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**IMPACT OF LAND USE CHANGE IN MOUNTAIN SEMI-DRY
MEADOWS ON PLANTS, DECOMPOSITION AND EARTHWORMS**

Master thesis

In partial fulfilment of the requirements

for the degree of

“Dipl.-Ing.”

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Mai 2018

Acknowledgements

First, I would like to thank Univ. Prof. Mag. Dr. Thomas Frank and Assoc. Prof. Dr. Johann Zaller for the chance to become a part of the project „Healthy Alps”, as well as for the professional supervision, guidance and the patience in answering my questions throughout the process of my research.

Furthermore, I want to thank DI Ronnie Walcher and Raja Imran Hussain, MSc. for the support in the fieldwork and statistical analyses. I also want to thank Dr. Andreas Bohner, who helped a lot with plant species determination in the field. In addition, I would like to thank all the people at the Institute of Zoology for the organizational help and the friendly integration in the institute.

Finally, I want to thank my family, friends and work colleagues for all the encouragement. Above all, I am grateful to my mother and Michael, who were both very patient, supportive and helped me during the whole process of my research.

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Abstract

Farming has created different agricultural landscape types and shaped the rural areas. However, ongoing socio-economic changes are following two trends on mountain meadows: intensification of sites that are easily accessible and abandonment of those that are difficult to manage. Both trends are known to affect plant diversity directly, while influencing indirectly litter decomposition via changes in abiotic conditions, plant assemblage and the quality of litter. Effects on plant diversity are additionally expected to affect earthworm activity, diversity and assemblages. It was investigated whether abandonment of extensively managed mountain meadows affects plant parameters, litter decomposition and earthworms. Four managed (mown once a year, no fertilization) and four abandoned (no mowing, no fertilization) semi-dry meadows in a mountain region in Austria were surveyed in June and August 2016. Plant parameters (species richness, plant cover, plant traits, biomass), litter decomposition (tea bag index) and earthworm parameters (species richness, density, biomass) were assessed. Additionally, soil parameters (temperature, moisture, electric conductivity) were measured. Plant species richness was significantly higher in managed than in abandoned meadows. Furthermore, management types resulted in different plant species assemblages. In managed meadows, hemi-rosette and ruderal plant species were more abundant, while more erect growing plant species occurred in abandoned meadows. The structure of plant biomass showed differences mainly in a higher necromass in abandoned sites. Decomposition rate was significantly higher in abandoned sites and correlated positively with higher necromass. Earthworm parameters showed marginal management effects, with marginally higher earthworm density in managed meadows. Moreover, the density of juvenile and endogeic earthworms was marginally higher in managed sites. Both management types harboured similar earthworm species. It is concluded that management has a strong impact on plants above ground, which subsequently alters microenvironmental conditions and soil community via various complex interactions. In order to sustain plant and earthworm biodiversity in this study region both abandoned and extensively managed meadows matter.

Zusammenfassung

Ländliche Gebiete sind geprägt von unterschiedlichen Landschaftstypen, die durch landwirtschaftliche Nutzung entstanden sind. Sozioökonomische Veränderungen haben zwei Trends zu Folge, die bis heute andauern: Nutzungsintensivierung von leicht zugänglichen Flächen und Auflassung von schwer zu bewirtschaftenden Flächen. Beide Trends haben direkte Auswirkungen auf die Pflanzenvielfalt. Zudem beeinflusst die landwirtschaftliche Nutzungsintensität indirekt den Streuabbau sowie die Regenwurmgemeinschaft durch Veränderungen der abiotischen Bedingungen, der Pflanzenzusammensetzung und der Streuqualität.

Diese Studie untersuchte, ob die Einstellung der Bewirtschaftung Auswirkungen auf die Vegetation, den Streuabbau und die Regenwürmer hat. Dazu wurden vier bewirtschaftete (jährliche Mahd, keine Düngung) und vier brachliegende (keine Mahd, keine Düngung) montane Halbtrockenrasen in Österreich im Juni und August 2016 untersucht. Die aufgenommenen Messdaten umfassten Pflanzenparameter (Artenreichtum, Deckung, Pflanzeigenschaften, Biomasse), Streuabbau (tea bag index), Regenwurmparameter (Artenreichtum, Dichte, Biomasse) sowie Bodenparameter (Temperatur, Feuchtigkeit, elektrische Leitfähigkeit).

