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# Only large and highly-connected semi-dry grasslands achieve plant conservation targets in an agricultural matrix

## Nur große, gut vernetzte Halbtrockenrasen erreichen botanische Naturschutzziele in einer von Äckern dominierten Landschaft

Philipp Sengl[1, 2, *], Martin Magnes[1], Viktoria Wagner[3], László Erdős[4] & Christian Berg[1]

[1]*Institute of Plant Sciences, University of Graz, Schubertstraße 51, 8010 Graz, Austria, nwsephi@gmx.at; martin.magnes@uni-graz.at; christian.berg@uni-graz.at;*
[2]*Civil Engineering Office Kofler Umweltmanagement, Traföß 20, 8132 Pernegg a. d. Mur, Austria;*
[3]*Department of Botany and Zoology, Masaryk University, Kotlářská 2, 611 37 Brno, Czech Republic, wagner@sci.muni.cz;*
[4]*Institute of Ecology and Botany, MTA Centre for Ecological Research, Alkotmány utca 2-4, 2163 Vácrátót, Hungary, erdos.laszlo@okologia.mta.hu*
**Corresponding author*

### Abstract

Semi-dry grasslands were once widely distributed communities, but today they represent some of the most vulnerable habitats in Central Europe. European and national legislation and non-governmental organizations have managed to protect some of the remaining fragments. However, despite their status as Natura 2000 habitats, they are often endangered due to improper management, fragmentation and edge effects from adjacent croplands. By using a sample of 44 semi-dry hay meadows in the south-eastern Alpine Foreland of Styria, we investigated how species-richness and trait composition of semi-dry grassland species respond to variation in patch size, connectivity, abiotic site factors and management regimes. We used linear regression models to identify the most important drivers for richness of typical semi-dry grassland species and thus conservation value. The number of typical semi-dry grassland species was highest in well-connected fragments, i.e. units that shared two or more borders with neighbouring species-rich grasslands. Furthermore, large semi-dry grasslands (> 8000 m²) had highest numbers of semi-dry grassland species and highest relevance for conservation; no difference was found among smaller fragment sizes. Unregular management was associated with increased presence of competitive species which replaced stress-tolerant specialists. Our study indicates that under eutrophication, small fragment size and isolation, only large semi-dry grasslands can sustain a high number of species with high conservation value. The conservation value of smaller semi-dry grassland fragments could be improved by buffer zones, adapted mowing treatments and periodical sheep grazing.

**Keywords:** dispersal, ecological strategy, Ellenberg indicator values, *Festuco-Brometea*, isolation, mowing, naturalness, phenology, plant traits, resilience

**Erweiterte deutsche Zusammenfassung am Ende des Artikels**

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## 1. Introduction

Although once widely distributed in Central Europe, semi-dry grasslands have become endangered in the last century due to land-use change (POSCHLOD & WALLISDEVRIES 2002, DOSTÁLEK & FRANTÍK 2012, HABEL et al. 2013). Nevertheless, they are still genuine hotspots of plant species diversity (DENGLER et al. 2014). In Austria the total area of semi-dry grasslands is estimated to be approximately 5000 ha, with the main area of distribution in the continental region and the Alpine Foreland (ELLMAUER & TRAXLER 2000). Efforts made on behalf of the European Habitats Directive, regional governments and non-governmental organizations were successful in protecting some of these semi-dry grassland fragments (SENGL & MAGNES 2008, ELLMAUER 2012) and have resulted in a stable total area (UMWELTBUNDESAMT 2013). However, despite their conservation status, semi-dry grassland species are still endangered by fragmentation (FISCHER & STÖCKLIN 1997, BRÜCKMANN et al. 2010), improper management (KLIMEŠ et al. 2013), and nutrient influx (RÖMERMANN et al. 2008) from adjacent arable land (NEITZKE 1998, ESSL et al. 2004, SENGL & MAGNES 2008). Additionally, some of these sites have suffered from conflicting protection aims (WALLISDEVRIES et al. 2002, TSCHARNTKE et al. 2012). For example, they can be managed to protect specific groups of organisms (insects, birds, plants) or certain species, which might require contrasting management regimes.

A large body of literature has shown that abandonment (STAMPFLI & ZEITER 1999, GALVÁNEK & LEPŠ 2008, JACQUEMYN et al. 2011, MUDRÁK et al. 2013), fragmentation and isolation (FISCHER & STÖCKLIN 1997, COUSINS 2009, MARINI et al. 2012, PURSCHKE et al. 2012, ZULKA et al. 2014) can lead to a decline of vascular plant species diversity in species-rich grasslands. However, fewer studies have explored the way in which different management regimes affect plant species richness (HANSSON & FOGELFORS 2000, HUMBERT et al. 2012, SOCHER et al. 2012, KLIMEŠ et al. 2013), and the prevalence of specific plant trait groups (PLUESS 2013). We aimed to close this gap including, besides the anthropogenic factor of management, a large set of abiotic site conditions (KLIMEŠ et al. 2013, CARBONI et al. 2015).

Our model region, located in the south-eastern part of the Alpine Foreland of Austria, hosts a small network of semi-dry grasslands that are unique to this region, characterized by several submediterranean-subcontinental species (*Cirsium pannonicum*, *Crepis praemorsa*, *Hypochaeris maculata*, *Thesium linophyllon*; cf. STEINBUCH 1995, SENGL & MAGNES 2008). However, the effects of management, fragmentation or connectivity, have never been thoroughly explored in these specific grasslands. Moreover, despite the fact that agro-environmental subsidies are linked to specific management instructions, no study has been conducted that thoroughly explores the impact of mowing frequency (once or twice per year, or unregularly) on plant species richness, composition and functional diversity in semi-dry grasslands (ZECHMEISTER et al. 2003, SUTCLIFFE 2015). Although species richness has been reported to respond negatively to increased land-use intensity, in particular mowing frequency (ALLAN et al. 2014, ZECHMEISTER et al. 2003), SOCHER et al. (2012) have shown that the impact of management intensity can differ significantly among regions. Additionally, we were interested whether management and connectivity are more important than soil nutrient concentration (KLEIJN et al. 2009, GRACE et al. 2014) and pH.

Specifically, we addressed the following questions: (1) How do management, connectivity and abiotic factors influence the diversity and occurrence of typical and/or endangered semi-dry grassland species on a local scale? (2) How is the prevalence of functional groups related to competition and dispersal affected by management, connectivity and abiotic factors?

Based on the findings of FISCHER & STÖCKLIN (1997) we expected that smaller, isolated sites surrounded by croplands would contain smaller amounts of typical semi-dry grassland species than larger, well-connected sites. We assumed that nutrient influx from bordering croplands (NEITZKE 1998) could negatively impact the diversity of semi-dry grassland species. In addition, we hypothesized that late annual mowing (HUMBERT et al. 2012) similarly to abandonment leads to a decline of semi-dry grassland species diversity. We expected an expansion of competitive, tall herbs and grasses that would eventually replace small, stress-adapted species of the class *Festuco-Brometea* (MUCINA & KOLBEK 1993) as found by DOSTÁLEK & FRANTÍK (2012) for annual sheep grazing in autumn.

The results of our study will increase the understanding of interrelationships between fragment size, connectivity, management, abiotic site conditions and species composition of semi-dry grasslands. Results can inform land managers about the critical fragment size and connectivity needed to sustain semi-dry grasslands with high conservation value and reveal whether a decreased mowing frequency, which is often a central component of agro-environmental schemes (ELLMAUER & ESSL 2005, HUMBERT et al. 2012, VALKÓ et al. 2012), can be a viable option for maintaining semi-dry grassland species diversity. Since the present state of the investigated grassland remnants is a result of the impact of management and site conditions during the past decades, our findings reveal whether measures besides mowing are necessary to ensure persistence of semi-dry grassland fragments (POSCHLOD & WALLISDEVRIES 2002, KAPFER 2010a, b).

## 2. Material and methods

### 2.1 Study area

The study area was located in the south-eastern Alpine Foreland of Austria near Sankt Anna am Aigen (46.81N/15.98E–46.81N / 15.99E; 260–320 m a.s.l.). Soils were non-calcareous Cambisols and Stagnosols and calcareous Leptosols (LEBENSMINISTERIUM 2012). Total annual precipitation was 830–840 mm and the annual average temperature 9.1–9.3 °C (1971–2000) (ZAMG 2012). Oak-hornbeam forests on deep nutrient-rich soils (specifically the association *Galio sylvatici-Carpinetum* Oberd. 1957) and oak forests (specifically the association *Genisto germanicae-Quercetum roboris* Aich. 1933) on more acidic soils (WILLNER 2007a, b) were the potential natural vegetation in this area.

