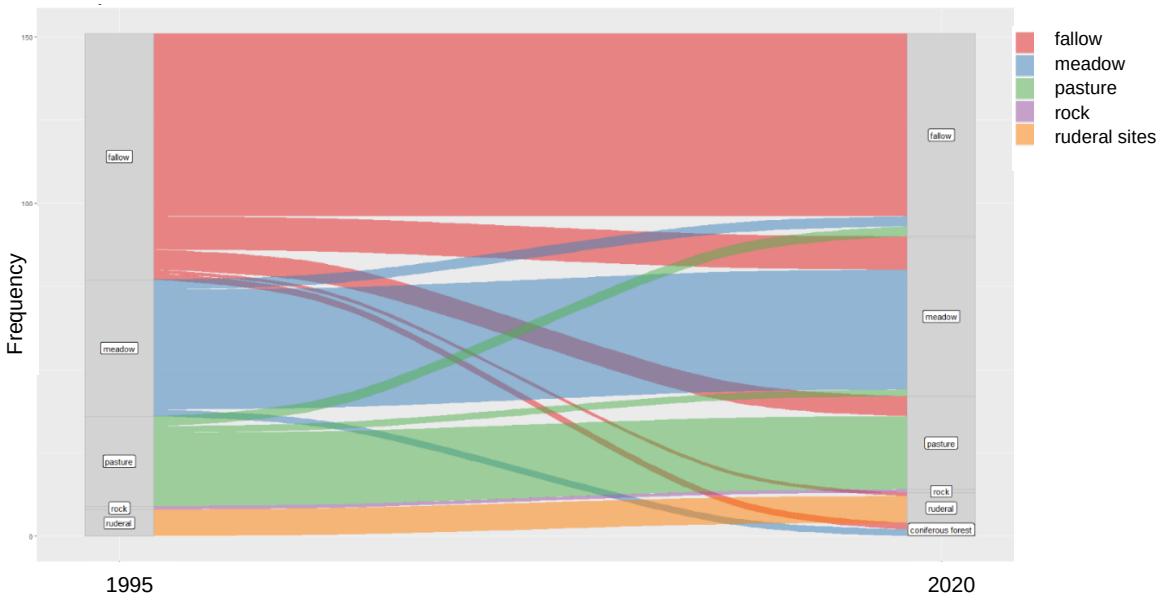

Figure 9: Land use changes over 25 years. Shown are the transitions between different land use types.

When analysing the effects of these land use transitions on species richness, I found a significant increase in species richness for land-use transitions from fallow to pasture (estimate = 18.17, p-value < 0.01) and a significant decrease in species richness for the transition from pasture to meadow (estimate = -28.00, p-value < 0.01). Additionally, the models show a non-significant increase in species richness in meadows (estimate = 4.08, p-value = 0.09) and pastures (estimate = 5.73, p-value = 0.06). Overall, the model explains only 11% of the variation in the data, indicating that other factors not sampled in this study explain a large fraction of changes in species richness. Additionally, for several transitions the number of replicates is too small to derive significant results: e.g., pasture to meadow (n=2) (Figure 10).

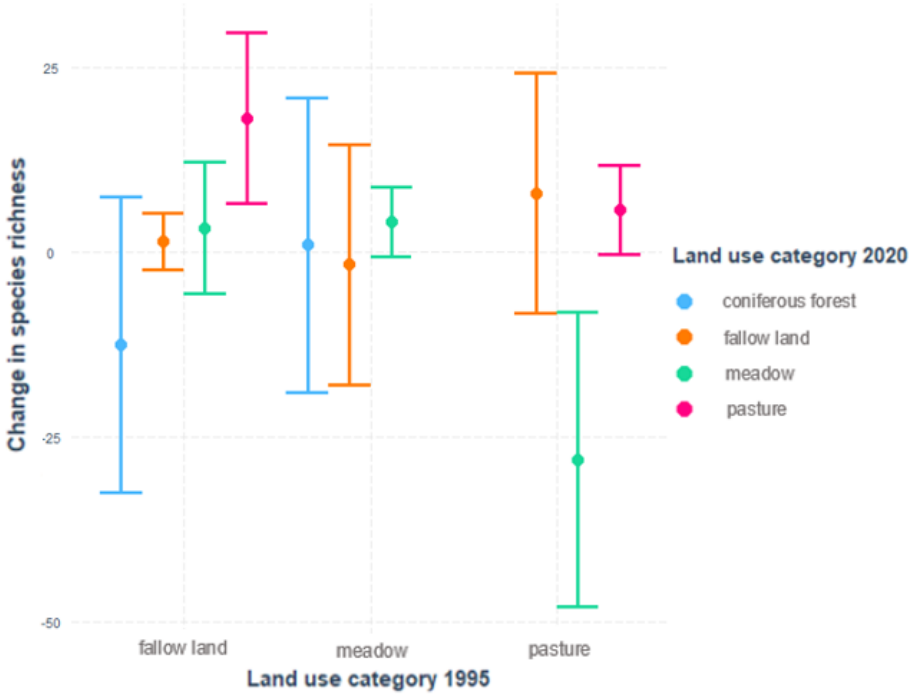

Figure 10: Changes in species richness due to land use transition effects.

Within the conservation area, grasslands are mainly used as meadows and pastures, and a considerable part is abandoned. However, the majority of the fallows is located outside the protected area boundaries, as well as are the ruderal sites (Figure 11).

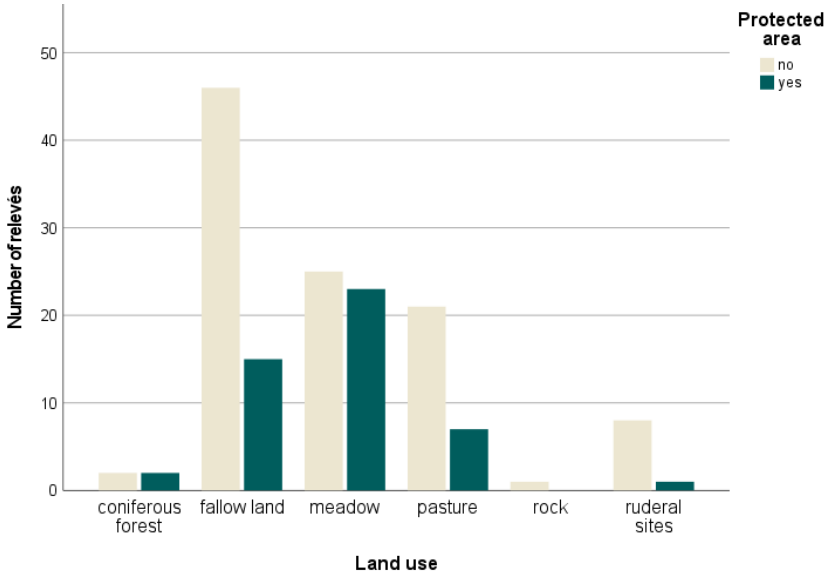

Figure 11: Land use of the relevés within and outside the protected area. Only the land use of the second survey period (2020) is shown.

In addition, the plots of the first and second survey period within the protected area differ significantly in mean plant species numbers. In particular, weighted community values for nutrients have significantly increased for relevés of several vegetation classes outside the protected areas (Festuco-Brometea, Calluno-Ulicetea and Scheuchzerio-Caricetea fuscae), whereas no such change occurred within the protected

area. In terms of land use, fallow land and pastures outside the protected area belong to the categories most affected by increase in EIV for nutrients.

