Universität für Bodenkultur Wien
University of Natural Resources and Life Sciences, Vienna

Effects of management cessation on bumblebees (Hymenoptera, *Bombus* sp.), hoverflies (Diptera, Syrphidae), heteropteran bugs (Hemiptera, Heteroptera), grasshoppers (Orthoptera, Caelifera/ Ensifera), plants, soil characteristics and humans in Austrian and Swiss mountain grassland ecosystems

Dissertation for the attainment of the doctoral degree at the University of Natural Resources and Life Sciences, Vienna

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Ronnie Walcher

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Abstract

Semi-natural grassland is one of the most species rich agroecosystem in the world. At present, around one third of Europe´s land surface is covered by permanent grassland, which is an important part of the agricultural landscape. Extensive land use by mowing or grazing preserved the high ecological value of grasslands and protected them as essential sources of regulatory, supportive and cultural ecosystem services. In recent decades, the issue of land use abandonment came more often in the focus of scientific research, as it is considered one of the greatest threats to grassland diversity and is leading to a decline in their total area. In order to identify its multifaceted consequences, the present thesis investigates the issue of land-use abandonment from different perspectives and examines (i) the effects of abandonment on bumblebees, hoverflies, true bugs and grasshoppers, (ii) the effects of abandonment on plant richness, vegetation characteristics, soil properties and litter decomposition and (iii) the relationships between biodiversity and humans in the context of management change. The studies were carried out in extensively managed and long-term abandoned meadows in three mountain regions in the Austrian and Swiss Alps. Management had positive effects on local bumblebee communities, however, hoverflies, true bugs and grasshoppers showed also an affinity for abandoned meadows. Plant richness declined markedly after abandonment, plant species assemblages differed between meadow types, and also examined soil parameters were affected. Litter decomposition was found to be higher in abandoned meadows. Overall, land-use abandonment had a clear impact on insect diversity, vegetation and soil parameters and the provision of important cultural ecosystem services. However, it was shown that the effects were not always negative. Abandonment created new habitats, which contributed to an increase in the local insect diversity within the agricultural landscape. This study is intended to show the high value of mountain grassland and provides arguments for the conservation of this ecosystem. The results of the studies shall support decision makers together with ecologists when developing management plans for mountain grasslands and show the importance to address diverse ecological and social aspects when developing agri-environmental schemes.

Key words: grassland, extensive management, land-use abandonment, biodiversity, insects, plants, soil parameter

Zusammenfassung

Naturnahes Grünland zählt zu den artenreichsten Agrarökosystemen der Welt. Derzeit ist rund ein Drittel der europäischen Landfläche von Dauergrünland bedeckt, welches einen wichtigen Bestandteil der Kulturlandschaft darstellt. Extensive Landnutzung durch Mähen oder Beweidung bewahrte den hohen ökologischen Wert von Grünland und bewahrte es als wesentliche Quelle für regulative, unterstützende und kulturelle Ökosystemleistungen. In den letzten Jahrzehnten stand das Thema Landnutzungsaufgabe immer öfter im Mittelpunkt der wissenschaftlichen Forschung, da es als eine der größten Bedrohungen für die Grünlandvielfalt gilt und zu einem Rückgang ihrer Gesamtfläche führte. Um die vielfältigen Folgen zu identifizieren, wurde in vorliegender Arbeit das Problem der Landnutzungsaufgabe von Bergwiesen aus verschiedenen Perspektiven untersucht. Die vorliegende Arbeit untersucht (i) die Auswirkungen der Landnutzungsaufgabe auf Hummeln, Schwebfliegen, Wanzen und Heuschrecken, (ii) die Auswirkungen der Landnutzungsaufgabe auf Pflanzenartenreichtum, Vegetationscharakteristika, Bodeneigenschaften und Streuzersetzung und (iii) die Beziehungen zwischen Biodiversität und Mensch im Kontext mit dem Bewirtschaftungswandel. Die Studien wurden auf extensiv bewirtschafteten und unbewirtschafteten Wiesen in drei Bergregionen der österreichischen und schweizerischen Alpen durchgeführt. Extensive Bewirtschaftung hatte positive Auswirkungen auf die lokalen Hummelgemeinschaften, jedoch zeigten Schwebfliegen, Wanzen und Heuschrecken auch eine Affinität zu unbewirtschafteten Wiesen. Der Pflanzenreichtum nahm nach der Landnutzungsaufgabe deutlich ab und die Pflanzenartengemeinschaften unterschieden sich deutlich zwischen den beiden Wiesentypen. Ebenfalls gab es Auswirkungen auf die untersuchten Bodenparameter. In den unbewirtschafteten Wiesen war die Streuzersetzung höher. Insgesamt wirkte sich die Aufgabe der Landnutzung eindeutig auf die Insektenvielfalt, die Vegetations- und die Bodenparameter und die Bereitstellung wichtiger kultureller Ökosystemleistungen aus. Es wurde jedoch gezeigt, dass die Auswirkungen nicht in jedem Fall negativ waren. Durch die Bewirtschaftungsaufgabe wurden neue Lebensräume geschaffen, welche zu einer Zunahme der lokalen Insektenvielfalt innerhalb der Agrarlandschaft beitrugen. Die Studie soll den hohen Wert von Grünland in Bergregionen aufzeigen und Argumente für den Erhalt dieses Ökosystems liefern. Die Ergebnisse sollen Entscheidungsträger zusammen mit Ökologen bei der Erstellung von Bewirtschaftungsplänen unterstützen und zeigen, wie wichtig es ist, bei der Entwicklung von Agrarumweltmaßnahmen vielfältige ökologische und soziale Aspekte zu berücksichtigen.

Schlüsselwörter: Grünland, extensive Landnutzung, Landnutzungsaufgabe, Biodiversität, Insekten, Pflanzen, Bodenparameter

1. General Introduction

Grasslands represent one of the most dominant parts of the European agricultural landscape and account for more than one-third of the total utilized area (Suttie et al. 2005). Generally, grasslands can be classified into two major types: natural and semi-natural grasslands (Dengler et al. 2020). Natural grasslands (e.g. alpine grassland) represent self-sustaining systems which never experienced any management by humans (Török et al. 2020). On the contrary, semi-natural grasslands, which in turn represent the majority of the European grasslands, are closely connected with human land use (Dengler et al. 2020). Regular management, either by mowing or grazing, maintained these biodiversity hotspots. Especially, extensive low input farming with low stocking rates and less frequent mowing sustained the high ecological value of semi-natural grasslands and consequently their value for the conservation of many plant and invertebrate species (Baur et al. 2006; Buchgraber et al. 2011; Chytrý et al. 2015; Littlewood et al. 2012; Wilson et al. 2012). In addition to providing valuable habitats for plants and animals, grasslands represent highly aesthetic landscape elements and support humans with important regulative, supportive and cultural ecosystem services (Pastur et al. 2016).

Considering that the proportion of extensively managed semi-natural grasslands in Europe has seriously declined since the second half of the 20th century, it quickly became clear how management changes affected this ecosystem in the past decades (Bullock et al. 2011). There are several reasons for this decline. On the one side, an increased demand for agricultural products along with an increased economic pressure and the development of modern agricultural practice with the introduction of advanced mechanization led to an intensification of grasslands or to conversion into arable land (Lieskovský et al. 2015; Marini et al. 2011). On the other side, traditional, extensive management, especially in mountain regions, became economically unimportant leading to the abandonment of formerly managed sites (Hinojosa et al. 2016; MacDonald et al. 2000; Osawa et al. 2016).

The abandonment of land use is often seen as a serious threat to biodiversity, affecting both plant and animal diversity (e.g. Uchida and Ushimaru 2015), and is also considered to affect human health and well-being (Arnberger et al. 2018). However, it is reported that these effects vary greatly between geographical regions and also between different taxa (Queiroz et al. 2014). The present thesis considers the issue of land use abandonment from different perspectives. In addition to the effects of abandonment on different groups of insects, the effects of abandonment on plants, soil properties and human health benefits are investigated in three different regions of the Austrian and Swiss Alps.

1.1. Bumblebees, syrphids, heteropteran bugs and grasshoppers and the consequences of abandonment

Semi-natural grasslands, in their various management forms as meadows or pastures, provide important habitats and foraging resources for numerous insect groups (Bonari et al. 2017, Öckinger et al. 2007; Uchida et al. 2016), among them bumblebees, hoverflies, true bugs and grasshoppers. Abandonment is assumed to alter the habitat conditions of formerly managed mountain meadows with a decline of plant species richness and the consequent decline of valuable resources for insects (Maurer et al. 2006; Pykälä et al. 2005; Valkó et al. 2018). Although, the four insect groups are important grassland dwellers, little is known whether and to what extent abandonment affects them. Especially, the heteropteran bugs are still underrepresented in ecological studies, especially in mountain areas. However, they have a high ecological relevance since they are important herbivores and play an important role as food source for higher trophic levels (Moir and Brennan 2007; Torma and Császár 2013; Torma et al. 2019). Publications I and III in the present thesis provide important contributions in order to show whether, how and to what extent bumblebees, heteropteran bugs and grasshoppers are affected by land-use abandonment in mountain regions taking also feeding types of the investigated insects and the plant- and landscape parameters as explanatory variables into account. Publication II investigates the effects of abandonment on hoverflies and their larval feeding types in relation to plant- and landscape factors in three mountain areas. Against the background of a continuous insect decline and the overall decrease of insect biomass in recent decades (e.g. Hallmann et al 2017), studies including several insect groups are important in order to possibly make suggestions and recommendations for insect conservation strategies in mountain regions in the future.

1.2. Plants, soil properties and litter decomposition and the consequences of abandonment

Primarily, land-use abandonment affects plant communities of extensively managed semi-natural grasslands, leading to a decline of plant species richness, especially of those species whose persistence depends on a regular management (Baur et al. 2006; Pykälä et al. 2005). Also, the consequent secondary succession after stopping land-use utilization leads to a gradual encroachment of shrubs and trees and a consequent conversion into closed forest (Baur et al. 2006; Bohner et al. 2012; Elias and Tischew 2016). Several studies have confirmed these effects of land-use abandonment on the plant species composition of meadows and pastures (Komac et al. 2013; Marini et al. 2009; Sanjuán et al. 2018). However, the research question on how soil properties such as soil microbial communities, carbon and nitrogen content of the soil or soil temperature and moisture are changing after management cessation, has been little investigated in the past. The question of the impact of abandonment of grasslands on vegetation characteristics, various soil properties and litter decomposition was examined in publication IV.

1.3. Linkages between grassland management and humans

The interactions between grasslands and humans and the benefits that humans derive from this ecosystem are manifold (Müller et al. 2019). Grassland is used for fodder production to ensure high quality and quantity of meat production, to ensure water supply and climate regulation or to prevent soil erosion (Bengtsson et al. 2019). In recent years, semi-natural grasslands have increasingly been discussed with regard to the provision of cultural ecosystem services such as recreational services, aesthetic value or cultural heritage (Müller et al. 2019; Plieninger et al. 2013). Semi-natural grasslands are one of the most species rich ecosystems in Europe and are more and more seen as restorative settings for humans (Arnberger et al. 2018), and as an important source of cultural ecosystem services (Nowak-Olejnik et al. 2020). Extensively managed meadows are often appreciated as highly biodiverse landscape elements by humans which assign a high ecological value to these habitats (Müller et al. 2019; Lindemann-Matthies and Matthies 2018). Further, it was shown that people perceived health benefits such as stress reduction and well-being after a stay in grassland habitats which positively affected human health (Arnberger et al. 2018). Abandonment of formerly extensively managed meadows may alleviate these positive effects. This topic has hardly been addressed so far in mountain meadows across the Alps. Thus, publication V of the present thesis builds a link between measured biodiversity attributes and perceived and measured health benefits in the context of grassland management. This contribution should provide another argument for the conservation of extensively managed grasslands in mountain regions.

2. Publications and objectives of the thesis

This thesis aims at investigating the effects of long-term abandonment of annually mown mountain grassland on several aspects of biodiversity, soil properties and the health and well-being of humans. The issue of abandonment has raised the following research questions:

1.) How does long-term abandonment of mountain meadows affect the species richness, abundance and species composition of bumblebees, syrphids, heteropteran bugs and grasshoppers, and to what extent does it impact their species composition? Additionally, the effect of plant and landscape variables and their effects on insects has been examined.
2.) Which impact has long-term abandonment of formerly mown meadows on vascular plant richness and assemblages, vegetation characteristics and local soil properties?
3.) Are there any relationships between management type – managed and abandoned meadows - and human health benefits and is there an association between humans and biodiversity?

Answering these questions is a key for understanding the multifaceted processes of abandonment and their consequences for biodiversity rich mountain grassland, in order to add arguments for their conservation.

To address the proposed research questions, this dissertation thesis consists of three core publications (I-III) on insects in mountain grasslands, one co-author publication (IV) on vegetation characteristics and soil properties and one co-author publication (V) examining relationships between biodiversity, human health and well-being in relation to management. The following publications are included in the present thesis in order of their appearance in the thesis:

I Walcher, R., Karrer, J., Sachslehner, L., Bohner, A., Pachinger, B., Brandl, D., Zaller, J. G., Arnberger, A., and Frank, T., 2017. Diversity of bumblebees, heteropteran bugs and grasshoppers maintained by both: abandonment and extensive management of mountain meadows in three regions across the Austrian and Swiss Alps. *Landscape Ecology*, **32**, 1937–1951, https://doi.org/10.1007/s10980-017-0556-1.

II Walcher, R., Hussain, R., I., Karrer, J., Bohner, A., Brandl, D., Zaller, J. G., Arnberger, A., Frank, T., 2020. Effects of management cessation on hoverflies (Diptera: Syrphidae) across

Austrian and Swiss mountain meadows. *Web Ecology*, **20**, 143-152, https://doi.org/10.5194/we-20-143-2020.

III Walcher, R., Hussain, R., I., Sachslehner, L., Bohner, A., Jernej, I., Zaller, J. G., Arnberger, A., Frank, T., 2019. Long-term abandonment of mountain meadows affects bumblebees, true bugs and grasshoppers: a case study in the Austrian Alps. *Applied Ecology and Environmental Research*, **17**, 5887-5908, https://dx.doi.org/10.15666/aeer/1703_58875908.

IV Bohner, A., Karrer, J., Walcher, R., Brandl, D., Michel, K., Arnberger, A., Frank, T., Zaller, J. G., 2019. Ecological responses of semi-natural grasslands to abandonment: case studies in three mountain regions in the Eastern Alps. *Folia Geobotanica*, **54**, 211-225, https://doi.org/10.1007/s12224-019-09355-2.

V Hussain, R., I., Walcher, R., Eder, R., Allex, B., Wallner, P., Hutter, H.-P., Bauer, N., Arnberger, A., Zaller, J. G., Frank, T., 2019. Management of mountainous meadows associated with biodiversity attributes, perceived health benefits and cultural ecosystem services. *Scientific Reports*, **9**, 14977, https://doi.org/10.1038/s41598-019-51571-5.

3. Study regions and sampling methods

This chapter introduces the study areas and the methods which were used to answer the proposed research questions.

3.1. Study regions

All studies of the present thesis were conducted on mountainous meadows in three regions across the Eastern Alps including two Austrian and one Swiss region (Figure 1). From east to west the regions comprised the Styrian part of the nature reserve Eisenwurzen (Central Ennstal, Austria), the Biosphere Reserve Val Müstair (Graubünden, Switzerland) and the Biosphere Reserve Großes Walsertal (Vorarlberg, Austria). In each region, six meadows were selected, among three of them were annually mown, non-fertilized and three of them were abandoned. For the third core-publication, which was carried out only in the nature reserve Eisenwurzen, I selected one more replicate of each meadow type summing up to four annually mown and four abandoned meadows. The age of the abandoned meadows was between 15 and 60 years with the shortest time since abandonment in the Biosphere Reserve Val Müstair and the longest time since abandonment in the Biosphere Reserve Großes Walsertal. The managed meadows were between 470 and 5150 m^2 and the abandoned meadows were between 300 and 4300 m^2 in size.

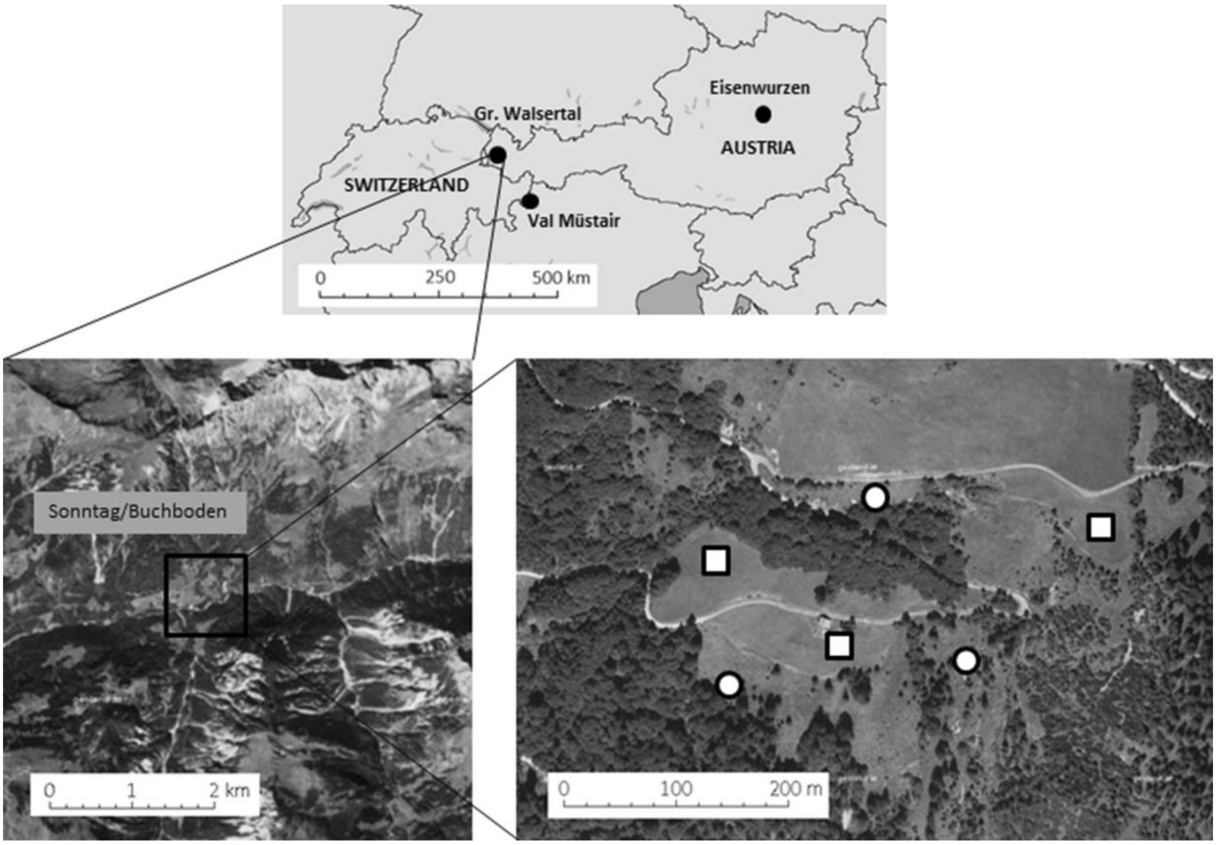

Figure 1: Location of the three selected study regions. The region Großes Walsertal is shown in detail. Managed meadows are marked with squares, abandoned meadows are marked with circles (data source: www.basemap.at).

3.2. Insect sampling

For insect sampling I used three different approaches. I carried out an observation plot method for bumblebees and syrphids, a sweep net method for syrphids and heteropteran bugs, and a soundscape method for grasshoppers. Species richness and abundance of bumblebees and syrphids were recorded by observing four rectangular plots within each meadow. The sizes of the observation plots were 20 m^2 for the bumblebees and 2 m^2 for the hoverflies. They were situated in the center of the meadows with defined distances between them (3, 9, 27 m). Each plot was monitored for 15 minutes leading to an observation time of 1 hour per meadow and per insect group. Bumblebees were identified at the species level on-site, hoverflies were collected with a small insect net and identified in the lab.
The sweep net method was primarily used to assess the species richness and abundance of heteropteran bugs, but also turned out to be an efficient method to sample syrphids because it increased the sampling efficiency. Sweep netting was carried out along three transects in the center of each meadow conducting 90 (3*30) sweeps per meadow. The collected insects

were sorted in the lab according to the insect groups syrphids and heteropteran bugs, and identified at the species level.

For assessing grasshoppers, a soundscape approach was used. This innovative method was introduced in Core publication I and III and describes an innovative and non-invasive method to collect data on grasshopper species richness. For this approach, I installed 80 cm high platforms, one in each meadow. On these platforms I placed a commercially available recording device (Olympus LS-12, Olympus Europa SE &CO. KG) connected to a heterodyne bat detector which served as an ultrasonic microphone in order to amplify the grasshopper sounds (Figure 2). The records took place within a time span of 7 hours between 10 a.m. and 5 p.m., and species were identified afterwards by listening to the records.

Figure 2: Soundscape approach for recording grasshopper sounds.

3.3. Vegetation surveys

Plant parameters were measured to assess the effects of abandonment on local vegetation characteristics and to explain distribution patterns of the investigated insect groups. In every meadow, vascular plant richness, vegetation cover and flower cover were surveyed in four 1 m^2 plots which were located in the center of each meadow. A frame of 1*1 m was placed on the ground and each plant species within the frame was identified to species level and percentage of vegetation and flower cover was evaluated. The individual plots had a distance of 5 m between them. Afterwards, recorded plants were grouped by plant strategy types

(Grime 1977) and Ellenberg indicator values (soil, moisture, light, nutrient availability). A detailed description of the vegetation survey methods is provided in publication IV.

3.4. Measurement of soil properties

Six soil samples were taken on each meadow and mixed afterwards to have one composite soil sample per meadow. Soil samples were taken from the upper 10 cm of the soil with a soil corer. This was done to get an overview of local soil parameters like total carbon and nitrogen and the pH-values of the soils. Further, the microbial phospholipid fatty acid composition was investigated in order to determine the microbial community composition of the soils. A further description of the methods and the utilized measuring instruments is described in publication IV.

3.5. Measurement of litter decomposition

The measurement of the litter decomposition was done in accordance with previous work from Keuskamp et al. (2013) using the tea bag index. This measurement was carried out in the center of the meadows. Totally, 20 tea bags were buried in each meadow around a circle with a diameter of 5 m. Pairs of bags of green tea and rooibos tea were buried in a depth of 8 cm and excavated after an incubation time of at least 52 days. After this procedure, the tea bags were cleaned from roots and soil particles, dried and weighed. Afterwards, the litter decomposition rate (k) and litter stabilization factor (S) were calculated. An exact method description is given in publication IV.

3.6. Landscape factors

In order to investigate the influence of the surrounding landscape structure on insects, the percentage of open land (pastures, intensive and extensive meadows) and forest was measured in ArcGIS. These two parameters were estimated within a 500 m radius around each meadow. Details are given in core publication I and III.

3.7. Assessing the effects of abandonment on recreation and human well-being

Altogether, 22 probands were selected to investigate the effects of grassland management on health benefits and well-being. The participating persons had the same cultural background and were of similar age. Within each region, they visited one managed and one abandoned meadow. The probands visited each site, sat on the meadow for 15 minutes and intently perceived their surroundings. To assess health effects, blood pressure and pulse rates were measured before and after the 15 minutes. Subsequently, after a few minutes, the probands had to fill out standardized questionnaires to find out how they perceived factors such as naturalness and recreation effects in both meadow types. A detailed description of the methods, questionnaires and measuring devices is part of publication V.

4. Publications

4.1. Publication I: Diversity of bumblebees, heteropteran bugs and grasshoppers maintained by both: abandonment and extensive management of mountain meadows in three regions across the Austrian and Swiss Alps.

Walcher, R., Karrer, J., Sachslehner, L., Bohner, A., Pachinger, B., Brandl, D., Zaller, J. G., Arnberger, A., and Frank, T., 2017. Diversity of bumblebees, heteropteran bugs and grasshoppers maintained by both: abandonment and extensive management of mountain meadows in three regions across the Austrian and Swiss Alps. *Landscape Ecology*, **32**, 1937–1951, https://doi.org/10.1007/s10980-017-0556-1.

Author contributions: This work was written as part of the "Healthy Alps" project. This project was designed and developed by Thomas Frank, Johann Zaller and Arne Arnberger.

Ronnie Walcher planned and conducted the field work, collected data on bumblebees, heteropteran bugs and grasshoppers, identified bumblebees and heteropteran bugs to species level, prepared and analyzed the data and wrote the manuscript.

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RESEARCH ARTICLE

Diversity of bumblebees, heteropteran bugs and grasshoppers maintained by both: abandonment and extensive management of mountain meadows in three regions across the Austrian and Swiss Alps

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Abstract
Context Abandonment of extensively managed meadows is an ongoing global challenge in recent decades, particularly in mountain regions, and directly affects plant diversity. However, the extent to which plant diversity further affects associated insect pollinators or herbivores is little investigated.
Objectives We focused on the effects of abandonment of mountain meadows on species richness and assemblages of bumblebees, bugs and grasshoppers. Specifically, we investigated the influence of vegetation cover, flower cover, plant richness and surrounding landscape on the three insect groups.
Methods Species richness, abundance and species assemblages of bumblebees, bugs and grasshoppers were surveyed in one Swiss and two Austrian regions: three meadows which had been abandoned for 15–60 years, and three extensively managed meadows (mown once a year, no use of fertilizers). We surveyed bumblebees and bugs by sweep net, and grasshoppers using the time-effective soundscape approach.
Results Bumblebee species richness and abundance were significantly higher in managed meadows, whereas bug and grasshopper richness and abundance showed no differences between both management types. Managed and abandoned meadows harboured significantly different species assemblages of bugs and grasshoppers, but not of bumblebees. Increasing flower cover and plant richness increased bumblebee

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richness, but correlated negatively with richness of bugs. Surrounding open landscape positively affected bugs. Caelifera positively correlated with surrounding forest cover and negatively with vegetation cover. Vegetation cover positively affected Ensifera.
Conclusions Abandoned and extensively managed meadows are important habitat types for the conservation of the three insect groups, thus suggesting the maintenance of both habitat types within mountain landscapes.

Keywords Mountain grassland · Species richness · Species assemblages · *Bombus* sp. · Heteroptera · Orthoptera

Introduction

Grasslands are an integral part of Central European cultural landscapes, and most grassland communities originate from human land use (Moog et al. 2002; Poschlod et al. 2009). Human land use is one of the most important determinants of grassland biodiversity (Maurer et al. 2006; Fischer et al. 2008; McGinlay et al. 2017). In recent decades, especially in European mountain grasslands, two contrasting trends could be observed: management of productive and easily accessible areas has been intensified, whereas areas that do not allow mechanised agricultural techniques have been abandoned (Tasser and Tappeiner 2002; Strijker 2005; Prévosto et al. 2011). Steep and inaccessible slopes in mountain regions, in particular, are more prone to abandonment (Tasser et al. 2007). Mountain meadows were maintained for centuries by local farmers (Tappeiner and Cernusca 1993). Due to socioeconomic factors, a cessation of grassland management is taking place, especially on grassland with marginal agricultural value (Bohner et al. 2012; Hinojosa et al. 2016) such as extensively managed meadows in mountain regions. Changes in agriculture either by intensification or abandonment have resulted in a reduction of semi-natural grasslands in Europe (Baur et al. 2006a; Graf et al. 2014). After land-use abandonment, succession starts immediately (Tasser and Tappeiner 2002), leading to shrub encroachment and establishment of woody species in open grassland (Komac et al. 2013; Wiezik et al. 2013). The process of shrub encroachment depends on several factors such as proximity to forest, altitude and steepness of the slope (Tasser et al. 2007). Regular management is important for the maintenance of semi-natural grassland (Fonderflick et al. 2014).

The aim of this study was to investigate the impact of abandonment on species richness, abundance and species assemblages of bumblebees, heteropteran bugs and grasshoppers within three regions across the Alps by comparing extensive (annually mown, non-fertilized) and abandoned meadows.

Bumblebees were studied because they are important pollinators in many areas (Corbet et al. 1991; Wood et al. 2016) and have been shown to be suitable bioindicators for human impacts at the landscape level (Sepp et al. 2004). In recent decades, bumblebees are known to be in decline due to e.g. reduction of floral resources or loss of suitable nest sites (Carvell 2002; Nieto et al. 2014). As bumblebees require unimproved, flower-rich grasslands (Williams 1988), the loss of flower-rich grasslands and consequent loss of suitable floral resources due to abandonment is assumed to decrease bumblebee species richness and abundance.

Heteropteran bugs were investigated because they are an appropriate indicator for total insect diversity in managed landscapes (Duelli and Obrist 1998). They are influenced by various vegetation factors (e.g. Frank and Künzle 2006; Zurbrügg and Frank 2006) and might respond differently to changes of microclimatic conditions (Di Giulio et al. 2001).

Many grasshopper species, which are important primary and secondary consumers in grasslands (Ingrisch and Köhler 1998), are tightly bound to their habitat, react very sensitively to environmental changes (Baur et al. 2006b) and are prone to grassland abandonment (Marini et al. 2009; Uchida et al. 2016). They are suitable indicators for land-use change as they show a clear response to succession (Fartmann et al. 2012).

In the present study, we expected that bumblebees, heteropteran bugs and grasshoppers would show a clear response to abandonment. Therefore, we included factors such as vegetation cover, flower cover, plant richness and surrounding landscape structure (forest cover and open landscape) in the analysis.

We addressed the following hypotheses:

1. There is a significant difference in species richness and species assemblages of bumblebees,

heteropteran bugs and grasshoppers between managed and abandoned meadows.

2. There is a specific influence of vegetation cover, flower cover, plant richness and surrounding landscape structure on species richness and abundance of bumblebees, heteropteran bugs and grasshoppers.

Materials and methods

Study regions and sites

The study was conducted in June and August 2015 in three regions across the Austrian and Swiss Alps (Fig. 1). The study regions comprised the Eisenwurzen region (Styria, Austria, mean annual air temperature: 6.9 °C, mean annual precipitation: 1 087 mm) with study sites in the municipalities of St. Gallen (47°41′N, 14°37′E), Stainach (47°32′N, 14°06′E) and Pürgg (47°31′N, 14°03′E), the Biosphere Reserve Großes Walsertal region (Vorarlberg, Austria, mean annual air temperature: 5.7 °C, mean annual precipitation: 1 630 mm) in the municipality of Sonntag/Buchboden (47°14′N, 9°57′E) and the Biosphere Reserve Val Müstair region (Graubünden, Switzerland, mean annual air temperature: 5.9 °C, mean annual precipitation: 810 mm) in the municipalities Tschierv (46°37′N, 10°20′E), Valchava (46°36′N, 10°24′E) and St. Maria (46°36′N, 10°25′E). Altogether, we surveyed six semi-dry meadows located on south-facing slopes within each study region, three of them extensively managed and three abandoned. Extensively managed meadows are mown once a year, usually between mid-July and the beginning of August, and receive no fertilizer treatment. Cessation of management in the abandoned meadows occurred at least 15 years ago, with the shortest time since abandonment in the Biosphere

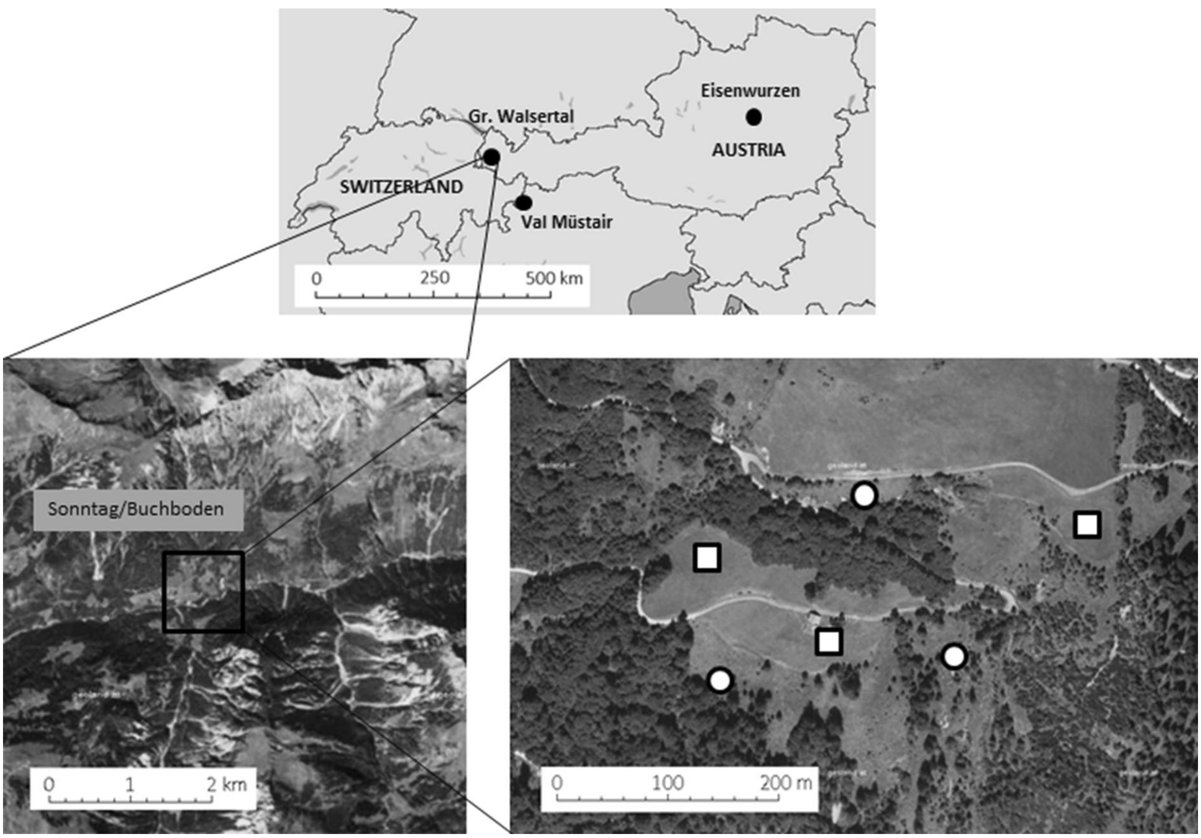


Fig. 1 Location of the three study regions Eisenwurzen, Großes Walsertal and Val Müstair. Detailed inset maps are shown for the study region Großes Walsertal (*open square* delineates location of managed meadows, *open circle* delineates location of abandoned meadows) (data source: www.basemap.at)

Reserve Val Müstair (15–20 years) and the longest time since abandonment in the Biosphere Reserve Großes Walsertal (35–60 years). Abandoned sites in the Eisenwurzen region were between 20 and 40 years old. Before cessation of management, abandoned meadows were used as extensively managed meadows and were never used as pastures. Information on former management was gathered via interviews with land owners. The meadows in the Eisenwurzen region were situated between 660 and 790 m above sea level, the meadows in the Biosphere Reserves Großes Walsertal and Val Müstair were situated between 1180 and 1250 m a. s. l., and between 1740 and 1800 m a. s. l., respectively. The sizes of managed meadows ranged between 470 and 5150 m^2, the sizes of abandoned meadows between 300 and 4300 m^2. There was no significant difference between size of abandoned and managed meadows for each of the three regions (Eisenwurzen: $F = 1.832$, $p = 0.247$; Großes Walsertal: $F = 3.561$, $p = 0.132$; Val Müstair: $F = 1.378$, $p = 0.306$; ANOVA). To assess the influence of the surrounding landscape structure, a circle with a radius of 500 m was drawn around the centre of each study site and the proportion of open landscape (intensive meadows, extensive meadows, pastures) and forest cover (closed forest) was measured in ArcGIS based on existing maps (ArcGIS basemap). Built-up land (single houses, villages, huts) was not considered since it occurred only at the circle margins of one site in the Eisenwurzen region and had a maximum proportion of only 5% within the 500 m radius.