The semi-dry meadows in the study area (Fig. 1) were described as a single, narrowly-distributed association described as *Cirsio pannonici-Brometum* Steinbuch 1995 (nom. inv. according to WILLNER et al. 2013), that probably belongs to the *Filipendulo vulgaris-Brometum* Hundt & Hübl ex Willner 2013 (WILLNER et al. 2013). Some characteristic species of this association were *Bromus erectus*, *Festuca rupicola*, *Cirsium pannonicum*, *Filipendula vulgaris*, *Thesium linophyllon* and *Euphorbia verrucosa*. These meadows harboured 218 species of vascular plants in total, of which 56 species are listed in the Rest list of Vascular Plants of Austria (NIKLFELD & SCHRATT-EHRENDORFER 1999). Detailed vegetation descriptions with tables are presented in SENGL & MAGNES (2008).

At the time of the study, a total of 44 semi-dry grassland patches (9.5 ha or 4.7% of the total area) prevailed in the open landscape area 'Aigener Feld' (total area: 2.2 km²). Most sites were relatively steep, located on the upper parts of the hills, facing mainly south. This relatively large extent of semi-dry grasslands in the study area can be explained in part by their designation as Natura 2000 sites (ASL 2009). Some of the larger sites were either purchased or rented by the nature conservation agency 'Naturschutzbund Steiermark'. Smaller semi-dry grassland remnants were often spared from conversion to agricultural fields due to low profitability (STEINBUCH 1995). However, a considerable number of the sites were not managed regularly and sometimes they were mown without biomass removal. Within our study area, most protected sites served primarily the conservation of bird and arthropod diversity (ASL unpubl.), which means they were mostly managed with the lowest possible intensity in order to

**Fig. 1.** Species-rich semi-dry grassland in the study area (*Cirsio pannonici-Brometum*) (Photo: P. Sengl, May 2008).

**Abb. 1.** Artenreicher Halbtrockenrasen im Untersuchungsgebiet (*Cirsio pannonici-Brometum*) (Foto: P. Sengl, Mai 2008).

prevent shrub encroachment (cf. KRUESS & TSCHARNTKE 2002). This means that meadows were mowed once or even less than once a year, and in late season (in or after July, KORN et al. 2015), which seems to be a suitable management option for maintaining arthropod diversity (WETTSTEIN & SCHMID 1999, HUMBERT et al. 2012). Moreover, like in other European regions (SUTCLIFFE 2015), hay is no longer needed for livestock feeding in the study area (SENGL & MAGNES 2008), and sometimes is disposed closed to the meadows after conservation mowing.

## 2.2 Data sampling and processing

The study comprised all semi-dry grassland patches in the study area covering an area ranging from 215 to 10574 $m^2$ ($n$ = 44). Every grassland patch was delineated by a margin that indicated different properties and, consequently, different management regimes, was counted as a single item (= utilization unit: UU) without giving consideration to within-site heterogeneity. We recorded one vegetation relevé per utilization unit. We placed plots randomly, but avoided ecotones, vicinity of forest edges or arable fields, and kept a minimum distance of 5 m to patch margins. Only utilization units containing at least three semi-dry grassland species typical for the region (Section 2.3) were included ($n$ = 41). Additionally, utilization units that lacked dispersal barriers (e.g. roads or hedges) were pooled into areas of coherent grassland units (GU). Consequently, for each relevé we calculated the area of (1) the utilization unit and (2) the coherent grassland unit. Sampling was carried out by the first author in the period of 2007 to 2014. We collected vegetation data in 4 m × 4 m plots as proposed by CHYTRÝ & OTÝPKOVÁ (2003) for temperate grasslands, and used an extended Braun-Blanquet cover-abundance scale according to DENGLER et al. (2008). Plant nomenclature followed FISCHER et al. (2008).

In every relevé we collected one soil sample (approximately 500–1000 g, consisting of three mixed subsamples taken within the relevé area) from the upper 10 cm mineral soil layer to analyse soil parameters (K, P, pH). The content of plant-available phosphor (P: mg / 1000 g), potassium (K: mg / 1000 g) and pH ($CaCl_2$ -solution) in the soil was analysed by the "Landwirtschaftliches Versuchszentrum – Boden und Pflanzenanalytik", a department of the provincial government. We used phosphor and potassium as indicators of the soil nutrient level and of fertilization impacts. To estimate effects of aspect and slope on diversity and structure of vegetation samples we calculated the PADI-radiation (RAD). The PADI-radiation is an equation model estimating the potential annual direct incident radiation using slope, aspect and latitude (MCCUNE & KEON 2002).

We geo-referenced and calculated the area of (1) each utilization unit (UU) and (2) the entire semi-dry grassland unit (GU), in ArcGIS 10.1 (ESRI 2012). Furthermore, we categorized both the area of the UU ($1 = x < 1000$ m²; $2 = 1000 \leq x < 4000$ m²; $3 = x \geq 4000$ m²), as well as the GU ($1 = x < 2000$ m²; $2 = 2000 \leq x < 8000$ m²; $3 = x \geq 8000$ m²) in three classes. Additionally, we calculated the area: perimeter ratio of both the utilization units and the coherent grassland units. We used three categories to describe the dominant management regime applied to each utilization unit: mowed unregularly, less than once per year (MU), mowed once per year (M1) or mowed twice per year (M2). Management was recorded through field observation by the first author throughout the study period. We used four levels to categorized connectivity to other mesic and semi-dry species-rich grasslands: (1) no connection, (2) species-rich grasslands are not bordering directly, but lie within a perimeter of 20 m, (3) utilization unit shares one border with other species-rich grasslands, and (4) utilization unit shares two or more borders with other species-rich grasslands. We chose a perimeter of 20 m around the utilization unit because previous studies (STAMPFLI & ZEITER 1999, SENGL et al. 2015) had shown that 20 m is the maximum distance that can be reached by most grassland species within a few years during re-colonization, if microsites for seedling establishment are available.

## 2.3 Community indices

For analysis of data in terms of diversity we calculated the total number of species and the number of semi-dry grassland species as response variables. Our set of semi-dry grassland species consisted of 48 diagnostic species according to MUCINA & KOLBEK (1993): (*Festuco-Brometea* Br.-Bl. et R. Tx. ex Klika et Hadač 1944: 17, *Brometalia erecti* Br.-Bl. 1936: 15, *Bromion erecti* Koch 1926: 6, plus 3 diagnostic species for associations of this alliance, *Cirsio-Brachypodion pinnati* Hadač et Klika in Klika et Hadač 1944: 6, *Koelerio-Phleetalia phleoides* Korneck 1974: 1) and ELLMAUER (1993): (*Calluno-Ulicetea* Br.-Bl. et R. Tx. ex Klika et Hadač 1944: 3). Additionally, we included five other species with high semi-dry grassland specifity in the study area (SENGL & MAGNES 2008). In order to estimate the conservation status of the relevés, we (1) counted the number of Red List species in each sample (NIKLFELD & SCHRATT-EHRENDORFER 1999), and (2) calculated its relevance for species conservation (BERG et al. 2014), which describes the suitability of a plant community to provide a habitat for endangered plant species. In the latter index, every species received a numeric value according to its Red List category: not endangered = 0, near threatened = 0.5, Red List category 3 (vulnerable) = 1, or Red List category 2 (endangered) = 2 (BERG et al. 2014). The somewhat special categories in NIKLFELD & SCHRATT-EHRENDORFER (1999) were revalued as follows: 3r!: söVL (vulnerable, but endangered within south-eastern Alpine Foreland) = 2; 3r!: other parts of Austria (vulnerable, but endangered outside of the south-eastern Alpine Foreland) = 1; r: söVL (regional vulnerable in the south-eastern Alpine Foreland) = 1; r: other parts of Austria (regional vulnerable outside of the south eastern Alpine Foreland) = 0.5. In order to obtain this relevance value the values for every relevé were summarized.

Furthermore, we used a naturalness indicator value (BORHIDI 1995) to estimate the degree of degradation within relevés. Naturalness indicator values are ordinal values ranging from -3 (invasives, indicating serious degradation) to +6 (specialists, indicating intact conditions). The idea rests on the observation that plant species have different tolerances against anthropogenic disturbances. In fact, it has been shown that certain plant species are significantly related to certain disturbance levels (e.g. KOWARIK 1990; KIM et al. 2002; KLOTZ et al. 2002), thus they are able to indicate the habitat's naturalness status. Naturalness indicator values seemed to perform well in earlier studies conducted in the

Carpathian Basin (e.g. MORSCHHAUSER 1995; TÖRÖK & SZITÁR 2010), and a former study (Erdős et al., unpublished data) has shown that this system, developed for the Pannonian biogeographical region, is applicable for semi-dry grasslands in the study area in south eastern Styria, too. We calculated the naturalness score for every relevé as a frequency weighted mean. Relevés were stored in Turboveg (HENNEKENS & SCHAMINÉE 2001) and imported into JUICE 7.0 (TICHÝ 2002) for further analysis.