5.4 Alien species

The number of alien species has increased from three species recorded in 1995 to 11 species recorded in 2020; in addition, the number of occurrences of alien species has increased. In the first sampling period, five occurrences of alien species were recorded, whereby this value increased to 48 in 2020. The most common alien species in the study area in 2020 was *Erigeron annuus* (annual fleabane), which was recorded in 14 plots (Figure 12).

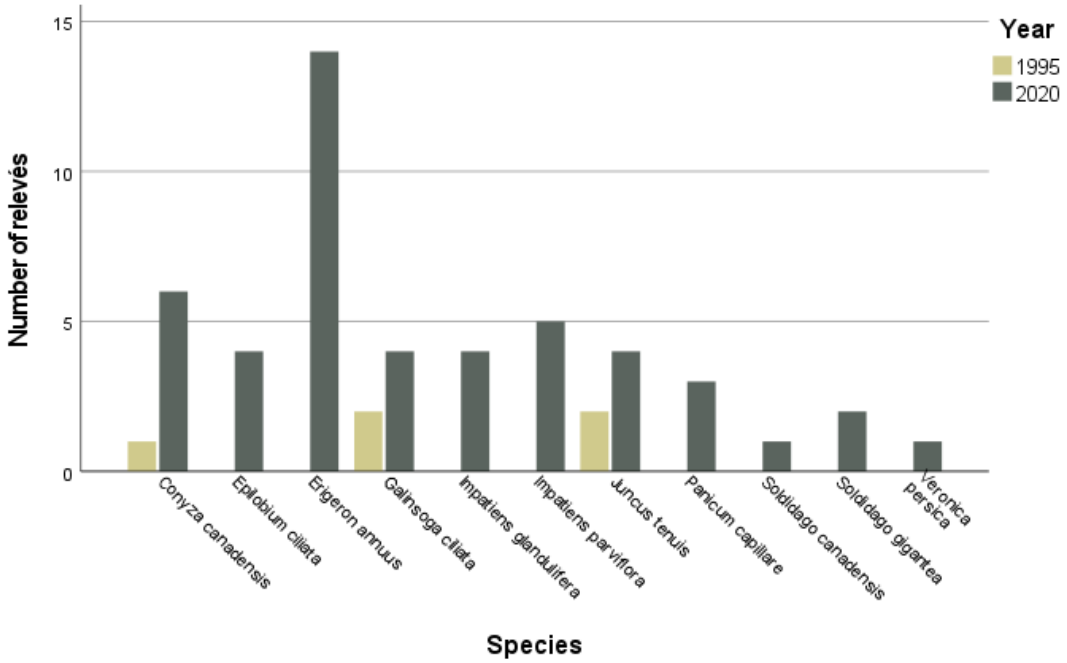

Figure 12: Number of occurrences of alien species in the 151 relevés at both sampling periods

Alien species were mostly recorded in plots of the Molinio-Arrhenateretea, Stellarietea and Galio-Urticetea (Figure 13A). Land use categories such as ruderal sites and fallows are more often invaded by alien species (Figure 13B) than sites with a regular disturbance regime (mowed and grazed areas).

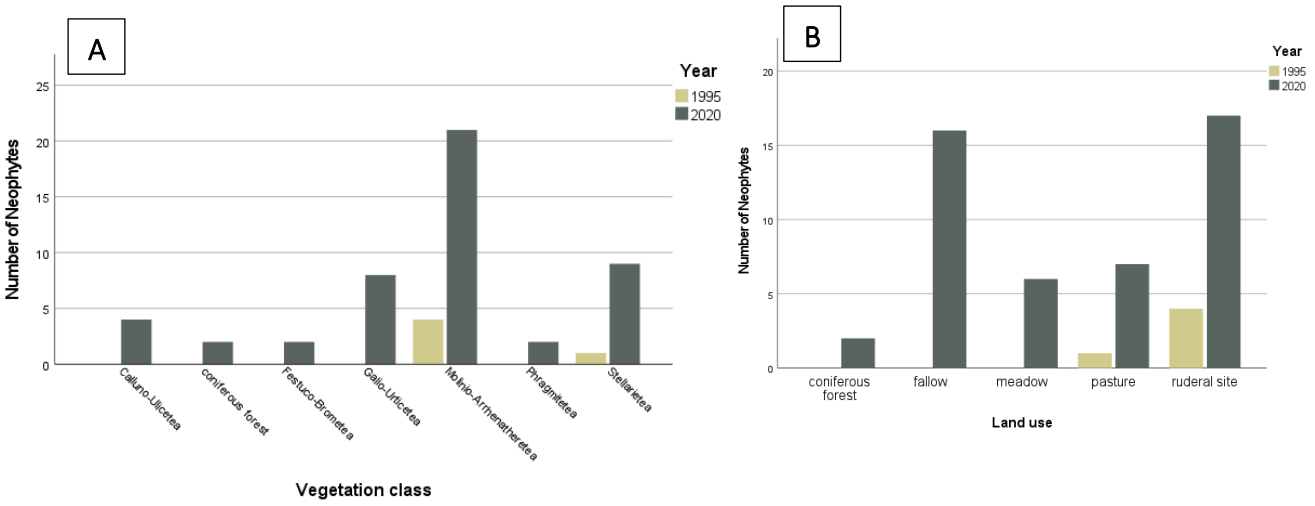

Figure 13: Number of recorded alien species A) in different vegetation classes and B) in different land use categories.

6. Discussion

6.1 Changes in species richness and species composition over time

With a total number of 421 species in the initial survey in 1995 and 424 species recorded in 2020, there is a slight increase in the total recorded species number. Similarly, mean species numbers in plots only changed little and changes were not significant in all vegetation classes. These findings are in contrast to other re-survey studies that revealed mean plant species richness declines in grasslands of many regions of Central Europe (e.g., Eichenberg et al., 2021; Hülber et al., 2017; Wesche et al., 2012; Bruelheide et al., 2020; Jansen et al., 2019). Though, a study from Denmark that analysed vegetation changes over more than 100 years in broad set of habitat types also showed an increase in mean species richness that was mostly attributed to increases in alien species richness outweighing a simultaneous decline in native species richness (Finderup Nielsen et al., 2019).

In the present study, species richness changes were marginal in most plots, with substantial increases or decreases in some others. At the same time, I observed substantial changes in species composition between both sampling periods. Regarding the newly recorded species in re-surveyed relevés, these are mainly species which prefer shadier sites (Oberndorfer, 2001). This result can be explained by the ongoing succession of abandoned sites, where encroachment of shrubs and trees is responsible for changes in light

conditions. The newly recorded species also include several alien species, which is in accordance with other studies (Eichenberg et al., 2021; Finderup Nielsen et al., 2019). While alien species richness and abundance increased, some native species disappeared completely. Species that have disappeared since the first survey are mostly species of nutrient-poor sites and species which were already rare in 1995 (Essl, 1998). Changes in land use such as intensification and fertilization, loss and change of habitats are the main causes for the decline of rare and threatened species in Central European grasslands (e.g., Zehm et al., 2020; Kempel et al., 2020). Further, the conspicuous decline of moderately common plants of nutrient-poor grasslands (Table 1) shows that widespread eutrophication has affected many plots. Several of these species are already listed as near threatened in the regional Red List (Hohla et al., 2009). Species suffering the highest losses prefer nutrient poor sites which is in line with other studies from Central Europe. Jansen et al. (2019) and Bruelheide et al. (2020), for example, show, that moderate common species of dry to wet habitats decreased the most in recent decades in Germany. In grasslands of the biosphere reserve Wienerwald, a similar set of species of nutrient-poor sites declined conspicuously (Hülber et al., 2017). Recently, Staude et al. (2022) reported changes in the vegetation of European habitats (trajectories across lowland grasslands, forests and mountain summits) towards a more nutrient-demanding species composition.