Die bewirtschafteten Halbtrockenrasen enthielten signifikant mehr Pflanzenarten als die brachliegenden. Hinsichtlich der Pflanzenartengemeinschaft gab es signifikante Unterschiede zwischen den Bewirtschaftungsformen. Halbrosettenpflanzen sowie ruderale Pflanzenarten kamen signifikant häufiger in bewirtschafteten Halbtrockenrasen vor. Hingegen waren aufrecht wachsende Pflanzenarten vermehrt in den aufgelassenen Halbtrockenrasen zu finden. Die Einstellung der Mahd führte zu einer Streuanhäufung. Die Zersetzungsrate war in den aufgelassenen Flächen signifikant höher und korrelierte positiv mit der Streuanhäufung. Bewirtschaftete Flächen zeigten eine marginal höhere Regenwurmdichte sowie marginal mehr juvenile und endogäische Regenwürmer. Es konnte kein Unterschied in der Artengemeinschaft der Regenwürmer zwischen den Bewirtschaftungsformen festgestellt werden.

Die Wiesenbewirtschaftung hat einen starken Einfluss auf die Pflanzen, welche wiederum in Wechselwirkung mit dem Mikroklima sowie dem Bodenleben stehen. Zur Erhaltung der Biodiversität von Pflanzen und Regenwürmern sind sowohl aufgelassene als auch extensiv bewirtschaftete Halbtrockenrasen von Bedeutung.

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1 Introduction

The rural area of Austria is characterized by a high variety of natural, semi-natural and agricultural landscapes (Schmitzberger et al. 2005). Grasslands constitute an integral part of these landscapes. Most of them were developed by human land use (Moog et al. 2002, Hejzman et al. 2013) and some areas are still managed traditionally (Schmitzberger et al. 2005). Traditional farming practices (e.g. extensive mowing) are often related with high species biodiversity, so called biodiversity hot-spots (Schmitzberger et al. 2005). In particular, semi-dry, nutrient poor meadows represent high species rich plant assemblages and host many rare and protected plant and animal species (Bohner et al. 2003, Wilson et al. 2012). To protect these species rich grasslands, a regular extensive management constitutes a major role in natural conservation (Moog et al. 2002, Bohner et al. 2003).

All along, ongoing changes in cultural landscape reflect the development of political circumstances and human society (Hejzman et al. 2013). Socio-economic trends lead to a decline of traditional farming practices. Furthermore, small farms are being replaced by modern and larger farms (Marini et al. 2011). Hence, two contrasting patterns have been observed: Intensification (fertilization, earlier and increased mowing) of easily accessible high-yield areas on the one hand, and abandonment on the other hand in areas that do not allow mechanized agricultural techniques (MacDonald et al. 2000, Tasser & Tappeiner 2002, Niederist et al. 2009). In this context, heavily farmed mountain meadows have been increasingly abandoned (Niederist et al. 2009) resulting in a reduction of these semi-natural grasslands within Europe (Baur et al. 2006) and a loss of these biodiversity hot-spots.

Land use changes are supposed to be the most important driving force for changes in the vegetation (Tasser & Tappeiner 2002). As succession starts immediately after abandonment, the vegetation type indicates the time passed since abandonment (Tasser & Tappeiner 2002). Succession is characterized by a decrease in plant species richness resulting in a plant assemblage dominated by only a few species. Furthermore, plant functional diversity changes and species composition shifts towards dwarf shrub or forest communities (Tasser & Tappeiner 2002, Maurer 2005, Niederist et al. 2009, Bohner et al. 2003, Rolecek et al. 2014).

A declining in plant diversity is accompanied by the decrease in essential ecosystem functions and services (Hooper et al. 2005). Decomposition of organic matter is a key process in ecosystems, e.g. driving the nutrient cycle through the breakdown of organic materials and the release of nutrient for the use of plants (Ebeling et al. 2014). Decomposition is therefore influenced by changes in species composition and the functional characteristics of the

vegetation (Hooper & Vitousek 1997, Meier & Bowman 2008). Furthermore, decomposition is affected by physical factors (e.g. climate) and the presence of decomposers, e.g. earthworms, since they influence soil microbial communities and thus the decomposition of organic matter (Lavelle et al. 1998, Seeber et al. 2006). Earthworms represent a large component of the animal biomass in soils (Lavelle & Spain 2001). They are considered as ecosystem engineers, playing an important role in the soil formation and the nutrient cycle (Lavelle et al. 1997, Blouin et al. 2013). Undoubtable, there are interactions between plants and earthworms (Zaller & Arnone III 1999, Zaller & Arnone III 1999a, Eisenhauer et al. 2009, Eisenhauer et al. 2009a, Van Groeningen et al. 2014, Mariotte et al. 2016). Earthworms are supposed to be sensitive to a reduction of plant diversity and a shift in key functional groups (Zaller & Arnone III 1999a, Spehn et al. 2000, Piotrowska et al. 2013), which come along with the abandonment of meadow management.