Bumblebee sampling

Species richness and abundance of bumblebees was surveyed once in June and once in August 2015. We observed four 20 m^2 (4×5 m squares) study plots within each meadow for 15 min each, and collected and counted every individual bumblebee occurring in these study plots. The first plot was chosen randomly, approximately in the centre of each meadow. Further plots were selected along a straight transect in a standardised manner at distances of 3, 9 and 27 m from the first plot (logarithmic distances). Sampling was carried out during suitable weather conditions (dry vegetation, no more than slight wind, temperature > 15 °C, sunshine) and between 9 a.m. and 5 p.m. On-site identification of species was performed following the approach proposed by Gokcezade et al. (2015). To identify bumblebees, single individuals were caught in plastic tubes and fixed at the bottom of the tube with a plastic foam plug. After immobilisation of a bumblebee, identification was conducted using a hand lens (magnification $\times 20$). After identification, bumblebees were released on-site. Any individual that could not be identified on-site was killed using acetic ether and stored in previously prepared plastic bags. Additionally, the collected individuals were treated with Thymol (2-isopropyl-5-methylphenol), a fungicide, inhibiting mould formation and infestation of collected bumblebees. Identification of collected bumblebees was subsequently performed in the laboratory using a stereo microscope, with reference to Mauss (1990). For further analysis, we classified bumblebees as long-tongued species (long- and intermediate long-tongued) and short-tongued species (short- and intermediate short-tongued) (von Hagen and Aichhorn 2014).

Heteropteran bug sampling

Heteropteran bug species richness and abundance was assessed once in June and once in August 2015. For sampling, a sweep net method was applied along defined transects approximately in the centre of each meadow. We conducted a total of 90 sweeps per meadow, separated in 3×30 sweeps. The net, consisting of a white heavy cloth, was approximately 70 cm long with an opening diameter of 40 cm, mounted on a stick of 1 m length. In the laboratory, identification of species was performed using a stereo microscope, with reference to Wagner (1952, 1966, 1967) and Strauss (2010). For further analysis, species were classified into phytophagous and zoophagous trophic levels. Overwintering strategy was classified, differentiating heteropteran bugs overwintering as imagoes or eggs. All information regarding food preference and overwintering strategy was gathered from Wagner (1952, 1966, 1967) and Strauss (2010).

Grasshopper sampling

Grasshoppers (Orthoptera: Ensifera and Caelifera) were surveyed once in August 2015 during the peak of almost all of the species' populations (Marini et al. 2010). Surveys were performed with recording devices (Olympus LS-12, Olympus Europa SE & CO. KG) to record sound production, which represents a suitable method for assessing species richness of grasshoppers within their environment (Chesmore and Ohya 2004; Lehmann et al. 2014). The soundscape approach provides a time-effective field method for examining species richness, compared to conventional methods (Gardiner and Hill 2006; Buri et al. 2013). A heterodyne bat detector was connected to the recorder as an ultrasonic microphone, in order to amplify grasshopper sounds (Batbox III D, Batbox Ltd. Steyning, UK). The frequency range of the heterodyne bat detector was adjusted to a frequency of 27 kHz with a bandwidth of 16 kHz. The recorders and the bat detectors were placed in the centre of each study site at a height of 80 cm. Sampling was carried out during dry weather conditions, sunshine, temperatures above 20 °C and no more than slight wind. The recording time lasted from 10 a.m. to 5 p.m., leading to a total recording time of 7 h per day. We identified species by listening to the records in the laboratory using acoustic comparison material from the field and archives (e.g. Roesti and Keist 2009). For further analysis, grasshoppers were subdivided into the suborders Ensifera and Caelifera in accordance with Baur et al. (2006b).

Plant parameters

To assess the influence of several plant parameters on bumblebees, bugs and grasshoppers, we investigated plant species richness, vegetation cover and flower cover in four randomly chosen 1 m^2 study plots in the centre of each meadow in June and August 2015. A frame of 1 m^2 size (1 × 1 m) was placed on the ground with the edges parallel to the hill slope (Karrer 2015), and each plant species within the 1 m^2 study plot was identified to species level. Vegetation cover in percent, including both necromass and living biomass, and proportion of open ground (bare soil, rocks) were estimated within the 1 m^2 frame. Proportion of flower cover was also assessed within the 1 m^2 frame. Individual plant species were subdivided into plants with open and hidden nectar flowers, since this is an important factor for bumblebees in relation to their tongue length.

Statistical analysis

We checked the data for normal distribution graphically by creating QQ-plots, and statistically using Shapiro-test. We tested for homogeneity of variances (homoscedasticity) using Bartlett-test. In order to assess the effects of the two habitat types—managed and abandoned meadows—on species richness and abundance of bumblebees, heteropteran bugs and grasshoppers, we calculated GLMs with a Poisson distribution, with management and region as explanatory variables (fixed factors). We tested data for over- and under dispersion by applying the function *dispersion.test()* in R (R-package "AER" 1.2-4, Kleiber et al. 2015). Many of the datasets were over- or under dispersed, which we corrected by specifying quasi-poisson errors (Crawley 2013). We also used GLMs to analyse differences between managed and abandoned meadows regarding trophic levels and overwintering strategy types of heteropteran bugs, tongue length of bumblebees, suborders of grasshoppers, effects of plant parameters (plant species richness, vegetation cover, flower cover, plants with hidden and open nectar flowers) and surrounding landscape structures on the three insect groups. After assessing possible correlations between plant parameters, we found it appropriate to test plant parameters separately, since plant parameters were highly correlated and could not be used in a single GLM model. To test for significant associations of any individual bumblebee, heteropteran bug and grasshopper species with managed or abandoned meadows, we calculated the point-biserial correlation coefficient r_{pb} for each species (Anjum-Zubair et al. 2015). To investigate associations of bumblebee, heteropteran bug and grasshopper species with study sites, we computed the strength and significance of the association using the R-functions *strassoc()* and *signassoc()* in R (R-package "indicspecies" 1.7.5, De Cáceres and Jansen 2015). We assessed the significance of the associations with two-sided permutation tests, and calculated confidence intervals by bootstrapping data 999 times with replacement, following Anjum-Zubair et al. (2015).

To assess differences in species assemblages of bumblebees, heteropteran bugs and grasshoppers between managed and abandoned meadows, we conducted a principal coordinate analysis (PCO) based on a resemblance matrix of Bray–Curtis similarity measures. We computed a permutational ANOVA (PERMANOVA) to test for significant differences in species assemblages between managed and abandoned meadows. As with the univariate analysis, we included region as a fixed factor.

Residuals were permuted 9999 times under a reduced model. In order to exclude the factors that did not differ in their dispersion, we conducted the PERMDISP-routine in analogy to a homogeneity test before applying an ANOVA. The test was performed on the basis of distances to the centroid with 9999 permutations. P-values were obtained by using permutation of residuals.

In addition, we conducted the SIMPER-routine (similarity percentages) to analyse the role of individual species in contributing to the differences between managed and abandoned meadows.

We conducted PCO, PERMANOVA, PERMDISP and SIMPER routines using the software Primer, version 6.1.13 with PERMANOVA + (PRIMER-E Ltd., Plymouth, UK). All other statistical tests were performed in R-Studio, version 3.1.3 (R Core Team 2015).

Results

Bumblebees

We recorded a total of 83 bumblebee individuals (*Bombus* sp.) of 14 species (Online Appendix Table 1). Fifty-seven individuals, belonging to 13 species, were identified in managed meadows, and 26 individuals belonging to 9 species were identified in abandoned meadows. One of the total 14 species was a cuckoo bumblebee (*Bombus* [*Psithyrus*] sp.). Seven of the 14 species were classified as long-tongued and 7 as short-tongued.

Total species richness of bumblebees was significantly higher in managed meadows compared to abandoned meadows (Table 1; Fig. 2a). Similarly, total number of individuals was also higher in managed meadows (Table 1; Fig. 2b). There was no effect of management on long-tongued and short-tongued species, nor on long-tongued and short-tongued individuals. Total number of individuals and number of individuals of short-tongued species differed significantly between regions (Table 1). Both flower cover and plant richness had a significant influence on total bumblebee species richness (Table 1). Bumblebee species richness increased with increasing flower cover and plant species richness (Table 1). Long-tongued species increased with increasing plant richness, number of short-tongued individuals increased with increasing flower cover (Table 1). No association was found between bumblebees and vegetation cover. Plants with open nectar flowers had a significant positive influence on total number of individuals, short-tongued bumblebee species and individuals (Table 1). A positive association was detected between plants with hidden nectar flowers, total species richness of bumblebees and species richness of long-tongued bumblebees (Table 1).

Neither percentage of open landscape nor forest area had an influence on bumblebees. Results of the point-biserial correlation did not indicate an association of any individual bumblebee species with either managed or abandoned meadows.

The graphical representation of species assemblages in the principal coordinate analysis (PCO) showed no clear separation of species assemblages between managed and abandoned meadows (PERMANOVA, main-test: $p = 0.1196$, Table 2). Both axes (PCO 1 and PCO 2) of the PCO explained 56% of the total variance (Fig. 3).

SIMPER-analysis showed that the average Bray–Curtis similarity in managed meadows was 25.02, where the five species *B. lucorum*, *B. terrestris*, *B. lapidarius*, *B. hortorum* and *B. humilis* explained 88.36% of the similarity. The average Bray–Curtis similarity in abandoned meadows was 6.37, due to the three species *B. lapidarius*, *B. pascuorum* and *B. humilis*, which explained 91.27% of the similarity. An average dissimilarity of 87.11 was detected between managed and abandoned meadows, where 78.91% of the dissimilarity was explained by the six species *B. lucorum, B. lapidarius, B. hortorum, B. terrestris, B. mucidus* and *B. humilis.*

Heteropteran bugs

We collected a total of 390 individuals comprising 35 bug species (Online Appendix Table 2). 187 individuals belonging to 21 species were found in managed meadows and 203 individuals belonging to 29 species were found in abandoned meadows. The majority of collected bugs were phytophagous, only three individuals belonging to three species were zoophagous. Regarding overwintering strategy, 28 of the bug species overwinter as imagoes and 9 species overwinter as eggs.

No significant effects of management could be detected for total species richness and total number of

Table 1 Residual deviance, degrees of freedom and p-values obtained from generalised linear models (GLM) showing the effects of management, region, vegetation cover, flower cover and plant species richness on bumblebees, heteropteran bugs and grasshoppers

	Management			Region			Vegetation cover			Flower cover			Plant richness			Flower classes: Open nectar			Flower classes: Hidden nectar		
	Res.dev.	df	p	Res.dev.	df	p	Res.dev.	df	p	Res.dev.	df	p	Res.dev.	df	p	Res.dev.	df	p	Res.dev.	df	p
Bumblebees																					
Total species	14.47	16	**0.019**	12.44	14	n.s.	19.22	16	n.s.	14.30	16	**0.016**(+)	15.74	16	**0.047**(+)	16.49	16	n.s.	13.53	16	**0.011**(+)
Total individuals	52.58	16	**0.043**	33.61	14	**0.044**	64.28	16	n.s.	51.00	16	n.s.	50.69	16	n.s.	48.73	16	**0.038**(+)	53.01	16	n.s.
Long-tongued species	15.36	16	n.s.	13.46	14	n.s.	17.06	16	n.s.	14.75	16	n.s.	12.55	16	**0.038**(+)	13.59	16	n.s.	11.52	16	**0.018**(+)
Short-tongued species	18.11	16	n.s.	13.32	14	n.s.	19.24	16	n.s.	17.66	16	n.s.	16.37	16	n.s.	13.71	16	**0.017**(+)	18.07	16	n.s.
Long-tongued individuals	47.05	16	n.s.	42.39	14	n.s.	47.69	16	n.s.	46.62	16	n.s.	45.16	16	n.s.	42.24	16	n.s.	37.68	16	n.s.
Short-tongued individuals	45.52	16	n.s.	22.48	14	**0.005**	47.46	16	n.s.	40.35	16	**0.038**(+)	38.39	16	n.s.	20.07	16	<**0.001**(+)	47.66	16	n.s.

	Management			Region			Vegetation cover			Flower cover			Plant richness			Surrounding landscape structure: Open landscape			Surrounding landscape structure: Forest cover		
	Res.dev.	df	p	Res.dev.	df	p	Res.dev.	df	p	Res.dev.	df	p	Res.dev.	df	p	Res.dev.	df	p	Res.dev.	df	p
Bugs																					
Total species	18.21	16	n.s.	12.92	14	n.s.	16.77	16	n.s.	14.42	16	**0.018**(−)	16.32	16	**0.043**(−)	12.72	16	**0.006**(+)	13.54	16	**0.013**(−)
Total individuals	308.75	16	n.s.	194.82	14	**0.039**	307.51	16	n.s.	288.02	16	n.s.	308.57	16	n.s.	201.81	16	**0.023**(+)	222.05	16	n.s.
Phytophagous species	16.95	16	n.s.	13.18	14	n.s.	15.93	16	n.s.	13.54	16	**0.034**(−)	14.18	16	**0.040**(−)	11.56	16	**0.010**(+)	12.77	16	**0.023**(−)
Overwinter egg species	6.60	16	n.s.	4.42	14	n.s.	6.86	16	n.s.	6.85	16	n.s.	6.65	16	n.s.	6.01	16	n.s.	5.37	16	n.s.
Overwinter imago species	29.62	16	**0.042**	27.04	14	n.s.	29.50	16	n.s.	24.19	16	**0.005**(−)	20.28	16	<**0.001**(−)	26.64	16	n.s.	29.41	16	n.s.
Phytophagous individuals	310.44	16	n.s.	198.90	14	**0.044**	309.43	16	n.s.	290.57	16	n.s.	310.07	16	n.s.	204.26	16	**0.024**(+)	225.34	16	n.s.
Overwinter egg individuals	279.87	16	n.s.	203.32	14	n.s.	317.17	16	n.s.	326.41	16	n.s.	261.01	16	n.s.	243.61	16	n.s.	248.15	16	n.s.
Overwinter imago indiv.	117.58	16	<**0.001**	59.42	14	**0.009**	170.06	16	n.s.	105.55	16	**0.011**(−)	85.24	16	<**0.001**(−)	178.18	16	n.s.	189.31	16	n.s.

	Management			Region			Vegetation cover			Flower cover			Plant richness			Surrounding landscape structure: Open landscape			Surrounding landscape structure: Forest cover		
	Res.dev.	df	p	Res.dev.	df	p	Res.dev.	df	p	Res.dev.	df	p	Res.dev.	df	p	Res.dev.	df	p	Res.dev.	df	p
Grasshoppers																					
Total species	2.49	16	n.s.	1.82	14	n.s.	2.62	16	n.s.	2.61	16	n.s.	2.32	16	n.s.	2.62	16	n.s.	2.61	16	n.s.
Caelifera	1.84	16	n.s.	1.25	14	n.s.	1.10	16	**0.001**(−)	1.69	16	n.s.	2.18	16	n.s.	1.75	16	n.s.	1.85	16	**0.024**(+)
Ensifera	7.02	16	n.s.	5.01	14	n.s.	6.30	16	**0.040**(+)	7.51	16	n.s.	7.31	16	n.s.	7.97	16	n.s.	7.86	16	n.s.

Effects of flower classes are shown for bumblebees, surrounding landscape is shown for heteropteran bugs and grasshoppers (significance level: $p < 0.05$, only significant p-values are shown, n.s. [not significant], (−) denotes negative effect, (+) denotes positive effect)

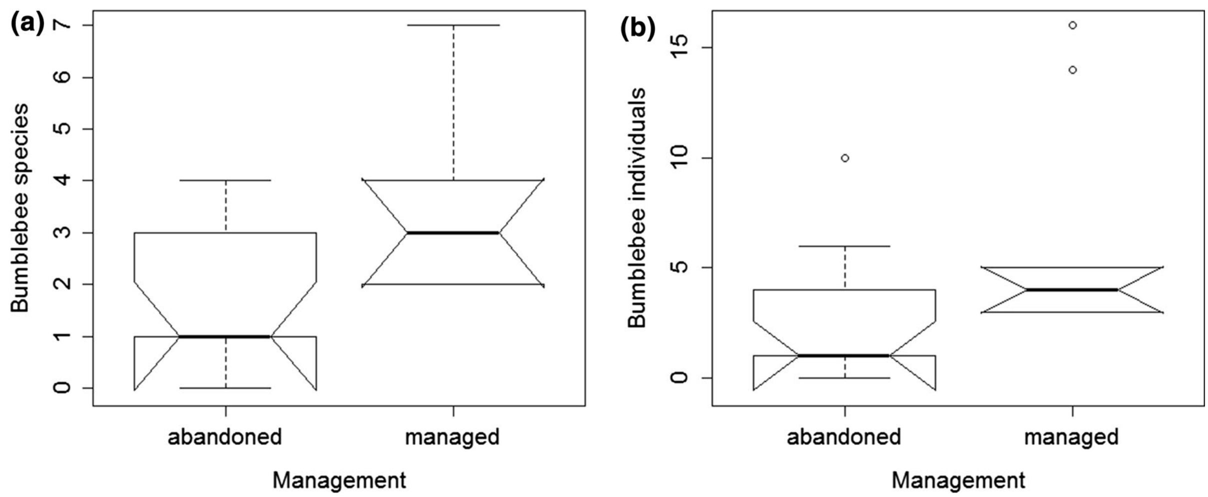


Fig. 2 Effects of management (managed and abandoned) on **a** bumblebee species richness and **b** bumblebee abundance. *Boxplots* show the medians, the 25 and 75% percentiles and the 10 and 90% percentiles (indicated as *dashed lines*), notches and outliers (o)

Table 2 PERMANOVA main-test for bumblebee, heteropteran bug and grasshopper species assemblages for the factors management, region and interaction between management and region (Manag × reg)

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Bumblebees						
Management	1	3185.3	3185.3	1.8233	0.1196	9945
Region	2	2027.5	1013.8	0.58027	0.8233	9930
Manag × reg	2	1537.2	768.6	0.43994	0.9227	9937
Res	12	20,964	1747			
Total	17	27,714				
Heteropteran bugs						
Management	1	8125.8	8125.8	2.8654	0.0107	9934
Region	2	16,240	8120	2.8633	0.0006	9917
Manag × reg	2	5714.4	2857.2	1.0075	0.4608	9899
Res	12	34,031	2835.9			
Total	17	64,111				
Grasshoppers						
Management	1	5726.5	5726.5	7.0071	0.0009	9960
Region	2	5484.1	2742	3.3552	0.0100	9952
Manag × reg	2	682.23	341.11	0.41739	0.8557	9965
Res	12	9807	817.25			
Total	17	21,700				

individuals, number of phytophagous species/individuals or number of species/individuals overwintering as eggs (Table 1). However, higher numbers of both species and individuals that overwinter as imagoes were found in abandoned meadows. The total number of individuals as well as the number of phytophagous individuals, and the number of individuals overwintering as imagoes differed between regions (Table 1). No significant influence of vegetation cover on bug parameters could be detected. Total species richness of

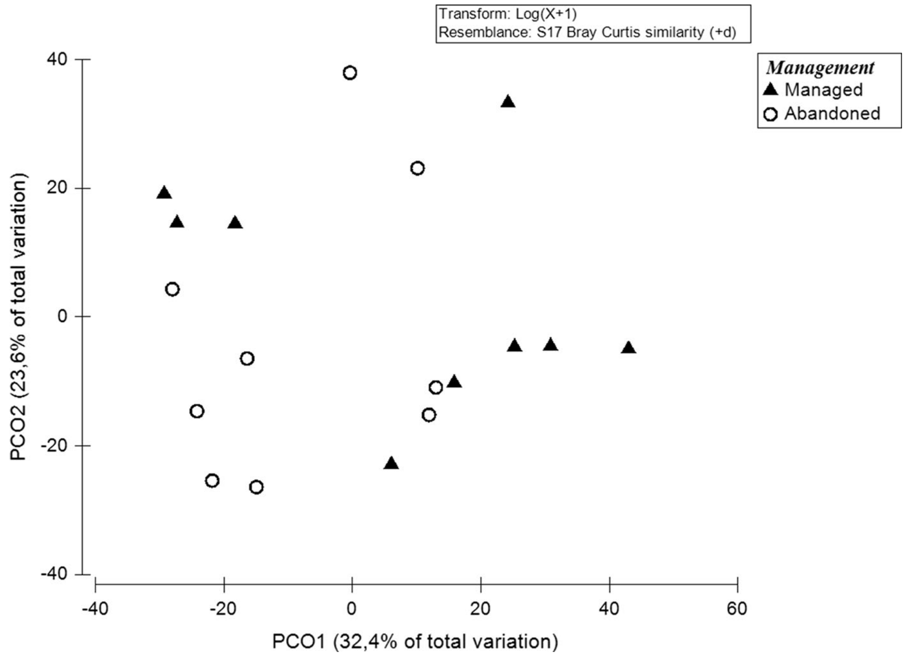


Fig. 3 Principal coordinate analysis (PCO) showing distribution of bumblebee species assemblages between managed and abandoned meadows

heteropteran bugs, richness of phytophagous species and number of species and individuals overwintering as imagoes decreased with increasing flower cover and plant species richness (Table 1). There was evidence that proportion of surrounding open landscape increased total species richness, total number of individuals, phytophagous species and number of phytophagous individuals (Table 1). Proportion of forest cover had a significant negative influence on total number of species and richness of phytophagous species (Table 1).

Bug species assemblages differed significantly between managed and abandoned meadows. In the PCO (Fig. 4), and confirmed by PERMANOVA analysis, both assemblages were clearly separated (PERMANOVA, main-test: $p = 0.0107$, Table 2). Both axes of the PCO (PCO 1 and PCO 2) explained 46.8% of the total variation. The average Bray–Curtis similarity in managed meadows according to the SIMPER-routine was 18.68, where the four species *Leptopterna dolabrata*, *Plagiognathus chrysanthemi*, *Carpocoris purpureipennis* and *Hadrodemus m-flavum* explained 90.43% of the similarity. An average Bray–Curtis similarity of 17.32 was observed in abandoned meadows, where *Myrmus miriformis, Stenodema holsata* and *Carpocoris purpureipennis* explained 76% of the similarity. An average dissimilarity of 88.4 was detected between managed and abandoned sites. Sixty-seven percent of the dissimilarity was explained by 10 species (*Leptopterna dolabrata*, *Myrmus miriformis*, *Stenodema holsata, Stenodema sericans, Plagiognathus crysanthemi, Carpocoris purpureipennis, Spilostethus saxatilis, Hadrodemus m-flavum, Dolycoris baccarum, Stenodema calcarata)*. The point-biserial correlation coefficient r_{pb} clearly indicated a significant positive association of *Myrmus miriformis* (r_{pb} association index: 0.54, lower and upper confidence intervals: 0.33 and 0.88, respectively) with abandoned meadows. None of the other species revealed associations with either managed or abandoned meadows.

Grasshoppers

A total of 17 species of grasshoppers were recorded in managed and abandoned meadows (Online Appendix Table 3). Fifteen species were detected in managed meadows and 14 species in abandoned meadows. Due to the method of assessing grasshopper diversity with soundscapes, no data on numbers of individuals was available. Six species belonged to the Ensifera and eleven species belonged to the Caelifera.

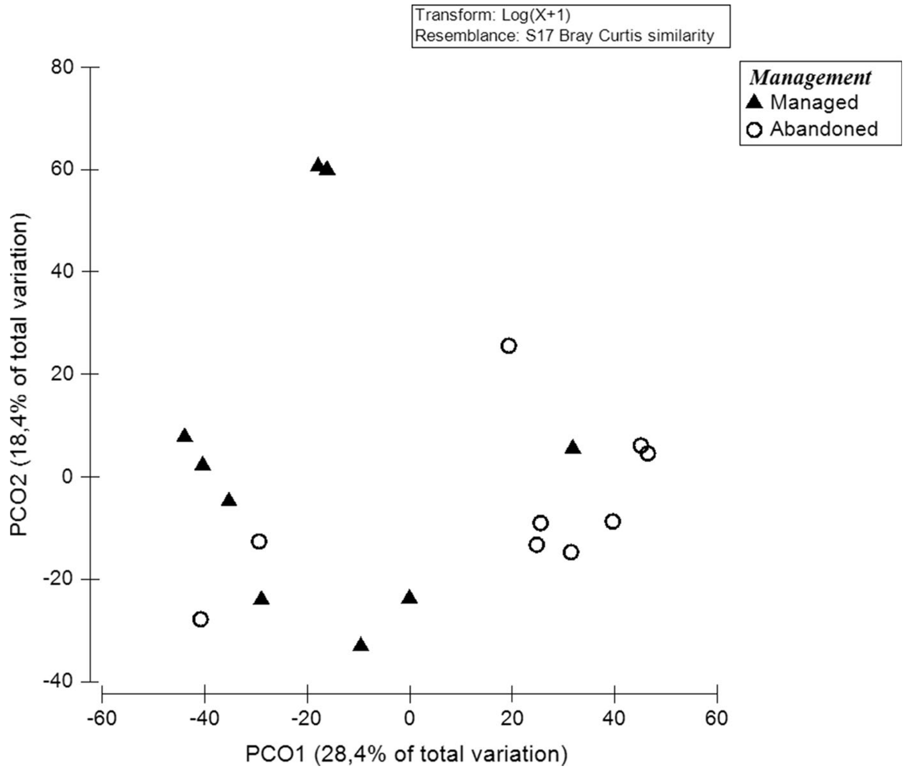


Fig. 4 Principal coordinate analysis (PCO) showing distribution of heteropteran bug species assemblages between managed and abandoned meadows

There were no significant effects of management on total species richness and no difference in grasshopper parameters between regions. Vegetation cover, flower cover and the proportion of open landscape and forest cover did not significantly influence total grasshopper species richness. Caelifera and Ensifera did not differ significantly between managed and abandoned meadows. Increasing vegetation cover significantly decreased the number of Caelifera, proportion of surrounding forest cover had a significant positive effect on Caelifera, and increasing vegetation cover had a significant positive effect on Ensifera (Table 1).

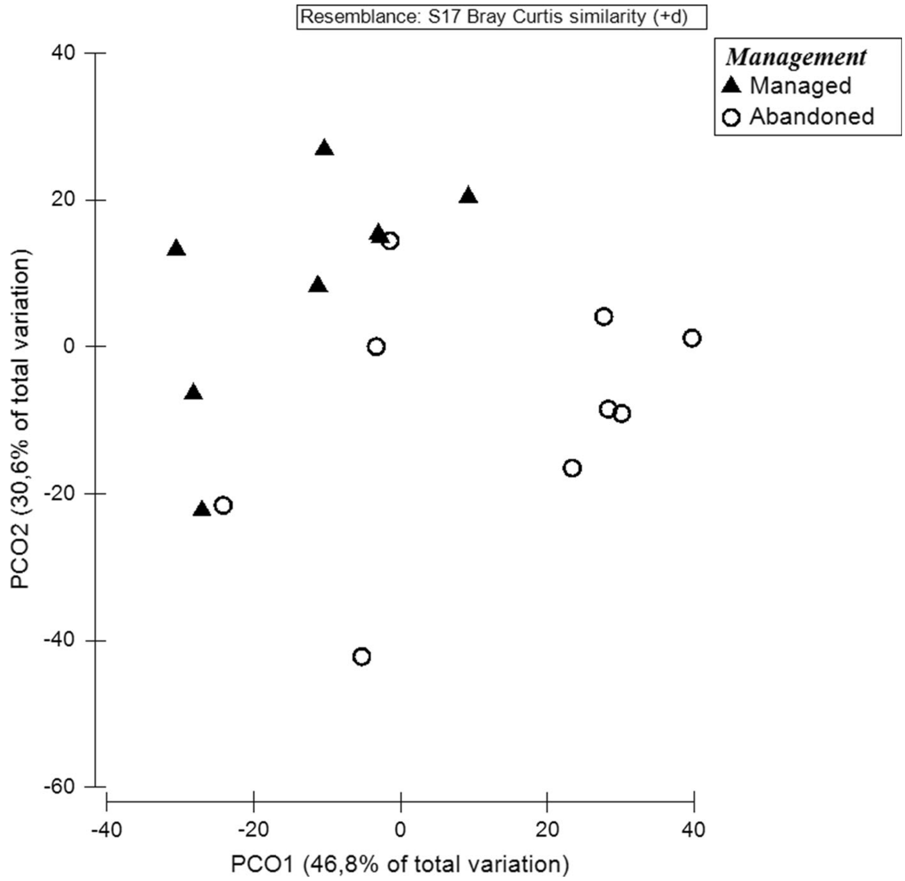
Grasshopper species assemblages differed significantly between managed and abandoned meadows. In the PCO (Fig. 5), and further confirmed by PERMANOVA analysis, both assemblages were clearly separated (PERMANOVA, main-test: $p = 0.001$, Table 2). Both axes of the PCO (PCO 1 and PCO 2) explained 77.4% of total variation. The average Bray–Curtis similarity in abandoned meadows according to the SIMPER-routine was 55.8, where five species (*Pseudochorthippus parallelus*, *Roeseliana roeselii*, *Euthystira brachyptera*, *Gomphocerippus rufus*, *Pholidoptera griseoaptera*) explained 81% of the similarity. An average Bray–Curtis similarity of 58.5 was observed in managed meadows made up by *Stenobothrus lineatus*, *Chorthippus biguttulus* and *Pseudochor thippus parallelus* which explained 74% of the similarity in managed meadows.

An average dissimilarity of 54.6 was detected between managed and abandoned sites where 68.9% was explained by eight species (*Stenobothrus lineatus*, *Gomphocerippus rufus*, *Pholidoptera griseoaptera*, *Chorthippus biguttulus*, *Tettigonia cantans*, *Metrioptera brachyptera*, *Euthystira brachyptera*, *Roeseliana roeselii*). The point-biserial correlation coefficient r_{pb} clearly indicated a significant positive association of *Stenobothrus lineatus* with managed meadows (r_{pb} association index: 0.89, lower and upper confidence intervals: 0.67 and 1, respectively). None of the other species revealed associations with either managed or abandoned meadows.

Vegetation parameters and landscape structure

Plant species richness and flower cover were significantly higher in managed than in abandoned meadows (ANOVA, $F = 16.31$; $p < 0.001$ and $F = 34.3$;

Fig. 5 Principal coordinate analysis (PCO) showing distribution of grasshopper species assemblages between managed and abandoned meadows



$p < 0.001$, respectively). Similarly, there were significantly more plants with hidden nectar flowers in managed meadows ($F = 24.43$; $p < 0.001$). Vegetation cover was significantly higher in abandoned than in managed meadows ($F = 6.52$; $p = 0.02$). No differences between habitat types were found for plants with open nectar flowers. Proportion of open landscape and forest cover were negatively correlated ($r = -0.95$, $p < 0.001$).

Discussion

Response of bumblebees to land-use change

Of the 47 bumblebee species occurring in Austria, Germany and Switzerland (Gokcezade et al. 2015), a third of the species could be recorded within the three study regions. Four species (*B. lucorum*, *B. humilis*, *B. lapidarius*, *B. hortorum*) comprised more than 60% of the total observations. A high abundance of few species has also been shown elsewhere (Dramstad and Fry 1995). Extensively managed meadows revealed a higher bumblebee species richness and abundance than abandoned meadows—as was expected by hypothesis 1. Loosing suitable foraging habitats and floral resources negatively affects bumblebees (Goulson et al. 2008). The present study indicates that abandonment has an adverse impact on bumblebee richness and abundance. Succession and a shift in the cover of dominant plant species (Pavlů et al. 2011) leads to a loss of floral resources. Both higher plant richness and flower cover in managed meadows increased bumblebee richness and abundance supporting the findings of other studies (Ebeling et al. 2008; Fründ et al. 2010). In the present study, higher flower cover was associated with higher plant species richness, illustrating the importance of maintaining a high plant species richness and flower cover within grassland habitats to benefit bumblebee richness. In addition, the diverse, plant species rich managed meadows provide sufficient food supply throughout the almost entire flight season of the bumblebees. Another important point is that managed meadows offer higher amounts of plants with hidden nectar being particularly important for long-tongued bumblebee species. The result that short-tongued bumblebees responded positively to plants with open nectar flowers and long-tongued bumblebees responded positively to plants with hidden nectar flowers is in line with other studies (Dramstad and Fry 1995; Carvell et al. 2004; Goulson 2010).

The majority of bumblebee species observed use a very broad range of habitat types (von Hagen and Aichhorn 2014; Gokcezade et al. 2015), which might explain the lack of difference between the bumblebee species assemblages of managed and abandoned meadows. An abandoned meadow generally undergoes different stages of succession, but some stages may remain stable for decades (Maag et al. 2001) and provide at least a certain amount of floral resources. Due to the high mobility of bumblebees (e.g. Darvill et al. 2004; Osborne et al. 2008) it is very likely that a high species turnover between managed and abandoned meadows occurred in this study since both meadow types were located within the action radius of the recorded bumblebees (e.g. Westphal et al. 2006).

Response of bugs to land-use change

The total number of heteropteran bugs was dominated by only a few species, of which *Leptopterna dolobrata* comprised more than 39% of the total observations. Hypothesis 1 could not be confirmed for total heteropteran bug species and abundance, but was confirmed for species and individuals overwintering as imagoes. Numbers of bug species and individuals overwintering as imagoes benefitted from the altered environmental conditions in the abandoned meadows. Since many bugs overwintering as imagoes are known to hibernate beneath the litter layer near their host plants (e.g. Rabitsch 2007), it can be assumed that the higher vegetation cover in abandoned meadows provides better protection against environmental influences such as high solar radiation and against dehydration and is therefore a preferred overwintering habitat.

The negative relationship between heteropteran bug species and flower frequency as well as plant richness was rather surprising as it contradicts available literature (e.g. Brändle et al. 2001; Frank and Künzle 2006; Zurbrügg and Frank 2006). Many phytophagous bug species are monophagous or oligophagous and thus require distinct plant species for their development. For example, *Leptopterna dolobrata*, the most abundant oligophagous species in the present study, feeds on tall grasses like *Phleum*, *Alopecurus*, *Holcus* and *Dactylis* (Wachmann et al. 2004). The restriction to a single plant species or only several distinct plant species might explain why higher plant species richness does not further increase phytophagous bug species richness. Since species overwintering as imagoes—which were negatively related to plant species richness—hibernate near their host plants, they will not benefit from increasing plant species richness. The positive relationship between bug species and surrounding open landscape may be explained by the fact that open land bugs can use surrounding meadows as retention sites during mowing of the extensive meadows.

Higher vegetation cover, above ground biomass and necromass in the studied abandoned meadows (Karrer 2015) most likely affect microclimatic conditions. Differences in microclimatic conditions are known to influence bugs (Di Giulio et al. 2001; Stoutjesdijk and Barkman 2014), which probably contributed to the significantly different bug assemblages observed between managed and abandoned meadows. For example, *Myrmus miriformis,* a character species for abandoned meadows in the present study, inhabits a wide range of habitats with the exception of xerothermic habitats (Wachmann et al. 2007). Higher above-ground biomass and necromass in abandoned meadows likely decrease temperature which makes this habitat type more suitable for *M. myriformis.* This suggests that microclimate has an important influence on the occurrence of this species, which could explain its almost exclusive occurrence in the abandoned meadows.