Conversely, the species that have increased most in occurrences are predominantly species of nutrient-rich sites (Table 1). These findings are again in line with the results of another resurvey study from Austria (Hülber et al., 2017) and Europe (Staude et al., 2022). Further, a study from Germany shows an increase of indifferent species and species of agricultural grasslands in nutrient poor acidic *Nardus* grasslands (Peppler-Lisbach et al., 2020).

6.2 Changes of weighted community values over time

A eutrophication trend is evident across all vegetation classes as shown by the changes in the Ellenberg indicator values for nutrients. All relevés put together, weighted community values for nutrients shows a significant increase. Hülber et al. (2017) observed the same

trend for oligotrophic habitats, like Brometalia. Here, I found such a significant trend of increasing nutrient community values in the class of Festuco-Brometea.

In the absence of data for relevant drivers of nutrient supply I can only speculate about the reasons of this change. A possible driver is atmospheric nitrogen deposition that is known as an important cause for the eutrophication of nutrient poor habitats (e.g. Bobbink et al. 2010, Pannek et al. 2015). However, for calcareous grasslands in northwestern Germany, no effect of atmospheric nitrogen deposition on species richness was found (Diekmann et al., 2014). Another line of argument relates to the intensification of land use and associated increases in fertilizer application that leads to higher nutrient supply. Numerous studies from Central Europe show evidence for the negative impact of land use intensification on oligotrophic species and their habitats (e.g. Diekmann et al., 2014; Halada et al., 2017; Peppler-Lisbach et al., 2020; Zehm et al., 2020; Jansen et al., 2019). Finally, in abandoned grasslands endogenous eutrophication may occur as in the absence of human land use, no nutrients are removed in the hay or by grazing.

The findings of Gossner et al. (2016) show an increase of generalistic species typical for intensively used grasslands in Germany. While it is well-known that traditional land use is important for the maintenance of semi-natural grasslands, intensification leads to the opposite (Diekmann et al., 2014; Halada et al., 2017. The reason why changes in land use have a minor importance in explaining changes in species richness in the present study could be due to the coarse classification of the land use categories. Conceivably, a differentiation between extensive and intensive mowing or grazing, would have given better insights.

Land use intensification is not only associated with changes in weighted community values for nutrients, but may also have knock-on effects on water supply of wet grasslands. Several of the wet grasslands were partly drained between both survey periods, and accordingly, weighted community values for moisture of the plots of Phragmitetea and Scheuchzerio-Caricetea fuscae became significantly less wet. Many of the rare wet habitats in the study area were already drained before the first investigation (Essl, 1998). Similarly to my results, the decline and degradation of wet habitats during recent decades can be observed in many regions of Central Europe (Kempel et al., 2020).

The significant increases in the community indices for temperature across vegetation classes provides evidence for thermophilization by climate change. This finding is widely supported by other studies of lowland (Martin et al., 2019) to alpine habitats (e.g. Gottfried et al. 2012) in Central Europe. Warm-adapted species increased relatively while cold-adapted ones declined during the study period.

6.3 Effects caused by of establishing a protected area

In 2014, a protected area has been established in a part of the study area, and a total of 48 plots are located within it. Since then, substantial conservation actions have been carried out there including the removal of 14 ha of forests and overgrown abandoned grasslands, and the re-establishment of extensive land use (mowing, grazing) in these areas (Priller, 2019). Accordingly, 19 plots – of which 12 are located in the protected area - that had been abandoned in 1995 have been used again in 2020.

Although the protected area was established nearly 20 years after the first survey – and thus conservation actions have only been established recently – differences in the trajectories of species change to the relevés located outside can already be identified. In particular, community values for nutrients within the conservation area did not increase significantly, while this was the case in the plots outside the protected area. Thus, it can be inferred that the management of the protected area has positive effects in halting eutrophication.

Several studies have shown that well-managed protected areas are able to halt – or reverse – species declines that are occurring in not-protected landscapes. For instance, a Bavarian study (Zehm et al., 2020) shows, that the decline of rare species outside protected areas is much stronger than inside protected areas. Still, protected areas are not large enough and not managed well enough to halt species declines altogether (Kempel et al., 2020). As a consequence, further measures have to be taken.

6.4 The spread of alien species (and effects of climate change)

In addition to major changes in the species composition of the native species, the number of alien species and their abundance has also changed during the 25 years elapsed

between both surveys. The number of alien species has increased from three (with a total of five occurrences) to 11 species (with a total of 48 occurrences) species. Still, the level of invasions is low with 2.6 % of all species being alien, and 0.7 % of all occurrences in the plots being alien species. This is also evident when compared to many regions in Europe, where alien species currently play a much bigger role, vegetation changes analyses by resurveyed relevés and (partly) outweigh the decline of native species (e.g., Eichenberg et al., 2021; Finderup Nielsen et al., 2019). Likely, one reason for the low level of invasion is that the study area is relatively distant to areas with high anthropogenic pressures (e.g., large settlements, large roads) that are associated with high propagule pressure and, consequently, higher abundances of invaders (Medvecká et al., 2013). Furthermore, the climatic conditions of the rather cool pre-alpine valley could have reduced the increase of alien species., as most alien species in Central Europe are confined to warm lowlands (Chyrtrý et al., 2009). With increasing altitude, the number of alien species is known to decrease drastically (Kueffer, 2011; Vorstenbosch et al., 2020). Nevertheless, more alien species are projected to migrate to higher altitudes in the future and expand into the montane and subalpine regions under further climate change (Becker et al. 2005; Kueffer et al. 2011). In addition, direct human impact in higher altitudes is also projected to increase due to rising land use intensity (Medvecká et al., 2013) and tourism, further increasing invasion risk at high altitudes (Kueffer, 2011; Dullinger et al., 2020).

Further, alien species in Central Europe prefer mostly nutrient-rich habitats (Kowarik, 2010; Jansen et al. 2011; Medvecká et al., 2013). Accordingly, aliens occur mostly in plots of nutrient-rich grasslands such as Molinio-Arrhenatheretea, Stellarietea and Galio-Urticetea. Combined with land use categories, it is likely that ruderal sites and abandoned land are even more invaded than habitats with a lack of nutrients (Medvecká et al., 2013).

The most common alien species in the study area, *Erigeron annuus* (14 plots), is a widespread species in Austria (Fischer et al., 2008). For example, vegetation surveys in semi-dry grasslands in the lowlands of Upper Austria recorded this species as the most frequent alien (Essl & Dirnböck, 2008). The closely related *Conyza canadensis* (Canadian horseweed), another widespread alien species, prefers also ruderal sites (Kowarik, 2010).

Both, *Erigeron annuus* and *Conyza canadensis* are currently not considered as invasive or potentially invasive species in Austria (Essl & Rabitsch 2002). Conversely, another species that was recorded only in the second survey, *Impatiens gladuliferia* (policeman's helmet) is classified as an invasive alien (Essl & Rabitsch, 2002). Shaded sites are invaded by another member of the Balsaminaceae, i.e., *Impatiens parviflora* (small-flowered touch-me-not). This invasive alien (Essl & Rabitsch, 2002) prefers forests and forest fringes on nutrient-rich soils (Kowarik, 2010). Likely, the few occurrences of the two invasive goldenrods species (*Solidago canadensis, S. gigantea*) will increase due to their high invasion potential (Szymura & Szymura, 2015). Even though the richness and abundance of invaders is still low, it can be assumed that the level of invasion in the study area will increase in the future. Finally, it is well-known that climate change will facilitate the spread of alien species (Kowarik, 2010). With increasing temperatures even more regions will become suitable for alien species (Kleinbauer et al., 2010).