### 2.4 Plant traits

We chose plant traits (Table 1) related to soil nutrient content (EIV-N), light availability (EIV-L), mean maximum plant height (cm), mowing tolerance, dispersal ability (seed weight, seed length/width-ratio, dispersal type, self-incompatibility) and phenological traits (begin of flowering, end of flowering and phenological group).

In addition, we analysed ecological strategy types (GRIME 1979) by deriving data from KLOTZ et al. (2002) (Table 1). We transformed a species strategy type to a numeric value (HUNT et al. 2004), e.g. a species with C strategy type would be characterized by the following vectors: C = 100, R = 0, S = 0, species with CS strategy type by C = 50, R = 0, S = 50 and species with CSR strategy type with C = 33.3, R = 33.3, S = 33.3. For all groups of relevés (MU; M1; M2, classes of connectivity, classes of utilization units and coherent grassland units) strategy values (C, R and S) were averaged and plotted in a triangular diagram. We extracted plant traits from the BIOLFLOR database (KLOTZ et al. 2002; Table 1). Missing data were completed based on GRIME (1979), FISCHER et al. (2008) and LANDOLT (2010).

**Table 1.** List of plant traits included in the analysis.

**Tabelle 1.** Liste der für die Analysen verwendeten Pflanzeneigenschaften.

| Trait | Levels/units |
|---|---|
| Dispersal type (LANDOLT 2010) | At (anthropochory); Au (autochory); Bo (boleochory); Dy (dysochory). En (endozoochory); Ep (epichory); Hy (hydrochory); Me (meteochory); My (myrmecochory) |
| Ellenberg values (ELLENBERG et al. 1991) | EIV-N (1–9); EIV-L (1–9) |
| Mean maximum plant height (FISCHER et al. 2008) | cm |
| Mean seed length/width-ratio (KLOTZ et al. 2002) | mm/mm-ratio |
| Mean seed weight (KLOTZ et al. 2002) | mg |
| Mowing tolerance (KLOTZ et al. 2002) | 1–9 |
| Naturalness indicator values (BORHIDI 1995) | -3–6 |
| Phenology (DIERSCHKE 1995, KLOTZ et al. 2002) | Begin of flowering (month), end of flowering (month), duration of flowering (months), phenological group (1–12) |
| Self sterility / self incompatibility (KLOTZ et al. 2002) | SC (self-compatible), C+ (more or less self-compatible), SI (self incompatibility), I+ (more or less self-incompatible) |
| Strategy type (KLOTZ et al. 2002) | C (competitors), CS (stress-tolerant competitors), CR (competitive ruderals), S (stress-tolerators), SR (stress-tolerant ruderals), CSR (intermediate strategists), R (ruderals) |

### 2.5 Statistical analysis

All predictors were tested for correlations before the analysis. Management was not correlated with connectivity ($p = 0.076$, Fisher´s exact test), or classes of utilization units ($p = 0.169$, Fisher´s exact test) allowing to treat them as independent variables. However, the area of coherent grassland units was significantly correlated to connectivity ($p = 0.001$, Fisher´s exact test), due to the fact that a grassland was counted as a coherent unit if it was connected to further grasslands. Additionally, we tested for correlation between all other abiotic explanatory variables using the Spearman-*Rho*-test (Supplement E1). To avoid collinearity among predictors we restricted linear modeling to the independent factors only abiding a significance threshold of $p < 0.01$.

We used general linear modeling to analyse the most important relationships between explanatory variables (site parameters: pH, PADI-radiation, area of utilization units (log-transformed continuous values), management and connectivity) and response variables (community indices: number of dry grassland species, number of Red List species, relevance for species conservation, naturalness indicator values). We applied model selection (best subsets) based on the Akaike Information Criterion (AIC).

Additionally, the particular effects of management (MU, M1, M2), connectivity (classes 1–4), area of utilization units (classes 1–3) and area of grassland units (classes 1–3) on all community indices (number of semi-dry grassland species, number of Red List species, relevance for species conservation, naturalness) as well as on all competitive traits (EIV-L, EIV-N, mean max. plant height, mowing tolerance), dispersal traits (seed weight, seed length/width ratio) and phenological traits (begin of flowering, end of flowering, duration of flowering, phenological group) were analysed by pooling all respective groups. We used first, the Kruskal-Wallis test to explore the overall differences among predictors and second, the pairwise Mann-Whitney test to explore differences between categories. Statistical analysis was performed in the software PAST 3.04 (HAMMER et al. 2001) and SPSS Statistics 23 (IBM 2015).

## 3. Results

### 3.1 Abiotic site conditions

Soils had relatively low P and K concentration (Phosphor: 14 mg / 1000 g; Potassium: 150 mg / 1000 g; Supplement E2). Ellenberg indicator values for nutrients were also low (2.8–5.6), while light availability was generally high (Ellenberg values: 6.6–7.4). Soil pH was relatively inhomogeneous among the grassland patches (range: 4.6–7.4). While pH and P were uniformly distributed among categories of management and classes of connectivity, utilization units and coherent grassland units, K was significantly lower in highly connected (connectivity class 4) and larger grasslands units (≥ 8000 m²). PADI-radiation was slightly higher in large grassland units (Supplement E2).

### 3.2 Community indices

Semi-dry grasslands of our study area harboured on average 46 species of vascular plants, including 13 semi-dry grassland species and 11 Red List species per relevé (Supplement E3). Highest scores of total species numbers were found both in unconnected as well as highly connected sites, but did not differ across different categories of management, area of utilization units and grassland units (Supplement E3). Consequently we dropped the total species number in further analysis.

According to linear modeling (Table 2), connectivity was the main factor promoting the number of semi-dry grassland species, explaining 37% of the total variance ($p < 0.001$). The number of Red List species was significantly explained by: pH ($p < 0.001$), PADI-radiation ($p = 0.009$) and connectivity ($p = 0.049$). The model explained 54% of the total variance.

**Table 2.** Linear relationship between explanatory variables (PADI-radiation, site size, soil characteristics, management and connectivity) and community indices (number of semi-dry grassland species, number of Red List species, relevance for species conservation, naturalness indicator values). Model selection was performed by selection of best subsets using the Akaike information criterion (AIC).

**Tabelle 2.** Lineare Beziehungen zwischen erklärenden Variablen (Einstrahlung, Flächengröße, Bodenfaktoren, Nutzung und Konnektivität) und Gemeinschafts-Indices (Anzahl an Halbtrockenrasen-Arten, Anzahl von Rote Liste Arten, Relevanz für den Artenschutz, Natürlichkeit). Die Modellselektion erfolgte durch Auswahl des besten Subsets unter Verwendung des Akaike information criterions (AIC).

| | Estimate | Standard error | *T* | *p* | Relative importance | Corrected $R^2$ |
|---|---|---|---|---|---|---|
| Semi-dry grassland species (N) | | | | | | |
| Connectivity | 9.667 | 1.996 | 4.843 | 0.000 | 1 | 0.371 |
| Red list species (N) | | | | | | |
| pH | -3.049 | 0.611 | -4.991 | 0.000 | 0.679 | |
| PADI-radiation | 18.521 | 6.715 | 2.758 | 0.009 | 0.208 | |
| Connectivity | 2.948 | 1.448 | -2.036 | 0.049 | 0.113 | 0.536 |
| Relevance for species conservation | | | | | | |
| pH | -1.931 | 0.503 | -3.842 | 0.000 | 0.589 | |
| PADI-radiation | 14.131 | 5.524 | 2.558 | 0.015 | 0.261 | |
| Connectivity | 2.309 | 1.191 | -1.939 | 0.061 | 0.150 | 0.445 |
| Naturalness | | | | | | |
| pH | -0.152 | 0.046 | -3.304 | 0.002 | 0.673 | |
| PADI-radiation | 1.107 | 0.408 | 2.301 | 0.027 | 0.327 | 0.232 |

The relevance for species conservation was explained by the same factors in the same order of importance (for details see Table 2). Naturalness was explained ($R^2 = 0.23$) by the factors pH ($p = 0.002$) and PADI-radiation ($p = 0.027$).

A closer look on the distribution of community indices (Fig. 2) revealed that the number of semi-dry grassland species was highest in the large grassland units (≥ 8000 m²) and well-connected sites (sharing two or more borders with further species-rich grassland); smaller and less connected sites did not differ in this respect. Several species occurred exclusively (*Hypochaeris maculata*, *Agrostis vinealis*, *Koeleria pyramidata*, *Antennaria dioica* and *Neotinea tridentata*) or predominantly (*Helianthemum ovatum*, *Anthyllis vulneraria* ssp. *carpatica* and *Prunella grandiflora*), in the largest coherent grassland units (≥ 8000 m²). Relevance for species conservation of sites was highest in grassland unit class 3 (≥ 8000 m²) and lowest in grassland unit class 2 (2000 ≤ x < 8000 m²). Grassland unit class 1 (< 2000 m²) was of slightly higher relevance for species conservation than class 2 (2000 ≤ x < 8000 m²). Naturalness of grassland sites was highest in grassland unit class 3 (≥ 8000 m²), but did not significantly differ in classes 1 (< 2000 m²) and 2 (2000 ≤ x < 8000 m²).