Response of grasshoppers to land use change

Vegetation cover, which was significantly higher in abandoned meadows, affected grasshoppers, in that Caelifera declined with increasing vegetation cover whereas Ensifera responded positively to increased vegetation cover. Several species of both suborders were restricted to either managed or abandoned meadows. Especially, *Stenobothrus lineatus* requires short vegetation and a certain amount of open soil (Behrens and Fartmann 2004). *S. lineatus* was a character species for managed meadows in the present study, and probably required regular mowing for its development and maintenance of viable populations (Marini et al. 2009). Maintenance of management was particularly important for species such as *Psophus stridulus, Omocestus rufipes* and *Decticus verrucivorus*, which are listed in the Red List of Austrian Orthoptera (Berg et al. 2005). These species show similar requirements to their habitat and, with the exception *P.stridulus*, occurred exclusively in managed meadows. Males of *P. stridulus* require at least some amount of dense vegetation (Hemp and Hemp 2003), which may explain its occurrence in abandoned meadows. Several Ensifera such as *Tettigonia cantans*, *Metrioptera brachyptera* and *Pholidoptera aptera* showed a particular preference for the abandoned meadows. These species require well-structured habitat types with a certain amount of shrubs and dense vegetation (Baur et al. 2006b), and mown meadows generally seem to be particularly unsuitable habitats for most Ensifera (e.g. Braschler et al. 2009). The positive response of Caelifera to surrounding forest cover must not be over-interpreted because Caelifera inhabiting open land would not select forest as suitable habitat. Only forest glades might be a suitable habitat for some species such as *Omocestus rufipes* (Baur et al. 2006b). It can be possible that forest edges act as refuge for Caelifera during mowing or are used as additional food resource.

The different species assemblages in managed and abandoned meadows are due to different habitat conditions. Thus, abandoned and managed meadows represent suitable habitats for distinct grasshopper species assemblages, and managed meadows proved particularly important for the conservation of three detected endangered species. Our results indicate that managed as well as abandoned meadows are crucial for maintaining grasshoppers in mountain grassland, as both promote distinct, co-existing species assemblages.

Conclusion

Whereas abandonment has often been shown to adversely affect arthropod diversity (e.g. Marini et al. 2009; Uchida and Ushimaru 2014), the present study showed that abandoned meadows that have not yet regrown with forest can provide valuable habitat for heteropteran bugs and grasshoppers. Thus, the occurrence of both managed and abandoned meadows may support the establishment of unique species assemblages, increasing the diversity of heteropteran bugs and grasshoppers across Central European mountain grassland. However, management schemes should aim at regularly removing shrubs and woody plants to prevent the establishment of closed forests on abandoned meadows, which in turn would be detrimental for many open land species. For the conservation of bumblebee diversity, annual mowing is an important management measure to maintain sufficient foraging sources in the long term. In conclusion, regarding conservation of the three insect groups investigated in mountain regions, we recommend that management measures should aim at preserving a heterogeneously structured landscape containing managed as well as abandoned meadows.

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Appendix: Species lists of bumblebees, heteropteran bugs and grasshoppers in the three study regions Eisenwurzen, Großes Walsertal and Val Müstair.

Tab.1: Number of species and individuals of bumblebees in managed and abandoned meadows in the three regions Eisenwurzen, Großes Walsertal and Val Müstair.

	Region					
	Eisenwurzen		Gr. Walsertal		Val Müstair	
Species	Managed	Abandoned	Managed	Abandoned	Managed	Abandoned
Bombus hortorum (Linnaeus)	6	0	1	1	2	0
B. humilis (Illiger)	2	5	1	2	1	0
B. hypnorum (Linnaeus)	1	0	0	0	0	0
B. lapidarius (Linnaeus)	4	3	1	1	1	1
B. lucorum (Linnaeus)	11	0	4	1	2	1
B. mesomelas (Gerstaecker)	0	0	1	0	0	0
B. mucidus (Gerstaecker)	2	0	1	0	1	4
B. pascuorum (Scopoli)	3	3	0	1	0	0
B. pratorum (Linnaeus)	1	0	0	0	1	0
B. (Psithyrus) rupestris (Fabricius)	2	0	0	1	0	0
B. soroeensis (Fabricius)	0	0	0	0	0	1
B. sylvarum (Linnaeus)	0	0	0	0	1	0
B. terrestris (Linnaeus)	2	1	3	0	1	0
B. wurflenii (Radoszkowski)	1	0	0	0	0	0

Tab. 2: Number of species and individuals of heteropteran bugs in managed and abandoned meadows in the three regions Eisenwurzen, Großes Walsertal and Val Müstair.

	Region					
	Eisenwurzen		Gr. Walsertal		Val Müstair	
Species	Managed	Abandoned	Managed	Abandoned	Managed	Abandoned
Aelia accuminata (Linnaeus)	3	0	0	0	0	0
Capsus ater (Linnaeus)	0	0	4	0	0	0
Carpocoris melanocerus (Mulsant & Rey)	0	0	0	1	0	0
Carpocoris purpureipennis (De Geer)	2	4	4	4	0	0
Coreus marginatus (Linnaeus)	0	0	0	0	0	1
Coriomeris denticulatus (Scopoli)	0	0	0	0	2	0
Cymus glandicolor (Hahn)	0	0	0	1	0	0

Dolychoris baccarum (Linnaeus)	1	0	0	2	1	2
Exolygus rutilans (Horvath)	0	0	0	1	0	0
Graphosoma lineatum (Linnaeus)	1	2	0	1	0	0
Hadrodemus m-flavum (Goeze)	0	0	10	1	0	0
Halticus apterus (Linnaeus)	2	1	0	0	0	0
Leptopterna dolobrata (Linnaeus)	38	23	92	0	0	0
Lygocoris pabulinus (Linnaeus)	0	0	0	0	0	1
Lygus punctatus (Zetterstedt)	0	0	0	0	0	3
Megalonotus chiragra (Fabricius)	1	0	0	0	0	0
Myrmus miriformis (Fallén)	0	2	1	14	1	12
Nabis ferus (Linnaeus)	0	1	0	1	0	0
Nabis limbatus (Dahlbom)	0	1	0	0	0	0
Nabis rugosus (Linnaeus)	0	0	1	1	0	0
Orthops basalis (A. Costa)	0	0	0	0	0	2
Orthops kalmii (Linnaeus)	3	1	0	0	0	0
Palomena prasina (Linnaeus)	1	0	0	2	0	0
Peritrechus geniculatus (Hahn)	0	0	1	0	0	0
Plagiognathus crysanthemi (Wolff)	2	0	1	0	7	1
Polymerus microphtalmus (Wagner)	1	2	0	0	0	0
Rhopalus subrufus (Gmelin)	0	0	0	1	0	2
Spilostethus saxatilis (Scopoli)	0	0	3	13	0	0
Stenodema calcarata (Fallén)	0	8	0	0	0	0
Stenodema holsata (Fabricius)	0	0	0	17	0	21
Stenodema laevigata (Linnaeus)	0	0	0	0	0	1
Stenodema sericans (Fieber)	0	0	0	48	0	1
Stenotus binotatus (Fabricius)	0	0	2	1	0	0
Stictopleurus crassicornis (Linnaeus)	1	0	0	0	0	0
Stictopleurus punctatonervosus (Goeze)	1	0	0	0	0	2

Tab. 3: Presence/absence of grasshopper species in managed and abandoned meadows in the three regions Eisenwurzen, Großes Walsertal and Val Müstair.

	Region					
	Eisenwurzen		Gr. Walsertal		Val Müstair	
Species	Managed	Abandoned	Managed	Abandoned	Managed	Abandoned
Chorthippus biguttulus (Linnaeus)	1	1	1	0	1	1
Chorthippus dorsatus (Zetterstedt)	1	0	0	0	0	0

Chorthippus mollis ignifer (Ramme)	0	0	0	0	1	1
Decticus verrucivorus (Linnaeus)	1	0	1	0	0	0
Euthystira brachyptera (Ocskay)	1	1	1	1	0	1
Gomphocerippus rufus (Linnaeus)	0	1	1	1	0	1
Metrioptera brachyptera (Linnaeus)	1	1	0	1	1	1
Omocestus rufipes (Zetterstedt)	0	0	0	0	1	0
Omocestus viridulus (Linnaeus)	0	0	0	0	1	0
Pholidoptera aptera (Fabricius)	0	0	0	1	0	0
Pholidoptera griseoaptera (De Geer)	0	1	1	1	1	1
Pseudochorthippus parallelus (Zetterstedt)	1	1	1	1	1	1
Psophus stridulus (Linnaeus)	0	0	0	0	1	1
Roeseliana roeselii (Hagenbach)	1	1	1	1	1	1
Stauroderus scalaris (Fischer von Waldheim)	0	0	0	0	1	1
Stenobothrus lineatus (Panzer)	1	0	1	0	1	1
Tettigonia cantans (Füssli)	1	1	0	1	0	0

4.2. Publication II: Effects of management cessation on hoverflies (Diptera: Syrphidae) across Austrian and Swiss mountain meadows.

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Ronnie Walcher planned and conducted the field work, collected data on syrphids, identified them to species level, prepared and analyzed the data and wrote the manuscript.

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Effects of management cessation on hoverflies (Diptera: Syrphidae) across Austrian and Swiss mountain meadows

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Abstract. Extensively managed grasslands, particularly in mountain regions, are considered to be one of the most diverse agroecosystems worldwide. Their decline due to land use abandonment affects the diversity of both plants and associated pollinators. Extensive grasslands constitute an important habitat type and food resource for hoverflies (syrphids); however, not much is known about the effects of abandonment on this important pollinator group. In the present study, we investigated how abandonment affects species richness and the composition of syrphids in mountainous meadows. We recorded the richness of vascular plants, vegetation cover, flower cover and the surrounding landscape to examine whether and how syrphids are affected by plant and landscape parameters. We investigated the species richness, abundance and species composition of syrphids by sweep netting and by using observation plots in 18 semidry meadows across two Austrian regions and one Swiss region. For each region, we selected three meadows abandoned for more than 20 years and three annually mown non-fertilized meadows. Abandonment or mowing had no significant effect on the total number of syrphid species or individuals or on the number of aphidophagous and non-aphidophagous species and individuals. However, the total number of species and the number of non-aphidophagous species significantly increased with the increasing number of plant species. The surrounding landscape and other plant parameters showed no association with the assessed syrphid parameters. Although syrphids were unaffected by abandonment, higher syrphid species numbers in response to a higher plant richness in annual mown meadows suggest that the management of mountain meadows is beneficial in preserving syrphid richness.

1 Introduction

Seminatural grasslands are considered one of the most valuable agroecosystems throughout Central European landscapes and are characterized by a high biodiversity (Chytrý et al., 2015; Habel et al., 2013; Maurer et al., 2006). In particular, extensive management by mowing or grazing is an important management scheme to maintain these habitats of high nature conservation value (Hansson and Fogelfors, 2000; Moog et al., 2002). Most of these grassland habitats have a long history and were maintained by local farmers for hay making and animal husbandry over hundreds of years (Chemini and Rizzoli, 2003; Poschlod and WallisDeVries, 2002). Since their conservation relies strongly on human land use activities, they are considered seminatural habitats (Heijcman et al., 2013). Due to a high economical pressure in recent decades, traditional management has become more and more unviable (Hinojosa et al., 2016; McGinlay et al., 2017). Thus, to increase the yield, new agricultural and cultivation techniques were developed which have led to an intensification of grasslands in favorable regions on the one hand and afforestation or abandonment in marginal

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regions on the other hand (Graf et al., 2014; Tasser et al., 2007). Besides economical reasons, ecological factors like slope inclination and accessibility are important drivers for farmers' decisions to cease management especially in mountainous landscapes (Tasser et al., 2007; Rey Benayas et al., 2007; Strijker, 2005). Abandonment has led to an ongoing decline of traditionally managed seminatural meadows, confining them to small patches within the landscape (Graf et al., 2014). Successional processes alter habitat conditions and have been leading to an increase in dominant grass species and the establishment of trees and shrubs on formerly managed meadows (Cremene et al., 2005; Diemer et al., 2001; Galvánek and Lepš, 2008; Tasser and Tappeiner, 2002). Consequently, plant species which demand regular management decline during this succession process (Hülber et al., 2017; Pykälä et al., 2005). Thus, an important research question is how insect populations might respond to changing vegetation characteristics after abandonment.

Generally, the extent of how abandonment affects insects depends very much on the considered insect groups (Bonari et al., 2017; Burel, 1991; Walcher et al., 2017) and can even differ between species within the same taxon (Jovičić et al., 2017). While some insect taxa benefit from the altered structural and environmental conditions in abandoned meadows, e.g., ants (Azcárate and Peco, 2011; Wiezik et al., 2013) and grasshoppers (Baur et al., 2006; Schirmel et al., 2011), recent studies showed detrimental effects of abandonment on pollinators such as butterflies (Öckinger et al., 2006) and bumblebees (Walcher et al., 2017). Until now, the response of hoverflies (syrphids) to the abandonment of extensively managed meadows in mountainous regions has been little studied.

Along with wild bees, syrphids are important pollinators of both wildflowers and crops (Jauker and Wolters, 2008). They may also play a role as pollinators in habitats which are unsuitable, for example, for wild and honey bees (Jauker et al., 2009; Rader et al., 2016). Besides providing important pollination services, hoverfly species whose larvae are aphidophagous contribute strongly to the efficient control of aphid populations (Leroy et al., 2014). Furthermore, hoverflies represent important bioindicators, which makes them an important insect group to study the effects of land use changes (Burgio and Sommagio, 2007).

In a study investigating hoverfly communities in regularly mown and abandoned mountainous grasslands, extensively managed meadows contained a higher number of hoverfly individuals compared to abandoned meadows (Hussain et al., 2017). Furthermore, the study found a positive relationship between flower cover and plant richness with hoverfly abundance. However, it is unclear whether these relationships vary among different regions. Thus, it is important to collect and merge data from several mountainous regions to obtain more generally valid results. Therefore, in the present study, we analyzed the data of three regions including those reported by Hussain et al. (2017). Analogous to their study, we tested the effects of abandonment, vegetation parameters and further surrounding landscape parameters on species richness and the abundance of syrphids in three regions across the Alps. In addition to the former study, here we further distinguished between species whose larvae have an aphidophagous of non-aphidophagous feeding mode. In the present study, we expected a clear response of hoverflies to abandonment due to altered vegetation characteristics, like decreasing plant and flower resources, which in turn are important determinants of hoverfly richness and abundance (Haenke et al., 2009). The surrounding landscape was included in the present study because it was reported to affect the number of hoverflies in grassland ecosystems (e.g., Gittings et al., 2006; Power et al., 2016).

We expected (i) different numbers of hoverfly species and individuals and a different hoverfly species composition between management types. Furthermore, we investigated (ii) whether and how hoverflies are affected by plant richness, flower cover, the cover of the vegetation and the surrounding landscape. Additionally, we investigated (iii) the effects of abandonment and plant and landscape parameters on both aphidophagous and non-aphidophagous hoverflies.

2 Material and methods

2.1 Study regions and sites

Investigations were carried out in June and August 2015. Altogether, 18 mountainous meadows in the Austrian and Swiss Alps were investigated. Two regions were located in Austria (central Ennstal and Großes Walsertal) and one region in Switzerland (Val Müstair) (Fig. 1). Investigations in the central Ennstal region were carried out in the municipalities of Sankt Gallen, Stainach and Pürgg, in Großes Walsertal in the municipality of Sonntag/Buchboden, and in the Val Müstair region in the municipalities of Valchava, St. Maria and Tschierv. The central Ennstal region is located in the Austrian federal state of Styria ranging from the Gesäuse national park in the east to Grimming mountain in the west. The meadows were situated at altitudes between 690 and 770 m above sea level (a.s.l.). Großes Walsertal is a biosphere reserve located in the Austrian federal state of Vorarlberg. Meadows were situated at altitudes between 1170 and 1280 m a.s.l. Val Müstair in the canton of Graubünden is situated in the Eastern Alps of Switzerland near the border with South Tyrol (Italy). Meadows in this region were situated at altitudes between 1740 and 1800 m a.s.l. Detailed information on the investigated meadows is shown in Table S1 in the Supplement. Within each region, six south-facing meadows were selected ($n = 18$). Three of the six meadows were annually mown and non-fertilized. The farmers usually mow the meadows from the end of July to the beginning of August depending on the annual weather conditions. Due to restricted accessibility with mowing machines, the meadows are mown manually with sickle bar mowers. Three of the six meadows had been abandoned for at least 20 years (Val

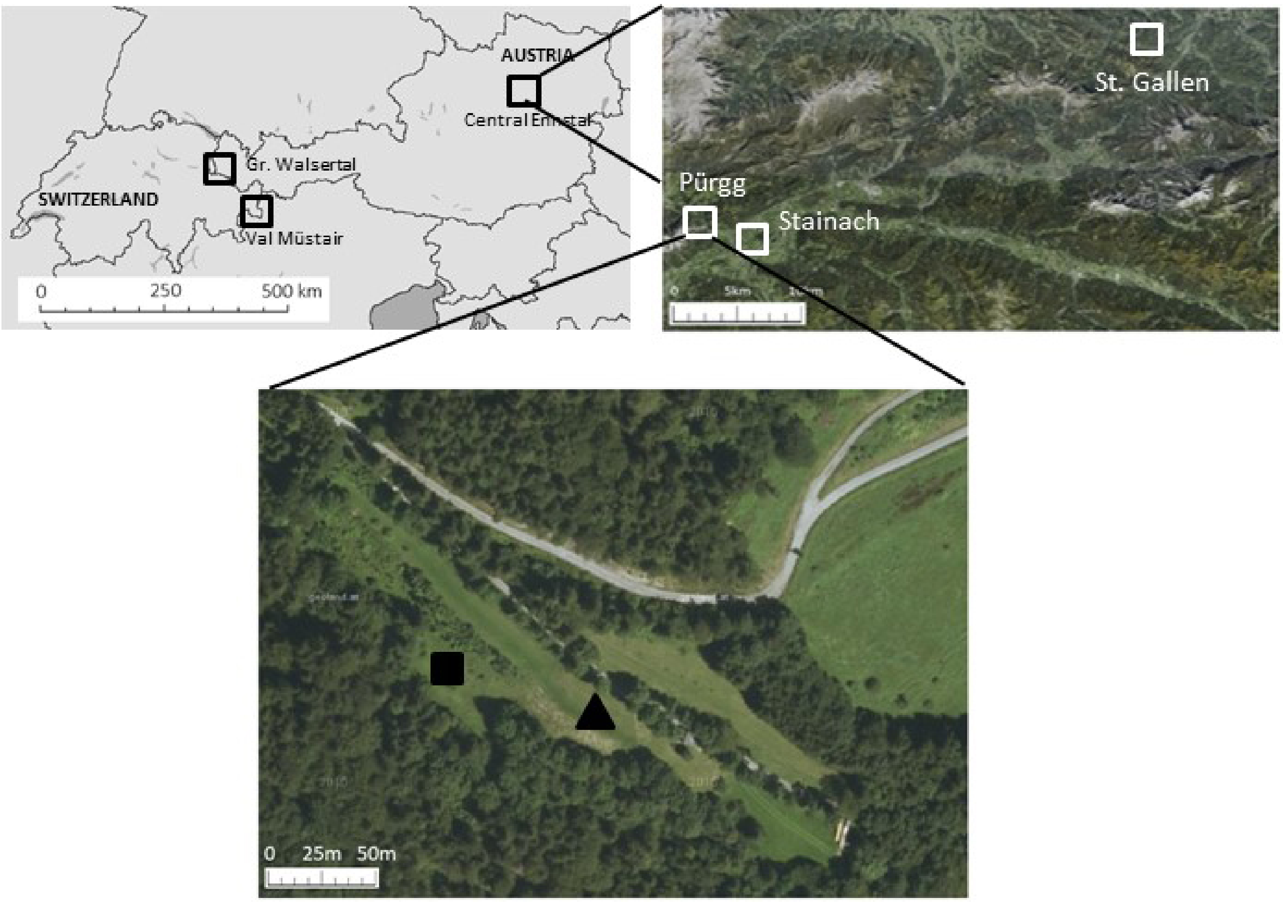

Figure 1. Location of the three study regions (central Ennstal, Großes Walsertal and Val Müstair). Detailed maps are shown for the central Ennstal region with the focus on two meadows in the municipality of Pürgg (the filled square outlines the location of one abandoned meadow, and the filled triangle outlines the location of one managed meadow). All panels are adapted from Basemap.at (2020), © data source: http://www.basemap.at (last access: April 2020), distributed under the Open Government Data Austrian license CC-BY 4.0.

Müstair 20 years, central Ennstal 20–40 years and Großes Walsertal 35–60 years since abandonment). Before the cessation of management, the abandoned meadows were annually mown and were never used as pastures. The annually mown meadows had an average area of 3049 m^2, and the abandoned meadows had an average area of 1366 m^2. The sizes of the abandoned and annually mown meadows were not significantly different within each region (t test: central Ennstal, $p = 0.295$; Großes Walsertal, $p = 0.131$; Müstair, $p = 0.323$).

2.2 Hoverfly sampling

We surveyed the number of hoverfly species and individuals once in mid-June and once in mid-August 2015 and finished one round of investigations within 2 d per month in each region. We started sampling at 10:00 and stopped at 17:00 (all times are in Central European time). In this time period, we found that optimal sampling conditions were a minimum temperature of 20 °C, dry vegetation and sunshine.

In order to increase sampling efficacy, we assessed the number of hoverfly species and individuals by sweep net sampling and an observation plot method (Hussain et al., 2018). Especially the observation plot method has been shown to increase the number of collected species and individuals (Hussain et al., 2018). Syrphid data from the central Ennstal region (Eisenwurzen) for June and August 2015 were provided by Hussain et al. (2017) who used the same sampling methods. Sweep net sampling was performed along three 15 m long and 2 m wide transects which were selected in the center of each meadow. Thus, we covered a sampling area of 90 m^2. The distances between the transects were 10 m. We used a sweep net consisting of a white cloth (40 cm opening diameter, 70 cm length). We conducted 30 sweeps per transect summing up to 90 sweeps per meadow. The contents of the sweep net were emptied after 30 sweeps and collected insects were killed with ethyl acetate and stored in previously prepared and labeled plastic vials. The sorting of hoverflies was carried out in the laboratory. Hoverflies were stored in glass vials filled with 70 % ethanol.

In addition to the sweep net method, we applied an observation plot method in which we observed four 2 m^2 plots each for 15 min within every meadow. The plots were distanced 3, 9 and 27 m from the first plot. The starting plot was selected approximately in the center of each meadow to avoid spillover effects from adjacent habitats. For the collection of single species, we used an insect net (20 cm opening diameter, 20 cm length) mounted on a handle 30 cm long. Syrphids entering an observation plot were caught and stored in plastic vials. In the laboratory, hoverfly individuals were preserved in glass vials in 70 % ethanol. For analysis, we pooled the individuals caught by sweep netting and those caught during the 15 min observations. Identification was performed using a binocular microscope and identification literature by Stubbs and Falk (1983) and van Veen (2010). For further analysis, we distinguished between hoverflies whose larvae are aphidophagous or non-aphidophagous. We did not consider hoverflies with saprophagous and phytophagous larvae separately due to the low number of species. Larvae of these species are all considered non-aphidophagous. The subdivision into feeding groups is an important aspect because the aphidophagous feeding group most likely contributes to an essential aphid control in nearby arable land. Thus, it is important to test whether the observed meadows can enhance aphidophagous syrphid populations.

2.3 Vegetation and landscape parameters

The assessment of plant parameters was carried out in June and August 2015 within 2 d in each month. We recorded plant parameters within four plots sized 1 m^2. As with the plots for syrphid sampling, these plots were situated in the center of the meadows. Within the plots, we identified all plants to the species level and assessed vegetation cover and flower cover. Besides living biomass, vegetation cover included necromass on the ground. For further analysis, we determined the amount of plant species with flowers having a flat corolla (hereafter designated as open nectar flowers, e.g., Ranunculaceae, Asteraceae and Apiaceae) because this flower type is an important food source for hoverflies. Additionally, we measured the surrounding landscape structure from orthophotos in ArcGIS (ArcGIS basemap). Therefore, we measured the percentage of open land (containing, for example, meadows and pastures in the surrounding) and forest (containing, for example, closed forest and hedges) within a 500 m circle drawn around the center of each meadow. We derived the vegetation and landscape data from the central Ennstal region (Eisenwurzen) for June and August 2015 from Hussain et al. (2017).

2.4 Statistical analysis

We used generalized linear models (GLMs) for count data and Poisson error distributions to analyze the effects of management and plant and landscape parameters on hoverfly species and individuals and aphidophagous species and individuals. We included the variable region as a fixed factor in the GLMs. Before testing plant and landscape parameters in a GLM, we ran correlation tests between them. Therefore, we first computed the *corr.test* function (R package *psych*; Revelle, 2019) to receive p values and correlation coefficients (r). We found certain correlations between plant and landscape parameters (Table 1). Furthermore, to assess for multicollinearity between predictor variables (management type and vegetation and landscape parameters), we computed the variance inflation factors (VIFs) using the R package *car* (Fox et al., 2020). Any variables with a VIF greater than 5 were removed from the models. Based on these results, we computed our GLMs. We found that the predictor variables of plant richness, flower cover, vegetation cover and open nectar flowers could have been included in one model (all predictor variables with a VIF less than 3) to evaluate their effects on hoverflies. To investigate the effects of open landscape and forest, we analyzed both factors in a separate model (VIF less than 5). Similarly, according to the VIF output, we also tested the variable management type separately. We accounted for over- and underdispersion of the data by computing the *dispersion.test* function in R (Kleiber and Zeileis, 2018). In cases of over- or underdispersion, we corrected the GLMs by using quasi-Poisson error distributions.

To avoid spatial autocorrelation, we performed the Moran's test by applying the *Moran.I* function (Paradis et al., 2017) for each region individually. Our analysis revealed no spatial autocorrelation between meadows within each region (central Ennstal, $p = 0.678$; Großes Walsertal, $p = 0.339$; Val Müstair, $p = 0.563$).

We performed a principal coordinate analysis based on a Bray–Curtis similarity matrix, to evaluate differences in hoverfly species composition between meadow types. As with the GLM, we included the variable region as a fixed factor. Possible significant differences in hoverfly species composition between meadow types were tested with a permutational ANOVA (analysis of variance; PERMANOVA). We calculated p values using 9999 permutations of residuals under a reduced model.

We used version 6.1.13 of the software PRIMER including PERMANOVA+ (PRIMER-e Ltd., Plymouth, UK) to conduct the principal coordinate analysis and PERMANOVA. We performed all other statistical analyses in R version 3.5.2 (R Core Team, 2018).

3 Results

We collected 175 syrphid individuals belonging to 30 species (Table S2). A total of 25 species with 84 individuals were detected in managed meadows and 18 species with 91 individuals in abandoned meadows. We distinguished between 15 aphidophagous and 12 non-aphidophagous species.

Table 1. Correlation between plant and landscape parameters. Significant and marginally significant r and p values are pointed out in bold.

	Plant species		Vegetation cover		Flower cover		Open flowers		Forest cover	
	r	p value	r	p value	r	p value	r	p value	r	p value
Vegetation cover	−0.22	0.375								
Flower cover	**0.66**	**0.003**	**−0.51**	**< 0.001**						
Open flowers	**0.77**	**< 0.001**	0.16	0.513	**0.42**	**0.084**				
Forest cover	−0.10	0.680	**−0.54**	**0.020**	0.40	0.103	−0.26	0.298		
Open landscape	−0.038	0.882	**0.40**	**0.097**	**−0.45**	**0.060**	**−0.95**	**< 0.001**	0.044	0.862

Table 2. Generalized linear models (GLMs) showing the effects of plant and landscape parameters on hoverfly species and individuals and on aphidophagous and non-aphidophagous species and individuals. Significant p values are shown in bold, and "df" signifies degrees of freedom.

Total hoverfly species						Total hoverfly individuals					
Variables	df	Estimate	Std. Error	z value	p value	Variables	df	Estimate	Std. Error	z value	p value
Intercept		0.430	0.702	0.612	0.540	Intercept		2.064	1.148	1.797	0.095
Flower cover	17	−0.148	0.188	−0.786	0.432	Flower cover	17	−0.215	0.325	−0.663	0.518
Plant species	17	0.043	0.021	2.037	**0.041**	Plant species	17	0.017	0.035	0.476	0.642
Vegetation cover	17	0.003	0.008	0.425	0.670	Vegetation cover	17	−0.004	0.128	−0.358	0.726
Open flowers	17	−0.173	0.157	−1.109	0.267	Open flowers	17	0.020	0.264	0.076	0.940
Variables	df	Estimate	Std. Error	z value	p value	Variables	df	Estimate	Std. Error	z value	p value
Intercept		8.809	4.795	1.837	0.066	Intercept		8.922	7.780	1.147	0.269
Open landscape	17	−0.062	0.048	−1.277	0.201	Open landscape	17	−0.071	0.081	−0.889	0.388
Forest cover	17	−0.082	0.050	−1.654	0.098	Forest cover	17	−0.064	0.079	−0.804	0.434
Aphidophagous hoverfly species						Aphidophagous hoverfly individuals					
Variables	df	Estimate	Std. Error	z value	p value	Variables	df	Estimate	Std. Error	z value	p value
Intercept		0.641	0.629	1.019	0.326	Intercept		2.419	1.195	2.023	0.064
Flower cover	17	−0.164	0.176	−0.929	0.369	Flower cover	17	−0.290	0.358	−0.812	0.431
Plant species	17	0.037	0.019	1.918	0.077	Plant species	17	0.007	0.037	0.199	0.845
Vegetation cover	17	0.001	0.007	0.088	0.931	Vegetation cover	17	−0.009	0.013	−0.682	0.507
Open flowers	17	−0.202	1.142	−1.426	0.177	Open flowers	17	0.068	0.282	0.242	0.812
Variables	df	Estimate	Std. Error	z value	p value	Variables	df	Estimate	Std. Error	z value	p value
Intercept		3.587	4.684	0.766	0.456	Intercept		6.968	8.653	0.805	0.433
Open landscape	17	−0.013	0.047	−0.279	0.784	Open landscape	17	−0.056	0.089	−0.634	0.536
Forest cover	17	−0.033	0.048	−0.684	0.504	Forest cover	17	−0.044	0.088	−0.501	0.624
Non-aphidophagous hoverfly species						Non-aphidophagous hoverfly individuals					
Variables	df	Estimate	Std. Error	z value	p value	Variables	df	Estimate	Std. Error	z value	p value
Intercept		−1.850	1.424	−1.299	0.216	Intercept		−2.345	1.840	−1.274	0.225
Flower cover	17	−0.639	0.425	−1.504	0.157	Flower cover	17	−0.428	0.510	−0.839	0.417
Plant species	17	0.113	0.052	2.161	**0.050**	Plant species	17	0.131	0.067	1.951	0.073
Vegetation cover	17	0.001	0.014	0.113	0.912	Vegetation cover	17	0.010	0.018	0.565	0.582
Open flowers	17	−0.477	0.343	−1.389	0.188	Open flowers	17	−0.677	0.434	−1.559	0.143
Variables	df	Estimate	Std. Error	z value	p value	Variables	df	Estimate	Std. Error	z value	p value
Intercept		3.587	4.684	0.766	0.459	Intercept		6.968	8.653	0.805	0.433
Open landscape	17	−0.013	0.047	−0.279	0.784	Open landscape	17	−0.056	0.089	−0.634	0.536
Forest cover	17	−0.033	0.048	−0.684	0.504	Forest cover	17	−0.044	0.088	−0.501	0.624

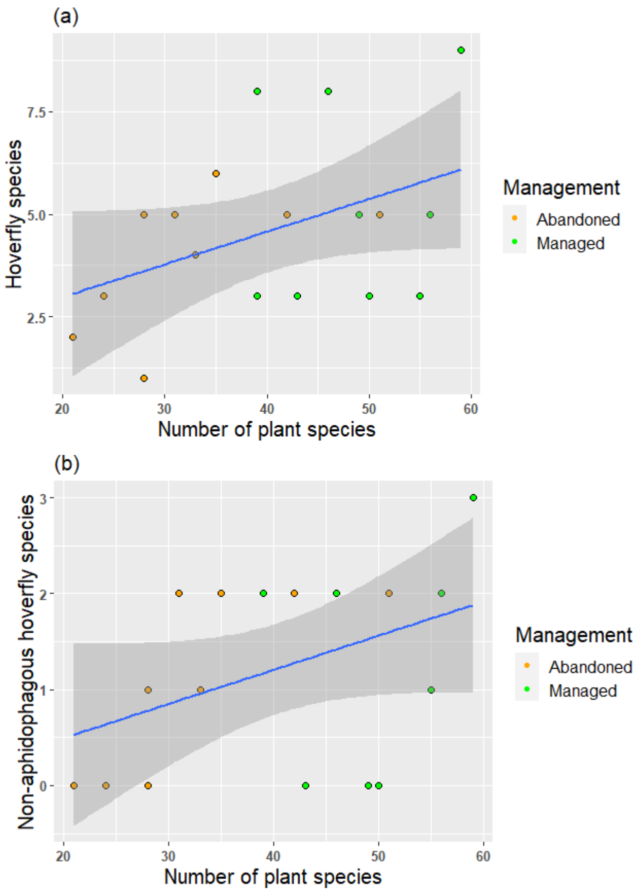

Figure 2. Regression showing **(a)** the significant relationship between the number of hoverfly species and the number of plant species and **(b)** the significant relationship between the number of non-aphidophagous species and the number of plant species in managed and abandoned meadows with a 95 % confidence interval.

Six species contributed to more than 75 % of the total individuals. These were *Melanostoma mellinum* (26.3 %), *Sphaerophoria scripta* (14.3 %), *Lapposyrphus lapponicus* (12 %), *Melanostoma scalare* (11.43 %), *Episyrphus balteatus* (7.43 %) and *Syritta pipiens* (4 %). Five species (*Orthonevra geniculata*, *Parasyrphus annulatus*, *Platycheirus albimanus*, *Rhingia borealis* and *Sphegina sibirica*) were only found in abandoned meadows; all other species were found in both meadow types. Three species which could only be identified to the genus level were not assigned to a feeding type. The total number of hoverfly species and individuals did not significantly differ between management types (GLM: $p = 0.158$ and $p = 0.823$, respectively), and this was also true for the number of aphidophagous and non-aphidophagous species and individuals (GLM: $p = 0.430$ and $p = 0.130$, respectively). The total number of species significantly increased with the increasing number of plant species (Fig. 2a; Table 2). Similarly, the number of non-aphidophagous species increased with the increasing number of plant species (Fig. 2b; Table 2). All other recorded plant and landscape parameters did not significantly affect the number of species and individuals of syrphids, and they also had no influence on the number of aphidophagous and non-aphidophagous species and individuals (Table 2). Regarding species composition, there was no difference between both meadow types (PERMANOVA: $p = 0.549$), which is also graphically represented in the principal coordinate analysis (PCO) (Fig. 3). Regarding plant parameters, the number of vascular plant species was significantly higher in mown meadows (ANOVA: $F = 16.31$ and $p < 0.001$). Flower cover and vegetation cover were higher in mown compared to abandoned meadows (ANOVA: $F = 34.3$ and $p < 0.001$; $F = 6.52$ and $p = 0.020$, respectively). A species list of identified plant species in the three study regions is attached in the Supplement (Table S3).

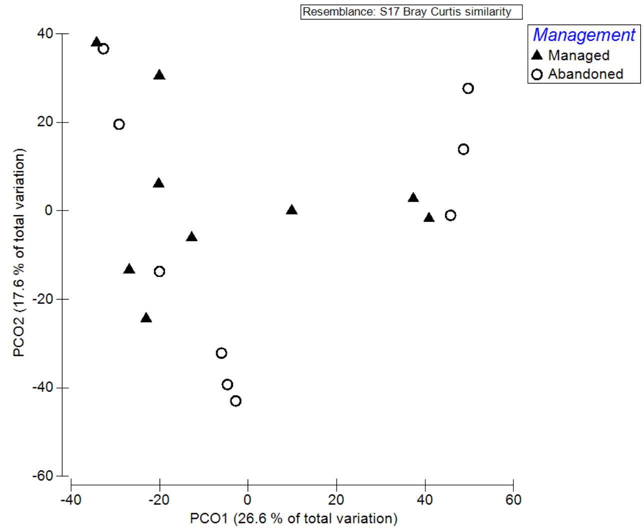

Figure 3. Principal coordinate analysis (PCO) showing hoverfly species composition in managed (▲) and abandoned (◯) meadows.