7. Conclusions

This resurvey-study reported moderate change in vegetation composition of grasslands in the Jaidhaus basin. Overall species richness and mean species richness of the plots changed little, but there were substantial changes in community indices, particularly for nutrients, temperature, and water. In addition, alien species have spread considerably during both survey periods. Finally, I found differences in vegetation changes between plots located inside and outside of a recently established protected area. Still, the reported changes are less pronounced as those reported from many other regions in Central Europe, likely because of the comparatively low human pressure in the study region.

This thesis underlines that conservation measures are highly important contributors for the maintenance of nutrient-poor, species-rich grassland habitats. Only a few years after the establishment of the conservation area, effects compared to the non-protected area can be seen regarding the community values for nutrients. Therefore, it is of great importance to maintain – and even expand - conservation measured and evaluate their success.

8. References

Aeschimann, D., Lauber, K., Moser, D. M., & Theurillat, J.-P. (2004). *Flora alpina* (Vol. 2). Bern: Haupt.

Aeschimann, D., Lauber, K., Moser, D. M., & Theurillat, J.-P. (2004). *Flora alpina* (Vol. 1). Bern: Haupt.

Alexander, J., Kueffer, C., Daehler, C. C., Edwards, P. J., Pauchard, A., Seipl, T., . . . Walsh, N. (2011). Assembly of nonnative floras along elevational gradients explained by directional ecological filtering. *Proceedings of the National Academy of Sciences - PNAS, Vol 108 (2)*, pp. 656-661. doi:10.1073/pnas.1013136108

Axmanová, I., Kalusová, V., Danihelka, J., Dengler, J., Pergl, J., Pysek, P., . . . Pärtel, M. (2021). Neophyte invasions in European grasslands. *Journal of Vegetation Science, vol. 32 (2)*, p. n/a. doi:10.1111/jvs.12994

Batáry, P., Dicks, L. V., Kleijn, D., & Sutherland, W. J. (2015). The role of agri-environment schemes in conservation and environmental management. *Conservation Biology, Vol. 29 (4)*, pp. 1006-1016. doi:10.1111/cobi.12536

Becker, T., Dietz, H., Billeter, R., Buschmann, H., & Edwards, P. J. (2005). Altitudinal distribution of alien plant species in the Swiss Alps. *Perspectives in plant ecology, evolution and systematics, Vol. 7 (3)*, pp. 173-183. doi:10.1016/j.ppees.2005.09.006

Bergwiesn Kulturlandschaftspflegeverein. (2021). *Bergwiesn*. Retrieved from http://bergwiesn.at/

BEV. (2021). *Austria Map Online*. (Bundesamt für Eich- und Vermessungswesen (BEV), Editor) Retrieved 11 03, 2021, from http://www.austrianmap.at/amap/

Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., . . . De Vries, W. (2010). Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecological Applications, Vol. 20 (1)*, pp. 30-59. doi:10.1890/08-1140.1

Bobbink, R., Tomassen, H., Weijters, M., van den Berg, L., Strengbom, J., Braun, S., . . . Hettelingh, J.-P. (2015). Effects and Empirical Critical Loads of Nitrogen for Europe. *Critical Loads and Dynamic Risk Assessments*, pp. 85 - 127. doi:10.1007/978-94-017-9508-1_4

Bohner, A., Starlinger, F., & Koutecky, P. (2012). Vegetation changes in an abandoned montane grassland, compared to changes in a habitat with low-intensity sheep grazing - A case study in styria, Austria. *Eco.mont, Vol. 4 (2)*, pp. 5-12. doi:10.1553/eco.mont-4-2s5

Braun-Blanquet, J. (1984). *Pflanzensoziologie. Grundzüge der Vegetationskunde* (3. ed.). Wien, New York: Springer Verlag.

Bruelheide, H., Jansen, F., Jandt, U., Bernhardt-Römermann, M., Bonn, A., Bowler, D., . . . Lütt, S. (2020). Using incomplete floristic monitoring data from habitat mapping programmes to detect species trends. *Diversity and Distributions, Vol.26 (7)*, pp. 782-794. doi:10.1111/ddi.13058

Bühler, C., & Roth, T. (2011). Spread of common species results in local-scale floristic homogenization in grassland of Switzerland. *Diversity and Distribution, vol. 17*, pp. 1089-1098. doi:10.1111/j.1472-4642.2011.00799.x

Bühler, C., & Roth, T. (2011). Spread of common species results in local-scale floristic homogenization in grassland of Switzerland. *Diversity & Distributions, vol. 17 (6)*, pp. 1089-1098. doi:10.1111/j.1472-4642.2011.00799.x

Chyrtrý, M., Pysek, P., Wild, J., Pino, J., Maskell, L. C., & Vilà, M. (2009). European map of alien plant invasions based on the quantitative assessment across habitats. *Diversity and Distributions, Vol. 15 (1)*, pp. 98 - 107. doi:10.1111/j.1472-4642.2008.00515.x

Diekmann, M., Jandt, U., Alard, D., Bleeker, A., Corcket, E., Gowing, D. J., . . . Duprè, C. (2014). Long-term changes in calcareous grassland vegetation in North-western Germany - No decline in species richness, but a shift in species composition. *Biological Conservation, Vol. 172*, pp. 170-179. doi:10.1016/j.biocon.2014.02.038

Dullinger, I., Gattringer, A., Wessely, J., Moser, D., Plutzar, C., Willner, W., . . . Dullinger, S. (2020). A socio-ecological model for predicting impacts of land-use and climate change on regional plant diversity. *Global Change Biology, vol. 26*, pp. 2336-2352.

Eggenberg, S., & Möhl, A. (2013). *Flora Vegetativa* (3. ed.). Bern: Haupt.

Eichenberg, D., Bowler, D. E., Bonn, A., Bruelheide, H., Grescho, V., Harter, D., . . . Jansen, F. (2021). Widespread decline in Central European plant diversity across. *Global Change Biology, Vol. 27 (5)*, pp. 1097-1110. doi:10.1111/gcb.15447

Ellenberg, H. (1992). *Zeigerwerte von Pflanzen in Mitteleuropa* (2. ed.). Göttingen: Goltze.

Ellenberg, H., & Leuschner, C. (2010). *Vegetation Mitteleuropas mit den Alpen* (6 ed.). Ulmer.

Essl, F. (1998). *Vegetation, Vegetationsgeschichte und Landschaftswandel der Talweitung Jaidhaus bei Molln/Oberösterreich.* Stapfia 0057.

Essl, F. (1999). *Projekt "Naturschutzgebiet Jaidhaus".* Gutachten vom Land Oberösterreich.

Essl, F., & Dirnböck, T. (2008). Diversity of native and alien vascular plant species of dry grasslands in central Europe. *Applied vegetation science, Vol. 11(4)*, pp. 441-450. doi:10.3170/2008-7-18527

Essl, F., & Rabitsch, W. (2002). *Neobiota in Österreich.* Wien: Umweltbundesamt.