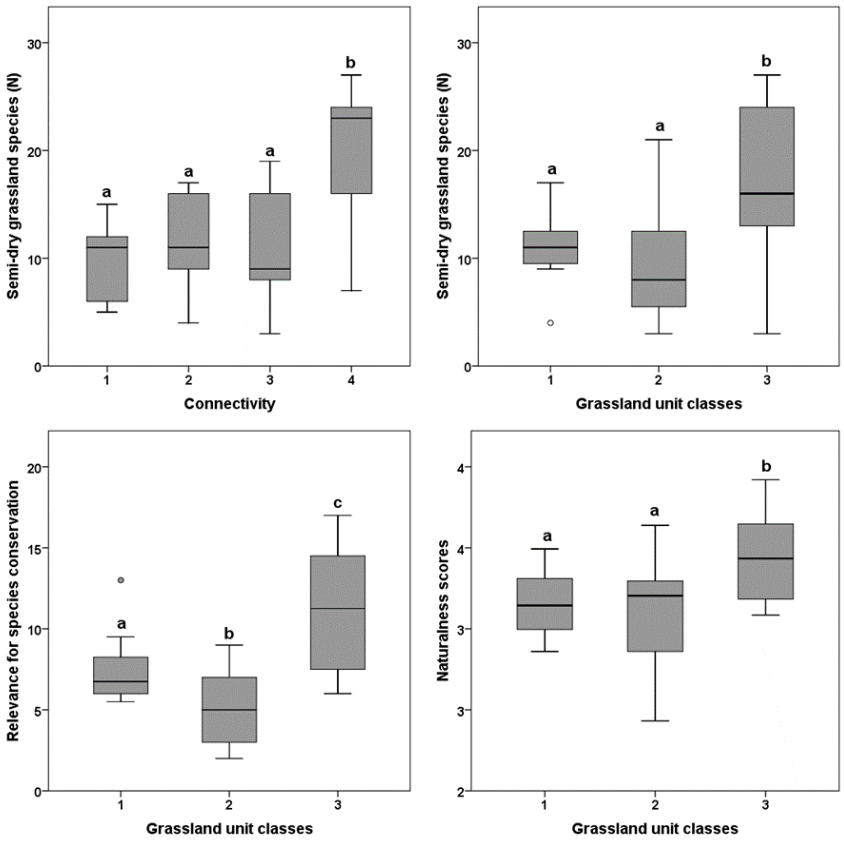


**Fig. 2.** Number of semi-dry grassland species, Relevance for species conservation and Naturalness among different categories of connectivity (1–4) and area of grassland units (1 = x < 2000 m²; 2 = 2000 ≤ x < 8000 m²; 3 = x ≥ 8000 m²). Different letters above boxplots indicate significant differences among categories ($p < 0.05$; Mann-Whitney test).

**Abb. 2.** Anzahl an Halbtrockenrasen-Arten, Relevanz für den Artenschutz und Natürlichkeitswerte in unterschiedlichen Kategorien von Konnektivität (1–4) und Grünlandeinheiten (1 = x < 2000 m²; 2 = 2000 ≤ x < 8000 m²; 3 = x ≥ 8000 m²). Unterschiedliche Buchstaben zeigen signifikante Unterschiede zwischen den Kategorien an ($p < 0{,}05$; Mann-Whitney-Test).

### 3.3 Plant traits

Traits related to competition revealed that well-connected and large coherent grasslands contained fewer species with high competition abilities (Fig. 3). This was reflected by higher EIV-L values and lower EIV-N values in grassland unit class 3 (≥ 8000 m²), as well as a lower mean max. plant height in this class. Also, mowing tolerance was lower in grassland unit class 3. The same pattern could be seen for the factor connectivity. While connectivity classes 1 (no connection to further species-rich grassland) to 3 (utilization unit shares one border with further species-rich grassland) showed no significant differences in Ellenberg values for light and nutrients, the highly connected grasslands of connectivity class 4 (utilization unit shares two or more borders with further species-rich grasslands) had higher EIV-L values and lower EIV-N values. However, management frequency and area of utilization units were not at all reflecting any significant pattern for competition-related traits.

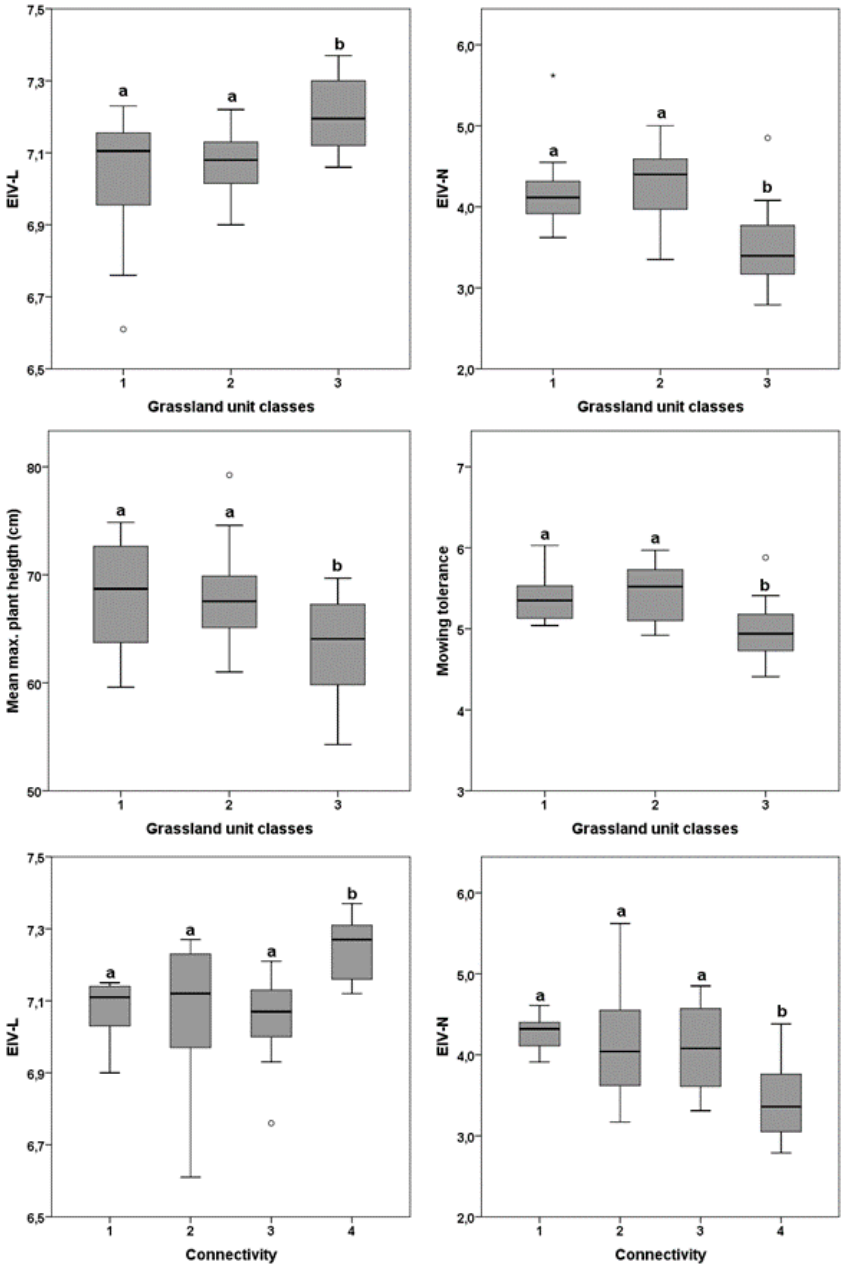


**Fig. 3.** Boxplot diagrams of competitive traits (EIV-L, EIV-N, mean maximum plant height, mowing tolerance) among different categories of grassland units (1 = x < 2000 m²; 2 = 2000 ≤ x < 8000 m²; 3 = x ≥ 8000 m²) and connectivity (1–4). Different letters above boxplots indicate significant differences among categories ($p < 0.05$; Mann-Whitney test).

**Abb. 3**. Boxplot Diagramme für Konkurrenz Eigenschaften (EIV-L, EIV-N, mittlere maximale Wuchshöhe, Mähtoleranz) in unterschiedlichen Größenkategorien von Grünlandeinheiten (1 = x < 2000 m²; 2 = 2000 ≤ x < 8000 m²; 3 = x ≥ 8000 m²) und Konnektivität (1–4). Unterschiedliche Buchstaben zeigen signifikante Unterschiede zwischen den Kategorien an ($p < 0{,}05$; Mann-Whitney-Test).