4 Discussion

With 46 individuals, *Melanostoma mellinum* was by far the most abundant hoverfly species in the present study. Furthermore, a higher abundance was made up of the eurytopic species *Sphaerophoria scripta*, *Lapposyrphus lapponicus* and *Melanostoma scalare*. These species are highly migratory, which can lead to a higher abundance in favorable years (Röder, 1990; Speight, 2014).

Regarding the total number of species and individuals, we found no differences between both meadow types. Considering the habitat requirements, most of the observed hoverfly species were eurytopic habitat generalists which use a variety of different habitats (Röder, 1990; Speight, 2014), and it can be assumed that both meadow types fulfilled hoverfly needs by providing similar resources and facilitating suitable microhabitats for their development. The most important factors which a habitat should provide for hoverflies are the availability of suitable floral resources (Hennig and Ghazoul, 2012; Moquet et al., 2018) and the presence of diverse larval habitats (Jauker et al., 2009; Weiner et al., 2014). Similar to the total number of species and abundance, the number of hoverfly species and individuals belonging to the aphidophagous and non-aphidophagous feeding guilds did not differ between meadow types. Especially the abundance of aphidophagous hoverflies is mainly determined by the presence of suitable aphid hosts (Almohamad et al., 2009). There is a very important contribution by Kök et al. (2020) which focused on the tritrophic relationships between plants, aphids and hoverflies. They found that plant species host different aphid species which in turn are a suitable prey for the larvae of aphidophagous hoverfly species like *Sphaerophoria scripta* and *Episyrphus balteatus*. This suggests that the choice of the habitats is mainly driven by these relationships.

Consistent with the lack of differences of species richness and abundance, we found a similar species composition in both meadow types. Only five species were confined to abandoned meadows and all other species were found in both meadow types. In contrast to, for example, bumblebees who have to provide pollen for their offspring, adult hoverflies are highly mobile, free in their dispersal (Meyer et al., 2009; Sutherland et al., 2001) and able to track suitable flower resources among a wide range of habitats (Jauker et al., 2009; Meyer et al., 2017).

The diversity of vascular plants turned out to be an important factor for hoverflies. Both the number of total hoverfly species and the number of non-aphidophagous species increased with an increasing plant richness. This indicates that a high variety of plant resources is most beneficial in maintaining hoverfly diversity in these grasslands (e.g., Meyer et al., 2009). The status of a high plant richness can only be preserved through regular extensive management. Grassland abandonment results in a decrease in plant richness (Pykälä et al., 2005) and consequently would have negative effects on hoverfly richness.

Surprisingly, we found no relationship between hoverflies and flower cover, contradicting the results of other studies (Meyer et al., 2009; Frank, 1999; Fründ et al., 2010; Power et al., 2016). However, our results are in line with those of Hussain et al. (2017) who reported that flower cover had no effect on syrphid richness and abundance. They mainly attributed this result to the presence of more flowers which have a deep, non-accessible corolla (e.g., *Salvia pratensis* and *Rhinanthus minor*), which is presumably also a good explanation for the findings in our study. For example, only a few syrphid species from the genus *Rhingia* developed specialized mouth parts to access the hidden nectar (Speight, 2014). However, with the exception of *Rhingia borealis*, these species were absent in our meadows. Another explanation for the missing relationship between flowers and hoverflies could be that hoverflies also feed on the honeydew from aphids that can be unrelated to the abundance of suitable flowers (van Rijn et al., 2013).

5 Conclusion

Although there was no overall effect of abandonment on syrphid richness, abundance and composition in the present study, plant richness turned out to be an important determinant for syrphid diversity in the investigated meadows, confirming also the results of other studies (e.g., Meyer et al., 2009; Hussain et al., 2017). In turn, this high plant richness can only be maintained by a regular extensive management. However, abandoned meadows also have the potential to contribute to a high hoverfly diversity in mountainous grasslands since some species were only found in abandoned meadows. Our results suggest that the maintenance of a heterogenous landscape containing both regularly mown and abandoned meadows is most beneficial for the conservation of hoverfly diversity in mountainous grasslands.

Data availability. The data used in this study are provided in the Supplement.

Supplement. The supplement related to this article is available online at: https://doi.org/10.5194/we-20-143-2020-supplement.

Author contributions. RW conducted field work, analyzed the data and wrote the paper. RIH and DB sampled and identified collected syrphids. RIH contributed hoverfly data from central Ennstal, and JK and AB recorded plant parameters. AA, JGZ and TF were the project leaders who designed and developed the "Healthy Alps" project. All authors reviewed the paper.

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Supplementary material:

Supplementary Table 1: Detailed information for the meadows in the three study regions Central Ennstal, Gr. Walsertal and Val Müstair.

		Mean annual temperature	Management type	Meadow size [m^2]	Altitude (meter a.s.l.)	Coordinates
Austria	Central Ennstal	6.9°C	managed	2731,74	552	47.668317, 14.596793
			managed	5154,08	805	47.517175, 14.125302
			managed	467,31	764	47.529405, 14.073971
			abandoned	1576,37	552	47.667813, 14.595772
			abandoned	656,11	545	47.663569, 14.594285
			abandoned	447,45	769	47.529468, 14.073386
Austria	Großes Walsertal	5.7°C	managed	3520,8	1250	47.250372, 9.972838
			managed	4726,5	1120	47.250044, 9.968447
			managed	5067,07	1100	47.249519, 9.969198
			abandoned	807,98	1200	47.250590, 9.970013
			abandoned	1708,84	1125	47.249461, 9.971204
			abandoned	4301,63	1050	47.249271, 9.968490
Switzerland	Val Müstair	5.9°C	managed	1152,78	1740	46.616116, 10.371446
			managed	3460,43	1730	46.615847, 10.371443
			managed	1167,99	1724	46.619523, 10.358019
			abandoned	1110,47	1740	46.616181, 10.370849
			abandoned	602,11	1730	46.616052, 10.370463
			abandoned	1087,17	1844	46.620209, 10.424658

Supplementary Table 2: Number of hoverfly individuals from the three study regions (Central Ennstal, Gr. Walsertal and Val Müstair). Aphidophagous species are emphasized with an “*”.

	Region					
	Central Ennstal		Gr. Walsertal		Val Müstair	
	Managed	Abandoned	Managed	Abandoned	Managed	Abandoned
Caliprobola speciosa	0	0	0	1	1	0
Cheilosia impressa	1	0	1	0	0	1
Cheilosia personata	1	0	0	0	0	0
Cheilosia sp.	1	0	0	0	0	0
Chrysotoxum cautum *	0	0	1	0	0	0
Episyrphus balteatus *	5	4	1	1	0	2
Epistrophe diaphana *	0	0	2	1	0	0
Eristalis jugorum	0	0	2	0	0	0
Lapposyrphus lapponicus *	6	14	0	0	0	1
Melanostoma mellinum *	7	0	1	0	10	28
Melanostoma scalare *	0	0	8	12	0	0
Merodon equestris	2	1	0	0	0	0
Myathropa florea	0	1	0	0	1	0
Orthonevra geniculata	0	1	0	0	0	0
Parasyrphus annulatus *	0	0	0	0	0	1
Paragus sp.	1	0	0	0	0	0
Pelecocera tricincta	0	0	1	0	0	0
Pipizella sp.	2	0	0	0	0	0
Pipizella viduata *	1	0	1	0	0	0
Pipizella virens *	1	1	1	0	0	0
Platycheirus albimanus *	0	0	0	0	0	1
Platycheirus sticticus *	0	0	0	0	1	0
Rhingia borealis	0	1	0	0	0	0
Scaeva pyrastri *	0	0	0	0	1	0
Sphaerophoria interrupta *	1	0	0	0	0	2
Sphaerophoria scripta *	7	8	5	2	1	2
Sphegina sibirica	0	1	0	0	0	0
Syritta pipiens	3	1	0	0	0	3
Syrphus ribesii *	1	0	0	0	0	0
Volucella bombylans	2	0	0	0	3	0

Supplementary Table 3: Presence/absence of plant species in the three study regions Central Ennstal, Val Müstair and Großes Walsertal.

	Region					
	Central Ennstal		Gr. Walsertal		Val Müstair	
	Managed	Abandoned	Managed	Abandoned	Managed	Abandoned
Acer pseudoplatanus	1	0	0	0	1	0
Achillea millefolium agg.	1	1	1	1	1	1
Acinos arvensis	0	0	0	0	1	0
Aegopodium podagraria	1	1	0	0	0	0
Agrostis capillaris	1	1	0	0	0	0
Ajuga genevensis	1	0	0	0	0	0
Ajuga reptans	0	1	0	0	0	0
Alchemilla monticola	0	0	1	0	1	1
Allium carinatum carinatum	1	1	1	1	1	1
Allium lusitanicum montanum	1	0	0	0	0	0
Alopecurus pratensis	0	0	0	1	0	0
Anthericum liliago	0	0	0	0	0	1
Anthericum ramosum	0	1	0	0	0	1
Anthoxanthum odoratum	1	1	1	1	1	1
Anthriscus sylvestris	0	0	0	1	1	0
Anthyllis vulneraria carpatica	1	0	1	0	1	0
Aquilegia atrata	1	0	0	0	1	1
Arabidopsis halleri	0	1	0	0	0	0
Arabis ciliata	0	0	1	0	0	0
Arabis hirsuta	0	0	1	0	1	0
Arenaria serpyllifolia	1	0	0	0	0	0
Arrhenatherum elatius	1	1	1	1	1	1
Astrantia major major	1	1	0	0	1	1
Avenula pubescens pubescens	1	1	0	0	0	0
Betonica alopecuros	1	1	0	0	0	0
Betonica officinalis	1	1	0	0	1	0
Betula pendula	1	0	0	0	0	0
Botrychium lunaria	0	0	1	0	0	0

Brachypodium pinnatum	1	1	1	1	1	1
Briza media	1	1	1	1	1	1
Bromus erectus	1	1	1	1	1	1
Buphthalmum salicifolium	1	1	0	0	1	1
Campanula glomerata glomerata	0	0	1	0	0	0
Campanula patula	0	0	0	0	0	0
Campanula rapunculoides	0	1	0	0	0	0
Campanula rotundifolia	1	1	0	1	1	1
Campanula scheuchzeri	0	0	1	1	0	0
Carduus defloratus viridis	1	0	0	0	0	0
Carex alba	1	1	0	0	0	1
Carex caryophyllea	1	0	0	0	0	0
Carex ericetorum	0	0	1	1	0	0
Carex flacca	1	1	1	0	0	0
Carex ornithopoda ornithopoda	1	1	1	0	0	0
Carex panicea	1	1	0	0	0	0
Carex spicata	1	1	0	0	0	0
Carex sylvatica	0	0	0	0	1	0
Carlina acaulis acaulis	1	0	1	0	1	1
Centaurea jacea	1	1	1	0	1	1
Centaurea scabiosa scabiosa	1	1	1	0	1	1
Cephalanthera damasonium	0	1	0	0	0	0
Cerastium holosteoides	1	0	1	1	0	0
Chaerophyllum aureum	0	1	0	0	0	0
Clinopodium vulgare	1	1	0	0	1	1
Colchicum autumnale	0	1	1	0	1	1
Convolvulus arvensis	0	1	1	0	0	0
Crepis biennis	0	0	0	0	0	0
Cruciata laevipes	0	1	0	1	0	0
Cyclamen purpurascens	0	1	0	0	0	0
Cynosurus cristatus	0	0	1	0	1	0
Dactylis glomerata	1	1	1	1	1	0
Dianthus carthusianorum carthusianorum	1	0	1	0	0	0
Dianthus deltoides	0	0	0	1	0	0

Echium vulgare	0	0	0	0	1	0
Epipactis atrorubens	0	0	0	0	0	1
Erica carnea	0	1	0	0	0	0
Euphorbia cyparissias	1	1	1	0	0	0
Euphrasia officinalis rostkoviana	1	0	0	0	0	0
Festuca pratensis	1	1	0	0	1	0
Festuca rubra rubra	0	0	1	1	1	1
Festuca rupicola	1	1	0	0	0	0
Festuca valesiaca	0	0	1	1	0	0
Fragaria viridis	0	0	1	1	1	0
Fraxinus excelsior	1	1	0	0	0	0
Galeopsis tetrahit	0	0	0	0	0	0
Galeosis speciosa	0	1	0	0	0	0
Galium album	1	1	0	1	1	1
Galium aparine	0	0	0	1	0	0
Galium pumilum	1	1	1	1	1	1
Gentiana verna	1	0	1	0	0	0
Gentianella aspera	0	0	1	0	0	0
Geranium phaeum phaeum	0	0	0	0	0	0
Geranium pratense	0	0	0	1	0	0
Glechoma hederacea	1	0	0	0	0	0
Gymnadenia conopsea conopsea	1	1	1	0	0	0
Helianthemum nummularium obscurum	1	1	1	1	0	1
Helleborus niger	0	1	0	0	0	0
Hepatica nobilis	0	0	0	1	0	0
Heracleum sphondylium	0	0	1	0	1	0
Hieracium pilosella	1	0	1	0	1	0
Hieracium spec.	1	0	0	1	1	0
Hippocrepis comosa	1	1	1	1	1	1
Holcus lanatus	1	0	0	0	1	0
Hypericum perforatum	0	1	0	0	0	0
Knautia arvensis arvensis	1	1	1	1	0	0
Knautia drymeia intermedia	1	1	1	0	0	0
Knautia maxima	0	0	0	0	0	0

Koeleria pyramidata pyramidata	1	1	1	0	0	0
Lamium album	0	0	0	1	0	0
Laserpitium krapfii gaudinii	0	0	0	1	0	0
Laserpitium latifolium	1	1	0	0	0	1
Lathyrus latifolius	0	0	0	1	0	0
Lathyrus pratensis	1	1	0	1	1	1
Leontodon hispidus hispidus	1	1	1	0	1	0
Leucanthemum ircutianum	1	0	1	0	1	0
Lilium bulbiferum bulbiferum	0	0	0	0	0	0
Linum catharticum	1	0	0	0	1	0
Lotus corniculatus	1	1	1	1	1	1
Luzula multiflora	0	0	0	0	1	0
Medicago falcata	1	1	0	0	0	0
Medicago lupulina	1	0	0	0	0	0
Melampyrum sylvaticum	0	1	1	1	0	0
Molinia caerulea	1	1	0	0	1	1
Myosotis alpestris	0	0	1	0	0	0
Myosotis arvensis	0	0	0	1	0	0
Nardus stricta	0	0	1	0	0	0
Onobrychis montana	0	0	1	0	0	0
Origanum vulgare vulgare	0	1	0	0	0	0
Orobanche gracilis	1	0	0	0	0	0
Phleum pratense	0	0	0	0	1	0
Phyteuma orbiculare	1	1	1	1	1	1
Pimpinella major major	1	1	0	0	0	0
Pimpinella saxifraga saxifraga	1	1	1	1	0	0
Plantago lanceolata	1	1	1	0	1	1
Plantago media	0	0	1	0	1	0
Platanthera bifolia	0	0	0	0	1	0
Poa angustifolia	1	1	1	1	1	0
Poa trivialis	0	0	1	0	0	0
Polygala alpestris	0	0	1	0	0	0
Polygala chamaebuxus	1	1	0	1	0	0
Polygala comosa	1	0	1	0	1	0
Polygonatum odoratum	0	0	1	0	0	0

Potentilla erecta	1	1	1	1	1	1
Primula elatior	0	1	1	1	1	1
Prunella grandiflora	1	1	0	0	1	1
Ranunculus acris acris	1	0	0	0	0	0
Ranunculus bulbosus	1	0	0	0	0	0
Ranunculus nemorosus	1	1	1	0	1	1
Ranunculus repens	0	0	0	0	0	0
Rhinanthus alectorolophus alectorolophus	0	1	1	1	1	0
Rhinanthus glacialis	1	1	0	0	0	0
Rhinanthus minor	1	0	1	0	0	0
Rosa spec.	0	0	0	1	0	0
Rubus idaeus	0	0	0	1	0	0
Rumex acetosa	1	1	0	0	1	0
Salvia verticillata	1	1	0	0	1	0
Sanguisorba minor	1	0	1	1	1	0
Scabiosa columbaria	1	0	0	0	1	0
Scabiosa lucida	0	0	0	0	1	0
Sesleria caerulea	1	1	0	1	1	0
Silene nutans nutans	1	0	1	0	0	0
Silene vulgaris vulgaris	0	0	0	1	1	0
Sorbus aucuparia	0	0	0	1	0	0
Stellaria graminea	0	0	0	0	0	0
Taraxacum officinale agg.	1	1	1	0	1	0
Teucrium chamaedrys	0	1	1	0	0	0
Thesium alpinum	0	0	1	0	0	0
Thymus pulegioides pulegioides	1	1	1	1	1	1
Tragopogon orientalis	1	0	1	1	0	0
Tragopogon pratensis	0	0	0	0	1	1
Trifolium arvense	0	0	1	0	0	0
Trifolium dubium	0	0	1	0	1	0
Trifolium medium medium	0	1	0	0	0	0
Trifolium montanum	1	1	1	1	1	1
Trifolium pratense pratense	1	0	1	0	1	0
Trifolium repens	1	0	1	0	1	0
Trisetum flavescens	1	1	1	0	1	0

Trollius europaeus	0	1	1	0	0	0
Vaccinium myrtillus	0	0	1	1	1	1
Valeriana officinalis	0	1	1	1	1	1
Verbascum spec.	0	0	0	1	0	0
Veronica chamaedrys chamaedrys	1	1	0	0	1	0
Veronica teucrium	0	0	0	1	0	0
Vicia cracca	1	1	1	1	1	0
Vicia sepium	0	1	0	1	0	0
Vincetoxicum hirundinaria	1	1	0	0	0	1
Viola hirta	1	1	0	0	0	0
Viola rupestris	1	1	0	0	0	0
Viola spec.	0	0	1	1	0	0

4.3. Publication III: Long-term abandonment of mountain meadows affects bumblebees, true bugs and grasshoppers: a case study in the Austrian Alps.

Walcher, R., Hussain, R., I., Sachslehner, L., Bohner, A., Jernej, I., Zaller, J. G., Arnberger, A., Frank, T., 2019. Long-term abandonment of mountain meadows affects bumblebees, true bugs and grasshoppers: a case study in the Austrian Alps. *Applied Ecology and Environmental Research*, **17**, 5887-5908, https://dx.doi.org/10.15666/aeer/1703_58875908.

Author contributions: This work was written as part of the “Healthy Alps” project. This project was designed and developed by Thomas Frank, Johann Zaller and Arne Arnberger.

Ronnie Walcher planned and conducted the field work, collected data on bumblebees, heteropteran bugs and grasshoppers, identified bumblebees and heteropteran bugs to species level, prepared and analyzed the data and wrote the manuscript.

LONG-TERM ABANDONMENT OF MOUNTAIN MEADOWS AFFECTS BUMBLEBEES, TRUE BUGS AND GRASSHOPPERS: A CASE STUDY IN THE AUSTRIAN ALPS

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Abstract. We investigated how abandonment of mountain meadows influences bumblebees, true bugs and grasshoppers in two years in the Eisenwurzen region (Austria). We surveyed abandoned (20-40 years old) and annually mown unfertilized meadows. Bumblebees were observed in 20 m^2 plots, bugs were collected by sweep netting and grasshoppers identified with a soundscape approach. The insect groups were analysed in relation to plant species richness, flower cover, vegetation cover and the surrounding landscape. Bumblebee species richness and richness of long-tongued species were significantly higher in managed meadows. Similarly, we found significantly more phytophagous bug species in managed meadows, whereas grasshoppers showed no difference between meadow types. Bumblebee species richness and abundance, the abundance of phytophagous bugs and total grasshopper species richness were associated with total flower cover. Surrounding forest area negatively affected bugs, while open landscape positively affected bugs, both regarding species richness and abundance, number of phytophagous species and individuals and individuals overwintering as egg. Species assemblages of the three insect groups did not significantly differ between meadow types. Extensive management is important to preserve bumblebee and bug richness. However, abandoned meadows, which are not yet re-grown into forest can still act as suitable habitats for the three insect groups.
Keywords: *extensive management, management cessation, grasslands, Bombus sp., Heteroptera, Orthoptera*

Introduction

More than 40 % of the earth´s terrestrial surface is covered by grasslands (Suttie et al., 2005). In Central European landscapes, they represent valuable ecosystems harbouring a high plant diversity (Dengler et al., 2013; Chytrý et al., 2015). Semi-natural grasslands were maintained for hundreds of years by local farmers and traditional land-use systems (Maurer et al., 2006; Fischer et al., 2008; Poschlod et al., 2009; Hejcman et al., 2013; Price et al., 2015). In Austria, 60% of the agriculturally used area is made up of grasslands, 90% of which are not ploughed for at least 20 years (Pötsch et al., 2005). Changes in farming practice and intensity have led to a reduction

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of semi-natural grasslands throughout European landscapes (Wesche et al., 2012). Main causes of this reduction are agricultural intensification and abandonment (e.g. Strijker, 2005; Baur et al., 2006a; Gellrich et al., 2007; Tasser et al., 2007; Prévosto et al., 2011; Graf et al., 2014). The reasons for the abandonment of extensively managed mountain meadows are manifold. Rey Benayas et al. (2007) identified some of the main drivers of land-use abandonment and mentioned socio-economic factors like rural depopulation and ecological factors like slope, altitude and accessibility as factors for management cessation. Especially, slopes with a high inclination are more often abandoned (Tasser et al., 2007; Niedrist et al., 2009). Land-use abandonment, and the consequent process of secondary succession (Komac et al., 2013), leads to forest-regrowth (Gellrich et al., 2007; Prévosto et al., 2011). Abandoned meadows undergo several successional stages (Tasser et al., 2007). Some of these stages remain stable for decades and abandoned grassland remains open for a long time (Walcher et al., 2017). Usually, regular mowing or grazing is necessary to maintain semi-natural grasslands without encroachment of woody vegetation (Hannson and Fogelfors, 2000; Maurer et al., 2006).

While there is a great body of evidence regarding the effects of abandonment on plants, knowledge regarding insect species is scarce. The effects of human-induced land-use changes strongly depend on the insect taxa being considered (Bonari et al., 2017; Lessard-Therrien et al., 2018). Therefore, studies taking different insect groups into account, are important in order to understand the consequences of management measures and to develop conservation strategies (Van Noordwijk et al., 2017).

The three insect groups investigated in the present study are scarcely studied in mountainous grasslands, and especially data on true bugs in mountainous grassland ecosystems are largely missing. This is surprising because bumblebees, bugs and grasshoppers are suitable organisms to study the effects of land-use abandonment in grassland ecosystems. The reduction of foraging resources and loss of suitable nesting sites are the main causes for bumblebee decline (Carvell, 2002; Goulson et al., 2005; Carvell et al., 2006; Nieto et al., 2014; Goulson et al., 2015). Long-tongued bumblebee species, in particular, often have specialized diets and are known to be in decline in many European countries (Goulson et al., 2005; Kosior et al., 2007). The true bugs are a diverse group, including generalist and specialist species, which are assumed to react differently to land-use changes such as abandonment. Along with grasshoppers, they respond sensitively to altered environmental conditions (Schwab et al., 2002; Frank and Kuenzle, 2006; Fartmann et al., 2012) and are suitable indicators for land-use changes (Duelli and Obrist, 2003; Fartmann et al., 2012). Especially, grasshoppers require specific habitat conditions (Baur et al., 2006b). They are particularly affected by the cessation of management (e.g. Marini et al., 2009; Uchida et al., 2016).

In the present study, we aimed at investigating how abandonment impacts richness and abundance of bumblebees, true bugs and grasshoppers. Therefore, we compared extensively managed annually mown meadows (no fertilizer application) with abandoned meadows in an Austrian region. The Eisenwurzen region is one of the largest nature reserve areas in Austria. This area contains a range of semi-natural habitats and is facing severe challenges due to abandonment (Haberl, 2009). We investigated the three insect taxa for the same reasons as in Walcher et al. (2017), but collected an additional year of data and one additional meadow per treatment. Data sampling over multiple years in mountainous grassland ecosystems is highly important in order to possibly give recommendations for management schemes and conservation strategies in the future. Thus, in the present study, we picked up the highly topical issue

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of land-use abandonment by conducting a 2-years research in such an important nature reserve area.

We hypothesized that (i) species richness and assemblages of the three insect groups differ significantly between meadow types and, (ii) surrounding landscape structure and vegetation parameters significantly influence the three insect groups.

Methods

Study region

The study was carried out in 2015 and 2016 in the Styrian part of the Eisenwurzen region (Austria). Sampling was carried out once in June (between 16th and 18th of June) and once in August (between 16th and 18th of August) in both years. The mean annual temperature in this region is 6.9°C and the mean annual precipitation is 1 087 mm. Eight southerly exposed meadows – four extensively managed and four abandoned – were selected in the three municipalities St. Gallen, Stainach, and Pürgg (*Fig. 1, Table 1*).

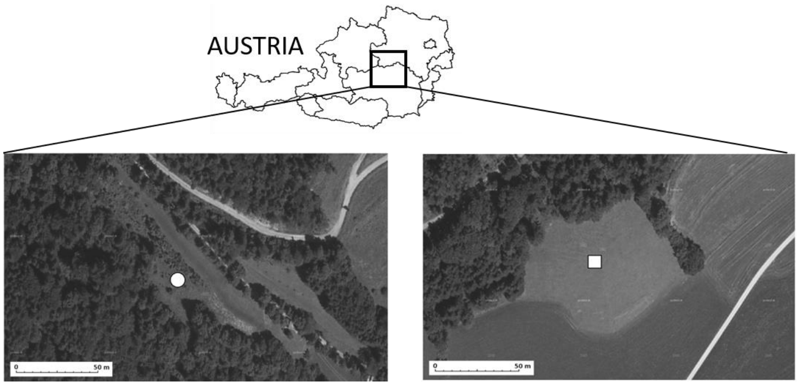

Figure 1. *Location of the study region Eisenwurzen. Orthophotos are shown for one abandoned (○) and one managed meadow (□) (data source: www.basemap.at)*

Table 1. *Coordinates of the investigated meadows in the Eisenwurzen region. Meadow A1-A4 are abandoned and meadows M1-M4 are managed meadows*

Meadow	Latitude	Longitude
A1	47°40'03.8" N	14°35'43.9" E
A2	47°39'51.5" N	14°35'39.6" E
A3	47°31'46.2" N	14°04'23.8" E
A4	47°31'01.1" N	14°07'26.9" E
M1	47°40'06.2" N	14°35'48.8" E
M2	47°39'53.3" N	14°35'42.7" E
M3	47°31'45.6" N	14°04'27.0" E
M4	47°31'01.8" N	14°07'31.4" E

Photos of the studied meadows give an impression of managed (*Fig 2 a* and *b*) and abandoned (*Fig 2 c* and *d*) meadows.

Due to technical problems with the soundscape method, we could only survey grasshoppers in three managed and three abandoned meadows, making a total of six meadows (n=6). The annually mown, non-fertilized managed meadows are usually

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mown at the beginning of August. In both years, 2015 and 2016, the meadows were mown mid-July. Thus, sampling in August took place four weeks after the last cut, thus ensuring new plants in flower for the second sampling round in August. Meadows are usually mown manually with bar mowers or, on very steep parts of the meadows, using a scythe. Abandoned meadows are between 20 and 40 years old and were used extensively before cessation of management. Information about former and current management of the investigated meadows and age of abandoned meadows was gathered by interviewing the land owners. The meadows were located at an average elevation of 670 m above sea level. The size of managed meadows ranged from 1095 to 4500 m^2, while the size of abandoned meadows ranged from 573 to 3370 m^2. The sizes of managed and abandoned meadows were not significantly different (F=0.959, p=0.365; ANOVA). We measured the percentage of surrounding open landscape (pastures, extensively and intensively used meadows) and the percentage of forest cover (closed forest) within a 500 m radius around the centre of each meadow, using ArcGIS (orthophotos, updated in 2017, ArcGIS basemap).

Figure 2. *Photos of study sites in the Eisenwurzen region (a and b are managed and c and d are abandoned meadows), Photos © R. Walcher*

Insect sampling

We sampled bumblebees and bugs in June and August 2015 and 2016 and grasshoppers in August 2015 and 2016. We assessed richness and abundance of bumblebees in four rectangular 20 m^2 (4 * 5) plots at each meadow. Sampling plots were selected randomly in the centre of the meadows. In order to guarantee standardisation of the sampling method, we selected distances of 3, 9 and 27 meters between the plots. Sampling was performed for 15 minutes per plot, summing up to 1 hour of observation time, and individual bumblebees were counted and identified on-site at the species level using an identification key by Gokcezade et al. (2015). However, single individuals had to be collected for complete confident identification in

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the lab. Furthermore, we grouped bumblebees into long- and short-tongued species and individuals. This classification is important because tongue length plays a major role in food plant selection.

For true bug sampling we carried out sweep-netting along defined transects. The distance between two transects was 15 metre. Specifically, we conducted 90 sweeps per meadow subdivided into 3 * 30 sweeps covering an area of total 90 m^2 (3 transects of 15 metre length * 2 m width of the transect). Collected bugs were identified using identification literature of Wagner (1952, 1966, 1967) and Strauss (2010). We gathered information on food preference (zoo- and phytophagous) and overwintering strategy (overwintering as egg or imagoes) from Wagner (1952, 1966, 1967).

To assess number of grasshopper species, we used digital recorders (Olympus LS-12, Olympus Europa SE & CO. KG, Hamburg, Germany) and connected them to bat detectors (Batbox III D, Batbox Ltd. Steyning, UK). We adjusted a frequency of 27 kHz on the detectors with a bandwidth of 16 kHz. We installed both devices on 80 cm high platforms. The records, which were conducted between 10 a.m. and 5 p.m., were afterwards analysed at the office by comparing them with acoustic material (e.g. Roesti and Keist, 2009). The recording range was approximately 30 meters. No analysis of grasshopper abundance can be made with the soundscape approach. All identified grasshoppers were assigned to Ensifera and Caelifera according to Baur et al. (2006b). All samples were taken during suitable weather conditions (low wind, sunny conditions, temperatures above 20°C, dry vegetation).

For bumblebee and true bug sampling, we carried out sampling in the meadows successively and not parallel. However, to avoid that the meadows were always sampled at the same time of the day, we investigated meadows, which were sampled in June in the morning, in August in the afternoon 2015. In the following year (2016) we sampled the meadows vice versa to 2015. A sketch showing the experimental setup of insect sampling is shown in *Figure 3*.

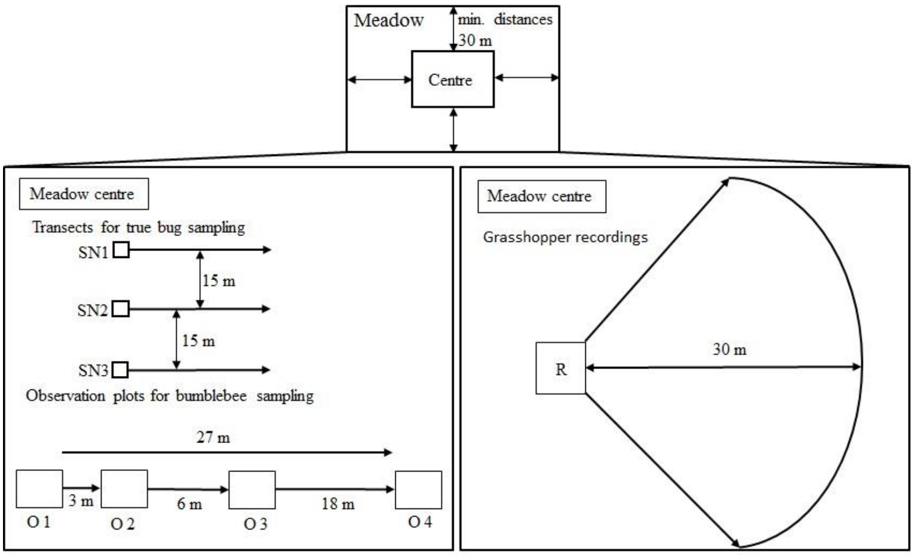

Figure 3. *Sketch showing sampling locations within one meadow. SN1-SN3 denotes transects for sweep sampling of true bugs. O1-O4 denotes observation plots for bumblebees. R denotes location of the recording devices. Measurements were carried out in the centre of each meadow keeping distances of minimum 30 meter to adjacent habitats*

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Plant sampling

To estimate the influence of vegetation parameters on the three insect groups, we examined vegetation cover as well as total flower cover and diversity of vascular plants in each meadow. Sampling was carried out in June and August 2015 and 2016. We selected four 1 m^2 plots in the centre of the meadows. For the purpose of vegetation assessments, we placed a 1 * 1 m frame on the ground and identified each plant to the species level. We recorded percentage of vegetation cover (including living biomass, necromass and open soil) and percentage of flower cover within the total plot area (1 m^2). We subdivided individual plant species into plant species providing open or hidden nectar flowers, which is an especially important vegetation parameter for bumblebees and their different tongue-length.

Statistical analysis

We used Shapiro-tests to check for normal distribution, and Bartlett- and Fligner-tests to check for homogeneity of variances of the data. We used generalized linear mixed models (GLMMs) to investigate the management effect on species richness and abundance of the three insect groups. Management was chosen as a fixed factor, and month (June and August) and year (2015 and 2016) as random factors. We investigated overdispersion in GLMMs by including an observation-level random effect (Harrison, 2014; Meyer et al., 2017). GLMMs were performed using the R-package *lme4* (Bates et al., 2015). We conducted generalized linear models (GLMs) to investigate differences between management types regarding tongue-length of bumblebees, feeding and hibernating strategy types of true bugs, suborders of grasshoppers, effects of vegetation parameters (vegetation and flower cover, plant species richness, plants providing hidden and open nectar flowers) and the structure of the surrounding landscape (open landscape and forest) on the three investigated insect groups. To test for over- or underdispersion, we used the *P__disp()* function (R-package “msme” version 0.5.1, Hilbe and Robinson, 2014) and the *dispersion.test()* function in R (R-package “AER”, version 1.2-4, Kleiber et al., 2015). We specified quasi-poisson errors to correct for over- or underdispersion in GLMs (Crawley, 2013). Before calculating GLM models, we investigated possible correlations between plant parameters and surrounding landscape structures. Since plant parameters and surrounding landscape structures were correlated, we decided to test them in single GLM-models. Furthermore, the point-biserial correlation coefficient r_{pb} was computed to detect possible significant associations of any individual species of the three insect groups with the two meadow types. This procedure calculates the strength (R-function *strassoc()*) and significance (R-function *signassoc()*) of possible associations. Both functions are included in the package “indicspecies” version 1.7.5 in R (De Cáceres and Jansen, 2015). Two-sided permutation tests were conducted to assess significant associations. We calculated confidence intervals and bootstrapped data 999 times with replacement (Walcher et al., 2017).

We analysed possible differences in species composition of the three insect groups conducting a principal coordinate analysis (PCO). We included month and year as random factors, similar to the univariate analysis. A permutational ANOVA (PERMANOVA) was conducted to evaluate significant differences in species assemblages of the three insect groups. We permuted residuals 9999 times under a reduced model. Furthermore, by conducting the SIMPER-routine (similarity

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percentages), we investigated how individual species contribute to the differences between meadow types.