Essl, F., & Rabitsch, W. (2013). *Biodiversität und Klimawandel: Auswirkungen und Handlungsoptionen für den Naturschutz in Mitteleuropa.* Berlin, Heidelberg: Springer. doi:10.1007/978-3-642-29692-5

European Commission. (2007). *Interpretation manual of European Union habitats.* Retrieved 01 2022, from European Commission, DG, Environment, Brussels: https://ec.europa.eu/environment/nature/legislation/habitatsdirective/docs/2007_07_im.pdf

Finderup Nielsen, T., Sand-Jensen, K., Dornelas, M., & Bruun, H. H. (2019). More is less: net gain in species richness, but biotic homogenization over 140 years. *Ecology letters, Vol.22 (10)*, pp. 1650-1657. doi:10.1111/ele.13361

Fischer, M., Oswald, K., & Adler, W. (2008). *Exkursionsflora für Österreich, Lichtenstein, Südtirol.* Linz: Biologiezentrum der Oberösterreichischen Landesmuseen.

Gossner, M. M., Lewinsohn, T. M., Kahl, T., Grassein , F., Boch, S., Prati, D., . . . Allan, E. (2016). Land-use intensification causes multitrophic homogenization of grassland communities. *Nature, Vol. 540 (7632)*, pp. 266-269. doi:10.1038/nature20575

Gottfreid, M., Pauli, H., & Futschik, A. (2012). Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*, pp. 111-115. doi:10.1038/nclimate1329

Grass, A., Bernhardt, K.-G., Tremetsberger, K., Hössinger, R., & Stoeckl, N. (2013). Veränderung der Artenvielfalt im pannonischen Niederösterreich - Auswertung des BOKU-Herbariums als Zeitzeuge. *Wiss. Mitt. Niederösterreichisches Landesmuseum*, pp. 173-200.

Habel, J. C., Dengler, J., Janisová, M., Török, P., Wellstein, C., & Wiezik, M. (2013). European grassland ecosystems: threatened hotspots of biodiversity. *Biodiversity and Conservation, Vol. 22*, pp. 2131-2138. doi:10.1007/s10531-013-0537-x

Halada, L., David, S., Hresko, J., Klimantova, A., Baca, A., Rusnak, T., . . . Vadel, L. (2017). Changes in grassland management and plant diversity in a marginal region of the Carpathian Mts in 1999-2015. *Science of the Total Environment, Vol. 609*, pp. 896-905. doi:10.1016/j.scitotenv.2017.07.066

Haseke, H. (1995). *Atlas der Geologie 1:20.000 des Nationalparkes Kalkalpen.* Linz: Amt der Oö. Landesregierung.

Hellmann, J. J., Byers, J. E., Bierwagen, B. G., & Duke, J. S. (2008). Five potential consequences of climate change for invasiv species. *Conservation Biology, Vol. 22 (3)*. doi:10.1111/j.1523-1739.2008.00951.x

Hohla, M., Stöhr, O., Brandstätter, G., Danner, J., Diewald, W., Essl, F., . . . Wittmann, H. (2009). *Katalog und Rote Liste der Gefäßpflanzen Oberösterreichs. - Stapfia 91.* Linz: Land Oberösterreich.

Hülber, K., Moser, D., Sauberer, N., Maas, B., Staudinger, M., Grass, V., . . . Willner, W. (2017). Plant species richness decreased in semi-natural grasslands in the Biosphere. *Agriculture, Ecosystems and Environment*, pp. 10-18. doi:10.1016/j.agee.2017.04.002

IPBES. (2019). Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Plattform on Biodiversity and Ecosystem Services. (J. S. E. S. Brondizip, Ed.) p. 1148. doi:https://doi.org/10.5281/zenodo.3831673

Jäger, E. J., Müller, F., Ritz, C. M., Welk, E., & Wesche, K. (2017). *Rothmaler Exkursionsflora von Deutschland Gefäßpflanzen: Atlasband* (13. ed.). Berlin Heidelberg: Springer. doi:10.1007/978-3-662-49710-4

Jansen, F., Bonn, A., Bowler, D. E., Bruelheide, H., & Eichenberg, D. (2019). Moderately common plants show highest relative losses. *Conservation Letters, Vol. 13 (1)*, p. n/a. doi:10.1111/conl.12674

Jansen, F., Ewald, J., & Zerbe, S. (2011). Ecological preferences of alien plant species in North-Eastern Germany. *Biological invasions, Vol. 13 (12)*, pp. 2691-2701. doi:10.1007/s10530-011-9939-4

Janssen, J., Rodwell, J., Gracia Criado, M., Gubbay, S., Haynes, T., Nieto, A., . . . Guisso del Galdo, G. (2016). European Red List of Habitats Part 2. Terrestrial and freshwater habitats. *European Commission*. doi:10.2779/091372

Kempel, A., Bornand, C. N., Gygax, A., Juillerat, P., Jutzi, M., Sager, L., . . . FIscher, M. (2020). Nationwide revisitation reveals thousands of local extinctions across the ranges of 713 threatened and rare plant species. *Conservation Letters, Vol.13 (6)*, pp. e12749-n/a. doi:10.1111/conl.12749

Kleinbauer, I., Dullinger , S., Klingenstein, F., May, R., Nehring, S., & Essl, F. (2010). Ausbreitungspotenzial ausgewählter neophytischer Gefäßpflanzen unter Klimawandel in Deutschland und Österreich. *BfN-Skripten, 275*, pp. 1-74.

Kowarik, I. (2010). *Biologische Invasionen. Neophyten und Neozoen in Mitteleuropa.* Ulmer.

Kueffer, C. (2011). Neophyten in Gebirgen – Wissensstand und Handlungsbedarf. *Gesunde Pflanzen, Vol.63 (2)*, pp. 63-68. doi:10.1007/s10343-011-0248-8

LandOÖ. (2010). *Agrarstrukturerhebung 2010 Überblick*. (LandOberösterreich, Ed.) Retrieved 11 03, 2021, from https://www.land-oberoesterreich.gv.at/119788.htm

Marini, L., Gaston, K. J., Prosser, F., & Hulme, P. E. (2009). Contrasting response of native and alien plant species richness to environmental energy and human impact along alpine elevation gradients. *Global ecology and biogeography, Vol. 18 (6)*, pp. 652-661. doi:10.1111/j.1466-8238.2009.00484.x

Martin, G., Devictor, V., Motard, E., Machon, N., & Porcher, E. (2019). Short-term climate-induced change in French plant communities. *Biology letters, Vol. 15 (7)*. doi:10.1098/rsbl.2019.0280

McCune, J., & Vellend, M. (2013). Gains in native species promote biotic homogenization over four decades in a human-dominated landscape. *Journal of Ecology, vol. 101 (6)*, pp. 1542-1551. doi:10.1111/1365-2745.12156

Medvecká, J., Jarolímeck, I., Senko, D., & Svitok, M. (2013). Fifty years of plant invasion dynamics in Slovakia along a 2,500 m altitudinal gradient. *Biological Invasions, Vol. 16 (8)*, pp. 1627 - 1638. doi:10.1007/s10530-013-0596-7

Mihoub, J.-B., Henle, K., Titeux, N., Brotons, L., Brummitt, N. A., & Schmeller, D. S. (2017). Setting temporal baselines for biodiversity: the limits of available monitoring data for

capturing the full impact of anthropogenic pressures. *Scientific reports, Vol. 7 (1)*, pp. 41591-13. doi:10.1038/srep41591

Mitchell, R., Hewison, R., Britton, A., Brooker, R., Cummins, R., Fiedling, D., . . . Riach, D. (2017). Forty years of change in Scottish grassland vegetation: Increased richness, decreased diversity and increased dominance. *Biological Conservation, vol. 212*, pp. 327-336. doi:10.1016/j.biocon.2017.06.027

Oberndorfer, E. (1992). *Süddeutsche Pflanzengesellschaften. Teil I: Fels- und Mauergesellschaften, alpine Fluren, Wasser-, Verlandungs- und Moorgesellschaften* (2. ed.). Jena, Stuttgart, New York: Gustav Fischer.