Consequently, management may alter the decomposition rate and the earthworm population indirectly via changes in plants above ground.

Based on this knowledge the aim of the current study was to investigate the impact of management on mountain semi-dry meadows on vegetation, decomposition rate and earthworms. Therefore, following hypothesis were set up and examined:

- (i) There is a difference in plant species richness, plant species assemblages, plant biomass and plant traits between abandoned and managed mountain semi-dry meadows.
- (ii) There is a difference in decomposition between abandoned and managed mountain semi-dry meadows.
- (iii) There is a difference in earthworm species richness, earthworm species assemblages, density, biomass and ecological groups of earthworms between abandoned and managed mountain semi-dry meadows.

2 Material and methods

This thesis is part of the research project „Alpine landscape under global change: Impacts of land-use change on regulating ecosystem services, biodiversity, human health and well-being” (short title: Healthy Alps). The project examines the impact of land-use management and whether there are connections between natural science and the human health. Regarding natural science, a recent study within the project reported an impact of management on species richness and abundance of bumblebees. Furthermore, there were different species assemblages of bugs and grasshoppers in managed and abandoned meadows (Walcher et al. 2017). Another study within the project Healthy Alps concluded a higher abundance of syrphids in managed than in abandoned meadows (Hussain et al. 2017).

The present master thesis is a partial replication of Johannes Karrer’s survey in 2015 (related to vegetation and decomposition) with an extension of the investigation of earthworms in Styria. The field work was carried out together with Ronnie Walcher, Raja Imran Hussain (both doctor students at BOKU Institute of Zoology) and Andreas Bohner (Plant ecologist at HBLFA Raumberg-Gumpenstein) in June and August 2016.

2.1 Study region

The study took place in the Central Ennstal (Long-Term Socio-economic and Ecosystem Research - LTSER region Eisenwurzen, Styria, Austria) across eight study sites in the municipalities of St. Gallen, Pürgg and Irdning. All sites are located in temperate sub-oceanic climate with an altitude of 660 – 790 m above sea level, mean annual air temperature of 6.9 °C and mean annual precipitation of 1087 mm.

The study was conducted in June and August 2016. Altogether, four extensively managed and four abandoned meadows were surveyed. Each managed meadow was mown once a year without any fertilizer input. The abandoned meadows were in cessation of mowing for 20-40 years. Before cessation, they were extensively managed and never grazed. The information about management was obtained from interviews with land owners.

2.2 Experimental setup and analysis

2.2.1 Vegetation

The experimental setup followed the study design of Johannes Karrer, which was done in 2015 on the same meadows (Karrer 2015).

For vegetation measurements (flower cover, plant species, plant biomass and plant traits), four equally distributed 1x1 m study plots were chosen randomly on each meadow. Therefore, a frame was placed on the vegetation (Figure 1A, B).



Figure 1: Plots of 1 m² for vegetation measurements on managed (A) and abandoned (B) meadows, and a plot where biomass was harvested (C).

2.2.1.1 Flower cover

In June, a top-view photo of the study plot was taken and analysed later to estimate the flower cover (%). Using EazyDraw (Version 2.10.6), a grid was placed on the photo with 100 sections in total. The same approach was planned for vegetation cover (calculating free spots of vegetation in the photo), but this had to be cancelled because it was not possible to identify these spots. In August, flower cover was estimated by using the same procedure as in June.

Flower cover was recorded for further analyses by Ronnie Walcher and Raja Imran Hussain for studies of pollinator diversity and activity.

2.2.1.2 Plant species

Many studies have shown that management influences the plant species richness. Both, intensification and abandonment of grassland can decrease species richness (Tasser & Tappeiner 2002, Bohner et al. 2003, Marini et al. 2007, Niederist et al. 2009, Rolecek et al. 2014). In contrast, regular extensive management is known to support high species richness (Moog et al. 2002, Bohner et al. 2003, Niederist et al. 2009). In this study species richness (number of species), complemented by Shannon index and Evenness, determine the above mentioned changes in plant species diversity.