We used the version 6.1.13 of the software Primer including PERMANOVA+ (PRIMER-E Ltd. Plymouth, UK) to conduct PCO, PERMANOVA, and SIMPER routines. We performed all other statistical analysis in R, version 3.1.3 (R Core Team, 2015).

Results

Bumblebees

In total, we collected 98 bumblebee individuals of 13 species (*Bombus sp.*, *Appendix A*). Twelve species with 64 individuals were found in managed, and 8 species with 34 individuals in abandoned meadows. We identified three cuckoo bumblebees (*Bombus* [*Psithyrus*] *sp.*). Further, we distinguished between 5 long- and 8 short-tongued species.

Managed meadows harboured a significantly higher total bumblebee richness and higher numbers of long-tongued species (GLMM, z=2.479, p=0.0132 and z=2.147, p=0.0318 respectively; *Fig. 4 a* and *b*).

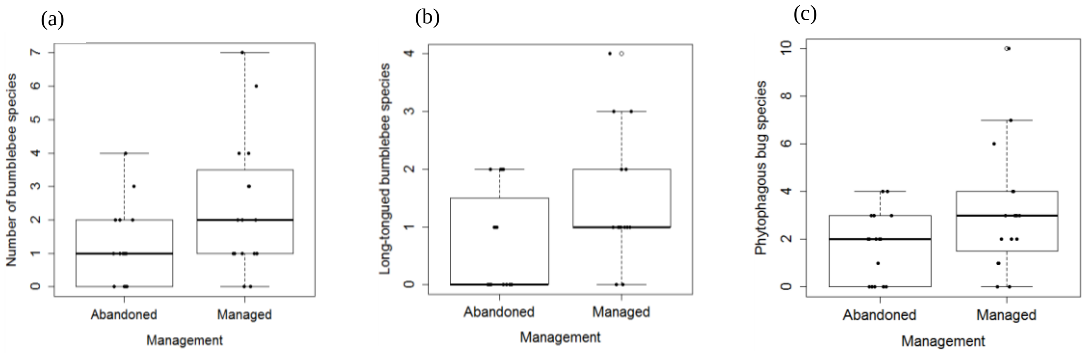

Figure 4. *Response of (a) total bumblebee species richness, (b) long-tongued bumblebee species richness and (c) phytophagous bug species richness on management. Boxplots show the median and the 25 % and 75 % percentiles. The dashed lines indicate the 10 % and 90 % percentiles. Outliers are indicated by (○). Data points are included as jitter-overlay*

Higher total flower cover increased total bumblebee species richness and abundance, and both number of short- and long-tongued species and individuals (*Table 2*, *Fig. 5a-f*).

Higher plant species with hidden nectar flowers significantly increased total bumblebee species richness as well as number of long-tongued species (*Table 2*, *Fig. 6 a* and *b*).

No relationship was found between number of bumblebee species and individuals, abundance of short-and long-tongued species and individuals and total plant species richness, surrounding landscape (open landscape and forest cover), vegetation cover and number of plant species with open nectar flowers. The point-biserial correlation did not show a significant association between individual bumblebee species and meadow types.

There was no significant difference between meadow types regarding bumblebee species assemblages (PERMANOVA, main-test: p = 0.145). We found an average

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similarity of 15.30 in annually mown meadows (SIMPER-analysis). 92.17% of the similarity was described by *B. lapidarius*, *B. hortorum*, *B. humilis* and *B. terrestris*. *Bombus humilis*, *B. pascuorum*, *B. hypnorum* and *B. terrestris* explained 91.42% of the similarity of 7.22 in abandoned meadows. Both meadow types revealed a dissimilarity of 91.49. *Bombus humilis*, *B. hortorum*, *B. lapidarius*, *B. pascuorum* and *B. terrestris* described 70.34% of the dissimilarity.

Table 2. *Generalized Linear Models (GLM, significance level: p<0.05) showing the effects of vegetation parameters on the three insect groups. The table shows the relationships between flower classes and bumblebees and the relationship between surrounding landscape structure, true bugs and grasshoppers. P-values which are significant are highlighted in bold (n.s: not significant, (-) indicates a negative effect, (+) indicates a positive effect, Res.dev. = Residual deviance, df = degrees of freedom)*

Bumblebees				Flower classes					
	Flower cover			Open nectar			Hidden nectar		
	Res.dev.	df	p	Res.dev.	df	p	Res.dev.	df	p
Total species	39.32	30	**<0.001 (+)**	51.05	30	n.s.	47.37	30	**0.022 (+)**
Total individuals	103.48	30	**0.004 (+)**	123.43	30	n.s.	124.14	30	n.s.
Long-tongued species	32.17	30	**0.008 (+)**	37.40	30	n.s.	32.85	30	**0.033 (+)**
Short-tongued species	37.02	30	**<0.001 (+)**	40.88	30	n.s.	44.64	30	n.s.
Long-tongued individuals	77.70	30	**0.044 (+)**	82.49	30	n.s.	86.32	30	n.s.
Short-tongued individuals	73.33	30	**0.008 (+)**	90.66	30	n.s.	84.19	30	n.s.
Bugs				Surrounding landscape structure					
	Flower cover			Open landscape			Forest cover		
	Res.dev.	df	p	Res.dev.	df	p	Res.dev.	df	p
Total species	57.73	30	n.s.	57.26	30	n.s.	54.69	30	**0.034 (-)**
Total individuals	280.76	30	n.s.	273.40	30	**0.049 (+)**	247.04	30	**0.011 (-)**
Phytophagous species	62.66	30	n.s.	60.41	30	**0.035 (+)**	56.72	30	**0.004 (-)**
Overwinter egg species	44.03	30	n.s.	43.47	30	n.s.	42.93	30	n.s.
Overwinter imago species	64.30	30	n.s.	65.08	30	n.s.	62.92	30	n.s.
Phytophagous individuals	303.24	30	**0.048 (+)**	289.55	30	**0.032 (+)**	258.92	30	**0.007 (-)**
Overwinter egg individuals	309.44	30	n.s.	290.30	30	**0.026 (+)**	262.88	30	**0.008 (-)**
Overwinter imago indiv.	122.18	30	n.s.	123.65	30	n.s.	122.32	30	n.s.
Grasshoppers				Surrounding landscape structure					
	Flower cover			Open landscape			Forest cover		
	Res.dev.	df	p	Res.dev.	df	p	Res.dev.	df	p
Total species	1.95	10	**0.009 (+)**	3.72	10	n.s.	3.76	10	n.s.
Caelifera	2.52	10	n.s.	1.99	10	n.s.	1.74	10	**0.046 (-)**
Ensifera	7.15	10	n.s.	7.82	10	n.s.	7.67	10	n.s.

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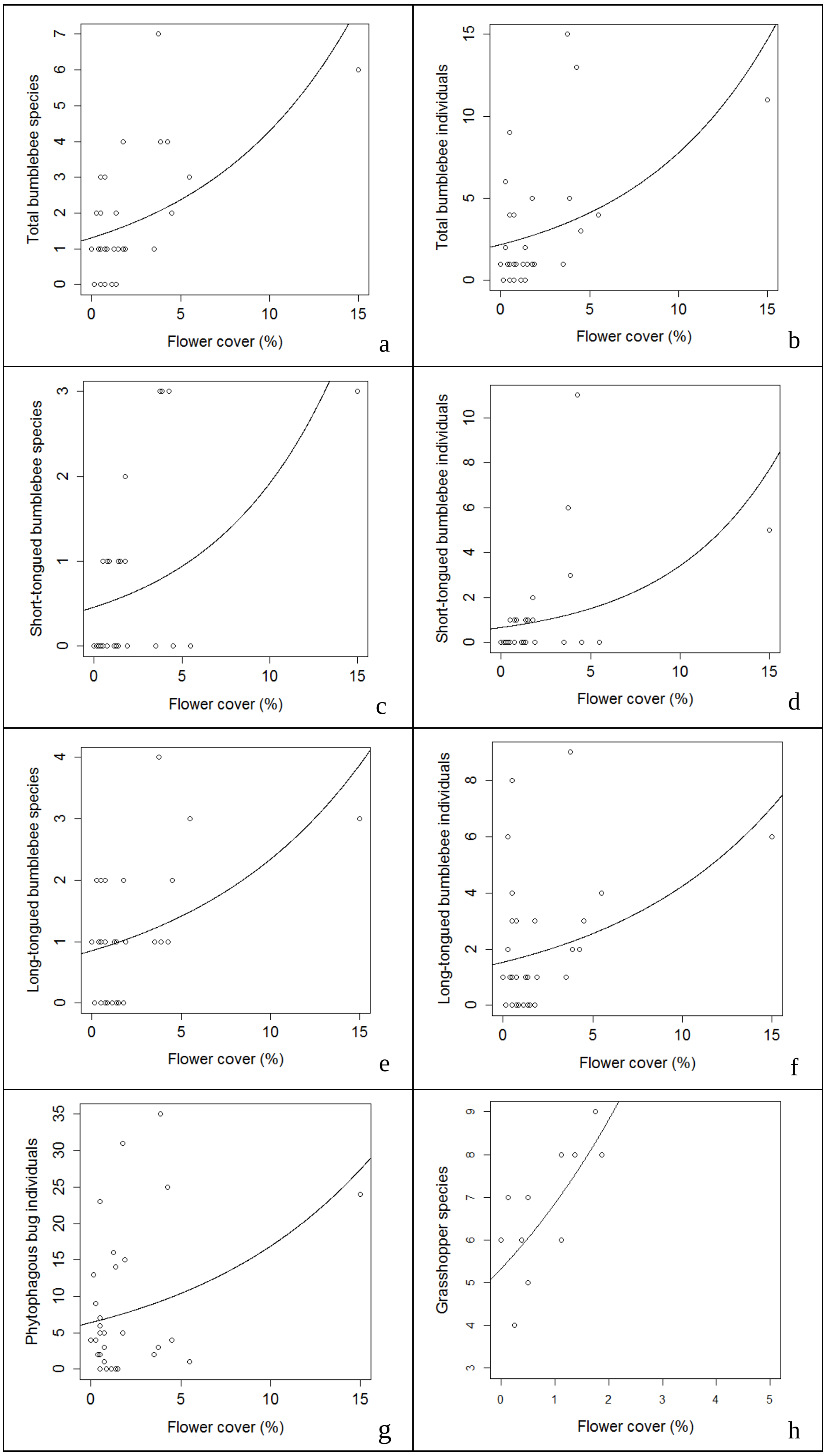

Figure 5. *Relationship between flower cover (in %) and (a) total bumblebee species, (b) total bumblebee abundance, (c) short-tongued bumblebee species, (d) short-tongued bumblebee abundance, (e) long-tongued bumblebee species, (f) long-tongued bumblebee abundance, (g) abundance of phytophagous bugs and (h) total grasshopper species. Fitted lines were drawn through the scatterplot using the predict-function in R*

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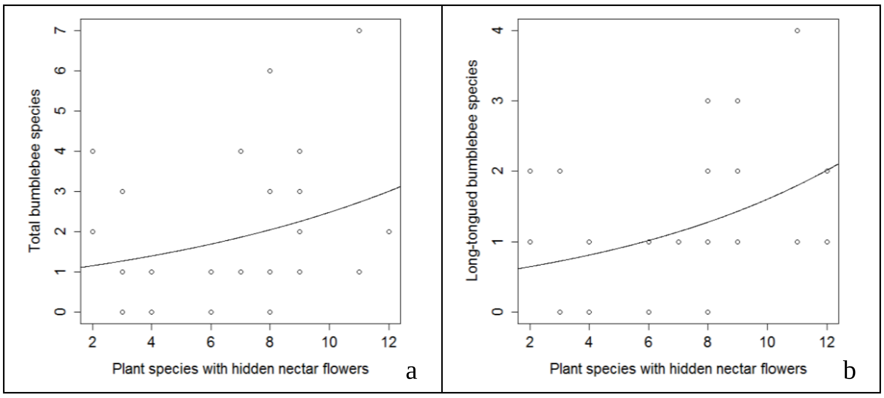

Figure 6. *Relationship between plant species with hidden nectar flowers and (a) total bumblebee species and (b) long-tongued bumblebee species. Fitted lines were drawn through the scatterplot using the predict-function in R*

True bugs

In total, we found 281 bug individuals of 32 species (*Appendix B*). We found 165 individuals of 27 species in managed, and 116 individuals of 13 species in abandoned meadows. Twenty-nine species were classified as phytophagous and three species as zoophagous. We classified 12 species as overwintering as eggs and 20 species as overwintering as imagos. We did not further include zoophagous bug species in the analysis due to the underrepresentation of this trophic group.

Managed meadows harboured significantly higher phytophagous bug species than abandoned meadows (GLMM, z=1.970, p=0.0488; *Fig. 4c*). Richness and abundance of true bugs, number of phytophagous bug species and individuals and individuals hibernating as eggs decreased with an increasing amount of forest cover in the surrounding landscape (*Table 2*). A larger proportion of open landscape in the surrounding landscape positively affected total number of individuals, individuals overwintering as eggs and species and individuals belonging to the phytophagous trophic group (*Table 2*). Increasing flower cover increased the number of phytophagous individuals (*Table 2*, *Fig. 5g*). No individual bug species was associated with either annually mown or abandoned meadows.

True bug species assemblages did not significantly differ between meadow types (PERMANOVA, main-test: p=0.565). The average Bray-Curtis similarity in the SIMPER-analysis in managed meadows was 7.19, with *Leptopterna dolobrata*, *Carpocoris purpureipennis*, *Orthops kalmii*, *Dolychoris baccarum*, *Graphosoma lineatum* and *Halticus apterus* explaining 91.58% of the similarity. Abandoned meadows revealed a similarity of 9.13. 91.11% of the similarity was due to the species *Nabis rugosus*, *Leptoperna dolobrata*, *Polymerus microphtalmus* and *Graphosoma lineatum*. We found an average dissimilarity of 92.30 between meadow types, where 62.70% of the dissimilarity was explained by the species *Leptopterna dolobrata*, *Nabis rugosus*, *Halticus apterus*, *Polymerus microphtalmus* and *Carpocoris purpureipennis*.

Grasshoppers

We detected a total of 15 grasshopper species in both meadow types (*Appendix C*). We found 12 species in managed and 13 species in abandoned meadows. We found eight Caelifera species and seven Ensifera species.

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There was no management effect on total species richness or on richness of Caelifera and Ensifera. Increasing total flower cover increased total grasshopper species richness (*Table 2, Fig. 5h*). Caelifera were significantly negatively affected by higher amounts of forest cover in the surrounding landscape (*Table 2*). We found *Stenobothrus lineatus* to be significantly associated with managed meadows.

Grasshopper species assemblages did not differ between meadow types (PERMANOVA, main-test: p=0.257). 94.01% of the similarity of 61.63 in managed meadows was due to the species *Chorthippus biguttulus*, *Stenobothrus lineatus*, *Pseudochorthippus parallelus*, *Metrioptera brachyptera*, *Roeseliana roeselii* and *Euthystira brachyptera*. 84% of the similarity of 53.42 in abandoned meadows was explained by the species *Euthystira brachyptera*, *Pholidoptera griseoaptera*, *Gomphocerippus rufus, Pseudochorthippus parallelus, Roeseliana roeselii*, and *Chorthippus biguttulus*. The average dissimilarity between meadow types was 52.36, with *Stenobothrus lineatus, Metrioptera brachyptera, Pholidoptera griseoaptera, Gomphocerippus rufus, Chorthippus biguttulus, Roeseliana roeselii, Barbitistes serricauda* and *Pholidoptera aptera* explaining 67.13% of the dissimilarity.

Landscape structure and vegetation parameters

Managed meadows comprised a significantly higher total plant species richness as well as a higher total flower cover compared to abandoned meadows (F=38.17, p<0.001 and F=6.06, p=0.019, respectively, ANOVA). Similarly, managed meadows harboured a significantly higher number of plant species with hidden nectar flowers (F=88.05, p<0.001). Vegetation cover as well as number of plant species with open nectar flowers did not differ between habitat types. Surrounding open landscape and surrounding forest cover were significantly negatively correlated (R^2=-0.96; p<0.001). Flower cover significantly increased with increasing numbers of plant species (R^2=0.44; p=0.012). Number of plant species were significantly positively correlated with number of plants with hidden nectar flowers (R^2=0.74; p<0.001) and number of plants with open nectar flowers (R^2=0.37; p=0.037). Numbers of hidden nectar plants marginally significantly increased with increasing flower cover (R^2=0.34; p=0.057). A list of the recorded plant species, the mean values for vegetation and flower cover and mean numbers of plant species providing open and hidden nectar flowers are given in *Appendix D*.

Discussion

Our results showed a positive effect of extensive management on total bumblebee species richness, particularly on long-tongued bumblebee species. This positive effect is mainly attributable to the higher total flower cover and the higher number of plant species which provided hidden nectar flowers in the investigated annually mown meadows. As a consequence of abandonment, it is likely that plant species richness decreased (e.g. Stampfli and Zeiter, 1999; Pykälä et al., 2005), which subsequently led to a reduction of floral resources (Maurer et al., 2005). In our study, there was also a positive association between total flower cover and plant species richness. This illustrates the importance of maintaining extensively managed, species-rich meadows to preserve local bumblebee richness. In addition, these meadows provide an adequate supply of suitable foraging resources throughout almost the entire activity period of bumblebees, except for the time between mowing and the emergence of new flowers. The importance of providing flower-rich habitats for bumblebees has already been

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stressed by numerous authors (e.g. Dramstad and Fry, 1995; Carvell et al., 2006; Ahrné et al., 2009). Similar species assemblages between meadow types suggests the provision of a sufficient amount of suitable foraging plants in abandoned meadows (Walcher et al., 2017). Further, bumblebees are highly mobile organisms which use a wide range of habitat types (e.g. Darvill et al., 2004; Westphal et al., 2006; Carvell et al., 2017), and both meadow types lay within their flight range.

Managed meadows contained significantly higher numbers of phytophagous bug species compared to abandoned meadows. Effects of management on several bug species were also shown in other studies (e.g. Di Giulio et al., 2001). Due to a reduced plant species richness in abandoned meadows we assume that suitable host plants for phytophagous bug species might be lost during the process of secondary succession (Tasser and Tappeiner, 2002). The managed meadows provided a range of suitable host plants for many bug species, as many of them were polyphagous species using a range of different plant species and families (e.g. Di Giulio and Edwards, 2003; Wachmann et al., 2004, 2007, 2008). True bugs were positively related with surrounding open landscape, revealing the importance of this landscape factor for the observed bugs (Torma et al., 2017). Most of the examined bug species in the present study are associated with open grassland habitats (e.g. Wachmann et al., 2004, 2007, 2008). This might explain the positive relationship with surrounding open landscape, because these species can utilize the supplementary resources in the surrounding meadows depending on their food specialization (Torma et al., 2017). In addition, these habitats can also be regarded as suitable refuges during mowing of the extensively managed meadows or as supplementary overwintering habitats. Most of the detected species were found in both habitat types. True bugs are usually very mobile organisms with a high dispersal potential (Bröring and Wiegleb, 2005; Yanhui et al., 2007; Reynolds et al., 2013). In addition, many of the bug species found in both managed and abandoned meadows were generalist species which do not depend on a specific habitat (e.g. Di Giulio et al., 2001; Wachmann et al., 2004, 2007, 2008). This and the ability to migrate over long distances might explain the lack of differences in species assemblages between both habitat types. The positive relationship between bug species and total flower cover confirms the results of some other studies (Frank and Kuenzle, 2006; Zurbrügg and Frank, 2006). Around 70% of the collected bugs are reported to feed or stay mainly on inflorescences (Wachmann et al., 2004, 2007, 2008). This explains the positive relationship between bugs and flower cover in the present study. In general, both managed and abandoned meadows are beneficial for various bug species, while abandoned meadows, which are not yet regrown with woody plants, are still a valuable habitat for many bug species inhabiting open landscapes.

Several studies on grassland habitats revealed a negative influence of land-use abandonment on grasshoppers, in which abandonment led to a decline in grasshopper species richness (Marini et al., 2009; Uchida and Ushimaru, 2014; Uchida et al., 2016). Our results, on the other hand, supports the findings of other studies (Bonari et al., 2017; Walcher et al., 2017), in that grasshoppers did not show any response to land-use abandonment. Most of our observed grasshopper species are considered to be habitat generalists. Therefore, we assume that they are well adapted to the habitat conditions of both managed and abandoned meadows. Interestingly, there was a positive relationship between total grasshopper species richness and flower cover. We interpret this as an indirect effect of management, as there is no evidence in literature of grasshoppers using inflorescences as a direct food source. Zahn et al. (2010) showed a positive correlation

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between grasshopper abundance and total flower cover. More likely, the factor flower cover is an indicator of habitat conditions and vegetation development in the two management types. Managed meadows are particularly important habitats for some of the observed grasshopper species. For example, *Stenobothrus lineatus* was found to be a characteristic species of the managed meadows. This species requires regularly mown meadows with a low sward height and some places of bare ground (Behrens and Fartmann, 2004). However, abandoned meadows were characterized by taller vegetation and the presence of certain bushes and small trees. In general, Ensifera prefer more structured habitat types containing trees and shrubs (Baur et al., 2006b; Marini et al., 2009) and some of the Ensifera species were exclusively or almost exclusively detected in abandoned meadows. A species which showed a particular preference for abandoned meadows was *Tettigonia cantans*. This species requires well-structured habitat types with dense vegetation (Baur et al., 2006b). The negative relationship between Caelifera and surrounding forest cover is due to the fact that none of the observed Caelifera species would choose closed forest as habitat type, since they are known to have an affinity for open habitats. There was no difference between species assemblages in managed and abandoned meadows. This result is in contrast to other studies (e.g. Fartmann et al., 2012; Walcher et al., 2017) who found that species assemblages differed between successional stages of grasslands. Most of the grasshopper species we observed have no special preference for a specific habitat type (Baur et al., 2006b) but are more sensitive to vegetation characteristics (Gardiner et al., 2002). It can be assumed that most of the observed grasshopper species found suitable microhabitats in both meadow types, and thus contain similar species assemblages.

Conclusion

Extensive management of meadows turned out to be an important management scheme to sustain bumblebee and true bug richness in the nature reserve Eisenwurzen region. High plant richness in the extensively mown meadows was associated with high flower cover, which contributed to high richness and abundance of the three insect groups studied. Both types of meadows harboured a similar composition of the three insect taxa. This shows that abandoned meadows, as long as they are not yet re-grown into forest, can act as suitable habitat for many of the observed species. However, a conversion into closed forest would deteriorate habitat conditions which are suitable for most species inhabiting open habitats. Thus, a regular removal of shrubs and trees is required for the maintenance of this meadow type.

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APPENDICES

Species lists of bumblebees, heteropteran bugs, grasshoppers and plants (with related vegetation parameters) in the study region Eisenwurzen.

Appendix A. *Number of individuals of bumblebees in managed and abandoned meadows in the Eisenwurzen region in 2015 and 2016 (M1-M4…managed meadows, A1-A4…abandoned meadows)*

	Eisenwurzen							
	Managed				Abandoned			
	M1	M2	M3	M4	A1	A2	A3	A4
Bumblebee species								
Bombus hortorum	5	6	0	3	0	1	0	1
Bombus humilis	2	1	2	1	0	0	15	2
Bombus hypnorum	0	0	0	1	0	0	0	2
Bombus lapidarius	4	2	2	0	0	0	3	0
Bombus lucorum	3	1	0	8	0	0	0	0
Bombus mucidus	0	0	3	0	0	0	0	0
Bombus pascuorum	3	3	0	0	0	1	3	0
Bombus pratorum	0	0	2	0	1	0	0	0
Bombus terrestris	3	3	0	0	1	0	2	0
Bombus wurflenii	1	0	1	0	0	0	0	0
Psithyrus barbutellus	0	0	0	0	0	0	1	1
Psithyrus bohemicus	0	1	0	2	0	0	0	0
Psithyrus campestris	0	0	1	0	0	0	0	0

Appendix B. *Number of individuals of heteropteran bugs in managed and abandoned meadows in the Eisenwurzen region in 2015 and 2016 (M1-M4…managed meadows, A1-A4…abandoned meadows)*

	Eisenwurzen							
	Managed				Abandoned			
	M1	M2	M3	M4	A1	A2	A3	A4
Bug species								
Adelphocoris lineolatus	0	0	0	0	0	0	0	1
Adelphocoris seticornis	0	4	3	0	0	0	0	0
Aelia accuminata	0	0	3	0	0	0	0	0
Capsus ater	0	0	1	0	0	0	0	0
Carpocoris purpureipennis	2	0	4	2	3	0	2	0
Catoplatus fabricii	0	0	0	1	0	0	0	0
Charagochilus gyllenhalii	0	0	0	0	0	1	0	1
Corizus hyoszyami	0	0	2	0	0	0	0	0
Dolychoris baccarum	0	2	7	1	0	0	0	0
Eurydema oleracea	0	7	0	0	0	0	0	0
Eurygaster maura	0	2	0	0	0	0	0	0
Exolygus rutilans	0	4	0	0	0	0	0	0
Graphosoma lineatum	0	1	2	0	0	1	3	0
Halticus apterus	0	0	11	2	0	1	23	0
Holcostethus vernalis	0	0	1	0	0	0	0	0
Leptopterna dolobrata	2	21	30	23	0	1	27	5
Lygus rugulipennis	0	2	0	0	0	0	0	0
Megalonotus chiragra	0	0	1	0	0	0	0	0
Myrmus miriformis	0	1	0	0	4	0	6	1
Nabis ferus	0	0	0	0	0	1	0	2
Nabis limbatus	0	0	0	0	1	0	0	0
Nabis rugosus	0	3	1	0	4	3	2	3
Orthops kalmii	2	0	2	0	0	0	1	0
Palomena prasina	0	1	2	0	0	0	0	0
Plagiognathus crysanthemi	1	0	0	1	0	0	0	0

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	Eisenwurzen							
	Managed				Abandoned			
Bug species	M1	M2	M3	M4	A1	A2	A3	A4
Polymerus microphtalmus	0	0	0	1	0	1	2	7
Polymerus unifasciatus	0	3	0	0	0	0	0	0
Rhopalus subrufus	1	0	0	0	0	0	0	0
Rubiconia intermedia	1	0	0	0	0	0	0	0
Stenodema calcarata	0	0	0	0	8	1	0	0
Stictopleurus crassicornis	0	0	3	0	0	0	0	0
Stictopleurus punctatonervosus	0	0	1	0	0	0	0	0

Appendix C. *Presence/absence of grasshopper species in managed and abandoned meadows in the Eisenwurzen region in 2015 and 2016 (M1-M4…managed meadows, A1-A4…abandoned meadows)*

	Eisenwurzen					
	Managed			Abandoned		
Grasshopper species	M1	M2	M3	A1	A2	A3
Barbitistes serricauda	0	1	0	1	1	1
Chorthippus biguttulus	1	1	1	1	0	1
Chorthippus dorsatus	0	0	1	0	0	0
Chrsyochraon dispar	0	1	0	0	0	1
Decticus verrucivorus	1	0	1	0	1	0
Euthystira brachyptera	1	1	0	1	1	1
Gomphocerippus rufus	0	0	0	1	1	0
Metrioptera brachyptera	1	0	1	1	0	0
Omocestus sp.	0	0	0	1	0	0
Pholidoptera aptera	1	0	0	1	1	1
Pholidoptera griseoaptera	1	1	1	1	1	1
Pseudochorthippus parallelus	1	1	1	0	1	1
Roeseliana roeselii	1	1	1	0	1	1
Stenobothrus lineatus	1	1	1	0	0	0
Tettigonia cantans	0	0	0	1	1	1

Appendix D. *Presence/absence of plant species and the means of vegetation cover (in %) and flower cover (in %) and mean numbers of plants with open nectar flowers and plants with hidden nectar flowers in managed and abandoned meadows in the Eisenwurzen region in 2015 and 2016 (M1-M4…managed meadows, A1-A4…abandoned meadows)*

	Eisenwurzen							
	Managed				Abandoned			
Vegetation parameters	M1	M2	M3	M4	A1	A2	A3	A4
Vegetation cover (in %)	84.925	78.93	71.75	77.77	75.915	85	80.475	74.175
Flower cover (in %)	2.53	5.53	1.8725	2.2175	0.74875	0.74875	0.75	0.875
Plants with open nectar flowers	5	6.5	3	6	5	5.5	3	4
Plants with hidden nectar flowers	11.5	8.5	7.5	7.5	3	5	2	3.5

	Managed				Abandoned			
Plant species	M1	M2	M3	M4	A1	A2	A3	A4
Acer pseudoplatanus	1	0	0	0	0	0	0	0
Achillea millefolium agg.	1	1	1	1	0	1	1	1
Acinos alpinus	1	0	0	0	0	0	0	0
Aegopodium podagraria	0	1	0	1	0	1	1	1
Agrostis capillaris	1	1	0	1	0	1	1	1
Ajuga genevensis	0	0	1	0	0	0	0	0

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	Managed				Abandoned			
	M1	M2	M3	M4	A1	A2	A3	A4
Plant species								
Ajuga reptans	0	1	1	1	0	1	0	0
Alchemilla monticola	0	1	0	1	0	0	0	0
Allium carinatum carinatum	1	0	1	0	1	1	1	1
Allium lusitanicum montanum	0	0	1	0	0	0	1	0
Anacamptis pyramidalis	1	0	0	0	0	0	0	0
Anthericum ramosum	0	0	0	0	1	0	0	0
Anthoxanthum odoratum	0	1	0	1	0	1	0	1
Anthriscus sylvestris	0	1	0	0	0	0	0	0
Anthyllis vulneraria carpatica	1	1	0	1	0	0	0	0
Aquilegia atrata	1	0	0	0	0	0	0	0
Arabidopsis halleri	0	1	0	0	0	1	0	0
Arabis hirsuta	0	1	0	1	0	0	0	0
Arenaria serpyllifolia	0	0	1	0	0	0	0	1
Arrhenatherum elatius	0	1	1	1	0	0	1	1
Astrantia major major	1	1	0	1	1	1	0	1
Avenula pubescens pubescens	1	1	1	1	0	1	1	0
Betonica alopecuros	1	0	0	0	1	1	0	0
Betonica officinalis	0	1	0	1	0	1	0	1
Betula pendula	1	0	0	0	0	0	0	0
Brachypodium pinnatum	1	1	1	1	1	1	1	1
Briza media	1	1	1	1	0	1	0	0
Bromus erectus	1	1	1	1	0	0	1	1
Buphthalmum salicifolium	1	1	1	1	1	1	1	0
Calamagrostis varia	0	0	0	0	1	0	0	0
Campanula patula	0	1	0	1	0	0	0	0
Campanula persicifolia	0	1	0	0	0	0	0	0
Campanula rapunculoides	0	0	1	0	0	0	1	0
Campanula rotundifolia	1	1	0	1	0	1	1	1
Cardamine pratensis	0	0	0	1	0	1	0	0
Carduus defloratus viridis	1	0	1	0	0	0	0	1
Carex alba	1	0	0	0	1	1	0	0
Carex caryophyllea	1	0	1	1	0	0	0	0
Carex flacca	1	0	0	1	1	1	1	0
Carex montana	0	1	1	0	0	0	0	0
Carex ornithopoda ornithopoda	1	0	0	0	1	0	0	0
Carex pallescens	0	0	0	0	0	1	0	0
Carex panicea	1	0	0	0	1	1	0	0
Carex spicata	0	0	1	0	0	0	1	0
Carex sylvatica	0	0	0	0	0	1	0	0
Carlina acaulis acaulis	1	0	0	0	1	1	0	0
Centaurea jacea	1	1	0	1	1	1	0	0
Centaurea scabiosa scabiosa	1	1	1	1	1	1	0	0
Cephalanthera damasonium	0	0	0	0	1	0	0	0
Cerastium holosteoides	0	1	1	1	0	0	0	0
Cerinthe minor	0	0	0	0	0	0	1	0
Chaerophyllum aureum	0	0	0	0	0	0	1	0
Chaerophyllum hirsutum	0	0	0	1	0	0	0	0
Cirsium erisithales	0	0	0	1	0	0	0	0
Clinopodium vulgare	0	1	0	1	1	1	1	1
Colchicum autumnale	0	0	0	0	0	1	0	0
Convolvulus arvensis	0	0	0	0	0	0	1	0
Corylus avellana	0	0	0	0	1	0	0	0
Crataegus monogyna	0	0	1	0	0	0	0	0
Crepis biennis	0	1	0	1	0	0	0	0
Cruciata laevipes	0	1	0	1	0	0	1	0
Cyclamen purpurascens	0	0	0	0	1	0	0	0
Cynosurus cristatus	0	1	0	1	0	0	0	0
Dactylis glomerata	1	1	0	1	0	1	1	1
Danthonia decumbens decumbens	1	1	0	0	0	0	0	0
Daucus carota	0	1	0	0	0	0	0	0
Dianthus carthusianorum carthusianorum	0	1	1	1	0	0	1	0

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	Managed				Abandoned			
	M1	M2	M3	M4	A1	A2	A3	A4
Plant species								
Erica carnea	0	0	0	0	1	0	0	0
Euphorbia amygdaloides	0	0	0	0	1	0	0	0
Euphorbia cyparissias	1	0	0	0	1	1	0	0
Euphrasia officinalis rostkoviana	1	0	1	1	0	0	0	0
Festuca pratensis	1	1	1	1	0	1	0	1
Festuca rubra rubra	1	1	1	1	1	0	1	1
Festuca rupicola	1	1	1	0	1	1	1	1
Fraxinus excelsior	0	0	1	1	0	1	1	1
Galeopsis tetrahit	0	0	0	0	0	0	0	1
Galeopsis speciosa	0	0	0	0	0	1	0	1
Galium album	1	1	1	1	1	1	1	1
Galium pumilum	1	1	0	1	1	1	1	1
Galium verum	0	1	0	0	0	0	0	1
Gentiana verna	0	0	0	1	0	0	0	0
Gentianella aspera	1	0	0	0	0	0	0	0
Geranium phaeum phaeum	0	1	0	0	0	0	0	0
Glechoma hederacea	0	1	1	0	0	0	0	0
Gymnadenia conopsea conopsea	1	1	0	1	1	0	0	0
Helianthemum nummularium obscurum	1	1	0	1	1	0	1	0
Helleborus niger	0	0	0	0	1	0	0	0
Hieracium pilosella	0	0	1	0	0	0	0	0
Hieracium spec.	0	0	1	0	0	0	0	0
Hippocrepis comosa	1	0	0	0	1	0	0	0
Holcus lanatus	0	1	0	1	0	0	0	0
Hypericum maculatum	0	0	0	0	0	1	0	0
Hypericum perforatum	0	0	0	0	0	0	1	0
Knautia arvensis arvensis	1	1	1	1	0	1	1	0
Knautia drymeia intermedia	1	1	1	1	1	0	0	1
Knautia maxima	1	1	1	1	0	0	0	1
Koeleria pyramidata pyramidata	1	1	1	1	1	1	1	1
Laserpitium latifolium	1	0	0	0	1	0	0	0
Lathyrus pratensis	0	1	1	1	0	1	1	1
Leontodon hispidus hispidus	1	1	1	1	1	0	0	1
Leucanthemum ircutianum	1	1	1	1	0	0	0	0
Lilium bulbiferum bulbiferum	0	0	0	0	0	0	0	1
Linum catharticum	1	1	0	1	0	0	0	0
Lotus corniculatus	1	1	1	1	1	1	1	0
Luzula multiflora	0	1	0	0	0	0	0	0
Medicago falcata	1	1	1	1	0	1	1	1
Medicago lupulina	1	1	1	1	0	0	0	0
Melampyrum sylvaticum	0	0	0	0	1	0	0	0
Mercurialis perennis	0	0	0	0	0	0	1	0
Molinia caerulea	1	0	0	0	1	0	0	0
Myosotis arvensis	0	1	0	1	0	0	0	0
Orchis coriophora	0	1	0	0	0	0	0	0
Origanum vulgare vulgare	0	0	0	0	1	0	0	0
Orobanche gracilis	0	1	0	1	0	0	0	0
Phyteuma orbiculare	1	0	0	0	1	1	0	0
Pimpinella major major	1	1	0	1	0	1	0	0
Pimpinella saxifraga saxifraga	1	1	1	1	1	0	1	1
Plantago lanceolata	1	1	1	1	0	1	0	0
Plantago media	0	0	1	0	0	0	0	0
Poa angustifolia	0	1	1	1	0	1	1	1
Poa trivialis	0	1	0	1	0	0	0	0
Polygala amarella	1	0	0	0	0	0	0	0
Polygala chamaebuxus	1	0	0	0	1	0	0	0
Polygala comosa	1	1	0	0	0	0	0	0
Polygonatum odoratum	0	0	0	0	1	0	0	1
Potentilla erecta	1	1	0	1	1	1	0	1
Potentilla reptans	0	0	1	0	0	0	0	0
Primula elatior	0	1	0	1	0	1	0	0

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	Managed				Abandoned			
	M1	M2	M3	M4	A1	A2	A3	A4
Plant species								
Prunella grandiflora	1	1	0	1	1	0	0	0
Prunella vulgaris	0	0	0	1	0	0	0	0
Quercus robur	0	1	0	0	0	0	0	0
Ranunculus acris acris	0	1	0	1	0	0	0	0
Ranunculus bulbosus	0	0	1	0	0	0	1	0
Ranunculus nemorosus	1	0	0	0	1	1	0	0
Ranunculus repens	0	1	0	0	0	0	0	0
Rhinanthus alectorolophus alectorolophus	0	1	0	0	0	1	0	0
Rhinanthus glacialis	1	0	0	1	1	0	0	0
Rhinanthus minor	0	1	0	1	0	0	0	1
Rubus caesius	0	0	0	0	0	0	0	1
Rubus idaeus	0	0	0	0	0	0	0	1
Rumex acetosa	0	1	1	1	0	0	1	0
Salvia glutinosa	0	0	0	0	1	0	0	0
Salvia verticillata	0	1	1	0	0	0	1	0
Sanguisorba minor	1	0	0	0	0	0	0	0
Scabiosa columbaria	1	1	1	1	0	0	0	0
Seseli libanotis	1	0	0	0	0	0	0	0
Sesleria caerulea	1	0	0	0	1	0	0	0
Silene nutans nutans	0	1	1	1	0	0	0	1
Silene vulgaris vulgaris	0	0	1	0	0	0	0	1
Stellaria graminea	0	0	0	0	0	0	0	1
Taraxacum officinale agg.	0	1	0	1	0	1	0	1
Teucrium chamaedrys	0	0	0	0	1	0	1	0
Thymus pulegioides pulegioides	1	1	1	1	1	0	1	0
Tragopogon orientalis	0	0	0	1	0	0	0	1
Trifolium medium medium	0	0	0	0	1	1	1	0
Trifolium montanum	1	1	0	1	1	0	0	1
Trifolium pratense pratense	1	1	1	1	0	0	0	0
Trifolium repens	0	1	1	1	0	0	0	0
Trisetum flavescens	0	1	1	1	0	1	1	0
Trollius europaeus	0	0	0	0	0	1	0	0
Valeriana officinalis	0	0	0	0	0	1	0	0
Verbascum nigrum	0	0	0	0	0	0	1	0
Veronica chamaedrys chamaedrys	0	1	1	1	0	1	1	1
Vicia cracca	0	1	1	1	1	0	1	1
Vicia sepium	0	0	0	0	0	1	0	0
Vincetoxicum hirundinaria	1	0	0	0	1	0	0	0
Viola arvensis arvensis	0	0	0	0	0	0	0	1
Viola hirta	1	1	1	1	1	0	1	1
Viola rupestris	1	1	0	1	1	1	1	1

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Ronnie Walcher planned the field work, helped to record the vegetation and soil parameters, provided help for data analysis and reviewed the manuscript.