Oberndorfer, E. (1992). *Süddeutsche Pflanzengesellschaften. Teil IV: Wälder und Gebüsche. A. Textband.* (2 ed.). Jena, Stuttgart, New York: Gustav Fischer.

Oberndorfer, E. (1992). *Süddeutsche Pflanzengesellschaften. Teil V: Wälder und Gebüsche. B. Tabellenband.* (2 ed.). Jena, Stuttgart, New York: Gustav Fischer.

Oberndorfer, E. (1993). *Süddeutsche Pflanzengesellschaften. Teil II: Sand- und Trockenrasen, Heide- und Borstgras-Gesellschaften, alpine Magerrasen, Saum-Gesellschaften, Schlag- und Hochstauden-Fluren* (3 ed.). Jena, Stuttgart, New York: Gustav Fischer.

Oberndorfer, E. (1993). *Süddeutsche Pflanzengesellschaften. Teil III: Wirtschaftswiesen und Unkrautgesellschaften* (3 ed.). Jena, Stuttgart, New York: Gustav Fischer.

Oberndorfer, E. (2001). *Pflanzensoziologische Exkursionsflora für Deutschland und angrenzende Gebiete* (8. ed.). Stuttgart: Ulmer.

Pannek, A., Duprè, C., Gowing, D., Stevens, C., & Diekmann, M. (2015). Spatial gradient in nitrogen deposition affects plant species frequency in acidic grasslands. *Oecologica, vol. 177(1)*, pp. 39-51. doi:10.1007/s00442-014-3120-6

Peppler-Lisbach, C., Stanik, N., Könitz, N., & Rosenthal, G. (2020). Long term vegetation changes in Nardus grasslands indicate eutrophication, recovery from acidification, and management change as the main drivers. *Applied vegetation science, Vol. 23 (4)*, pp. 508-521. doi:10.1111/avsc.12513

Priller, D. (2014). Streuwiese Jaidhaus in Molln. (N. Oberösterreich, Ed.) *Informativ*.

Priller, D. (2019). Wiesenrekultivierung im Naturschutzgbiet Jaidhaus. (Naturschutzbund Oberösterreich, Ed.) *Informativ*(95).

R Core Team. (2019). *R: A language and environment for statistical computing [WWW Document]. R Found. Stat. Comput.* Retrieved 11 29, 2021, from https://www.R-project.org/

Ridding, L., Bullock, J., Walker, K., Bealey, C., & Pywell, R. (2021). Responses of calcareous grassland plant communities to changed seasonal grazing management: Results of a 31year study. *Journal for Nature Conservation, vol. 62*, p. 126026. doi:10.1016/j.jnc.2021.126026

Runge, F. (1986). *Die Pflanzengesellschaften Mitteleuropas.* Münster: Aschendorff.

Staude, I., Pereira, H., Daskalova, G., Bernhardt-Römermann, M., Diekmann, M., Pauli, H., . . . Wipf, S. (2022). Directional turnover towards larger-ranged plants over time and across habitats. *Ecology Letters, Vol. 25 (2)*, pp. 466-482. doi:10.1111/ele.13937

Sutcliffe, L. M., Batáry, P., Kormann, U., Báldi, A., Dicks, L. V., Herzon, I., . . . Konstiuková, J. (2015). Harnessing the biodiversity value of Central and Eastern European farmland. *Diversity and Distributions, Vol. 21 (6)*, pp. 722-730. doi:10.1111/ddi.12288

Szymura, M., & Szymura, T. H. (2015). Growth, phenology, and biomass allocation of alien Solidago species in central Europe. *Plant species biology, Vol. 30 (4)*. doi:10.1111/1442-1984.12059

Tälle, M., Deák, B., Poschlod, P., Valkó, O., Westerberg, L., & Milberg, P. (2016). Grazing vs. mowing: A meta-analysis of biodiversity benefits for grassland management. *Agriculture, Ecosystems & Environment, Vol. 222*, pp. 200-212. doi:10.1016/j.agee.2016.02.008

Tüxen, R., & Ellenberg, H. (n.d.). *Der systematische und ökologische Gruppenwert. EIn Beitrag zur Begriffserklärung und Methodik der Pflanzensoziologie* (Vol. 3). (m. F.-S. Arbeitsgemeinschaft, Ed.) 1937.

van der Maarel, E. (1979). Transformation of Cover-Abundance Values in Phytosociology and its Effects on Community Similarity. *Plant Ecology, vol. 39 (2)*, pp. 97-114. doi:10.1007/BF00052021

Vellend, M., Baeten , L., Myers-Smith, I. H., Elmendorf, S. C., Beauséjour, R., Brown, C. D., . . . Wipf, S. (2013). Global meta-analysis reveals no net change in local-scale plant biodiversity over time. *Proceedings of the National Academy of Sciences - PNAS, Vol. 110 (48)*, pp. 19456-19459. doi:10.1073/pnas.1312779110

Vorstenbosch, T., Essl, F., & Lenzner, B. (2020). An uphill battle? The elevational distribution of alien plant species along rivers and roads in the Austrian Alps. *NeoBiota, 63*, pp. 1-24. doi:doi.org/10.3897/neobiota.63.55096

Wesche, K., Krause, B., Culmsee, H., & Leuschner, C. (2012). Fifty years of change in Central European grassland vegetation: Large losses in species richness and animal-pollinated plants. *Biological Conservation, vol. 150 (1)*, pp. 76-85. doi:https://doi.org/10.1016/j.biocon.2012.02.015

ZAMG. (2020). *ZAMG Jahrbuch*. (Zentralanstalt für Meteorologie und Geodynamik, Editor) Retrieved 11 03, 2021, from https://www.zamg.ac.at/cms/de/klima/klimauebersichten/jahrbuch

Zehm, A., Klotz, J., Horn, K., Wecker, M., von Brackel, W., Blachnik, T., . . . Wimmelbrücker, A. (2020). Rückgang seltenster Pflanzenarten ist ungebremst – Freilanduntersuchungen zur Bestandsentwicklung vom Aussterben bedrohter Gefäßpflanzenarten Bayerns. *Berichte der Bayrischen Botanischen Gesellschaft*, pp. 5-42.