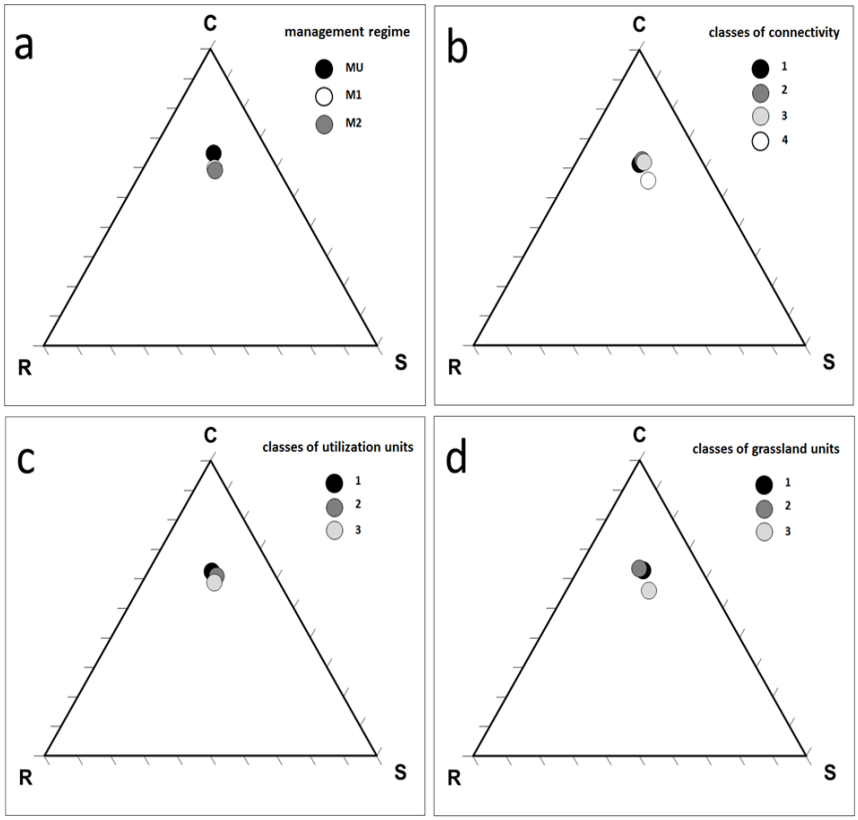


**Fig. 4.** Triangle plot of Grime´s strategy types under (a) different management regimes (MU, M1, M2), (b) classes of connectivity (1–4), (c) size classes of utilization units (1 = x < 1000 m²; 2 = 1000 ≤ x< 4000 m²; 3 = x ≥ 4000 m²), and (d) size classes of grassland units (1 = x < 2000 m²; 2 = 2000 ≤ x < 8000 m²; 3 = x ≥ 8000 m²). C = competition; R = disturbance; S = stress.

**Abb. 4.**Triangular Diagramm der Strategietypen nach Grime bei (a) unterschiedlichem Management (MU, M1, M2), (b) Konnektivitätsklassen (1–4), (c) Größenkategorien von Nutzungseinheiten (1 = x < 1000 m²; 2 = 1000 ≤ x< 4000 m²; 3 = x ≥ 4000 m²) und (d) Größenkategorien von Grünland-einheiten (1 = x < 2000 m²; 2 = 2000 ≤ x < 8000 m²; 3 = x ≥ 8000 m²). C = Konkurrenz; R = Störung; S = Stress.

These findings were also supported by the analysis of Grime´s strategy types. However, while the pattern for connectivity and area of grassland units was similar as compared with the analysis above (Fig. 3), the triangular plots in Figure 4 gave additional information about the amount of competitors and stress-tolerators, respectively, according to management regime and area of utilization units. It could be seen first, that unregularly mowed sites contained a higher amount of competitors than sites mowed once or twice, while a number of stress-adapted, small-growing species never occurred in unregularly mown sites (*Rhinanthus minor* [SR], *Linum catharticum* [SR], *Cerastium brachypetalum* [SR], *Hieracium bauhinii* [CS], *Ononis spinosa* [CS], *Sedum sexangulare* [S]). Second, the larger size of site areas was related to higher portion of stress tolerance related traits.

**Table 3.** Mean values and standard deviation (SD) of plant traits among different groups of management, connectivity, utilization units and grassland units. Significance in overall distribution among test variables is indicated by bold characters ($p < 0.05$; Kruskal-Wallis test). Significant differences among categories are indicated by different characters (a, b, c; $p < 0.05$; Mann-Whitney test).

**Tabelle 3.** Mittelwerte und Standardabweichung (SD) von Pflanzeneigenschaften bei unterschiedlichen Managementkategorien, Konnektivität, Nutzungseinheiten und Grünlandeinheiten. Signifikanz in der Gesamtverteilung der Testvariablen wird durch Fettdruck dargestellt ($p < 0{,}05$; Kruskal-Wallis-Test). Signifikante Unterschiede zwischen den einzelnen Kategorien wird durch unterschiedliche Buchstaben dargestellt (a, b, c; $p < 0.05$; Mann-Whitney-Test).

| | EIV-L | | EIV-N | | Mean max. height (cm) | | Mowing tolerance | | Seed weight (mg) | | Seed L/W-ratio | | End of flowering (month) | | Duration of flowering (months) | | Phenological group | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | SD | Mean | SD | Mean | SD | Mean | SD | Mean | SD | Mean | SD | Mean | SD | Mean | SD | Mean | SD |
| Management | | | | | | | | | | | | | | | | | | |
| Mowing unreg. | 7 | 0.2 | 4.3 | 0.7 | 70 | 5.3 | 5.3 | 0.4 | 2.8 | 0.7 | 1.5 | 0.1 | 7.9 | 0.2 | 3.4 | 0.2 | 5.8 | 0.3 |
| Mowing 1x p.a. | 7.1 | 0.1 | 4 | 0.6 | 65.8 | 5.2 | 5.3 | 0.4 | 2.4 | 0.6 | 1.4 | 0.1 | 7.9 | 0.2 | 3.5 | 0.2 | 5.7 | 0.3 |
| Mowing 2x p.a. | 7.1 | 0.1 | 3.8 | 0.5 | 64 | 5 | 5.2 | 0.3 | 2.7 | 0.5 | 1.4 | 0.1 | 8 | 0.2 | 3.6 | 0.3 | 5.7 | 0.3 |
| Connectivity | | | | | | | | | | | | | | | | | | |
| Class 1 | **7.1 a** | **0.1** | **4.3 a** | **0.2** | 65.7 | 4.4 | 5.5 | 0.2 | **2.5 a** | **0.5** | 1.4 | 0.1 | 7.9 | 0.3 | 3.5 | 0.3 | **5.5 a** | **0.2** |
| Class 2 | **7.1 a** | **0.2** | **4.1 a** | **0.8** | 68.2 | 5.3 | 5.3 | 0.4 | **3.1 b** | **0.5** | 1.5 | 0.1 | 8 | 0.2 | 3.5 | 0.3 | **5.6 ab** | **0.3** |
| Class 3 | **7.1 a** | **0.1** | **4.2 a** | **0.5** | 67.5 | 6.2 | 5.3 | 0.3 | **2.5 a** | **0.7** | 1.4 | 0.1 | 7.9 | 0.2 | 3.4 | 0.2 | **5.6 a** | **0.3** |
| Class 4 | **7.2 b** | **0.1** | **3.5 b** | **0.5** | 63.5 | 4.8 | 5 | 0.5 | **2.1 a** | **0.4** | 1.4 | 0.1 | 8 | 0.1 | 3.5 | 0.1 | **5.9 b** | **0.2** |
| Utilization unit | | | | | | | | | | | | | | | | | | |
| 1 (x < 1000 m²) | 7 | 0.2 | 4.3 | 0.6 | 67.9 | 5.3 | 5.4 | 0.4 | **2.8 a** | **0.5** | 1.5 | 0.1 | **8.1 a** | **0.2** | **3.6 a** | **0.3** | 5.7 | 0.2 |
| 2 (1000 ≤ x < 4000 m²) | 7.1 | 0.1 | 3.9 | 0.6 | 66.5 | 6.3 | 5.2 | 0.4 | **2.4 b** | **0.7** | 1.4 | 0.1 | **7.9 b** | **0.2** | **3.4 b** | **0.2** | 5.7 | 0.4 |
| 3 (x ≥ 4000 m²) | 7.2 | 0.1 | 3.9 | 0.6 | 64.5 | 3.9 | 5.3 | 0.5 | **2.3 b** | **0.6** | 1.4 | 0.1 | **7.9 ab** | **0.2** | **3.5 ab** | **0.2** | 5.7 | 0.2 |
| Grassland unit | | | | | | | | | | | | | | | | | | |
| 1 (x < 2000 m²) | **7.0 a** | **0.2** | **4.2 a** | **0.2** | **68.0 a** | **5.2** | **5.4 a** | **0.3** | **2.9 a** | **0.6** | 1.4 | 0.1 | 7.9 | 0.3 | 3.5 | 0.3 | 5.6 | 0.3 |
| 2 (2000 ≤ x < 8000 m²) | **7.1 a** | **0.1** | **4.3 a** | **0.5** | **68.0 a** | **5** | **5.4 a** | **0.4** | **2.6 a** | **0.6** | 1.4 | 0.1 | 8 | 0.2 | 3.5 | 0.3 | 5.7 | 0.3 |
| 3 (x ≥ 8000 m²) | **7.2 b** | **0.1** | **3.5 b** | **0.5** | **63.1 b** | **4.9** | **5.0 b** | **0.4** | **2.2 b** | **0.6** | 1.4 | 0.1 | 7.9 | 0.2 | 3.4 | 0.2 | 5.8 | 0.2 |
| Total | 7.1 | 0.1 | 4 | 0.6 | 66.3 | 5.4 | 5.3 | 0.4 | 2.5 | 0.6 | 1.4 | 0.1 | 7.9 | 0.2 | 3.5 | 0.2 | 5.7 | 0.3 |