In June, vascular plant species within the plots were identified (Fischer et al. 2008) and noted if flowering. As a next step, plant species cover was estimated according to Braun-Blanquet (1964) with a modified scale for species cover containing three subdivisions per cover class (Bohner et al. 2012). For the purpose of statistical analyses, means of each adapted Braun-Blanquet scale were calculated, as each cover class stands for a range between a minimum and maximum cover value in per cent (r = 0.1 %, + = 0.6 %, 1a = 1.5 %, 1 = 3 %, 1b = 4.5 %, 2a = 8.5 %, 2 = 16 %, 2b = 23 %, 3a = 28 %, 3 = 38.5 %, 3b = 48 %, 4a = 53 %, 4 = 62.5 %, 4b =

72 %, 5a = 78 %, 5 = 88 %, 5b = 97.5 %). Number of plant species (species richness) were counted per meadow and mean plant cover was calculated for each meadow.

Shannon index and Evenness were calculated in Excel (Microsoft 2017). Shannon index considers the number of species and the relative frequency. Evenness is a value for equal distribution of individuals and complements the Shannon index. The closer the Evenness is to 1, the higher is the equal species distribution in the meadows (Mühlenberg 1993).

In August again, plant species which have not been listed in June, were added to the list, by using the same procedure as in June. In addition, the number of flower-classes and flower-colours of present flowering species were counted for further research by Ronnie Walcher and Raja Imran Hussain.

While the identification of plant species and estimation of plant species cover was done together with Andreas Bohner in June, the repeated check of plant species in August was done only by the thesis author.

2.2.1.3 Plant biomass

Besides the species richness, the composition of plant functional groups is an important determinant of ecosystem processes (Tilman et al. 1997, Hooper & Vitousek 1997). As land use changes are known to influence the cover of functional groups (Dullinger et al. 2003), these shifts may also appear in the structure of plant biomass. Additionally, abandonment is supposed to cause an increase in litter accumulation (Kelemen et al. 2014). To detect the mentioned changes in plant biomass, the biomass was divided into necromass and living biomass of three functional groups, namely grasses (Poaceae, Juncaceae and Cyperaceae), legumes (Fabaceae) and non-legume herbs (including mosses and seedlings of woody vegetation if present). Due to the ability to directly use atmospheric nitrogen, legumes play a key role in nitrogen accumulation in grassland and affect the nitrogen budget of plant communities (Spehn et al. 2002). Grasses are supposed to be more resistant against above-ground management because their leaves and apical meristems are situated below ground (Maurer 2005). Furthermore, grasses are superior competitors in grassland systems and can suppress the biomass of herbs (Del-Val & Crawley 2005). Management can increase necromass due to accumulation of dead plant material in abandoned meadows, which is a major mechanism in structuring grassland diversity (Kelemen et al. 2013, Kelemen et al. 2014).

In June, for this purpose, all four 1 m²-plots were separated in four sections of 0.25 m² using two sticks. One section of each plot was harvested at a height of 4 cm and separately collected in labelled bags (Figure 1C). In the laboratory, necromass and functional groups (grasses,

legumes and non-legume herbs) were sorted and packed in small labelled paper bags. To calculate the dry biomass, the bags were dried at 60°C for 72 hours in a Memmert UF 260 drying oven (Memmert GmbH Co. KG, Schwabach FRG, Germany) and then weighted with a Mettler PC440 balance (Mettler-Toledo Intl-Inc., Greinfensee-Zürich, Switzerland). For preparing statistical data, weight was extrapolated to plot size of 1 m² and the mean for each abandoned and managed meadow was computed using Excel (Microsoft 2017).

2.2.1.4 Plant traits

For further determination of changes in biodiversity, analyses of plant traits in a community can be useful (McGill et al. 2006, Fontana et al. 2014). Therefore, the list of plant species was complemented by Ellenberg indicator values (Ellenberg 1992), rosette-types and plant strategy types, extracted from BIOLFLOR Database (Klotz et al. 2002).

By means of Ellenberg indicator values, the ecological performance of species and the abiotic conditions in the study sites can be estimated. The following indicators were chosen for the study: light availability, soil humidity and soil fertility (Ellenberg 1992).