8.1 Figure captions

8.2 Table captions

9. Supplementary information

Table S 1: GPS coordinates of the resurveyed plots. Coordinate system: WGS84

plot code	latitude (N)	longitude (E)	plot code	latitude (N)	longitude (E)
1	47,84935°	14,35185°	77	47,82808°	14,35447°
2	47,84852°	14,35232°	78	47,84925°	14,37015°
3	47,84702°	14,35372°	79	47,84973°	14,36952°
4	47,84702°	14,36282°	80	47,85015°	14,36332°
5	47,84502°	14,3638°	81	47,853333°	14,35945°
6	47,84275°	14,36905°	82	47,8498°	14,355567°
7	47,84292°	14,3724°	83	47,848567°	14,35655°
8	47,84357°	14,36887°	84	47,8493°	14,35345°
9	47,8406°	14,37977°	85	47,84705°	14,355167°
10	47,84105°	14,3676°	86	47,84525°	14,35585°
11	47,84037°	14,3688°	87	47,830117°	14,35535°
12	47,84035°	14,36983°	88	47,832283°	14,356917°
13	47,84512°	14,35547°	89	47,821783°	14,365167°
14	47,8294°	14,35557°	90	47,822317°	14,365317°
15	47,82392°	14,35848°	91	47,824867°	14,359483°
16	47,82517°	14,35708°	92	47,84455°	14,352317°
17	47,832031°	14,356158°	93	47,843483°	14,351783°
18	47,84387°	14,34885°	94	47,84325°	14,351717°
19	47,84398°	14,35015°	95	47,843083°	14,351883°
20	47,84152°	14,35223°	96	47,843667°	14,353267°
21	47,84125°	14,35207°	97	47,843017°	14,353383°
22	47,83992°	14,35202°	98	47,842783°	14,35385°
23	47,83965°	14,352033°	99	47,850633°	14,35105°
24	47,838717°	14,351833°	100	47,8509°	14,35037°
25	47,843667°	14,355333°	101	47,85117°	14,35045°
26	47,835217°	14,36245°	102	47,85017°	14,35123°
27	47,829117°	14,359117°	103	47,85073°	14,35097°
28	47,8386°	14,352367°	104	47,85053°	14,34985°
29	47,82915°	14,35902°	105	47,85053°	14,34985°
30	47,84908°	14,3526°	106	47,84252°	14,3696°
31	47,84795°	14,35343°	107	47,8422°	14,369983°
32	47,83652°	14,35602°	108	47,842833°	14,37625°
33	47,84342°	14,35353°	109	47,84345°	14,376067°
34	47,84308°	14,37357°	110	47,84435°	14,376333°
35	47,83933°	14,35872°	111	47,840767°	14,348717°

36	47,83603°	14,35617°	112	47,84105°	14,349833°
37	47,83617°	14,35582°	113	47,839067°	14,350233°
38	47,84252°	14,36533°	114	47,837433°	14,353117°
39	47,8425°	14,34762°	115	47,834733°	14,356317°
40	47,84222°	14,34785°	116	47,833983°	14,3559°
41	47,84052°	14,3545°	117	47,825367°	14,3601°
42	47,83992°	14,35442°	118	47,8257°	14,361483°
43	47,83742°	14,3518°	119	47,827133°	14,358083°
44	47,8376°	14,35255°	120	47,841367°	14,370617°
45	47,83773°	14,35315°	121	47,8401°	14,369717°
46	47,83845°	14,35322°	122	47,836283°	14,381017°
47	47,83843°	14,3531°	123	47,839483°	14,348617°
48	47,83897°	14,35328°	124	47,83805°	14,34785°
49	47,83963°	14,35513°	125	47,841033°	14,35055°
50	47,83943°	14,35547°	126	47,834117°	14,357367°
51	47,83893°	14,35463°	127	47,833683°	14,3588°
52	47,83822°	14,35513°	128	47,829733°	14,3595°
53	47,83842°	14,35232°	129	47,829883°	14,359617°
54	47,83913°	14,3563°	130	47,83025°	14,359367°
55	47,83898°	14,35645°	131	47,832333°	14,360017°
56	47,84265°	14,35645°	132	47,835617°	14,36065°
57	47,84272°	14,3564°	133	47,833183°	14,362967°
58	47,8418°	14,35668°	134	47,840236°	14,357858°
59	47,83888°	14,36078°	135	47,837917°	14,364767°
60	47,84205°	14,35368°	136	47,8381°	14,364933°
61	47,84188°	14,3535°	137	47,838383°	14,365333°
62	47,8415°	14,35113°	138	47,839133°	14,36495°
63	47,846°	14,3641°	139	47,83935°	14,36505°
64	47,8455°	14,36143°	140	47,839983°	14,358817°
65	47,84473°	14,36373°	141	47,84005°	14,35865°
66	47,84787°	14,36585°	142	47,850067°	14,3582°
67	47,84843°	14,36652°	143	47,85025°	14,342367°
68	47,84748°	14,35702°	144	47,849817°	14,345617°
69	47,83917°	14,35995°	145	47,843733°	14,350867°
70	47,83435°	14,36187°	146	47,845317°	14,350583°
71	47,83457°	14,362°	147	47,84585°	14,350317°
72	47,83497°	14,3623°	148	47,847517°	14,35155°
73	47,83558°	14,3625°	149	47,851033°	14,349133°
74	47,84932°	14,35203°	150	47,851583°	14,35195°
75	47,82452°	14,35652°	151	47,84005°	14,354575°
76	47,82855°	14,35512°			

Table S 2: Overview of completely disappeared and newly arrived species. Alien species are highlighted (yellow). Note that this table reflects the disappearances and gains within the re-surveyed plots, but not in the study area in general.

disappeared species	Number of relevés	newly recorded species	Number of relevés
Antennaria dioica	5	*Acer campestre*	1
Asplenium trichomanes	1	*Actaea spicata*	2
Asplenium viride	1	*Agrimonia eupatoria*	1
Aster amellus	3	*Alopecurus pratensis*	10
Athamanta cretensis	1	*Aruncus dioicus*	1
Betula pendula	2	*Athyrium filix-femina*	5
Bidens tripartita	1	*Calystegia sepium*	1
Calycocorsus stipitatus	1	*Cardamine trifolia*	1
Campanula cespitosa	1	*Carex muricata* agg.	6
Campanula glomerata	1	*Carex sylvatica*	17
Carex sempervirens	2	*Clematis vitalba*	12
Carex spicata	3	*Crataegus laevigata*	1
Cerastium carinthiacum ssp. *carinthiacum*	1	*Dactylorhiza maculata* s.lat. (inkl. *fuchsii*)	5
Crepis alpestris	12	*Dentaria bulbifera*	2
Crepis praemorsa	2	*Digitalis grandiflora*	1
Crocus albiflorus	2	*Dryopteris filix-mas*	4
Dactylorhiza majalis	3	*Elymus caninus*	1
Dryopteris carthusiana	1	*Epilobium ciliatum*	4
Eleocharis quinqueflora	1	*Epilobium montanum*	2
Equisetum fluviatile	1	*Erigeron annuus*	14
Euphrasia stricta	1	*Euphorbia amygdaloides*	2
Fallopia convolvulus	1	*Festuca arundinacea*	1
Gentianella aspera	15	*Festuca gigantea*	1
Geranium sanguineum	2	*Galeobdolon montanum*	1
Glyceria notata	1	*Galium aparine*	19
Heracleum austriacum	2	*Gymnocarpium robertianum*	3
Hieracium bauhinii	1	*Hedera helix*	1
Hieracium piloselloides	1	*Hepatica nobilis*	6
Hieracium sabaudum	1	*Impatiens glandulifera*	4
Hypericum montanum	3	*Impatiens parviflora*	5
Hypochoeris maculata	12	*Lamium purpureum*	1
Lembotropis nigricans	3	*Lunaria rediviva*	2
Lilium bulbiferum	1	*Luzula multiflora* s.lat.	1
Lycopodium clavatum	1	*Lysimachia nummularia*	8
Lysimachia nemorum	1	*Matricaria chamomilla*	1
Mentha arvensis	1	*Moehringia muscosa*	2
Ononis spinosa	2	*Orobanche flava*	3
Ophioglossum vulgatum	1	*Panicum capillare*	3