In general, dispersal-related traits (seed weight, seed length/width-ratio) as well as phenological traits (end of flowering, duration of flowering and phenological group) showed less distinct responses to management frequency, connectivity and area of grassland sites (Table 3). Seed weight was significantly higher in small grassland units (< 1000 m²), particularly owing to the numbers of *Fabaceae* (*Medicago lupulin*a, *Onobrychis viciifolia*, *Vicia angustifolia*). The end of flowering was later and the duration of flowering longer in small (< 1000 m²) and large utilization units (≥ 4000 m²) than in medium-sized utilization units (1000 ≤ x < 4000 m²). A similar pattern occurred for phenological groups and the factor connectivity.

Dispersal type, self-compatibility and germination type did not show any significant difference in distribution among any management frequency, connectivity and area classes of coherent grasslands (Supplement E4), except dispersal type, which was slightly different compounded in utilization class 1 (<1000 m²) (Supplement E5) as compared with utilization classes 2 and 3 ($X^2 = 27$, $df = 16$, $p = 0.041$). Utilization unit class 1 was the only class to contain the dispersal types boleochory (*Arenaria serpyllifolia*, *Astrantia major*, *Erysimum cheiranthoides*), hydrochory (*Lycopus europaeus*) and dysochory (*Capsella bursa-pastoris*, *Vicia villosa*, *Cirsium oleraceum*). Additionally, in small utilization units (< 1000 m²) the amount of endozoochory and meteorochory was slightly smaller than in larger units, whereas the amount of autochory (*Capsella bursa-pastoris*, *Viola arvensis*, *Viola riviniana*, *Vicia sepium*, *Vicia villosa* and *Vicia sativa*) was considerably higher.

## 4. Discussion

In Central Europe considerable efforts were made to maintain species-rich semi-dry grasslands (POSCHLOD & WALLISDEVRIES 2002). In fact, conservation-oriented management has become rather expensive (POSCHLOD et al. 2005), due to the fact that hay of extensively used grasslands is no longer needed in modern agriculture (STOATE et al. 2009). Conservation of semi-dry grassland currently relies on subsidies to farmers who remove the biomass. However, evaluations in Austria have revealed that the amount of subsidies was not related to conservation success (ZECHMEISTER 2003). In our study, we aimed to identify key factors underlying the diversity of typical and endangered semi-dry grassland species in a fragmented landscape (LAUTERBACH et al. 2013) and to provide recommendations for agencies, habitat managers and farmers how to maximize conservation success for vascular plants (JANIŠOVÁ et al. 2011).

### 4.1 Abiotic site conditions

The majority of studied grassland patches contained soil nutrient levels below the upper limits restraining plant species diversity (JANSSENS et al. 1998). However, we observed lower potassium amounts in both highly connected (connectivity class 4: utilization unit borders to two or more further species-rich grassland) and large grassland (grassland unit class 3: ≥ 8000 m²) sites. This can most likely be explained by the fact that larger and well-connected sites suffer less from nutrient influx than smaller and isolated sites (NEITZKE 1998). As a result of considerable differences in the pH contents of sites, semi-dry grasslands in the study area differed in dominance of stress-adapted or competitive species, respectively, which had a significant impact on the number of Red List species, relevance for species conservation and naturalness (Section 4.2).

### 4.2 Community indices

We found significant thresholds in connectivity and fragment size that increased the richness of semi-dry grassland patches. For the number of semi-dry grassland species, connectivity could be identified as the main factor (Table 2). Well-connected sites, sharing at least two borders with further species-rich grasslands, contained twice the number of semi-dry grassland species than less connected sites. Similarly, coherent grassland units larger than 8000 m² showed highest numbers of semi-dry grassland species; no difference was found among smaller grassland units (Fig. 2). This is in line with other studies that investigated the negative effect of habitat fragmentation for richness of specialist species (BRÜCKMANN et al. 2010, ZULKA et al. 2014). However, the study of SCHAFFERS (2002) showed that long and narrow grasslands harboured more species than grasslands with low perimeter:area ratios, possibly due to the effect of neighbouring different vegetation types. We found the opposite effect taking semi-dry grassland species numbers into account.

The fact that less connected and smaller patches had low richness of semi-dry grassland species could first, be explained by nutrient influx from bordering croplands, which promoted competitive species and thus caused competitive exclusion of habitat specialists (SCHAFFERS 2002). The lower potassium content in well-connected and large sites (Supplement E1) underlines this assumption. Our results support findings by NEITZKE (1998), who discovered that bordering croplands within a distance of ≤ 8 m had a negative effect on nitrogen supply and, consequently, on the species composition of calcareous grasslands, therefore suggesting a ´boundary zone´. Second, it could be a direct size effect following the habitat fragmentation paradigm, as it was found for dry grassland specialist species in the study of ZULKA et al. (2014). According to this concept small populations in isolated grassland fragments are more prone to stochastic extinction events with a lower probability of recolonization. Furthermore, small population size was found to be connected to lower genetic variation and, consequently, lower plant fitness (LEIMU et al. 2006).

We identified soil-pH, PADI-radiation and connectivity as the main drivers of conservation value (number of Red List species, relevance for species conservation) and naturalness. While the effect of connectivity can be explained as above, the negative effect of pH is more difficult to explain because soil pH has been shown previously to be positively related to plant species richness in Central European vegetation (e.g. EWALD 2003). One explanation for this discrepancy is that soil pH is overlaid by more important factors, like productivity (CHYTRÝ et al. 2003). Although we did not measure this parameter, we observed dense *Bromus erectus*-dominated vegetation on sites with high pH. As Red List species in semi-dry grasslands tend to be poor competitors, they might have been subpressed in sites with high productivity and soil pH by competitive exclusion (PIPENBAHER et al. 2013).

We found a positive relationship between PADI-radiation on the one hand and number of Red List species, relevance for species conservation and naturalness on the other hand. This supports findings of BENNIE et al. (2006), who observed that steep and south-facing dry grasslands were more resilient to the invasion by competitive grasses than more shallow areas. This effect might be explained by strong micro-climatic differences and low water availability at steeps slopes, similar to conditions found in more continental dry grasslands (HENSEN 1995). As many endangered semi-dry grassland species are stress-tolerant specialists, they could outperform more competitive generalist species at these sites.

A large body of literature deals with the effects of management on species diversity in grasslands. Taken together, these studies portray a unimodal relationship between management regime and diversity. Since both a high mowing frequency (ZECHMEISTER et al. 2003,

SOCHER et al. 2012, ALLAN et al. 2014) and complete abandonment (HANSSON & FOGELFORS 2000, KAHMEN et al. 2002, JACQUEMYN et al. 2011, KLIMEŠ et al. 2013) affect species richness negatively, an intermediate mowing frequency should have the most positive effect on plant species diversity. In our study management did not explain differences in semi-dry grassland species diversity (Table 2). We see several explanations for this unexpected result. First, our study did not take the date of mowing into consideration, although this factor can influence species diversity in grasslands (HUMBERT et al. 2012). For example, delaying mowing from spring to fall or from early summer to later can have negative effects on species diversity. JACQUEMYN et al. (2011) showed that mowing once a year at the end of the growing season leads to a decrease in species richness, most likely explained by the absence of microsites for seedling establishment. Second, the effect of mowing frequency has to be considered carefully, taking into account regional environmental factors like mesoclimate, soil type, soil moisture or atmospheric N deposition (SOCHER et al. 2012). Third, the typical nature conservation dogma of decreased mowing frequency is relatively new (KAPFER 2010a, b). For instance, mowing once annually was in fact traditionally accompanied by grazing in early spring and autumn. However, the cessation of traditional management cannot unfold its effects not within several years (KLIMEŠ et al. 2013). The study of BÜHLER & ROTH (2011) showed a general increase of common species in grasslands that had been managed continuously for ten years, which led to taxonomic homogenization but not yet to a decrease of uncommon specialists. Last but not least, our study focused on current management but it is possible that past management would be a better predictor for species richness and conservation value (FAHRIG 2003, ZULKA et al. 2014).