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ORIGINAL RESEARCH PAPER

Ecological responses of semi-natural grasslands to abandonment: case studies in three mountain regions in the Eastern Alps

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Abstract Semi-natural, extensively managed, grasslands are among the most species-rich agroecosystems in Europe. However, they are threatened by abandonment. We investigated the response of semi-natural grasslands to cessation of mowing at ten sites in three UNESCO Biosphere Reserves in Switzerland and Austria. We assessed vegetation characteristics, topsoil properties and microbially mediated soil processes by comparing once-a-year mowed with adjacent long-term abandoned grasslands on semi-dry, nutrient-poor, base-rich soils. Plant litter decomposition was determined using standardized substrates (Tea Bag Index). Soil microbial community composition was assessed by phospholipid fatty acid analysis. Abandonment altered floristic composition by replacing shade-intolerant or low-growing grassland species, in particular character species of the alliance *Bromion erecti*, with medium- to tall-sized grasses (e.g. *Brachypodium pinnatum*) and tall herbs (e.g. *Laserpitium latifolium*). Time since abandonment had an influence on the magnitude of successional changes after abandonment. Cessation of mowing increased above-ground phytomass but decreased plant species richness and evenness. Abandonment increased soil microbial biomass, promoted litter decomposition and led to an increased soil organic carbon, C:N ratio, and inorganic N supply. Our findings also showed that abandoned grasslands dominated by grasses remained shrub- and treeless for several decades.

Keywords mountain grasslands · grassland ecology · plant ecology · biodiversity · agroecosystems · soil ecology · agricultural management · abandonment

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Introduction

Mountain regions are worldwide of utmost importance to biodiversity (MacDonald et al. 2000). In the Eastern Alps and in many other European mountain regions, unfavourable topographical and climatic conditions preclude an intensive agricultural land use. Thus, the agricultural landscape is characterized by a high proportion of extensive grasslands. Extensively managed grasslands (one cut each year in mid-summer without organic or inorganic fertilization, no over-sowing or herbicide treatment) in the montane and subalpine regions represent low productive, species-rich, semi-natural plagioclimax communities. Especially semi-natural, dry, calcareous grasslands belong to the most species-rich agroecosystems in Europe, and thus have a great nature conservation value (Poschlod and Wallis De Vries 2002). During the twentieth century, the number and area of this habitat type decreased dramatically due to intensification of grassland management, abandonment, afforestation or conversion to other land-use types. Nowadays, semi-natural calcareous grasslands are threatened throughout Europe (Poschlod and Wallis De Vries 2002). The maintenance of these species-rich grasslands by extensive management is therefore an important conservation target in Europe.

Several studies have investigated the ecological consequences of grassland abandonment (Moog et al. 2002; Niedrist et al. 2009; Walcher et al. 2017; Hussain et al. 2018). However, little information is available on concurrent changes of soil properties (Köhler et al. 2001; Oelmann et al. 2017; Zeller et al. 2001).

From a climate change point of view, information on alterations in litter decomposition and soil organic carbon (SOC) sequestration after abandonment are important because of their feedbacks on climate processes. Also, from an environmental and nature conservation viewpoint, more detailed information on soil and vegetation changes induced by abandonment are desirable because alterations in plant diversity, composition and structure of grassland communities as well as changes in soil physical, chemical and microbiological properties may have long-term consequences for the provision of ecosystem services (ESs).

Litter decomposition in the soil influences build-up of soil organic matter (SOM) and provides the primary source of inorganic N for plants and soil organisms in semi-natural grasslands (Parton et al. 2007). Soil N supply, in turn, plays a major role in determining species composition, plant diversity and productivity of the grassland vegetation, thereby influencing the rate and pattern of successional changes in grassland communities after abandonment (Tilman 1987). Litter decomposition is mainly controlled by microclimate, litter quality and by the diversity, composition and activity of the soil decomposer community (Scherer-Lorenzen 2008). Soil microbial communities are strongly influenced by climate (especially precipitation), vegetation, soil properties and land use (De Vries et al. 2012). Abandonment may alter the size, activity and composition of the soil microbial biomass through vegetation changes (plant biomass production, rhizodeposition, vegetation composition, species dominance, plant diversity) and soil changes (pH, N supply, quantity and quality of SOM, soil temperature and moisture).

For landscape management it is important to know whether the environmental impacts of abandonment are primarily site- or habitat-specific. If semi-natural grasslands from different mountain regions in the Eastern Alps respond to abandonment consistently, we would be able to identify a general successional pattern and to predict the environmental impacts of abandonment more generally. This, in turn, is important for setting priorities in species and habitat conservation as well as for developing general landscape management recommendations.

The objective of this study was to evaluate the ecological responses of semi-natural grasslands to abandonment in different mountain regions in the Eastern Alps. We hypothesized that abandonment leads to consistent changes of vegetation, soil and microbial properties within the same habitat type under different climatic conditions, which in turn influences major ecosystem processes (plant biomass production, litter decomposition, SOC sequestration, N cycling) in a similar vein. We focused on extensively managed grasslands on semi-dry, nutrient-poor, base-rich soils because this habitat type is threatened throughout Europe by land-use change.

Material and methods

Study regions and study sites

The study was conducted in three mountain regions (Val Müstair, Central Ennstal, Great Walsertal) in the Swiss and Austrian Alps representing low-, intermediate- and high-rainfall areas, respectively (Fig. 1, Table 1). Within each study region, we compared long-term (> 30 years) extensively managed grasslands with immediately neighbouring abandoned grasslands. Altogether, we surveyed ten regularly managed (mown) and ten abandoned (unmown) grasslands at various sites in different regions. At each study site, managed and adjacent abandoned grasslands did not differ in their abiotic site conditions (topography, bedrock, soil type, soil thickness). The study sites were particularly suited for this ‘paired-site’ study because they enabled the use of chronosequences (space-for-time substitution) to study the long-term ecological consequences of grassland abandonment (Walker et al. 2010).

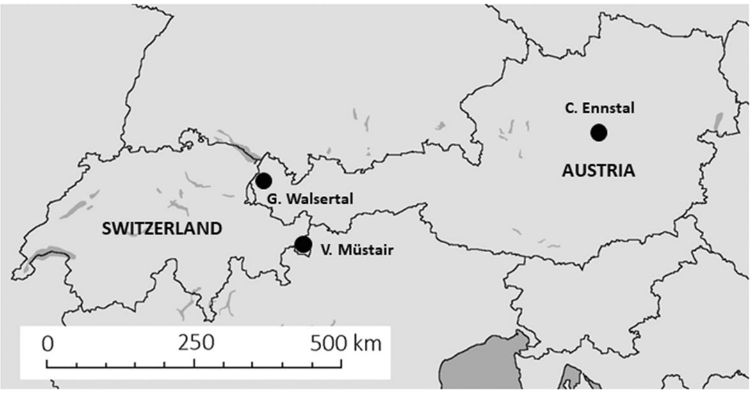

Fig. 1 Location of the study regions in the Swiss and Austrian Alps

The study sites were located in the montane and subalpine belt on south-facing slopes. Altitude varied from 660 to 1,800 m a.s.l. (Table 1). Soil types were nutrient-poor, well-aerated Rendzinas and calcic Cambisols developed over limestone or marl with mull humus and a loose, porous crumb structure in topsoil. Thickness of A horizon varied from 20 to 90 cm. The managed grasslands were mown once a year, usually between mid-July and the beginning of August, and received neither farmyard manure nor mineral fertilizers. None of the traditionally managed grassland sites was grazed, re-seeded or irrigated. Before cessation of mowing, the abandoned grasslands were also used as extensively managed grasslands. Therefore, we assume that the initial plant species composition, species richness, soil properties and soil microbial community composition of both land-use types were similar. The time elapsed since abandonment varied from 15 to 60 years. During the successional time, there was no human-mediated disturbance at the studied abandoned grassland sites. However, localized natural biotic disturbance through the activity of small rodents (e.g. voles) or browsing by wild animals (e.g. deer) cannot be ruled out. Phytosociologically, the managed grasslands belonged to the alliance *Bromion erecti*, which is widely distributed throughout Europe (Mucina et al. 2016; Willner et al. 2019). The plant communities within this alliance are characterized by a restricted water and nutrient supply (lack of plant available nitrogen and phosphorus), low productivity and high vascular plant

Table 1 Characteristics of the study regions and study sites

Environmental variables and management history	G. Walsertal (Vorarlberg, Austria)	V. Müstair (Graubünden, Switzerland)	C. Ennstal (Styria, Austria)
Geographic location of the study sites	47°14′ – 47°15′ N 9°57′ – 9°58′ E	46°36′ – 46°37′ N 10°21′ – 10°25′ E	47°31′ – 47°40′ N 14°04′ –14°35′ E
Number of study sites	3	3	4
Years since abandonment	35–60	15–20	20–40
Altitude of the study sites [m a.s.l.]	1,180–1,250	1,740–1,800	660–790
Mean annual air temperature [°C]	+5.7	+5.9	+6.9
Mean air temperature January [°C]	−2.4	−2.8	−3.9
Mean air temperature July [°C]	15	16	17
Mean annual precipitation [mm]	1,637	811	1,219

species richness (Köhler et al. 2001). The abandoned grasslands represented plant communities in a successional stage characterized by the dominance of tall grasses (*Brachypodium pinnatum* stage). The surrounding vegetation of the study sites were forests, hedgerows, shrub communities and more intensively managed permanent meadows.

Vegetation survey and phytomass harvest

Vegetation surveys were carried out in June 2015. At each site an area was selected which was fairly uniform with respect to topography, soil type and vegetation. Within this area, four plots (1 × 1 m), each spaced 5 m apart, were placed side by side (Fig. 2). The choice of the plot size (1 m^2) for the measurement of vegetation characteristics was governed by the need to compare our results with data from literature. To avoid edge effects, at each study site the spatial distance between managed and abandoned plots was at least 20 m. Vegetation surveys were carried out with a modified Braun-Blanquet scale for species cover consisting of three subdivisions per cover class (Supplementary Table S1; Braun-Blanquet 1964). Only vascular plant species were recorded. Taxonomy and nomenclature follows Fischer et al. (2008). All plots were revisited in August 2015 to ensure that late-flowering species had not been missed. For vegetation analyses, means of the minimum and maximum of modified Braun-Blanquet cover-class-ranges were used.

To assess vegetation changes due to abandonment, the following plant parameters were analysed (i) total vegetation cover, cover of plant functional groups (grasses, herbs, legumes) and individual cover of all vascular plant species; (ii) species richness (number of species per plot), Shannon index and evenness; (iii) flower traits (colour, abundance, cover); (iv) plant strategy types according to (Grime 1977) and four plant traits (life span, type of reproduction, Raunki*æ*r life form, type of rosettes, unweighted in each case); (v) unweighted Ellenberg indicator values for light, soil moisture and nutrient availability (Ellenberg et al. 2001).

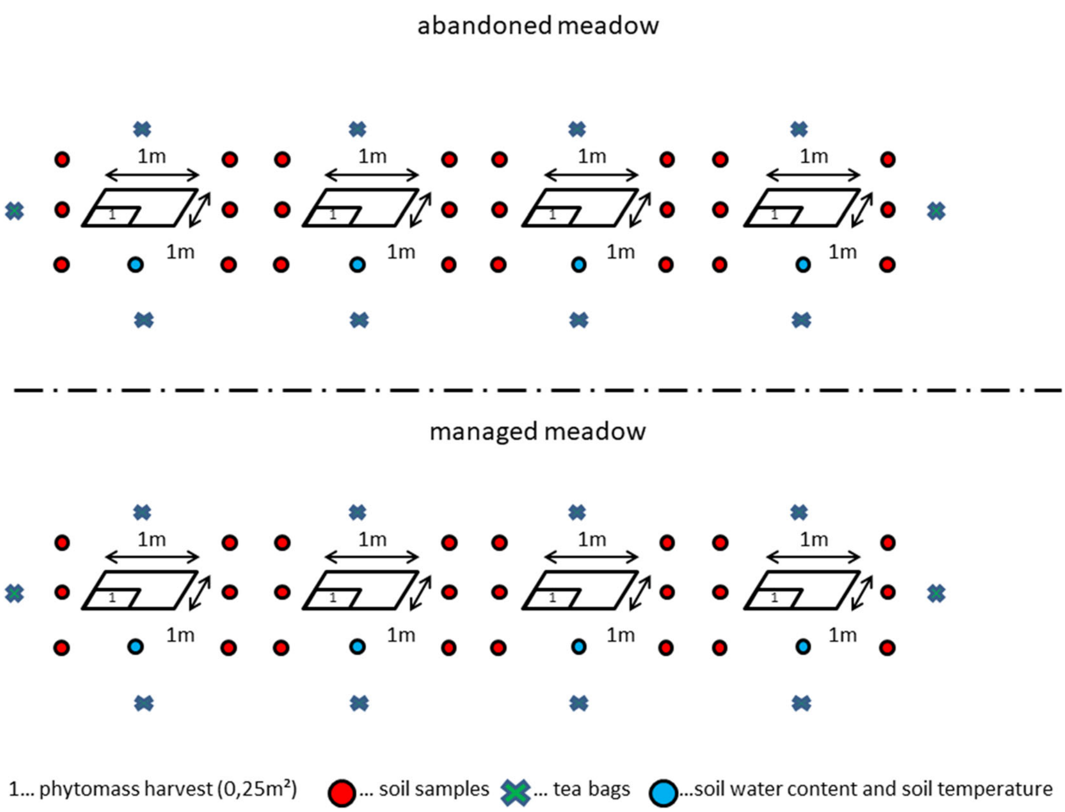

Fig. 2 Schematic overview of the study and sampling design

Total vegetation cover, flower cover and cover of plant functional groups were recorded as percentage cover per m^2. The flower cover was estimated both in June and August 2015, reflecting different phenological stages of the plant community. Plant traits were selected based on field experience and from information in the literature (Prévosto et al. 2011). Plant strategy types, plant traits and flower colour were abstracted from the BIOLFLOR database (Klotz et al. 2002). Both plant traits and Ellenberg indicator values were not weighted by abundance because in species-rich vegetation types weighted and unweighted averages usually give similar results (Diekmann 2003).

Standing phytomass was assessed on a 50 × 50 cm area of each plot in June 2015 (Fig. 2). The plants were clipped by hand shears at the soil surface. The harvested phytomass was sorted into five categories: grasses, herbs, legumes, necromass and biomass. In this study, we distinguished between biomass (living green plant tissue), necromass (dead tissue on the plant), phytomass (biomass plus necromass) and plant litter (dead plant material at the soil surface). Plant samples were dried at 60°C for 72 h.

Soil sampling and soil analysis

At each study site, six individual soil samples were taken randomly outside of each vegetation plot at a distance of 1 m with a soil corer (4 cm diameter). Soil sampling was performed in June and August 2015 from the main rooting zone of the plants (0–10 cm depth). Samples were mixed to obtain one composite sample per site and sampling date (Fig. 2). We only sampled the uppermost 10 cm of the soil because this soil layer responds most sensitively to changes in grassland management (Bohner et al. 2016). Soil samples were transported to the laboratory in cool boxes and stored at −20°C until analyses. An aliquot of each sample was air-dried and passed through a 2-mm sieve for the analysis of basic soil parameters. Total carbon (C_{tot}) and total nitrogen (N_{tot}) were determined by dry combustion (1,250°C) using an elemental analyser (LECO TruMac, LECO Corp., St. Joseph, USA). Carbonate was measured gas-volumetrically. Organic carbon (C_{org}) was calculated as the difference between total C and carbonate C. Soil pH was measured in 0.01 M $CaCl_2$ solution at a soil-to-solution ratio of 1:2.5 using a glass electrode. NH_4-N and NO_3-N were determined colourimetrically after extraction with 1 M KCl (Hood-Nowotny et al. 2010). Soil microbial community composition was assessed in June and August 2015 by analysing the microbial phospholipid fatty acid (PLFA) composition (Hackl et al. 2005). Therefore, soil (1.5 g fresh weight) was extracted with a buffer mixture consisting of chloroform:methanol:citrate buffer (1:2:0.8, v/v/v). The lipids were separated into neutral lipids, glycolipids and phospholipids on a silicic acid column. After a mild alkaline methanolysis the phospholipid methyl esters were separated on an Agilent 6890 gas chromatograph equipped with a flame ionization detector (Agilent Inc., Santa Clara, CA, USA). Methyl non-adecanoate fatty acid (19:0) was added as internal standard in order to quantify peak areas. A standard qualitative bacterial acid methyl esters mix (BAC mix) and a standard qualitative fatty acid methyl esters mix (FAME mix; both Sigma Aldrich Co., St. Louis, MO) were also measured to allow identification of the fatty acid peaks. In total, 31 PLFAs were identified. The total amount of PLFAs was used as a measure of the active soil microbial biomass (Zeller et al. 2001).

At each study site, in June and August 2015 gravimetric soil water content was determined using four soil cores (0–10 cm depth, diameter 4 cm) and soil temperature was measured in 5 cm depth using four insertion thermometers (Voltcraft DET3R, Conrad Electronic SE, Hirschau, Germany). The measurements were taken outside of the vegetation plots at a distance of 1 m (Fig. 2).

Litter decomposition

Litter decomposition was determined using the 'tea bag index' (TBI; Keuskamp et al. 2013). The TBI consists of two parameters: litter decomposition rate (k) expresses the velocity of decomposition, while litter stabilization factor (S) expresses the inhibiting effect of environmental conditions on the decomposition. Both parameters are based on weight loss of litter material. Two tea types with contrasting decomposition characteristics were used: green tea (*Camellia sinensis*; Lipton, EAN 87 22700 05552 5) with high cellulose content and expected fast decomposition and rooibos tea (*Aspalathus linearis*; Lipton, EAN 87 22700 18843 8) with high lignin content and expected slow decomposition (Keuskamp et al. 2013). At each study site, ten pairs of green and rooibos tea bags were buried in June 2015 in

8 cm soil depth outside of the vegetation plots at a distance of 1 m (Fig. 2). The tea bags were retrieved after a field incubation period of 52 and 79 days. The tea bags were cleaned from adhered soil particles and roots, dried at 70°C for 48 h and weighed. Stabilization factor S and decomposition rate k were calculated using the hydrolysable fraction of green tea (0.842 $g \cdot g^{-1}$) and rooibos tea (0.552 $g \cdot g^{-1}$).

Statistical analysis

Normal distribution of residuals was checked with qq-plots and Shapiro-Wilk tests, homogeneity of variances with histograms and Bartlett-tests. When assumptions were met, we performed analyses of variances (ANOVAs) with management, sampling date and region (block) as factors. When sampling date was not significantly different, means between the two sampling dates were analysed. If assumptions for parametric statistics were not met we applied Box-Cox transformations or performed non-parametric Kruskal-Wallis tests. For post-hoc comparisons of ANOVAs, we used Tukey tests. Correlations were tested with Pearson's correlation coefficient. Differences in plant species composition were analysed by principal coordinate analyses (PCO) using PerMANOVA by applying a Bray-Curtis distance matrix and 9,999 permutations. The assumption of homogeneity of multivariate dispersions among treatments for PerMANOVA was checked. PerMANOVA was carried out with Primer (Primer6 and Permanova+ 2003), all other statistical analyses with R (version 3.1.1; R Development Core Team 2014). All results were stated as statistically significant if $P < 0.05$.

Results

Vegetation characteristics

In all study regions, mean species richness, Shannon-Index and evenness were significantly lower on abandoned than on managed plots (Tables 2 and 3). Across study regions, species composition of the vegetation was significantly affected by abandonment. Abandoned plots were clearly separated from managed plots by the first axis in the PCO-plot (Fig. 3). In each study region, vegetation composition differed considerably between abandoned and managed plots but was quite similar within the abandoned and managed plots (Fig. 3).

Table 2 ANOVA and Kruskal-Wallis results for the effects of management and region on vegetation characteristics

Parameter	Treatment	Region	Treatment × region
	$F_{1, 78}$	$F_{2, 77}$	$F_{2, 77}$
Total vegetation cover	41.921*	39.440*	6.846*
Ag phytomass	25.451*	5.807*	2.242
Ag plant biomass	5.054*	18.099*	1.241
Necromass	34.853*	2.631	
Species richness	135.320*	12.962*	3.196*
Shannon-Index	84.779*	1.621	3.456*
Evenness	56.534*	0.580	5.575*
EIVl	40.322*	1.994	1.722
EIVm	5.714*	1.978	0.437
EIVn	0.408	7.306*	6.169*
Legumes	27.984*	4.974*	8.107*
Herbs	13.670*	6.190*	4.340*
Grasses	0.055	4.812*	0.492

*After values refer to significant differences ($P < 0.05$). Ag – Above-ground, EIVl – Ellenberg light indicator, EIVm – Ellenberg soil moisture indicator, EIVn – Ellenberg nutrient availability indicator

The dominant species in managed plots was *Bromus erectus*. In abandoned plots, however, *Brachypodium pinnatum* was dominant (Supplementary Table S2). Most of the plant species in abandoned plots were common and widespread species whereas character species of the alliance *Bromion erecti* were scarce. Only a few species were restricted to abandoned plots (*Trifolium medium*, *Vicia sepium*, *Cephalanthera damasonium*, *Epipactis atrorubens*, *Galeopsis tetrahit*, *Anthericum ramosum*, *Lilium bulbiferum* subsp. *bulbiferum*, *Hypericum perforatum*, *Rubus idaeus*, *Rosa* species). Most of them are usually found in forests, forest edges and forest clearings. In abandoned plots, seedlings of *Fraxinus excelsior* were the most abundant woody plants (cover: always less than 0.5 %, frequency: 15%).

Managed plots were dominated by light-demanding and drought-tolerant, low soil fertility grassland species. The mean Ellenberg indicator value for light was significantly lower on abandoned than on managed plots whereas that for soil moisture was significantly higher. The mean Ellenberg indicator value for nutrient availability, however, showed no consistent trend in response to abandonment (Tables 2 and 3).

Table 3 Vegetation parameter of the managed and abandoned grasslands under study

Parameter	Region	Managed grasslands	Abandoned
Total vegetation cover [%]	G. Walsertal	98.3 ± 1.3	99.0 ± 0.0
	V. Müstair	97.1 ± 1.9	99.4 ± 0.5
	C. Ennstal	92.6 ± 6.8	97.8 ± 1.4
Above-ground phytomass [g·m^{-2}·DM]	G. Walsertal	391.8 ± 138.3	559.8 ± 116.0
	V. Müstair	298.1 ± 81.1	428.5 ± 219.0*
	C. Ennstal	520.5 ± 115.2	560.4 ± 112.8*
Above-ground plant biomass [g·m^{-2}·DM)	G. Walsertal	258.2 ± 57.9	266.2 ± 61.6
	V. Müstair	143.4 ± 40.4	166.6 ± 83.6
	C. Ennstal	189.9 ± 66.8	248.1 ± 63.6*
Necromass (g·m^{-2}·DM)	G. Walsertal	4.1 ± 2.3	27.9 ± 35.7*
	V. Müstair	2.3 ± 2.8	95.4 ± 78.6*
	C. Ennstal	12.0 ± 21.2	63.5 ± 55.5*
Species richness	G. Walsertal	30.8 ± 3.6	13.7 ± 2.4*
	V. Müstair	25.0 ± 5.1	12.6 ± 3.1*
	C. Ennstal	31.3 ± 7.1	20.3 ± 6.1*
Shannon index	G. Walsertal	2.21 ± 0.2	1.38 ± 0.2*
	V. Müstair	2.48 ± 0.2	1.11 ± 0.4*
	C. Ennstal	2.46 ± 0.6	1.51 ± 0.5*
Evenness	G. Walsertal	64 ± 0.1	53 ± 0.1*
	V. Müstair	78 ± 0.1	44 ± 0.2*
	C. Ennstal	72 ± 0.1	50 ± 0.1*
Ellenberg light indicator	G. Walsertal	7.2 ± 0.2	6.7 ± 0.2*
	V. Müstair	7.2 ± 0.1	6.8 ± 0.5*
	C. Ennstal	7.1 ± 0.2	6.8 ± 0.2*
Ellenberg soil moisture indicator	G. Walsertal	4.1 ± 0.2	4.4 ± 0.4*
	V. Müstair	4.1 ± 0.2	4.2 ± 0.4
	C. Ennstal	4.3 ± 0.5	4.4 ± 0.4
Ellenberg nutrient availability indicator	G. Walsertal	3.7 ± 0.3	3.1 ± 0.3*
	V. Müstair	3.1 ± 0.4	3.6 ± 0.8
	C. Ennstal	4.0 ± 0.8	4.0 ± 0.9

*After values refer to significant differences within a region ($P < 0.05$). Means ± *SD*, $n = 3$ for G. Walsertal and V. Müstair, $n = 4$ for C. Ennstal, DM – dry mass

Grasses were the dominant functional group across all sites. The proportion of both herbs and legumes was significantly lower on abandoned than on managed plots (Table 4). Vegetation on all plots was dominated by perennials which accounted for more than 90% of the total vegetation cover. Proportion of perennials was significantly higher on abandoned than on managed plots, while that of biennials was significantly lower. Proportion of species reproducing by seeds only was significantly lower on abandoned than on managed plots. Proportion of hemicryptophytes was significantly lower and that of chamaephytes was slightly lower on abandoned than on managed plots, while the proportion of both geophytes and phanerophytes was comparatively higher; proportion of therophytes was similar in both land-use types. Proportion of erosulate plants was significantly higher on abandoned than on managed plots, while that of hemirosette plants was significantly lower. Proportion of competitors was significantly higher on abandoned plots compared to managed plots whereas that of ruderals was significantly lower. Proportion of stress-tolerators was unaffected.

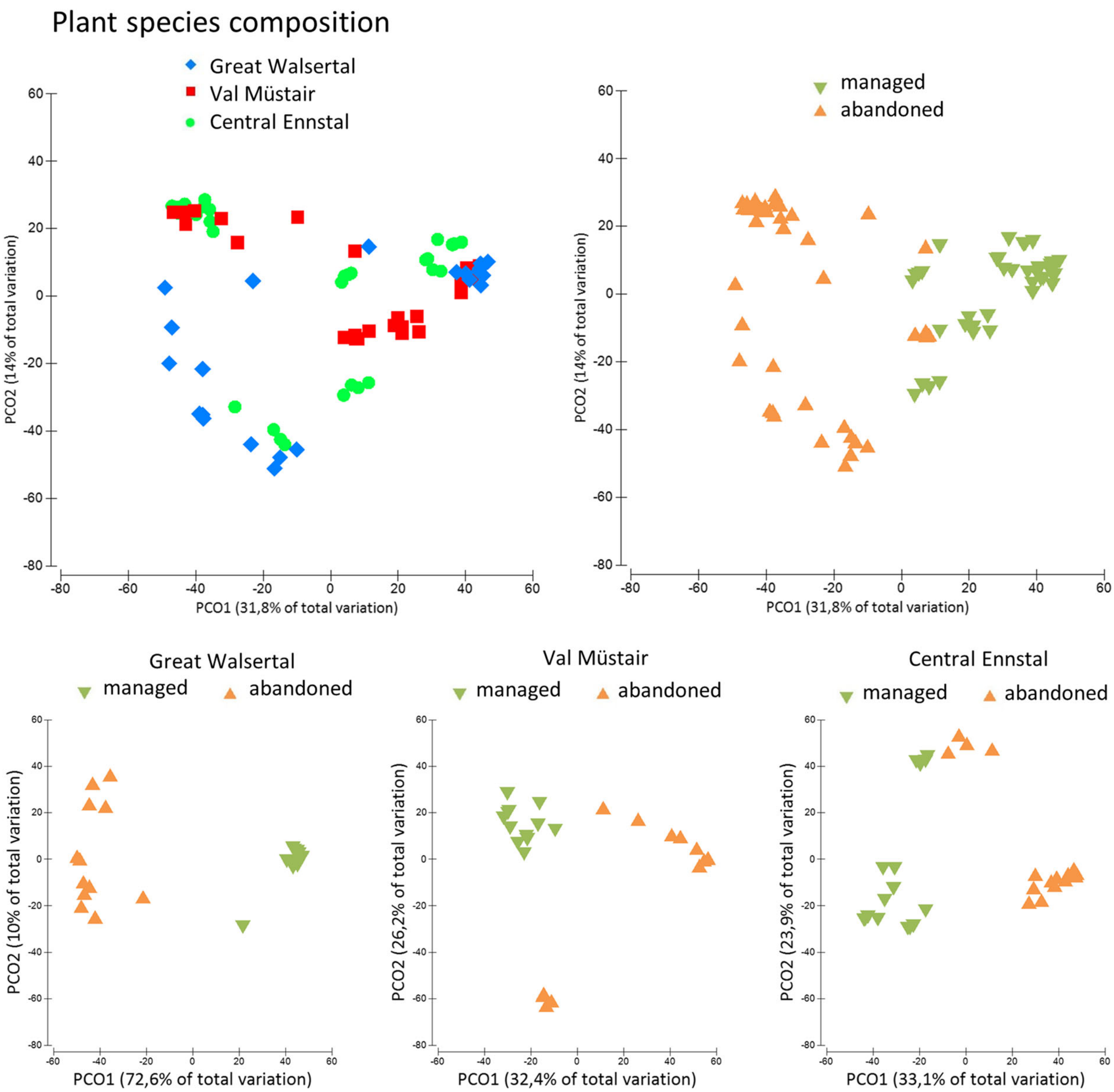

Fig. 3 Principal coordinate analysis (PCO) showing plant species composition in managed and abandoned grasslands in three different regions in the Eastern Alps. $n = 3$ for G. Walsertal and V. Müstair, $n = 4$ for C. Ennstal

At peak season, total vegetation cover, above-ground phytomass, above-ground plant biomass and necromass were significantly higher on abandoned than on managed plots (Table 2). Biomass to necromass ratios varied from 2 to 10 in abandoned and from 16 to 63 in managed plots. In both land-use types, the necromass was mainly composed of dead grass leaves, which were concentrated in the lower canopy layer.

At peak flowering season in June, the percentage of flowering species and the flower cover were significantly lower on abandoned than on managed plots whereas in August after mowing both parameters were comparatively higher, though not significantly, on abandoned plots (Table 4). In both land-use types, the prevalent flower colours of blooming plants were yellow and white. On managed plots, the flower colours were more evenly distributed than on abandoned plots.

Table 4 Vegetation parameter of the managed and abandoned grasslands under study

Parameter	Managed grasslands	Abandoned
Plant functional groups		
Grasses [%]	64	76
Herbs [%]	28	21*
Legumes [%]	8	3*
Life span		
Annual [%]	3.8	3.1
Biennial [%]	3.7	0.5*
Perennial [%]	92.5	96.4*
Type of reproduction		
Only by seed [%]	24.8	17.4*
Mostly by seed, rarely vegetatively [%]	23.0	24.6
By seed and vegetatively [%]	50.4	53.9
Mostly vegetatively, rarely by seed [%]	1.8	4.1
Raunkiaer life form		
Therophytes [%]	3.3	3.2
Hemicryptophytes [%]	83.2	77.9*
Geophytes [%]	5.1	8.2
Chamaephytes [%]	4.2	3.0
Phanerophytes [%]	4.2	7.7
Type of rosettes		
Erosulate plant [%]	24.9	36.8*
Hemirosette plant [%]	63.6	53.0*
Rosette plant [%]	11.5	10.2
Plant strategy types		
Competitors [%]	53	60*
Stress-tolerators [%]	26	26
Ruderals [%]	21	14*
Flower colour (flowering plants)		
Blue [%]	10.5	2.5*
Brown [%]	1.2	0.8
Yellow [%]	35.8	48.2
Green [%]	2.8	1.6*
Red [%]	17.6	16.3*
White [%]	32.1	30.6
Flower abundance (June)		
Flowering species [%]	30.7	17.7*
Flower cover [%]	3.85	0.80*
Flower abundance (August)		
Flowering species [%]	3.6	7.1
Flower cover [%]	0.28	0.29

*After values refer to significant differences ($P < 0.05$)

Topsoil properties

Across study regions, both the concentration of C_{org} and the C:N ratio in topsoil were significantly higher on abandoned than on managed plots (Table 5). The soil organic C (SOC) accumulation as a result of abandonment was associated with N_{tot} enrichment in all study regions, except V. Müstair. At the sampling date in June, the NH_4-N concentration in topsoil was significantly higher on abandoned plots compared to managed plots (Table 5). In the uppermost soil layer of both land-use types, the concentration of NO_3-N was significantly lower than that of NH_4-N. The topsoils (0–10 cm depth) of both land-use types were in the carbonate buffer range (pH $CaCl_2$: > 6.2; Table 6). Soil temperature in 5 cm depth at the two sampling dates in June and August 2015 was significantly lower on abandoned than on managed plots in V. Müstair and C. Ennstal (Table 6). In all study regions, except V. Müstair, soil moisture in the layer 0–10 cm tended to be higher in abandoned than in managed plots.