Depending on natural competition, stress and disturbances, three different main forms of strategy types have developed during the evolution of plants (Grime 1977). These forms are supplemented through secondary strategies, which are adapted to intermediate intensities. The main strategies are competitors, stress-tolerators and ruderals. Generated in relatively undisturbed conditions, competitors evolved selection for highly competitive abilities. They are characterized by small seed production, rapid growth rate and lateral shoot spread above and below ground. Stress tolerators own adaptations which allow endurance in unproductive condition. These plants have a wide range of shoot growth form, a slow growth rate and small seed production. The shoots of ruderals are limited by lateral spread, have a short life span, grow rapidly and have a high annual seed production. These characteristics allow ruderals to be present in severely disturbed areas (Grime 1977). The strategy types were calculated as follows (numbers in brackets indicate weighted characteristics of the different strategy types, i.e. competitors, stress tolerators, ruderals): c (competitor) = (1, 0, 0); s (stress tolerate) = (0, 1, 0); r (ruderal) = (0, 0, 1); cs (competitive, stress tolerate) = (0.5, 0.5, 0); cr (competitive, ruderal) = (0.5, 0, 0.5); sr (stress tolerate, ruderal) = (0, 0.5, 0.5); csr (completely intermediate) = (0.33, 0.33, 0.33).

Growth form of plants can be associated with land use (Cornelissen et al. 2003) and can be influenced through changes in management (Mitchly & Willems 1995). To analyze the management effect on plant growth form in this study, the following forms were selected (Klotz

et al. 2002): rosette: compressed internodes, crowded arranged leaves, only lower-bearing section consists of stretched internodes, hemi-rosette: shoot axis consisting of a rosette-forming and a stretched part, and erect growing: stretched shoot axis with leaves in equal distance to each other.

Besides this plant traits, life form, life span, reproduction, flower colour and flower class were attached from BIOLFLOR Database (Klotz et al. 2002) as a need for further research by Ronnie Walcher and Raja Imran Hussain.

After adapting all plant species with the above mentioned parameters, means of the different traits were computed for each managed and abandoned meadow in Excel (Microsoft 2017).

2.2.2 Litter decomposition

Decomposition of organic matter is a key ecosystem process, transforming dead organic material into simpler states with the release of biological nutrients for further use by microorganisms and plants (Lavelle & Spain 2001). Litter decomposition is influenced by abiotic conditions, decomposers, plant community and quality of litter (Lavelle & Spain 2001, Seeber et al. 2006, Ebeling et al. 2014). Hence, discussion of possible (indirect) management effects on decomposition is obvious.

For determining litter decomposition, the “Tea Bag Index” (TBI) was calculated following the approach of Keuskamp et al. (2013). The TBI is a novel approach to measure decomposition rate in the soil and furthermore, to compare carbon decomposition dynamics between ecosystems. TBI is based on the weight loss of litter material and comprises two parameters, decomposition rate k and litter stabilization factor S . While k defines rapidly decomposed plant material with easily degradable compounds, S is the labile fraction, which stabilise and become recalcitrant during decomposition (Keuskamp et al. 2013).

Therefore, Lipton rooibos tea bags (EAN: 87 22700 18843 8) and Lipton green tea bags (EAN: 87 22700 05552 5) were dried at 70 °C for 1 hour in a Memmert UF 260 drying oven (Memmert GmbH Co. KG, Schwabach FRG, Germany). Then each tea bag was weighted separately and marked. In June, 20 tea bags were buried pairwise in 8 cm depth in each meadow (Figure 2). To find all tea bags after incubation time, tea bag labels were tacked with a nail visible on the surface. In addition to that, location characteristics were mapped. The tea bag pairs were buried in a circle of 2 m radius within a representative area in the meadow (exposition, slope, shading by trees). After 68-71 days, tea bags were removed and sorted into labelled bags per each site. If tea bags could not be found, a metal detector was used.

Since hardly any roots remained in the tea bags, as recorded contrary by Karrer (2015), the further procedure was done in accord with Keuskamp et al. (2013). In the laboratory tea bags were cleaned from soil particles with a toothbrush and dried in a Memmert UF 260 drying oven (Memmert GmbH Co. KG, Schwabach FRG, Germany) for 48 h at 70 °C and weighted.

For the calculation of the TBI the provided calculated hydrolysable fraction (H; 0.842 g g⁻¹ for Green tea; 0.552 g g⁻¹ for Rooibos tea) was used (Keuskamp et.al 2013). Afterwards, the mean per meadow was computed for statistical analyses in Excel (Microsoft 2017).



Figure 2: Burrowing pairs of tea bags in the meadows.