Orchis mascula	3	*Paris quadrifolia*	2
Orobanche reticulata	1	*Phyteuma spicatum*	2
Persicaria hydropiper	1	*Polygala amara*	13
Persicaria maculosa	1	*Polygonatum multiflorum*	3
Persicaria vivipara	1	*Polygonatum verticillatum*	1
Pinus sylvestris	1	*Polypodium vulgare*	1
Potentilla heptaphylla	1	*Prenanthes purpurea*	1
Primula vulgaris	1	*Pulmonaria officinalis*	3
Prunus avium	1	*Rubus fruticosus* agg.	6
Pyrola rotundifolia	2	*Sanicula europaea*	2
Ranunculus aconitifolius	1	*Solidago canadensis*	1
Rosa pendulina	2	*Solidago gigantea*	2
Salix caprea	4	*Sonchus asper*	10
Selinum carvifolia	1	*Sonchus oleraceus*	1
Sherardia arvensis	1	*Ulmus glabra*	1
Tephroseris crispa	2	*Verbascum nigrum*	1
Thymus praecox ssp. *praecox*	1	*Veronica hederifolia* agg.	1
		Veronica persica	1
		Viola mirabilis	2
		Viola reichenbachiana	3

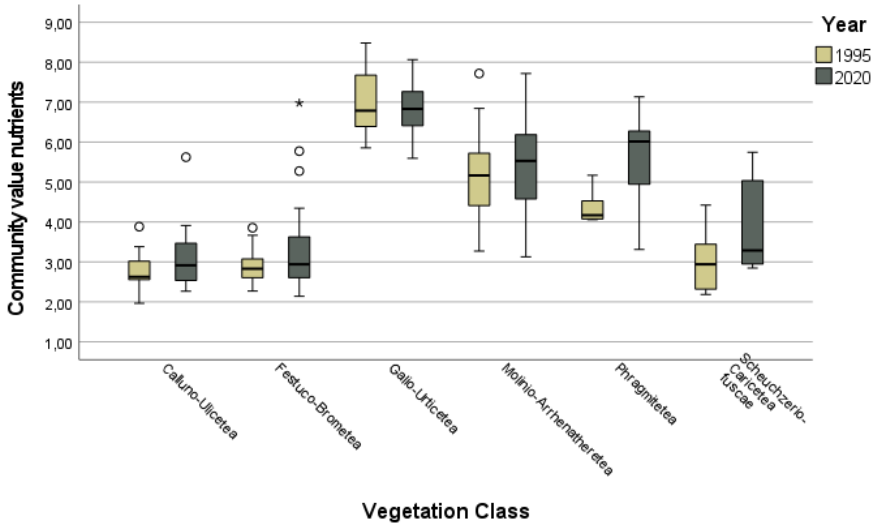

Figure 14: Community values for nutrients grouped by the most frequent vegetation classes. Allocation to the classes corresponds to the classes as observed 1995 versus the ones as observed in 2020. 1995) Calluno-Ulicetea (N=11), Festuco-Brometea (N=64), Galio-Urticetea (N=6), Molinio-Arrhenatheretea (N=48), Phragmitetea (N=5), Scheuchzerio-Caricetea fuscae (N=11); 2020) Calluno-Ulicetea (N=7), Festuco-Brometea (N=54), Galio-Urticetea (N=10), Molinio-Arrhenatheretea (N=49), Phragmitetea (N=9), Scheuchzerio-Caricetea fuscae (N=8). Outliers marked with a circle/star are located 1.5 times respectively 3 times above the interquartile distance.

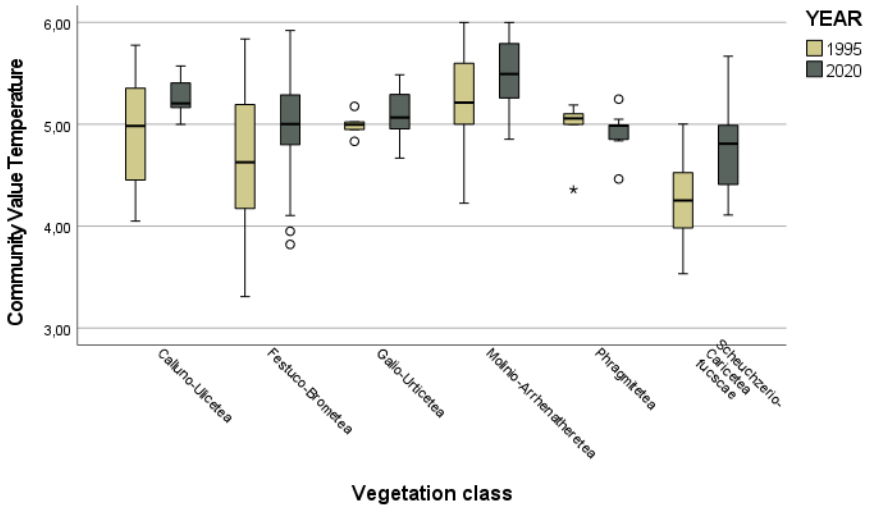

Figure 15: Community values for temperature grouped by the most frequent vegetation classes. Allocation to the classes corresponds to the classes as observed in 1995 versus the ones observed in 2020. 1995) Calluno-Ulicetea (N=11), Festuco-Brometea (N=64), Galio-Urticetea (N=6), Molinio-Arrhenatheretea (N=48), Phragmitetea (N=5), Scheuchzerio-Caricetea fuscae (N=11); 2020) Calluno-Ulicetea (N=7), Festuco-Brometea (N=54), Galio-Urticetea (N=10), Molinio-Arrhenatheretea (N=49), Phragmitetea (N=9), Scheuchzerio-Caricetea fuscae (N=8). Outliers marked with a circle/star are located 1.5 times respectively 3 times above the interquartile distance.

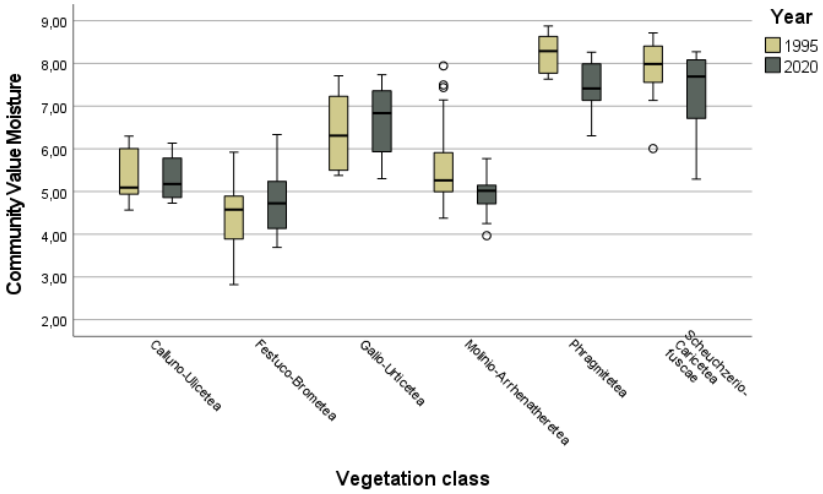

Figure 16: Community values for moisture grouped by the most frequent vegetation classes. Allocation to the classes corresponds to the classes as observed in 1995 versus the ones as observed in 2020. 1995) Calluno-Ulicetea (N=11), Festuco-Brometea (N=64), Galio-Urticetea (N=6), Molinio-Arrhenatheretea (N=48), Phragmitetea (N=5), Scheuchzerio-Caricetea fuscae (N=11); 2020) Calluno-Ulicetea (N=7), Festuco-Brometea (N=54), Galio-Urticetea (N=10), Molinio-Arrhenatheretea (N=49), Phragmitetea (N=9), Scheuchzerio-Caricetea fuscae (N=8). Outliers marked with a circle/star are located 1.5 times respectively 3 times above the interquartile distance.