### 4.3 Plant traits

We found that small (< 8000 m²) and less connected sites (sharing no or only one border with further species-rich grasslands) promoted typical *Arrhenatherion* Koch 1926 species, i.e. tall growing plants adapted to efficient extraction of nutrients (Table 3, Fig 4d). By contrast, species with a high specificity for semi-dry grasslands, i.e. often CS-species (e.g. *Danthonia decumbens*, *Medicago falcata*, *Koeleria pyramidata*, *Koeleria macrantha* and *Cervaria rivini*) did not occur in smaller patches. These results match observations by MARINI et al. (2012) from grassland fragments in Central and N-Europe. The higher edge to core proportion in smaller patches means that small semi-dry grasslands suffer from higher nutrient influx (NEITZKE 1998). These conditions increase plant height (HEIJCMAN et al. 2007) and reduce light availability for small grassland species. Furthermore, from a meta-population perspective, stress-tolerant species could be more prone to local extinction events due to demographic stochasticity, genetic drift, and reduced probability of re-colonization events (FISCHER & STÖCKLIN 1997). As long as small patches are dominated by competitive species, more stress-tolerant species will be bound to large sites where they can maintain stable populations (ZULKA et al. 2014).

We did not find any effect of management on the prevalence of stress-adapted species in semi-dry grasslands, given that mowing was performed at least once annually. However, mowing unregularly led to higher portions of competitive species (Fig. 4). In contrast to VALKÓ et al. (2012), who stated that a decreased mowing frequency (lower than once per year) can be a suitable option for dry-mesophilous mountain meadows in NE Hungary, our study showed that unregular management is unsuitable for typical, stress-adapted semi-dry grassland species in the Alpine Foreland of Styria (Fig. 4). Eventually, our findings go well together with the model suggested by SCHAFFERS (2002), in which maximum species rich-

ness occurs on sites where stress and disturbance and light competition are in balance. This is also supported by ZULKA et al. (2014) who found out that above-ground standing phytomass was negatively correlated to species richness of dry grassland specialists.

In contrast to our hypothesis, site size, management and connectivity were not related to plant traits connected to dispersal (MARINI et al. 2012), germination type and selfing (Supplement E4). In particular, we found that small, isolated sites did not contain more wind-dispersed and more self-compatible species than larger, well-connected sites. This could be explained by the dominance of tall-growing species, which prevents efficient anemochory of small species (THOMSON et al. 2011, LAUTERBACH et al. 2013, SENGL et al. 2015). Our results could indicate that dispersal and establishment must be less important than persistence in semi-dry grasslands (MAURER et al. 2003) or that our study sites lack microsites for seedling establishment (JACQUEMYN et al. 2011, MUDRÁK et al. 2013). However, in line with COUSINS (2009) and PURSCHKE et al. (2012) we conclude that the extinction debt may not yet be paid in fragmented grasslands due to long-term persistence ability of lots of species. Additionally, we have to admit that it was not possible in this study to take into account which grassland fragments were part of a larger continuum in the past (FAHRIG 2003, ZULKA et al. 2014). Consequently, grassland fragments could still harbour plants with short distance dispersal traits which are expected to occur in well-connected sites only.

### 4.4 Management recommendations

Small semi-dry grassland fragments had a low number of semi-dry grassland species and low relevance for species conservation and naturalness. Several management actions could improve these conditions. First, buffer zones around grassland remnants (VRAHNAKIS et al. 2013) could protect them from nutrient influx (NEITZKE 1998) and thus foster diversity of semi-dry grassland species (KRÁLOVEC et al. 2009). Restoration of such buffer zones could be implemented easily and cost effectively by natural colonization (TÖRÖK et al. 2011), due to the fact that source populations are nearby (SENGL et al. 2015). Second, the introduction of growth-adapted management could avoid an increase of competitive, tall herbs and grasses and favor more stress-adapted and endangered semi-dry grassland species (DIERSCHKE & BRIEMLE 2002, SCHAFFERS 2002).

Similar to ČÍŽEK et al. (2012) and VALKÓ et al. (2012) we think that a diversified, periodically changing management regime could increase species diversity, taking into account the requirements of various different taxa such as plants, birds and insects (JANIŠOVÁ et al. 2011, ALLAN et al. 2014, HILLER & BETZ 2014). Nevertheless, we recommend a minimum management frequency of one cut per year for semi-dry grasslands in our model region. In that respect sheep grazing should be tested as a management option of semi-dry grassland in the region. After all, grasslands in Central European lowlands have a 6000-year old history as pastures (KAPFER 2010a, b), while the production of hay in greater extent started not earlier than in the late medieval. The close connection of grazing of grasslands can still be observed by the high amount of zoochorous species (Supplement E5). So, periodical sheep grazing (KAPFER 2010b, AUFFRET 2011) could create an opportunity to reconnect grassland remnants, increase diaspore exchange and create microsites for the establishment of seedlings.

## 5. Conclusions

With our study in the SE Alpine Foreland we aimed to figure out the abiotic and anthropogenic prerequisites for efficient conservation measures of species-rich semi-dry grassland communities. Our study revealed that only large, well-connected semi-dry grassland sites support high richness of typical *Festuco-Brometea* species. In contrast, small and isolated semi-dry grassland sites had lower diversity of typical semi-dry grassland species, most possibly due to nutrient input from bordering crop fields. Similarly, unregular mowing proved to be insufficient for conservation of semi-dry grasslands because it promoted competitive *Arrhenatherion* species and suppressed stress-adapted semi-dry grassland specialists. Researchers and Managers need to evaluate to what extent buffer zones and growth-adapted management, incl. periodical shepherding, can improve the quality of semi-dry grassland remnants in the region.

## Erweiterte deutsche Zusammenfassung

**Einleitung –** Artenreiche Halbtrockenrasen sind in ganz Europa selten geworden und zählen zu den gefährdetsten Lebensraumtypen (HABEL et al. 2013). Oftmals handelt es sich dabei um Überbleibsel früher weit verbreiteter Pflanzengesellschaften (DOSTÁLEK & FRANTÍK 2012). In der Steiermark (Österreich) gelang es durch Bemühungen seitens der Landesregierung und verschiedener Naturschutzorganisationen einige dieser Halbtrockenrasen-Fragmente zu erhalten (SENGL & MAGNES 2008). Obwohl diese Fragmente weitestgehend in das Natura2000-Schutzregime eingebettet wurden, ist deren Erhaltungszustand oftmals unzureichend (UMWELTBUNDESAMT 2013). In manchen Flächen beobachteten wir unterschiedliche und sich zum Teil widersprechende Schutzzielen, ein Umstand der auch aus anderen Ländern berichtet wird (WALLISDEVRIES et al. 2002). Dies resultiert mitunter in einer, für die langfristige Erhaltung der Flächen, nicht zielführenden Pflegenutzung (POSCHLOD & WALLISDEVRIES 2002). Auch können negative Einflüsse zunehmender Fragmentierung und Isolation (FISCHER & STÖCKLIN 1997), sowie die Wirkung von Randeffekten benachbarter Intensiväckern (NEITZKE 1998) zu einer ungünstigen Entwicklung der Halbtrockenrasen führen. In unserer Studie haben wir die Auswirkungen abiotischer Standortparameter sowie von Flächengröße, Konnektivität und Management auf die Artendiversität, Artenzusammensetzung und Vorkommen von Merkmalsgruppen von Gefäßpflanzen untersucht.

**Material und Methoden –** Das Untersuchungsgebiet liegt im Südöstlichen Alpenvorland Österreichs in der Nähe der Marktgemeinde Sankt Anna am Aigen (46.80N/15.98E–46.81N/15.99E; 281–297 m a.s.l.). Die Böden sind hier mehrheitlich Braunerden und Pseudogleye mit saurer Reaktion, jedoch verlaufen auch einige schmale Kalkbänder durch das Untersuchungsgebiet (LEBENSMINISTERIUM 2012). Der Jahresniederschlag beträgt 830–840 mm und die Jahresmitteltemperatur beträgt etwa 9,2°C (1971–2000: ZAMG 2012). Das Untersuchungsgebiet beinhaltet unterschiedlich große Halbtrockenrasen, die ein- bis zweimal jährlich, oder auch nur unregelmäßig gemäht werden. Sämtliche untersuchte Flächen sind der lokalen Gesellschaft *Cirsio pannonici-Brometum* (STEINBUCH 1995, WILLNER et al. 2013) zuzuordnen. Zwischen 2007 und 2014 wurden insgesamt 44 Vegetationsaufnahme (4 m × 4 m, je eine Aufnahme pro Halbtrockenrasen) gemacht und Bodenproben genommen. Diese wurden auf Phosphor- und Kaliumgehalt sowie pH-Wert untersucht, außerdem wurde die Nutzung sämtlicher Flächen erhoben. Die Halbtrockenrasen wurden hinsichtlich der Mahdfrequenz (unregelmäßig, ein- oder zweimal pro Jahr), der Konnektivität zu weiterem artenreichen Grünland (vier Klassen), sowie der Flächengröße der Nutzungseinheit (drei Klassen) und des gesamten, zusammenhängenden Grünlandes (drei Klassen) eingeteilt. Es wurde eine lineare Modellierung mit anschließender Modellselektion durchgeführt, bei der Management, Konnektivität, Flächengrößen sowie weitere abiotische Faktoren (pH, Nährstoffgehalt, Einstrahlung) als Prädiktoren dienten. Ziel der Untersuchung war es, die Hauptfaktoren für das Auftreten gebietstypischer Halbtrockenrasen-Arten, sowie des naturschutzfachlichen

Wertes der Halbtrockenrasen herauszufinden (vgl. GRACE et al. 2014). Darüber hinaus wurden die Verteilungen konkurrenz- und ausbreitungsrelevanter Pflanzeneigenschaften unter dem Einfluss von Flächengröße, Mahd-Frequenz und Konnektivität untersucht.