2.2.3 Earthworm sampling

While effects of grassland management have been well studied for plant communities, little is known about effects on soil organisms such as earthworms. However, some studies explored an interaction between plants and earthworms (Brown 1995, Zaller & Arnone III 1999, Zaller & Arnone III 1999a, Eisenhauer et al. 2009, Eisenhauer et al. 2009a, Van Groenigen et al. 2014, Mariotte et al. 2016). Earthworms are known to influence the density, diversity, structure and activity of microfloral and faunal community. This happens through their soil activities (comminution, burrowing and casting, grazing and dispersal) which alter the soil's physico-chemical and biological status (Brown 1995). In this context, management can influence the earthworm population indirectly via vegetation changes.

The earthworm survey was done in June and August following the same approach. On each meadow five sampling plots were chosen randomly in equal distance of five meter. Next, a 25x25x25 cm hole was dug using a frame supporting to bury the correct size (Figure 3A, B). The excavated cube was put on a plastic sheet and every earthworm found was collected in a labelled plastic bottle filled with a solution of 4 % formol.

The earthworm data contain earthworm species, density (number of earthworms) and earthworm biomass in abandoned and managed meadows. In addition, specific biomass was computed to see whether individual earthworm weight is affected by management. Furthermore, age structure and ecological groups were differentiated within the data. In scientific literature, earthworm species are divided in three ecological groups, namely endogeic,

anecic and epigeic (Bouché 1977). Classification depends upon the services they provide based on their burrowing and feeding activities, and vertical distribution in the soil. Endogeic species are unpigmented or lightly pigmented, of medium size, make horizontal burrows in the upper 10-15 cm of soil and feed on mineral soil with rotted organic matter. Anecic species are usually dorsally pigmented, large, make vertical burrows down into mineral soil horizon and feed on decomposing litter on the soil surface pulled into the burrows. Epigeic species are pigmented ventrally and dorsally, small, live in the upper few centimeters of soil and feed on decomposing litter on the soil surface (Bouché 1977).

In the laboratory, each sample was washed first and selected into juvenile and adult earthworms. Juvenile earthworms without a clitellum (as a clitellum is needed for exact identification) were sorted into ecological groups, counted and weighted. Adult earthworms (with a clitellum) were identified after Brohmer (1984), allocated to the ecological groups, counted and weighted. Except for number of earthworm species (earthworm species richness, counted per meadow), the data were extrapolated to plot size of 1 m². Specific biomass and the mean of each parameter in every abandoned and managed meadow was calculated using Excel (Microsoft 2017).

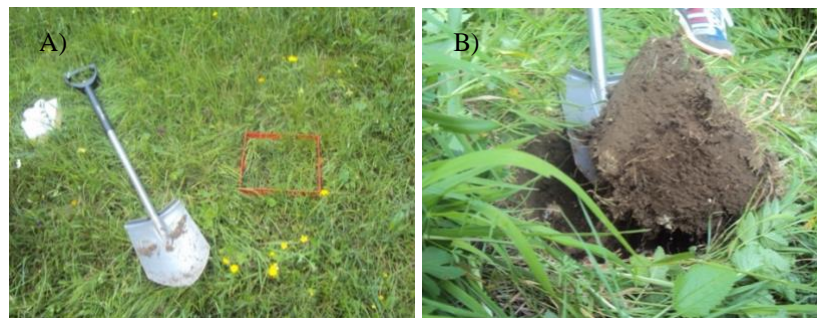


Figure 3: Frame of 25x25x25 cm (A) and the excavated cube of soil (B).

The study intended to examine earthworm activity through collecting earthworm surface casts in the meadows. Due to the high and partially dense vegetation, this sampling approach was not possible and had to be cancelled.

Earthworm abundance is affected by various external factors and biotic interactions within soil communities (Curry 1998). As climate and soil parameters determine the earthworm habitat, it is important to include soil temperature, soil moisture, electric conductivity (EC) and pH in the analyses. Therefore, before digging the hole, soil moisture, temperature and electric conductivity (EC) were measured on each earthworm sampling plot in June and August using the time domain reflectometry (TRIME®-PICO 64/32, HD2, IMKO Micromodultechnik GMBH, Ettlingen, Germany). The pH results were used from Karrer (2015). For statistical analyses, the mean per meadow was calculated.

3 Statistical analyses

All variables were checked for normal distribution using Shapiro-test. Using Fligner-test and Bartlett-test, the homogeneity of variance (homoscedasticity) was tested.

The effects of the management type (managed and abandoned) were examined using GLMs with a Poisson distribution for species richness and GLMs with a Gaussian distribution for variables fulfilling the assumptions for parametric tests. In addition, time effects and the interaction between management and time were checked. Effects of management on parameters which were not fulfilling the assumptions, were analysed using non-parametric Kruskal-Wallis test and Scheirer-Ray-Hare test to check management and time interactions.