Soil microbial community composition varied considerably among study regions. The total amount of PLFAs and the relative proportions of the functional groups of soil microorganisms revealed no significant differences between managed and abandoned plots (Table 5). In all study regions, the soil microbial community was dominated by bacteria (Supplementary Table S3). Generally, gram-negative bacteria represented the largest proportion of total PLFAs. In each study region, the proportions of gram-positive bacteria, gram-negative bacteria and arbuscular mycorrhizal fungi (AMF) were slightly higher in abandoned than in managed plots. For other functional groups, no consistent trend was observed. The ratio of gram-positive to gram-negative bacteria was only slightly affected by abandonment. The ratio of bacterial to fungal PLFA was higher, though not significantly, in abandoned than in managed plots. The total amount of PLFAs correlated positively with concentrations of C_{org} ($\rho_{sumPLFA,Corg} = 0.900$, $P < 0.001$), N_{tot} ($\rho_{sumPLFA,Ntot} = 0.887$, P < 0.001), NH_4-N in August ($\rho_{sumPLFA,NH4\text{-}N} = 0.789$, $P < 0.001$), NO_3-N in August ($\rho_{sumPLFA,NO3\text{-}N} = 0.663$, P = 0.003) and soil moisture ($\rho_{sumPLFA,moisture} = 0.805$, $P < 0.001$).

Table 5 ANOVA results for the effects of management and region on soil physical and chemical parameters, soil microbial community composition and litter decomposition

Parameter	Treatment F	Region F	Treatment × Region F
Soil physical and chemical parameters[1]			
Soil temperature [°C]	22.870*	52.230*	1.800
Soil moisture [% of pore volume]	1.921	46.711*	2.405
pH ($CaCl_2$)	1.236	1.859	0.794
C_{org} [g kg^{-1}]	7.922*	23.394*	2.103
N_{tot} [g kg^{-1}]	1.963	27.333*	1.733
C:N ratio	15.622*	10.447*	0.796
NH_4-N [μg·g^{-1} dry soil] – June	11.906*	2.805	1.181
NO_3-N [μg·g^{-1} dry soil] – June	1.238	0.670	0.090
NH_4-N [μg·g^{-1} dry soil] – August	3.135	8.504*	2.329
NO_3-N [μg·g^{-1} dry soil] – August	0.002	11.828*	0.435
Soil microbial community[1]			
Total PLFAs [nmol·g^{-1} dry soil]	3.271	19.596*	0.183
Gram$^+$ bacteria [%]	0.526	12.375*	0.010
Gram$^-$ bacteria [%]	0.270	2.419	0.158
Fungi [%]	0.094	25.780*	1.243
Arbuscular mycorrhizal fungi [%]	0.544	12.848*	0.044
Actinomycetes [%]	0.016	15.356*	0.522
Unspecific bacteria [%]	0.003	4.207*	0.002
Protozoa [%]	0.007	9.793*	0.004
Others [%]	3.716	50.242*	0.451
Bacteria:fungi ratio	1.005	30.520*	0.126
Litter decomposition [2]			
Litter decomposition rate k	51.042*	18.128*	6.453*
Stabilization factor S	42.841*	141.984*	7.371*

*After values refer to significant differences ($P < 0.05$). [1] : *d.f.* treatment: 1, 16; region: 2, 15. [2] : *d.f.* treatment: 1, 190; region: 2, 189

Litter decomposition

Across study regions, litter decomposition rate and stabilization factor were significantly higher on abandoned than on managed plots. Both parameters varied considerably among study regions, being highest at the subalpine site V. Müstair (Table 5, Fig. 4). Decomposition rate and stabilization factor correlated positively with necromass ($\rho_{k,necromass} = 0.638$, $P = 0.006$; $\rho_{S,necromass} = 0.521$, $P = 0.030$). Stabilization factor correlated negatively with N_{tot} in the topsoil ($\rho_{S,Ntot} = -0.537$, $P = 0.022$).

Discussion

Vegetation changes due to abandonment

Abandonment caused a marked decrease in species richness, Shannon-Index and evenness on all study sites, illustrating the importance of regular mowing for the maintenance of high plant species richness in semi-natural grasslands (Ryser et al. 1995; Bohner et al. 2012). Our findings also suggested that the similarity in plant species composition between abandoned and adjacent managed grasslands decrease with increasing

Table 6 Basic soil physical and chemical properties of the studied managed and abandoned grasslands. Mean values from two sampling dates in June and August 2015

Parameter	Region	Managed grasslands	Abandoned
Soil temperature [°C][x]	G. Walsertal	15.8 ± 0.7	14.9 ± 1.0
	V. Müstair	13.9 ± 0.5	11.9 ± 0.9*
	C. Ennstal	20.6 ± 1.8	16.9 ± 1.9*
Soil moisture [% of pore volume][x]	G. Walsertal	80.0 ± 8.8	83.4 ± 15.4
	V. Müstair	45.5 ± 4.7	42.5 ± 7.4
	C. Ennstal	29.8 ± 13.0	43.6 ± 14.3
pH [$CaCl_2$][x]	G. Walsertal	6.4 ± 0.8	7.0 ± 0.2
	V. Müstair	6.4 ± 1.3	6.3 ± 0.8
	C. Ennstal	6.7 ± 0.9	7.1 ± 0.2
C_{org} [g kg^{-1}][x]	G. Walsertal	107.9 ± 20.2	138.1 ± 42.1*
	V. Müstair	62.6 ± 5.0	62.2 ± 7.9
	C. Ennstal	55.2 ± 21.3	90.7 ± 22.6*
N_{tot} [g·kg^{-1}][x]	G. Walsertal	10.6 ± 1.9	11.8 ± 3.9
	V. Müstair	5.2 ± 0.4	4.5 ± 0.9
	C. Ennstal	5.2 ± 2.0	7.7 ± 1.2
C:N ratio[x]	G. Walsertal	10.2 ± 0.2	11.9 ± 0.8
	V. Müstair	12.0 ± 0.4	14.2 ± 2.3
	C. Ennstal	10.7 ± 0.4	11.7 ± 1.3
NH_4-N [μg·g^{-1} dry soil] – June[y]	G. Walsertal	15.9 ± 1.1	24.9 ± 7.4
	V. Müstair	19.9 ± 5.0	21.5 ± 1.0
	C. Ennstal	13.5 ± 1.6	20.0 ± 4.7
NO_3-N [μg·g^{-1} dry soil] – June[y]	G. Walsertal	1.3 ± 0.6	2.1 ± 1.7
	V. Müstair	0.9 ± 0.5	1.7 ± 1.6
	C. Ennstal	0.6 ± 0.6	1.2 ± 0.6
NH_4-N [μg·g^{-1} dry soil] – August[y]	G. Walsertal	39.5 ± 3.1	44.9 ± 9.1
	V. Müstair	34.8 ± 3.4	33.0 ± 4.6
	C. Ennstal	26.4 ± 3.1	35.1 ± 4.8
NO_3-N [μg·g^{-1} dry soil] – August[y]	G. Walsertal	10.8 ± 3.4	10.1 ± 0.7
	V. Müstair	6.7 ± 0.8	6.1 ± 0.8
	C. Ennstal	6.1 ± 1.3	6.8 ± 0.7

*After values refer to significant differences within a region ($P < 0.05$). Means ± *SD*, ^{x}: $n = 6$, ^{y}: $n = 3$

successional age. After cessation of mowing the dominant species shifted from the tussock-forming grass *B. erectus* to the vegetatively propagating grass *B. pinnatum* with extensive rhizomes and therefore highly competitive in abandoned grasslands (Grime et al. 1988).

Only a few plant species were restricted to abandoned grasslands, indicating a low habitat-specific species pool of grass-dominated successional communities. With just a few exceptions (e.g. *L. bulbiferum* subsp. *bulbiferum*), regionally rare or endangered plant species did not benefit from abandonment. Abandonment favoured tall and broad-leaved grasses (*B. pinnatum, Arrhenatherum elatius*) at the expense of small- to medium-sized, fine-leaved grasses (*Festuca rupicola, F. rubra*). A few legumes (*T. medium, V. sepium*) also benefited from abandonment. *Vicia sepium* is a scrambling legume with leaf tendrils, which is advantageous on abandoned sites. Tall herbs (especially *Laserpitium latifolium*) and clonally proliferating species such as *Galium album* were also promoted by abandonment. Based on results from this study and in accordance with

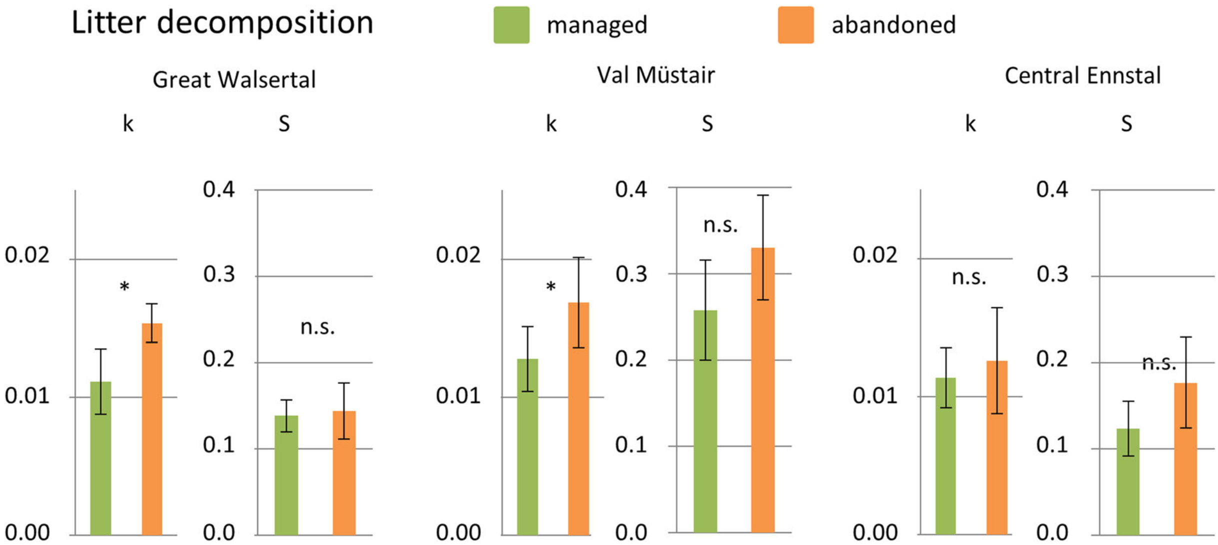

Fig. 4 Litter decomposition rate (*k*) and stabilization factor (*S*) in managed and abandoned grasslands in three different regions in the Eastern Alps. Means ± *SD*, n = 3 for G. Walsertal and V. Müstair, n = 4 for C. Ennstal. * denotes significant differences between managed and abandoned grasslands (Tukey-HSD, $P <$ 0.05), n.s. no significant differences

other studies (Bohner et al. 2012; Prévosto et al. 2011), the following plant attributes appear to be important in grassland succession: tall stature, leaves evenly distributed along the erect stem (erosulate plants), broad leaves, competitive strategy, perennial life cycle, below-ground reserve organs (geophytes), vegetative propagation via rhizomes (rhizomatous species), scrambling life form (leaf tendrils), tolerance to low light availability at different stages.

In the abandoned grasslands under study, there was no significant invasion of shrubs and trees even after 60 years of secondary succession. We assume that the germination and establishment of woody plants is impeded by a virtually closed sward and by accumulated necromass, retarding further succession to shrub communities. This finding is supported by several other studies (Bohner et al. 2012; Moog et al. 2002).

The managed and abandoned grasslands studied differed greatly in physiognomy and flowering phenology, which might also affect insects (Walcher et al. 2017; Hussain et al. 2018).

Topsoil changes due to abandonment

Across study regions, abandoned grasslands had significantly higher soil C_{org} concentrations than managed grasslands primarily due to higher rates of soil C inputs resulting from greater above-ground phytomass. Across study regions, abandonment increased soil C:N ratio, indicating that the cessation of mowing favours accumulation of less humified organic matter in topsoil. Since SOC accumulation generally involves the sequestration of soil N (Stevenson and Cole 1999), grassland abandonment frequently leads to enrichment of N_{tot} in the surface soil layer. In abandoned grasslands, the soil N supply was higher than in managed meadows because of higher rates of N inputs to the soil resulting from plant litter decomposition. At all study sites, NH_4^+ was the major form of inorganic soil N at the time of sampling, indicating a low nitrifying capacity of the studied semi-dry, nutrient-poor grassland soils. Similar effects of grassland abandonment on topsoil properties were observed in many other studies (Knops and Tilman 2000; Köhler et al. 2001; Tilman 1987; Zeller et al. 2001). The higher above-ground plant biomass and the denser surface layer of necromass at abandoned sites reduced average soil temperature and increased soil moisture (Facelli and Pickett, 1991).

Soil microbial community composition (PLFA) differed significantly among study regions but was not significantly affected by abandonment. This indicates that functional groups of soil microorganisms are more strongly influenced by local abiotic site conditions than by species composition of the vegetation (litter quality), plant community productivity (litter quantity) and plant species richness (litter diversity). This finding is in agreement with that of other studies (De Vries et al. 2012; Zeller et al. 2001). For most of the functional groups of soil microorganisms no consistent response to abandonment was obvious except for gram-positive bacteria, gram-negative bacteria and AMF, which slightly benefited from the cessation of mowing. Abandonment increased the bacteria:fungi ratio, presumably because of an enhanced soil water and inorganic soil N supply (De Vries et al. 2012; Hackl et al. 2005). The results of our correlation analysis suggested that microorganisms benefit from a high concentration of C_{org} in topsoil, from an enhanced inorganic soil N supply and improved soil water availability, indicating that resource availability (nutrients, water) has a strong influence on soil microorganisms (De Vries et al. 2012).

Changes in litter decomposition due to abandonment

The decomposition rate of both litter types was significantly higher on abandoned than on managed plots, indicating more favourable soil environmental conditions for decomposer microorganisms in abandoned semi-dry grasslands (Zhang et al. 2008). Thus, abandonment may accelerate litter decomposition in the topsoil at least during dry periods through increased soil water availability, leading to a faster N cycling and hence higher grass cover (Tilman and Downing 1994) in abandoned grasslands. Under semi-dry soil conditions, the positive effect of higher soil water availability after abandonment on microbial litter decomposition might be stronger than the negative effect of lower soil temperature (Butenschoen et al. 2011; Garcia-Palacios et al. 2016). Across study regions, litter stabilization factor, which is indicative for long-term C storage (Keuskamp et al. 2013), was significantly higher on abandoned plots compared to managed plots. We assume, that abandonment of semi-natural grasslands promotes SOC sequestration in the topsoil despite higher litter decomposition rates because a higher proportion of plant litter presumably enters the permanent (passive) SOM pool (Schulze et al. 2000). Our results demonstrate that abandonment of semi-natural grasslands promotes SOC sequestration in the topsoil not only by increasing plant litter inputs to the soil (Bohner et al. 2006), but also by converting more plant litter into SOM.

Ecosystem services

The cessation of mowing promotes SOC sequestration but can have detrimental effects on ESs linked to aesthetic values, if abandonment leads to grass-dominated, less colourful plant stands and can even affect human health aspects (Arnberger et al. 2018a, b). A high aesthetic value of semi-natural grassland communities as a result of great herb diversity is hardly compatible with SOC sequestration because annual mowing without manuring over a long period together with removal of the mown biomass inevitably leads to C losses in the topsoil (Bohner et al. 2016). To optimize the provision of ESs at the landscape scale, a mosaic of different land-use types and management intensities, including abandoned grasslands of different successional age, seems necessary.

Conclusions

Contrary to our hypothesis, the results show that several vegetation, soil and microbial parameters display no consistent trend during secondary succession in semi-natural grasslands on semi-dry, nutrient-poor, base-rich soils under different climatic conditions. Our study shows that vegetation parameters in general respond more sensitively and less site-specific to abandonment than soil and microbial parameters at the plant community scale, making the former a more reliable indicator of successional changes. Among the studied soil parameters, C:N ratio in topsoil seems to be the best parameter for monitoring successional changes due to abandonment.

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4.5. Publication V: Management of mountainous meadows associated with biodiversity attributes, perceived health benefits and cultural ecosystem services.

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Management of mountainous meadows associated with biodiversity attributes, perceived health benefits and cultural ecosystem services

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Associations between biodiversity, human health and well-being have never been discussed with reference to agriculturally managed, species-rich mountainous meadows. We evaluated these associations between extensively managed (one mowing a year, no fertilization) and abandoned (no mowing since more than 80 years, no fertilization) semi-dry meadows located in the Austrian and Swiss Alps. We quantified the richness and abundance of plants, grasshoppers, true bugs, bumblebees, syrphids and landscape characteristics in the surroundings of the meadows. Associations between these biodiversity attributes and short-term psychological and physiological human health effects were assessed with 22 participants (10 males, 12 females; mean age 27 years). Participants´ pulse rate, systolic blood pressure (SBP) and diastolic blood pressure (DBP) were not affected during visits to managed or abandoned meadows. However, perceived health benefits (e.g., stress reduction, attention restoration) were higher during their stays in managed than in abandoned meadows. Also, the attractiveness of the surrounding landscape and the recreation suitability were rated higher when visiting managed meadows. Perceived naturalness was positively correlated with plant richness and flower cover. A positive correlation was found between SBP and forest cover, but SBP was negatively correlated with the open landscape. A negative association was found between grasshoppers and recreational and landscape perceptions. We suggest to discuss biodiversity attributes not only in connection with agricultural management but also with cultural ecosystem services and health benefits to raise more awareness for multifaceted interrelationships between ecosystems and humans.

The association between biodiversity, ecosystems services and human health and well-being has gained increased consideration in global scientific and political debates in the past few years[1–3]. European alpine grasslands have been extensively managed for hundreds of years by local farmers and traditional land-use, bearing high plant and insect diversity[4,5]. However, changes in agricultural practices and low farm incomes have resulted in abandonment of these alpine grasslands[6–9]. Mountainous meadows do provide restorative benefits[10] and are considered to promote human health[11]. However, there is a lack of direct evidence in linking biodiversity, ecosystem services, human health and well-being with meadow management intensity.

Ecosystems offer services valuable to human health and well-being positively affecting mental health, the cardiovascular system and stress levels[12–18]. Although biodiversity plays a key role for delivering ecosystem and regulating services[19] and is important for human health and well-being[20], relationships between biodiversity and

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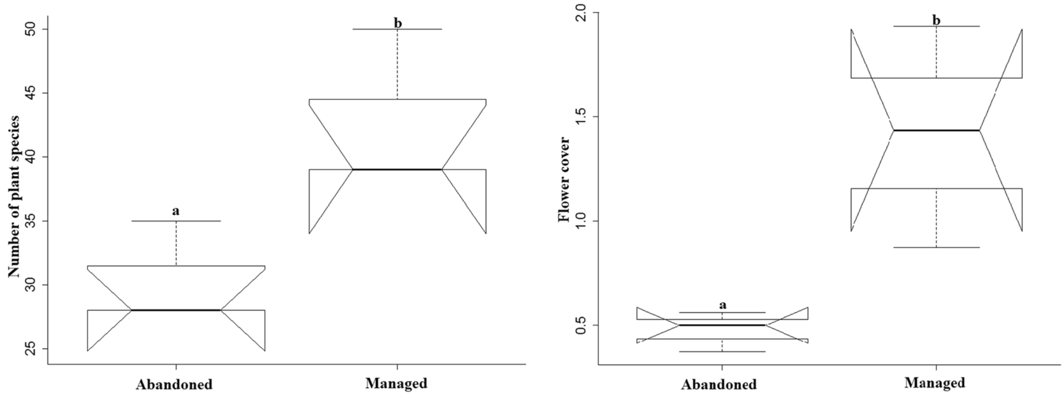

Figure 1. Plant richness and flower cover in abandoned and managed meadows. Dissimilar letters above box plots show significant differences.

human health and well-being are not uniform[21,22]. Fuller *et al.*[23] assumed that plants are the most evident and stationary element of biodiversity. They are visible to people and may be useful indicators for the relationships between biodiversity and human health[24]. Several studies found positive associations between perceived health benefits and birds or plant diversity[25,26] while others did not find a consistent relationship between plant richness and psychological benefits[27]. Further investigations are required to clarify potential knowledge gaps on the association between biodiversity and human health[21,28].

Studies on the associations between the biodiversity, physiological and well-being benefits and the degree of naturalness and human health were primarily carried out in the urbanized context or only on specific organisms such as butterflies[29] or birds[3]. Our explorative study for the first time aims in getting an understanding on the relationships between biodiversity and human health on meadows by considering several insect groups. While butterflies are very obvious to humans and well investigated[23,25], other pollinators like bumblebees, true bugs, grasshoppers and syrphids have not been investigated so far in that context, although these insects are characteristic elements of the fauna of alpine meadows. Grasshoppers and true bugs, for example, are abundant species in meadows and can be experienced by the people in many ways, namely at tactile, visual and audible perception levels. When people sit in the meadow, they can easily interact with insect groups.

The objective of the present work was to collectively evaluate associations between several biodiversity attributes, landscape characteristics and cultural ecosystem services on human health and well-being and how much agricultural management intensity affects these associations. The goal of our study was to explore the association between health and well-being benefits and measured biodiversity attributes in two grassland management regimes. In contrast to previous studies[23,30], our study relied on both perceived and measured health benefits when correlating these with several biodiversity attributes of alpine meadows. We hypothesized that meadows with a higher biodiversity would reduce stress levels and other psychological health parameters that would further translate into measurable physiological health benefits. The investigations were carried out with 22 participants (10 males, 12 females; mean age 27 years) in mountain landscapes in the Austrian and Swiss Alps. Biodiversity attributes and landscape parameters were assessed by standardized sampling methods.

Results

Species and plant richness. In total, we found 12 grasshopper, 16 true bug, 8 syrphid, 5 bumblebee and 115 plant species in both managed and abandoned meadows (Supplementary Table S1). *Bromus erectus* was the dominant plant species in managed meadows. The grasses *Brachypodium pinnatum*, *Molinia caerulea* and the non-leguminous herb *Laserpitium latifolium* were the dominant species in abandoned meadows.

Plant richness ($F_{1,6} = 8.053$, $p = 0.047$) and flower cover ($F_{1,6} = 9.04$, $p = 0.027$) differed significantly between managed and abandoned meadows (Fig. 1). Species richness and abundance of true bugs, grasshoppers, syrphids and bumblebees were non-significant between management types, as was also for surrounding landscape (Supplementary Table S2). However, there was a slight trend of increasing grasshopper abundance in managed meadows. When data of three study sites were pooled together then we found a significant difference only in bumblebees' abundance and richness between Austria and Switzerland study sites (Supplementary Fig. S1).

Cardiovascular parameters and perceptions of participants. We tested whether there are differences in pulse rates and blood pressure (SBP, DBP), perceived health benefits, recreation and landscape related attributes between managed and abandoned meadows. Overall, participants perceived various health benefits (stress reduction, attention restoration, increase in well-being) during their stay in the meadows (Table 1). We run a repeated measures analysis (including site, order of visits and management type) and found that the order of visits (main effect, as well as interaction effects) had no influence on the perceptions of naturalness ($p > 0.05$).

The results of the GLMs with repeated measures showed that there were no significant differences between the managed and abandoned meadows in pulse rate ($F_{1,22} = 0.655$, $p = 0.300$), SBP ($F_{1,22} = 0.599$, $p = 0.448$) and DBP ($F_{1,22} = 0.064$, $p = 0.803$). Significant differences were found for perceived stress reduction, attention restoration, well-being and degree of naturalness between managed and abandoned meadows (stress reduction $F_{1,22} = 15.464$, $p = 0.001$; attention restoration $F_{1,22} = 5.047$, $p = 0.036$; well-being ($F_{1,22} = 6.687$, $p = 0.017$), degree

Perceived health benefits and ecosystem services (Mean)	Abandoned meadow	Managed meadow
Stress reduction*	2.03	1.80
Attention restoration*	2.13	1.99
Change in well-being*	1.86	1.70
Landscape beauty*	2.25	1.43
Naturalness*	2.36	1.21
Suitability for recreation*	2.52	2.25
Noise perception-site*	2.89	3.07
Noise perception-background*	2.67	2.82
Probability to revisit	2.68	2.33
Meadow beauty	2.25	1.43

Table 1. Perceived health effects and cultural ecosystem services in two management types across Austrian and Swiss Alps. Answer scales: Stress reduction (1 = very good, 5 = absolutely not); attention restoration (1 = very good, 5 = absolutely not); change in well-being (1 = enhanced, 3 = unaffected, 5 = decreased); landscape beauty and naturalness (1 = very good to 5 = absolutely not); suitability for recreation (1 = very appropriate, 5 = not appropriate); noise perception-site (1 = noiseless to 5 = very intense); noise perception-background (1 = very pleasing to 5 = not pleasant); probability to revisit and meadow beauty (1 = very good to 5 = absolutely not). *Significant at the 0.05 probability level.

of naturalness ($F_{1,22} = 36.713$, $p < 0.001$), suitability for recreational purposes ($F_{1,22} = 4.309$, $p = 0.050$), landscape beauty ($F_{1,22} = 7.117$, $p = 0.014$), and noise perceptions ($F_{1,22} = 5.318$, $p = 0.031$). No differences were found for beauty of the meadow and the probability of a revisit.

Relationships between biodiversity and cardiovascular health and landscape perceptions. Perceived naturalness was positively correlated with number of plant species ($r = 0.87$, $p = 0.023$) and flower cover ($r = 0.86$, $p = 0.028$). We also detected a positive correlation between systolic BP (T1) and forest cover within the 500 m radius ($r = 0.973$, $p = 0.001$), and between the probability to revisit a meadow and bumblebee abundance ($r = 0.82$, $p = 0.043$). Systolic BP (T1) was negatively correlated with level of openness of the landscape ($r = -0.969$, $p = 0.001$). Grasshopper richness was negatively correlated with perceived stress reduction ($r = -0.89$, $p = 0.01$), attention restoration ($r = -0.09$, $p = 0.004$), change in well-being ($r = -0.82$, $p = 0.043$), landscape beauty ($r = -0.85$, $p = 0.028$), suitability for recreation ($r = -0.90$, $p = 0.012$), noise perceptions ($r = -0.80$, $p = 0.05$) and probability to revisit meadows ($r = -0.93$, $p = 0.006$) (Fig. 2). No correlations were found between human health perceptions and vegetation cover, true bugs and syrphids diversity ($p > 0.05$).

Discussion

To the best of our knowledge, this is the first study which analyzed the relationships between measured biodiversity attributes and perceived as well as measured human health benefits among alpine grassland management regimes. Extensively managed alpine grasslands are biodiversity hotspots of mountain landscapes, however are steadily disappearing due to abandonment. We found several negative and positive correlations between biodiversity attributes and human health and well-being and cultural ecosystem services. Agricultural management appeared to only play a minor role in this context.

Managed and abandoned meadows are characterized by different plant richness. Our results highlight that perceived naturalness has an association with plant richness. In our study, we followed Fuller *et al.*[23] who stated that plants are the most evident and stationary element of biodiversity. When management has an influence on plant richness and plant richness affects perceived naturalness, then there is actually also an indirect effect of management. Previous research has shown that people have a positive response to higher plant richness[31], although recognizing plant richness just by sighting itself can be quite imprecise[32], while Qiu *et al.*[33] found that lay people can recognize differences in biodiversity within an urban green space. Perceived naturalness was positively related to plant richness and flower cover, which suggests that when participants are in managed meadows, that contain high plant richness and flower cover, they perceive more naturalness[29].

Flowers have been an indicator as social, ravishing, spiritual and emotional symbol[34]. People often benefit from contacts with images of flowers, as well as advantages from interaction with real nature[35]. Higher flower cover in managed meadows seems representative of perceived naturalness by the participants not only due to their influential effect on mood[36] but also on health and well-being[37]. However, in contrast to previous studies[38,39], plant richness and flower cover were not related to human health. This might be due to healthy participants with similar age and same cultural background used in the study design.

Several studies revealed a decline in blood pressure in natural or semi-natural grasslands linked to urban settings[40,41], while others were unable to find such patterns[42,43]. In the present study we did not find differences between management regimes but found a negative relationship between SBP and openness of the landscape and a positive relationship between surrounding forest cover and SBP, indicating that in a more open landscape the SBP is lower.

All managed meadows provided higher self-reported health benefits (stress reduction, attention restoration, change in well-being), naturalness and cultural ecosystem services (landscape beauty, suitability for recreation and noise perception) assuming that a stay in managed meadows is more beneficial for mental and physiological

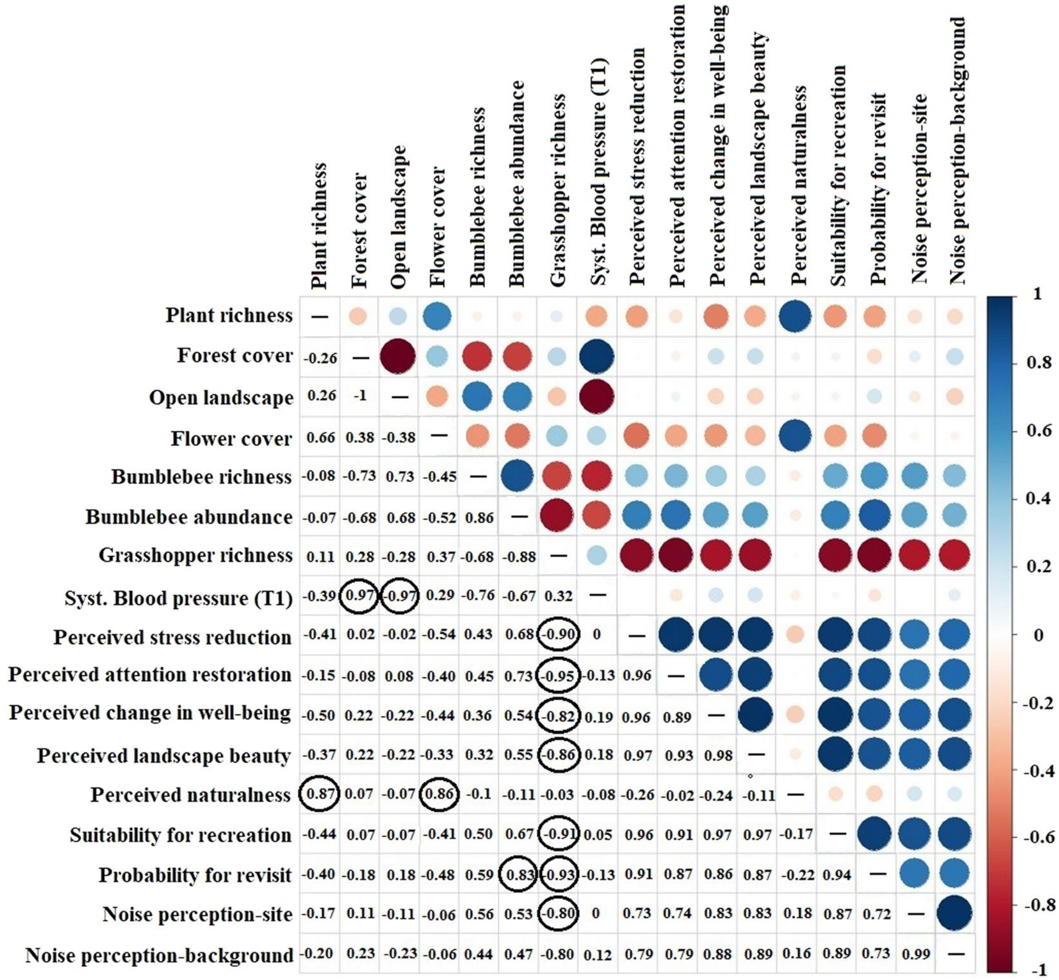

Figure 2. Correlation matrix showing co-occurrences of biodiversity attributes, landscape characteristics, cultural ecosystem services and human health and well-being. Negative correlations in red color and positive correlations are presented in blue. The size of the circle and color intensity is relative to the correlation coefficients. In the right side of the matrix, the legend color shows the corresponding colors and the correlation coefficients. Statistically significant correlations are marked by circles.

restoration than a stay in an abandoned meadow. Although participants valued positively both management regimes in terms of beauty and probability to revisit, managed meadows, richer in flower cover and plant species than abandoned meadows, were rated higher. This also showed that mountainous meadows differ in their perceived health effects[10].

A consistent negative relationship was found between grasshopper diversity and many landscape quality and health perceptions. Andujar[44] observed that grasshopper noises were not pleasant to those people who are uninspired by insects. Besides producing sounds, adult grasshoppers fly and jump, and combined with their high numbers, become more noticeable to participants compared to most other species living in the meadows. The occurrence of different grasshoppers flying around and on participants while they were sitting in the meadows may have caused a disordered impression. We think this might have evoked some biophobia[45] of grasshoppers to participants[46]. Previous research has also shown that landscapes evaluated as chaotic, confusing and very complex are not perceived as restorative environments, which may not provide health benefits to humans[47]. This might explain why participants discouraged the presence of grasshoppers for stress reduction, attention restoration, landscape beauty and suitability for recreation. Instead, participants preferred to revisit the meadows in the presence of many bumblebees. We assume that for our participants a good quality of life emerges from the functioning of pollinators as sign of identity and an aesthetically significant factor in landscapes[48]. We also assume that participants' aesthetic appreciation and naturalness were linked with the visual observation of biodiversity attributes[49]. The interactions of grasshoppers and bumblebees with participants made participants more perceptive, compared to the less visible syrphids and true bugs.