**Ergebnisse –** Die Ergebnisse der Studie zeigen, dass große, gut vernetzte Halbtrockenrasen in der Regel eine größere Anzahl gebietstypischer Halbtrockenrasen- und Rote-Liste-Arten aufwiesen. Ein hoher pH-Wert in Verbindung mit hohem Nährstoffniveau wirkten sich deutlich negativ auf die Artenzusammensetzung aus. Während unregelmäßige Mahd zu deutlich höheren Anteilen an Konkurrenzstrategen führte, waren die Unterschiede zwischen ein- und zweimaliger Mahd nicht signifikant. Obwohl einige Halbtrockenrasen-Arten eine offensichtliche Widerstandsfähigkeit gegen unregelmäßige Pflegenutzung aufwiesen, hatten sie dennoch unter dem Konkurrenzdruck mesophiler Grünlandarten zu leiden. Ausbreitungsrelevante sowie phänologische Pflanzeneigenschaften unterschieden sich kaum zwischen unterschiedlich großen, unterschiedlich vernetzten und unterschiedlich bewirtschafteten Halbtrockenrasen.

**Diskussion** – Die Ergebnisse zeigen, dass neben lokalen Boden- und Standortfaktoren, Flächengröße und Konnektivität entscheidende Faktoren für die Anzahl typischer Halbtrockenrasen-Arten und somit dem naturschutzfachlichen Wert der Flächen darstellen (cf. BRÜCKMANN et al. 2010). Ein hohes Nährstoffniveau in Verbindung mit einem hohen pH-Wert, was besonders bei kleineren, isolierten Flächen vermutlich aus Einträgen aus benachbarten Ackerflächen resultierte, wirkte sich deutlich zu Gunsten von Konkurrenz-Strategen aus (NEITZKE 1998). Zudem schienen typische Halbtrockenrasen-Arten stärker auf große, zusammenhängende Flächen angewiesen zu sein. Ursache dafür könnte eine höhere Aussterbewahrscheinlichkeit kleiner, lokaler Populationen sein (FISCHER & STÖCKLIN 1997). Wir fanden keine signifikanten Unterschiede bezüglich Diversität und Artenzusammensetzung zwischen einmal- und zweimal gemähten Flächen. Jedoch zeichnete sich ein Trend zu höheren Deckungswerten konkurrenzkräftiger Arten in nur unregelmäßig gemähten Flächen ab (SCHAFFERS 2002). Dies führt zu Dominanz hochwüchsiger, konkurrenzstarker Fettwiesen-Arten, die kleine, stresstolerante Arten, welche in der Regel einen höheren naturschutzfachlichen Wert besitzen, verdrängten (SCHAFFERS 2002). Allerdings ist die naturschutzorientierte, extensive Pflegenutzung (einmalige, späte oder unregelmäßig durchgeführte Mahd) in Mitteleuropa noch relativ jung (KAPFER 2010b), sodass sich der Effekt noch nicht deutlich manifestiert haben könnte (vgl. BÜHLER & ROTH 2011). Nicht gestützt wurde unserer Erwartung, dass kleine, isolierte Flächen einen höheren Anteil anemochorer Arten aufweisen sollten. Dieser Umstand führt zu der Annahme, dass Wiederbesiedelung von Standorten insgesamt ein seltenes Ereignis bei Mäh-Halbtrockenrasen-Arten darstellt (JACQUEMYN et al 2011, MAURER et al. 2003). Insgesamt ergab die Analyse ausbreitungsrelevanter und phänologischer Pflanzeneigenschaften kaum eindeutig interpretierbare Ergebnisse.

**Schlussfolgerungen** – Die Ergebnisse unserer Studie zeigen, dass nur große und gut vernetzte Halbtrockenrasen besonders hohe Diversität sowie hohe naturschutzfachliche Wertigkeit aufweisen. Zudem fanden wir einen deutlichen Zusammenhang zwischen Produktivität und Diversität von Halbtrockenrasen. Hohe Produktivität kann dabei aus einer zu geringen Nutzungsfrequenz (KAPFER 2010a, b) oder Nährstoffeinträgen aus benachbarten Ackerflächen (NEITZKE 1998) resultieren. Gerade unter dem Gesichtspunkt, dass artenreiches Grünland durch jahrhundertelangen Nährstoffentzug entstanden ist (HANSSON & FOGELFORS 2000), benötigen wir ein standortsangepasstes, aufwuchs-orientiertes Management um die langfristige Erhaltung der Struktur und des Artenreichtums von Halbtrockenrasen im Gebiet zu gewährleisten. Schutzgebietsmanager sollten zudem die Einrichtung von Pufferflächen um kleinere bis mittelgroße Halbtrockenrasen in Erwägung ziehen, um den Einfluss von Nährstoffeinträgen zu vermindern (KRÁLOVEC et al. 2009, VRAHNAKIS et al. 2013). Zusätzlich dazu könnte periodische Beweidung (AUFFRET 2011) die Flächen besser vernetzen, einen Diasporenaustausch zwischen isolierten Flächen ermöglichen und gleichzeitig Keimungsnischen erzeugen.

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## Supplements

**Additional supporting information may be found in the online version of this article.**

**Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.**

**Supplement E1.** Spearman-*Rho* correlation matrix among abiotic site conditions (soil content, PADI-radiation [RAD]) and site size (area utilization unit; area/perimeter utilization unit; area grassland unit; area/perimeter grassland unit).

**Anhang E1.** Spearman-*Rho* Korrelations-Matrix zwischen abiotischen Standortverhältnissen (Bodenfaktoren, Einstrahlung (RAD) und Flächengröße, sowie Flächen/Umfang-Verhältnis von Nutzungseinheiten und zusammenhängendem Grünland.

**Supplement E2.** Mean values and standard deviation (SD) of abiotic site conditions (pH, phosphor content, potassium content, and PADI-radiation [RAD]) across different categories of management, connectivity, utilization units and grassland units.

**Anhang E2.** Mittelwerte und Standardabweichung (SD) von abiotischen Standortverhältnissens (pH, Phosphor, Kalium, Einstrahlung [RAD]) bei unterschiedlichen Managementkategorien, Konnektivität, Nutzungseinheiten und Grünlandeinheiten.

**Supplement E3.** Mean values and standard deviation (SD) of species numbers, number of semi-dry grassland species, number of Red List species, Relevance for species conservation and Naturalness among different categories of management, connectivity, utilization units and grassland units.

**Anhang E3.** Mittelwerte und Standardabweichung (SD) von Artenzahl, Anzahl an Halbtrockenrasenarten, Anzahl an Rote Liste Arten, Relevanz für den Artenschutz und Natürlichkeitswerte bei unterschiedlichen Managementkategorien, Konnektivität, Nutzungseinheiten und Grünlandeinheiten.

**Supplement E4.** Contingency analysis between frequency of management (mowing unregularly; mowing 1 x p.a.; mowing 2 x p.a.), classes of connectivity (1–4), utilization unit classes (1–3), and grassland unit classes (1–3).

**Anhang E4.** Kontingenzanalyse zwischen den Faktoren Management-Frequenz (unregelmäßige Mahd, Mahd 1 x pro Jahr, Mahd 2 x pro Jahr), Konnektivitätsklassen (1–4), Klassen der Nutzungseinheiten (1–4) sowie Klassen zusammenhängenden Grünlandes (1–4).

**Supplement E5.** Distribution of dispersal traits among species in different utilization unit classes ($1 = x < 1000$ m²; $2 = 1000 \leq x < 4000$ m²; $3 = x \geq 4000$ m²).

**Anhang E5.** Verteilung der verschiedenen Ausbreitungsstrategien von Pflanzen unter unterschiedlichen Größenklassen der Nutzungseinheiten ($1 = x < 1000$ m²; $2 = 1000 \leq x < 4000$ m²; $3 = x \geq 4000$ m²).

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