The relationships between different parameters were analysed using Pearson correlation and Spearman correlation, for not normally distributed variables. All statistical analyses were performed in R version 3.3.1 (R Core Team., 2016) using an alpha level of 0.05.

To assess differences in species assemblages of plants and earthworms between abandoned and managed meadows, a principal coordinate analysis (PCO) was conducted based on a resemblance matrix of Bray-Curtis similarity measures. PERMANOVA was computed to test for significant differences in species assemblages between abandoned and managed meadows. Residuals were permuted 9999 times under a reduced model. PCO and PERMANOVA were performed in the Primer version 6.1.13 with PERMANOVA+ (PRIMER-E Ltd., Plymouth, UK).

4 Results

4.1 Vegetation

4.1.1 Plant species

In total 149 different plant species were recorded in the meadows. 93 species were found in abandoned and 118 in managed meadows. Management had a significant effect on species diversity. Species richness (Figure 4A), Shannon-index (Figure 4B) and Evenness (Figure 4C) were significantly higher in managed compared to abandoned meadows.

The dominant species in abandoned meadows was *Brachypodium pinnatum* which occurred in all sampling plots with a mean cover of 31.84 %, followed by *Laserpitium latifolium* (mean cover 7.50%). In contrast, the cover of individual species in managed meadows was more equal. *Bromus erectus*, which was present in half of the plots with a mean cover of 8.88 %, was the predominant species in managed meadows, followed by *Astrania major major* and *Festuca rubra rubra* with a mean cover of 7.88 % and 6.18 %, respectively (Table 1). Plant cover was similar in abandoned and managed sites (Table 2).

PCO revealed a clear separation of species assemblages between abandoned and managed meadows (Figure 5), which was significantly different (PERMANOVA, $P = 0.028$).

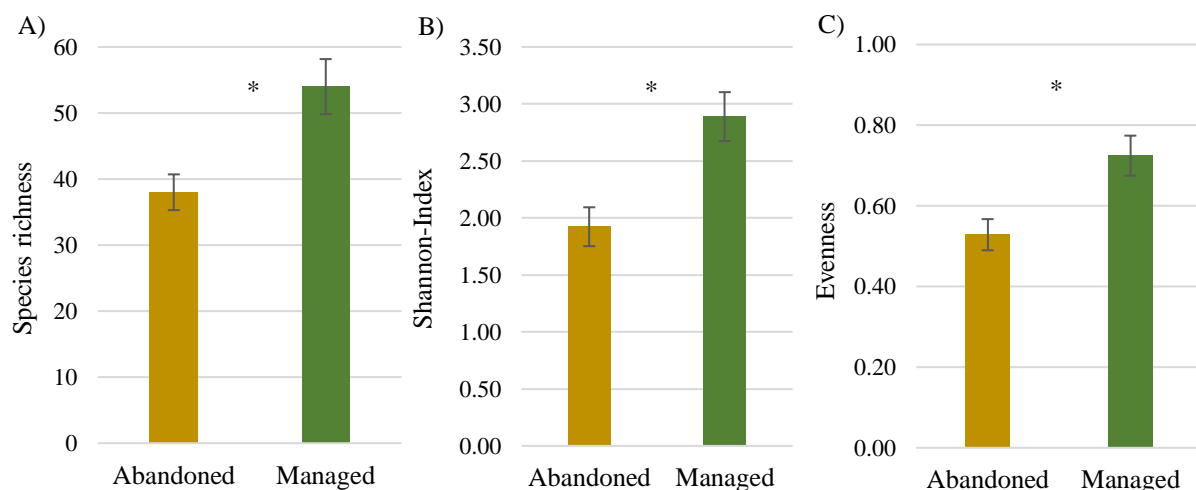


Figure 4: Species richness, Shannon-Index and Evenness describing plant species diversity in abandoned and managed meadows. * denotes significant difference between management types ($p < 0.05$). Mean \pm SD, $n = 4$.

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Table 1: Most frequent species in abandoned and managed meadows with mean cover and frequency. Species are ordered by descending cover.