A stay in these meadows positively influenced the subjective well-being of participants, confirming previous research on restorative effects of natural and semi-natural areas on human health and well-being[14–18]. However, participants perceived higher health benefits during their stay in managed meadows than abandoned meadows. The beauty of managed meadows and the surrounding landscape were rated higher, although the surrounding

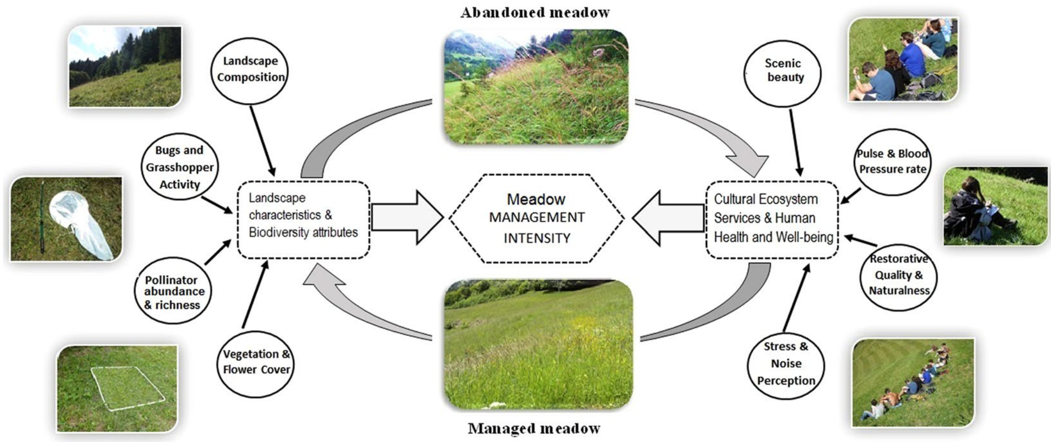

Figure 3. Conceptual framework illustrating links between the impacts of biodiversity attributes, landscape characteristics, cultural ecosystem services and human health and well-being. These services are interconnected by influential impact of two mountain management regimes.

Country/Federal State	Region	Municipality	Mean temperature in August	Mean annual rainfall	Altitude a.s.l*	GPS coordinate
Austria/Styria	Eisenwurzen	Pürgg	20 °C	1088 mm	790 m	47°31′N, 14°03′E
Austria/Vorarlberg	Großes Walsertal	Sonntag/Buchboden	23 °C	1633 mm	1200 m	47°14′N, 09°57′E
Switzerland/Graubünden	Val Müstair	Tchierv	25 °C	811 mm	1740 m	46°36′N, 10°20′E

Table 2. Study sites and their regional characteristics along an altitudinal gradient in Austria and Switzerland. *Above sea level.

landscape was the same for each meadow pair. One explanation might be that managed meadows were richer in flower cover. Flower cover may be the most noticeable visual cue between the two managements through which participants perceived variations in the environment around them[23], and may be the main factor influencing their perceptions of biodiversity. Another explanation for the higher health benefits of managed meadows might be that participants had perceived lower noise levels in abandoned meadows.

Biodiversity attributes revealed some relationships with cultural ecosystem services and perceived health benefits. However, these relationships might get obscured in the absence of the two management types (Fig. 3). Managed meadows, rich in plant species and flowers, provide more cultural ecosystem services but not more measured health benefits compared to abandoned meadows. Further expansion of our study by increasing participant numbers and having greater variety of cultural and educational backgrounds would also help to reveal additional aspects that might alter associations between biodiversity attributes and perceived and measured health benefits in areas with different agricultural management intensities.

Conclusion

We conclude that several biodiversity attributes were associated with cultural ecosystem services and health benefits within two studied grassland management regimes. These relational effects have been addressed the first time by means of visiting managed and abandoned meadows of Austrian and Swiss Alps. Although humans probably cannot directly sense ecological quality[50], there is a trend built on perceptions, that ecological quality has some connections with grassland management. Managed meadows having high plant richness and flower numbers increased the perception of naturalness which highlights their importance as natural element. Our conclusion not only helps to promote grassland management but also indicates its significant cultural value for human health and well-being. We suggest to discuss biodiversity attributes not only in connection with agricultural management intensity but also with cultural ecosystem services and health benefits in order to raise more awareness for the importance of interrelationships between ecosystems and humans.

Material and Methods

Study regions. The research was carried out in August 2015 in three UNESCO-LTSER biodiverse regions of the Austrian and Swiss Alps (Table 2). The study sites were six semidry meadows, three of them managed and three abandoned, comprised in the regions Eisenwurzen (M1: Styria, Austria), the Großes Walsertal Biosphere Reserve (M2: Vorarlberg, Austria) and the Val Müstair Biosphere Reserve (M3: Graubünden, Switzerland). Managed meadows were mown annually since more than 80 years, usually between mid-July and the beginning of August. Abandoned sites were between 20 and 40 years old. The sizes of abandoned meadows ranged between 300 and 4300 m^2, the sizes of managed meadows ranged between 470 and 5150 m^2. We did not find any significant differences between sizes of meadows for each of the three regions (ANOVA: M1: $F = 1.832$, $p = 0.25$; M2:

$F=3.561$, $p=0.13$; M3: $F=1.378$, $p=0.31$). In all three regions, the managed and the abandoned meadows were bordering, separated from each by some trees or tree lines.

Biodiversity attributes measurement. Syrphid species richness and abundance were surveyed using two different methods: line transects and observation plots[51,52]. For the line transect method, three transects were established in each meadow. Each transect was 15 m long and 2 m wide and the distance between each transect was 10 m. Additionally in each meadow, four 2 m^2 observation plots were selected in a straight line at distances of 0 m, 3 m, 9 m and 27 m. Observations were recorded over a period of 15 minutes for each plot. The two methods were carried out simultaneously in each meadow, therefore, field conditions during sampling were similar.

The data obtained from both methods were combined per study site. Since the survey was carried out on six meadows (three managed and three abandoned meadows), the number of statistical units was 6 in the analysis. We sampled bumblebees on four 20 m^2 study plots in each meadow for 15 minutes. Every individual bumblebee specimen was collected by sweep netting and counted. Bumblebees were set free on-site after identification[8]. Heteropteran bugs were sampled by sweep netting. We applied a total of 90 sweeps separated in 3×30 sweeps in the center of each meadow[53]. Species identification was performed in the laboratory using a taxonomic key provided by Wagner[54] and Strauss[55]. Grasshoppers were assessed with recording devices, which considered as an appropriate method for recording grasshoppers richness within their habitat[56]. We attached a bat detector (heterodyne) to the recording device to enhance sounds (Batbox III D). Later, grasshoppers were identified at species level by listening using auditory assessment material from the field[57].

Plant and landscape parameters. Vegetation and flower cover were based on the estimation of how much area a plant or flower covers in a defined area. This method also assessed the amount of canopy cover that occurred on a study site[58]. Plant species richness, vegetation cover (%) and flower cover (%) were assessed by four 1 m^2 (1×1 m) frames in each meadow. Each frame was subdivided into 4 sections of 0.25 m^2 and the distance between each frame was 5 m. The frame was set on the highest level of the vegetation and every plant species within each section was identified[52,59]. Later, plant community data per study site were used in the analysis. At each of the managed and abandoned sites an area was selected which was fairly uniform with respect to topography, soil and vegetation. This procedure was adopted randomly in June and August on each study site to measure vegetation representative of each meadow. This also ensured that late-flowering species had not been missed. Vegetation cover and flower cover were estimated using a modified Braun- Blanquet scale[60] for species cover[61,62].

Surrounding landscape structure (forest cover and open landscape) was assessed within a 500 m radius around the center of each study site by means of GIS[63] (geographical information system). In every circle, the percentage of open landscape and forest cover were calculated in ArcGIS (basemap). Open landscape was almost entirely covered by grassland. All sampling was conducted between 10 a.m. to 5 p.m. when climatic conditions were suitable, i.e. minimum temperature 15 °C, no rain or wind and dry vegetation.

Human health and recreational effects measurements. According to the World Health Organisation of the United Nations (WHO) health is a state of physical, mental and social well-being and not merely the absence of disease or infirmity; well-being is described as the state of being relaxed and healthy[19,64]. A sample of 22 healthy participants, balanced in gender (10 males, 12 females) and of a fairly similar age (mean age = 27, ranging from 22 to 36 years; non-smokers), was used for the assessment of short term effects on human well-being and recreation. The study fulfilled national ethical requirements and participants gave informed written consent before they joined the study. Also, the study was performed in accordance with the Declaration of Helsinki, and the study protocol was approved by the ethics committee of the Earth System Sciences (ESS) programme. Participants were briefed about the objective of the study, methodology and associated issues. The participants consisted of employed individuals and students from different Austrian institutions with similar culture background and educational levels. For the chosen research design and sample size, we expected that the test strength would be adequate[65].

The participants visited in different sessions each meadow in a standardized manner[17,18] at very similar weather conditions. Two separate visits per meadow were made in order to obtain more robust results. Participants started with the abandoned meadow in the morning of the first day, and visited the managed one in the afternoon. Next day, we reversed the visit order, i.e. the managed meadow was visited in the morning and the abandoned one in the afternoon. At the next region, we started with the abandoned meadow in the morning, followed by the managed one in the afternoon.

The approximate duration of a single visit was about two and a half hours at each study site. Participants' blood pressure (t1) and pulse rates were measured on the study site, after a bus ride of between 25–30 minutes. On reaching at the meadow, after a very easy 10-minute walk or shuttle transport, participants then sat and perceived the study sites for 15 minutes, after that we note down blood pressure (t2) and pulse rates. Then participants perceived the landscape over again for few minutes and completed several questionnaire forms. When participants were sitting in the meadows they were directly exposed to the environmental conditions perceiving plants and insects with all their senses in short distances. The difference between pulse and blood pressure were indicated as T1 ($t1 - t2$). The same procedure was followed at all study sites.

To test physiological factors of the cardiovascular system (pulse, systolic (SBP) and diastolic blood pressure (DBP)), self-inflating blood pressure cuffs (boso medilife S) were used. Over the years, research has found that both SBP and DBP are equally important in monitoring heart health. Greater risk of heart disease related to higher systolic pressures (>130 mm Hg)[66].

Pulse, SBP and DBP were recorded when sitting in upright position, quietly for 5 minutes prior to measurement. Talking was not allowed. We measured pulse, SBP and DBP three times per measurement at each study site. We used the third (most reliable) measurement of pulse and blood pressure for analyses[22]. During each visit, noise levels were permanently checked using measurement device (Voltcraft SL-451). Based on 30 minutes of observations, an average noise level was recorded for each study site.

Questionnaire. Perceived health benefits (i.e. stress relief, well-being, and attention restoration) were evaluated using 5-point response scales. Participants were questioned whether a visit in the meadow had reestablished their attention (1 = very good, 5 = absolutely not), decreased their stress (1 = very good, 5 = absolutely not), and altered their psychological well-being (1 = enhanced, 3 = unaffected, 5 = decreased). Landscape quality indicators included perceptions of naturalness and sound, and the attractiveness of the neighboring landscape and of the meadows applying 5-point response scales. Landscape and study site attractiveness were judged by a response scale ranged from 1 = very good to 5 = absolutely not. The answer scale of the sound level perception ranged from 1 = noiseless to 5 = very intense; background sound ranged from 1 = very pleasing to 5 = not pleasant. Participants had to estimate the appropriateness of study site for recreation (1 = very appropriate, 5 = not appropriate), and if they would visit again this study site on a scale from 1 = very good to 5 = absolutely not.

Statistical analysis. In the first step, all biodiversity attributes and physiological human health data were analyzed for normal distribution and homogeneity of variance to fulfill the prerequisite for ANOVA by using the Levene's test and box plots. We used General Linear Models (GLM) to analyse differences in perceived health effects, blood pressures and pulse rates between the study sites with Poisson error distribution (corrected by quasi-poisson when there was overdispersion). Pearson rank correlation was computed to assess the relationship between different biodiversity attributes (species numbers of true bugs, syrphids, plants, grasshoppers, and bumblebees), landscape characteristics (percentage of open land, forest and vegetation cover) and perceptions of cultural ecosystem services (naturalness, recreation, landscape beauty, noise perception) as well as perceived health benefits, blood pressure and pulse. Previous research analyzing relationships between biodiversity and human health and well-being typically relied on correlations[3,25,26]. The *corrplot* package was used for graphical presentation of correlation coefficient matrix because it contains algorithms to do matrix reordering. All statistical calculations were performed using R version 3.3.1[67,68] by using an alpha level of 0.05.

Data availability

All data generated or analyzed during this study are included in this published article (and its Supplementary Information Files).

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Author contributions
R.I.H., R.W., R.E. and B.A. conducted field work, A.A., R.E., P.W., H.P.H. and N.B. measured human health effects, R.I.H. analyzed the data and wrote the manuscript, J.G.Z., A.A. and T.F. project leaders, designed and developed the "Healthy Alps" project, all authors reviewed the manuscript.

Competing interests
The authors declare no competing interests.

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Supplementary Material:

Supplementary Table S1: List of species of biodiversity attributes in two management types across Austrian and Swiss Alps. Species presence is marked with "X" while empty space indicates absence.

Biodiversity attributes	Species list	Abandoned Meadow	Managed Meadow
Grasshoppers	*Chorthippus biguttulus*	X	X
	Decticus verrucivorus		X
	Euthystira brachyptera	X	X
	Gomphocerippus rufus	X	
	Metrioptera brachyptera	X	X
	Omocestus rufipes		X
	Pholidoptera griseoaptera	X	X
	Chorthippus parallelus	X	X
	Psophus stridulus	X	X
	Roeseliana roeselii	X	X
	Stenobothrus lineatus		X
	Tettigonia cantans	X	
True Bugs			
	Carpocoris melanocerus	X	
	Carpocoris purpureipennis	X	X
	Cymus glandicolor	X	
	Graphosoma lineatum	X	X
	Megalonotus chiragra		X
	Myrmus miriformis	X	
	Nabis ferus	X	
	Orthops kalmii	X	X
	Palomena prasina	X	X
	Rhopalus subrufus	X	
	Spilostethus saxatilis	X	X
	Stenodema holsata	X	
	Stenodema laevigata	X	
	Stenodema sericans	X	
	Stictopleurus crassicornis		X
	Stictopleurus punctatonervosus		X
Syrphids			
	Cheilosia impressa	X	
	Epistrophe diaphana		X
	Episyrphus balteatus	X	X
	Eupeodes lapponicus	X	X
	Melanostoma mellinum	X	X
	Pipizella varipes		X
	Pipizella virens		X
	Syritta pipiens	X	X

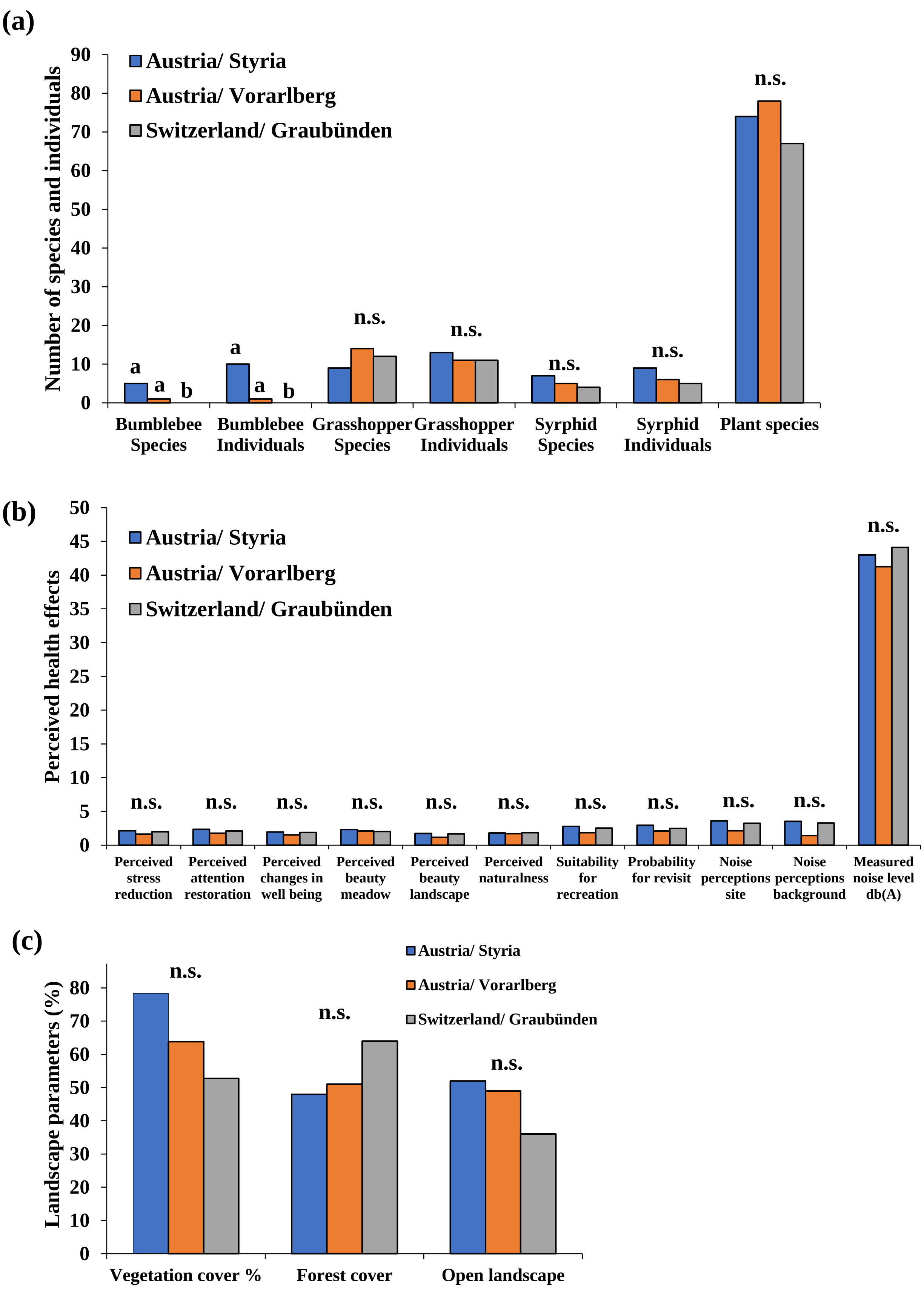
Bumblebees			
	Bombus humilis	X	
	Bombus lapidarius	X	X
	Bombus pascuorum	X	
	Bombus mucidus		X
	Bombus pratorum		X
Vascular Plants			
	Achillea millefolium agg.	X	X
	Aegopodium podagraria	X	
	Ajuga genevensis		X
	Alchemilla monticola	X	X
	Allium carinatum	X	X
	Allium lusitanicum		X
	Anthericum liliago	X	
	Anthoxanthum odoratum	X	X
	Anthriscus sylvestris		X
	Anthyllis vulneraria carpatica		X
	Aquilegia atrata	X	
	Arabis hirsuta		X
	Arenaria serpyllifolia		X
	Arrhenatherum elatius	X	X
	Avenula pubescens pubescens	X	X
	Brachypodium pinnatum	X	X
	Briza media	X	X
	Bromus erectus	X	X
	Buphthalmum salicifolium	X	X
	Campanula rapunculoides	X	
	Campanula rotundifolia	X	
	Carduus defloratus viridis		X
	Carex alba	X	
	Carex ericetorum	X	X
	Carex flacca		X
	Carex spicata	X	X
	Carex sylvatica		X
	Carlina acaulis acaulis	X	X
	Centaurea jacea	X	X
	Centaurea scabiosa scabiosa	X	X
	Cerastium holosteoides		X
	Chaerophyllum aureum	X	
	Clinopodium vulgare	X	X
	Colchicum autumnale	X	X
	Convolvulus arvensis	X	

Cruciata laevipes	X	
Cynosurus cristatus		X
Dactylis glomerata	X	X
Dianthus carthusianorum		X
Dianthus deltoides	X	
Epipactis atrorubens	X	
Euphorbia cyparissias		X
Festuca pratensis		X
Festuca rubra rubra	X	X
Festuca rupicola	X	X
Festuca valesiaca	X	X
Fragaria viridis	X	X
Fraxinus excelsior	X	X
Galium album	X	X
Galium pumilum	X	X
Gentianella aspera		X
Geranium pratense	X	
Glechoma hederacea		X
Gymnadenia conopsea		X
Helianthemum nummularium obscurum	X	X
Hepatica nobilis	X	
Heracleum sphondylium		X
Hieracium pilosella		X
Hieracium spec.	X	X
Hippocrepis comosa	X	X
Hypericum perforatum	X	
Knautia arvensis arvensis		X
Knautia drymeia intermedia		X
Koeleria pyramidata pyramidata		X
Laserpitium krapfii gaudinii	X	
Lathyrus pratensis	X	X
Leontodon hispidus hispidus		X
Leucanthemum ircutianum		X
Linum catharticum		X
Lotus corniculatus	X	X
Medicago falcata	X	X
Melampyrum sylvaticum	X	
Molinia caerulea	X	
Onobrychis montana		X
Phyteuma orbiculare	X	X
Pimpinella saxifraga saxifraga	X	X
Plantago lanceolata		X

Plantago media		X
Poa angustifolia	X	X
Poa trivialis		X
Polygala comosa		X
Polygonatum odoratum		X
Potentilla erecta	X	X
Primula elatior	X	X
Prunella grandiflora	X	X
Ranunculus bulbosus		X
Ranunculus nemorosus		X
Rhinanthus alectorolophus alectorolophus		X
Rhinanthus minor		X
Rosa spec.	X	
Rumex acetosa	X	X
Salvia verticillata	X	X
Sanguisorba minor	X	X
Scabiosa columbaria		X
Scabiosa lucida		X
Silene nutans nutans		X
Silene vulgaris vulgaris		X
Sorbus aucuparia	X	
Taraxacum officinale agg.		X
Teucrium chamaedrys	X	
Thymus pulegioides pulegioides	X	X
Tragopogon pratensis		X
Trifolium dubium		X
Trifolium medium medium	X	
Trifolium montanum		X
Trifolium pratense pratense		X
Trifolium repens		X
Trisetum flavescens	X	X
Vaccinium myrtillus	X	
Valeriana officinalis	X	X
Veronica chamaedrys chamaedrys	X	X
Vicia cracca	X	X
Viola hirta	X	
Viola rupestris	X	
Viola spec.	X	

Supplementary Table S2: Number of statistical units (N), degrees of freedom (df), F and P-values showing the effects of management on true bugs, grasshoppers, syrphids and bumblebees.

		Management			
		N	df	F	P
True bugs					
	Total species	6	4	0.73	0.44
	Total individuals	6	4	1.88	0.24
Grasshoppers					
	Total species	6	4	0.10	0.77
	Total individuals	6	4	0.18	0.76
Syrphids					
	Total species	6	4	0.21	0.67
	Total individuals	6	4	0.18	0.80
Bumblebees					
	Total species	6	4	0.10	0.90
	Total individuals	6	4	0.19	0.68



Supplementary Figure S1: (a) Biodiversity attributes, (b) perceived health effects and (c) landscape composition in three regions of Austria and Switzerland. Different letters show significant relationship ($p < 0.05$): n.s. no significant difference.

5. General Discussion

Management cessation had significant effects on insects, plants and humans. The extent of these effects varied greatly between the organisms studied. Generally, extensive land utilization maintains the diversity of grasslands (Babai and Molnár 2014). In this chapter, I discuss the most important effects of abandonment on insects, plants, soil properties and humans and present the main results. The present work on the abandonment of mountain meadows is intended to contribute to the understanding of the consequences of human-induced land-use change and to draw attention to the conservation needs of this ecosystem. Hereinafter, the insects, plants and soil properties, and the relationship between grassland management and humans, are discussed separately for a better overview.

5.1. Response of bumblebees to land-use abandonment

Bumblebees responded considerably to grassland abandonment and to the consequent changes in local habitat conditions. This result was consistent among both studies on bumblebees in mountain grassland. Abandonment resulted in a decrease of both number of species and individuals of bumblebees. The positive relationships between plant richness, flower cover and bumblebee richness suggested that the maintenance of flower-rich, unimproved mountain grassland by annual management is most important for the conservation of local bumblebee diversity (Carvell 2002; Diaz-Forero et al. 2013; Goulson et al. 2008).

Further, the results showed that abandoned and managed meadows differed markedly in terms of flower physiognomy which was proved to affect bumblebees with regard to their tongue-length. Long-tongued bumblebee species showed a preference for long-tubed flowers (hidden nectar flowers) whereas short-tongued species showed a preference for flowers with a flat corolla (open nectar flowers). A loss of suitable foraging resources due to abandonment, which was for example shown by a decline of long-tubed flowers after management cessation, might affect bumblebee populations and may lead to an extinction of certain species in mountain grassland (Carvell et al. 2006; Goulson and Darvill 2004; Goulson et al. 2005). Considering that bumblebees declined in many regions of the world (Goulson et al. 2008; Jacobson et al. 2018; Ornosa et al. 2017; Rollin et al. 2020), this adds an important aspect for the conservation of mountain meadows and thus for the conservation of bumblebees.

5.2. Response of heteropteran bugs to land-use abandonment

Both investigations on heteropteran bugs (publications I and III) revealed different relationships between management, vegetation characteristics and bugs suggesting large regional differences. Most likely, this inconsistency can be explained due to different species inventories of bugs having distinct ecological requirements (Moir and Brennan 2007; Körösi et al. 2012). However, both investigations showed a positive relationship between surrounding open landscape (meadows and pastures) and heteropteran bugs. These habitats can be assumed to provide additional food sources, overwintering habitats and refuge areas (Di Giulio et al. 2001; Friess et al. 2017; Jovičić et al. 2017). Overall, it was proved that heteropteran bugs benefitted from the conditions of both meadow types. In particular, among the three regions, abandonment has been shown to support local species diversity in that different species assemblages could co-exist. Some species were even strongly connected with abandoned meadows. Thus, for the conservation of heteropteran bugs, both meadow types played a crucial role in maintaining a high species diversity in mountain grassland.

5.3. Response of grasshoppers to land-use abandonment

Although there was no overall effect of abandonment on grasshoppers, several vegetation characteristics which in turn are dependent on management activity had a great influence on grasshoppers, especially when considering the Orthopteran suborders Caelifera and Ensifera species separately. A higher vegetation cover, as a consequence of abandonment, was positively related with the numbers of Ensifera species while a regular management was shown to be positively related with the numbers of Caelifera species. Most importantly, among the three regions, managed meadows provided an important habitat for three endangered species, two of them were even exclusively found in managed meadows. But there were also species of the suborder Ensifera which particularly preferred the abandoned meadows as habitat. There was some inconsistency between both studies on grasshoppers (publications I and III) regarding species composition of both meadow types, however, this can, as with the bugs, most likely explained by regional differences and differing species inventories (Baur et al. 2006; Bazelet and Samways 2011). Overall, both meadow types supported grasshoppers and displayed important habitats to maintain their species richness in mountain grassland ecosystems.

5.4. Response of hoverflies to land-use abandonment

According to other studies (e.g. Moquet et al. 2018), the preservation of a high diversity of vascular plants by annual mowing was proved to support and maintain a high diversity of hoverflies in the investigated meadows. Thus, a decrease of plant resources due to management cessation may consequently lead to a decline of hoverfly richness. However, the effects of abandonment on hoverflies were less pronounced than for example for the bumblebees. This was demonstrated by the fact that neither management nor other plant parameters other than the number of plant species had an effect on hoverfly richness and abundance. Both richness and abundance are also driven by the diversity and availability of larval habitats, and in case of aphidophagous species, depend on the availability of suitable hosts (Kök et al. 2020). Due to the fact that the identified hoverflies are very mobile (Doyle et al. 2020; Meyer et al. 2017), most of them occurred in both meadow types, which was also shown by similar species communities. However, some species preferred the abandoned meadows as habitat over the managed meadows. This suggested that maintaining both the abandoned and managed meadows support a high diversity of hoverflies in mountain grassland.

5.5. Response of vegetation, soil parameters and litter decomposition to land-use abandonment

Among all the organisms studied, plants showed the most pronounced response to land use abandonment which was clearly reflected by a decrease in the number of vascular plant species, evenness and Shannon-diversity in abandoned meadows confirming also the results of other studies (Pruchniewicz 2017). Likewise, abandoned and managed meadows differed markedly in terms of plant species composition. The results obtained proved that after abandonment the secondary succession resulted in a shift in the dominant plant species (Aldezabal et al. 2015; Pavlů et al. 2011) and favored those species which had certain characteristics such as broad leaves or the ability to reproduce vegetatively (Bohner et al. 2012). Considering that all of the abandoned meadows studied were not managed for more than 20 years, it was interesting that the proportion of trees and shrubs in abandoned meadows was still relatively low, even after 60 years of management cessation. This was due to the fact that a dense sward and a dense necromass layer prevented woody plants from germinating and trees and shrubs from establishing on the abandoned sites (Galvánek and Lepš 2012).

Overall, the vegetation parameters showed a more distinct response to abandonment than the measured soil parameters. This has been demonstrated, for example, for the microbial community composition of the soil, suggesting a regional effect rather than an abandonment effect. With the exception of a higher carbon-nitrogen ratio in the soil, a higher bacteria-fungi ratio and a higher litter decomposition rate in abandoned meadows, there was hardly any effect of abandonment on soil characteristics. Thus, it could have been shown that the vegetation parameters responded less site-specific to land use abandonment than the soil and microbial parameters, which in turn makes them more reliable indicators for land-use changes in mountain grasslands. However, also the carbon-nitrogen ratio may be used as measure of the impact of abandonment in mountain grassland.

5.6. Relationships between biodiversity and humans in the light of grassland management

People perceived naturalness of grasslands to be strongly connected with both plant richness and flower cover which indicated a positive effect of management. This is also consistent with other studies showing positive human appreciation for unimproved species- and flower-rich grasslands (e.g. Graves et al. 2017; Müller et al. 2019). Further, flowers have been shown to have positive effects on mood and social behavior (Haviland-Jones et al. 2005), most likely positively affecting people´s appreciation for managed grassland. Also, the positive relationship between health benefits and managed grassland indicated higher restoration effects in managed meadows compared to the abandoned meadows.

An interesting link has been uncovered between humans and different insect taxa. This link revealed a negative association of people and grasshoppers but a positive association with bumblebees. High levels of noise caused by grasshoppers, combined with their sudden movements and appearance, may have raised some kind of biophobia (Soga et al. 2020) which in turn may have resulted in disturbances that have impaired a recreational effect and reduced the suitability of grassland for recreational purposes. Depending on the age, cultural and educational background, there is generally a positive attitude towards bees and bumblebees which has been shown for example in a study by Sieg et al. (2018). Also, a better sensitization of people for the importance of pollinators in the last decades may have affected the positive link between people and bumblebees (e.g. Althaus et al. 2021). Other insect taxa were not considered in the present investigation because hoverflies and heteropteran bugs are hardly susceptible to humans

6. Summary

Extensive management in the sense of annual mowing is an important conservation activity which sustains the high plant species richness of mountain grasslands. The maintenance of this ecosystem is critical to support bumblebees and hoverflies with sufficient foraging resources and to provide habitat for a variety of heteropteran bug and grasshopper species. However, also abandoned meadows proved to be valuable habitats for a great variety of heteropteran bugs, grasshoppers and hoverflies and thus can contribute to increasing insect diversity in mountain landscapes. Management should therefore aim to create a highly structured, heterogenous landscape and maintain both meadow types within the mountain landscape. However, most importantly, abandoned meadows should be provided from a conversion into closed forest which in turn will lead to a rapid decline in species that depend on open habitats. From a human perspective, the maintenance of extensively managed mountain meadows is of great importance for the provision of cultural ecosystem services that have a positive impact on health. Managed meadows gave people a sense of higher naturalness and also increase the probability of a re-visit of the meadows. This can be an important factor to increase the value of mountain regions which can be particularly important in terms of tourism (Lindemann-Matthies et al. 2010).

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8. Index of figures

9. Curriculum vitae

Personal dates

Name	Ronnie Walcher
Date of birth	20.11.1981
Place of birth	Waidhofen/Ybbs, NÖ
Country	Austria
Citizenship	Austria

Education

Career

2015-2021 - Doctoral Degree in Agriculture (UH 788 890), University of Natural Resources and Life Sciences, Vienna
2011-2013 - Master´s Degree in Agricultural Biology (UH 066 459), University of Natural Resources and Life Sciences, Vienna
2003-2011 - Bachelor´s Degree in Biology with focus on Zoology, University of Vienna

Employments

Research work

2020-Present – Research assistant in the project “DivRESTORE”: Transforming grasslands to achieve insect diversity restorative goals and human well-being, funded by the Austrian Academy of Sciences (ÖAW)
2018-2020 – Research assistant in the project “REGRASS”: Re-establishing grasslands to promote farmland biodiversity and key ecosystem services, funded by the Wissenschaftsfonds (FWF)
2018-2019 – Insect monitoring as part of the project „Blühstreifenversuch St. Florian", Recording of bumblebees, hoverflies, heteropteran bugs, ladybeetles and lacewings in flower strips with different seed mixtures, funded by the Bienenzentrum Oberösterreich (Landwirtschaftskammer, OÖ)
2015-2018 – Research assistant in the project “Healthy Alps”: Alpine landscapes under global change: Impacts of land-use change on regulating ecosystem services, biodiversity, human health and well-

being, funded by the Austrian Academy of Sciences (ÖAW), Dissertation topic

Publications

Research articles in scientific journals

2020:

Maderthaner, M., Weber, M., Takács, E., Mörtl, M., Leisch, F., Römbke, J., Querner, P., **Walcher, R.**, Gruber, E., Székács, A., Zaller, J. G., 2020. Commercial glyphosate-based herbicides effects on springtails (Collembola) differ from those of their respective active ingredients and vary with soil organic matter content. *Environmental Science and Pollution Research*, **27**, 17280-17289.

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Bohner, A., Karrer, J., **Walcher, R.**, Brandl, D., Michel, K., Arnberger, A., Frank, T., Zaller, J. G., 2019. Ecological responses of semi-natural grasslands to abandonment: case studies in three mountain regions in the Eastern Alps. *Folia Geobotanica*, **54**, 211-225.

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2018:

Hussain, R. I., **Walcher, R.**, Brandl, D., Arnberger, A., Zaller, J. G., Frank, T., 2018. Efficiency of two methods of sampling used to assess the abundance and species diversity of adult Syrphidae (Diptera) in mountainous meadows in the Austrian and Swiss Alps. *European Journal of Entomology*, **115**, 150-156.

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Walcher, R., Karrer, J., Sachslehner, L., Bohner, A., Pachinger, B., Brandl, D., Zaller, J. G., Arnberger, A., Frank, T., 2017. Diversity of bumblebees, heteropteran bugs and grasshoppers maintained by both: abandonment and extensive management of mountain meadows in three regions across the Austrian and Swiss Alps. *Landscape Ecology*, **32**, 1937-1951.

Contributions to scientific events and conferences

2019:

Frank, T., Arnberger, A., Bohner, A., Brandl, M., Hussain, R. I., Maas, B., Moser, D., **Walcher, R.**, Zaller, J. G., 2019. Agrobiodiversity: abandonment of mountainous grasslands and establishment of lowland grasslands.

[49th Annual Conference of the Ecological Society of Germany, Austria and Switzerland (GfÖ), Münster, GERMANY, Münster, GERMANY, SEP 9-13, 2019] In: *Gesellschaft für Ökologie, Verhandlungen der Gesellschaft für Ökologie*, **49**, 120-120.

2018:

Bohner, A., Karrer, J., **Walcher, R.**, Brandl, D., Michel, K., Arnberger, A., Frank, T., Zaller, J. G., 2018. Ökologische Auswirkungen der Flächenstilllegung von gemähten Halbtrockenrasen: Fallstudien in drei Bergregionen in den Ostalpen. [18. Österreichische Botanik-Tagung & 24. Internationale Tagung der Sektion für Biodiversität und Evolutionsbiologie der Deutschen Botanischen Gesellschaft, Klagenfurt am Wörthersee, September 19-22, 2018], *Carinthia II*, **68**, 15-15.

Hussain, R. I., **Walcher, R.**, Brandl, D., Jernej, I., Arnberger, A., Zaller, J. G., Frank, T., 2018. Influence of abandonment and monitoring methods on syrphid composition in mountainous meadows of Austrian and Swiss Alps. [Poster] [48th Annual Conference of the Ecological Society of Germany, Austria and Switzerland (GfÖ), Vienna, AUSTRIA, 10.09.2018 - 14.09.2018] In: *Gesellschaft für Ökologie e.V. (GfÖ), Verhandlungen der Gesellschaft für Ökologie*, Band **47/48**.

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2017:

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