Abandoned meadows			Managed meadows		
Species	Cover (%)	Frequency (%)	Species	Cover (%)	Frequency (%)
<i>Brachypodium pinnatum</i>	31.84	100.00	<i>Bromus erectus</i>	8.88	50.00
<i>Laserpitium latifolium</i>	7.50	25.00	<i>Astrantia major major</i>	7.88	56.25
<i>Galium album</i>	6.53	81.25	<i>Festuca rubra rubra</i>	6.18	100.00
<i>Astrantia major major</i>	4.85	43.75	<i>Rhinanthus glacialis</i>	4.94	50.00
<i>Festuca rubra rubra</i>	4.26	68.75	<i>Sesleria caerulea</i>	4.00	25.00
<i>Trifolium medium medium</i>	1.35	31.25	<i>Betonica alopecuros</i>	3.10	25.00
<i>Betonica officinalis</i>	1.08	37.50	<i>Thymus pulegioides pulegioides</i>	3.01	62.50
<i>Rubus caesius</i>	1.00	6.25	<i>Medicago falcata</i>	2.57	25.00
<i>Aegopodium podagraria</i>	0.97	50.00	<i>Prunella grandiflora</i>	2.48	43.75
<i>Clinopodium vulgare</i>	0.94	62.50	<i>Euphorbia cyparissias</i>	2.38	25.00
<i>Poa angustifolia</i>	0.83	43.75	<i>Potentilla erecta</i>	2.19	62.50

Table 2: Plant parameters in response to meadow management. Means \pm SD, n = 4. GLM and Kruskal-Wallis¹⁾ results. Values written in bold denote significant results.

Parameter	Management		Statistical difference		
	Abandoned	Managed	Res. dev.	χ^2	p
Plant cover (%)	72.20 \pm 3.48	82.93 \pm 16.90		1.33	0.248 ¹⁾
Total biomass (g m ⁻²)	359.54 \pm 81.29	226.06 \pm 67.32	33432.00		0.045
Living biomass (g m ⁻²)	241.98 \pm 48.39	191.49 \pm 42.84	12530.00		0.169
Ellenberg indicators					
Light indicator	6.77 \pm 0.23	7.00 \pm 0.14	0.21		0.136
Humidity indicator	4.66 \pm 0.52	4.42 \pm 0.47	1.48		0.529
Fertility indicator	3.96 \pm 0.57	3.72 \pm 0.84	3.10		0.647

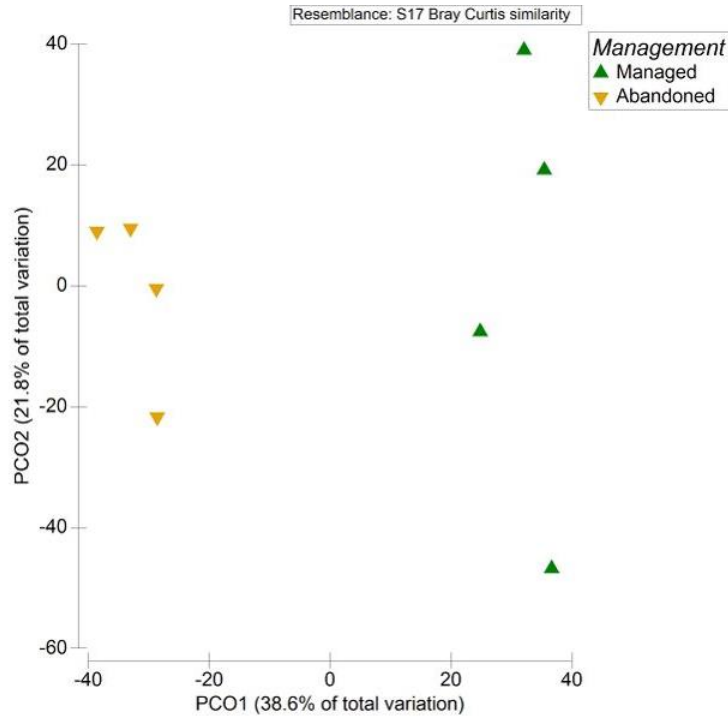


Figure 5: Principal coordinate analysis (PCO) showing the distribution of plant species assemblages between managed and abandoned meadows.

4.1.2 Plant biomass

Total biomass was significantly higher in abandoned meadows (Table 2). Furthermore, the structure of functional groups in the plant assemblage was influenced by management. Analysed in detail, legumes constitute the smallest and grasses the major part of total biomass in both management types. Abandoned meadows had significantly higher necromass, and grasses were marginally higher in this management type. Herbs and legumes exhibited no differences in management (Figure 6A). In contrast, considering the proportion of total biomass (%), herbs and necromass differed significantly due to management, with higher proportion of herbs in managed meadows and necromass in abandoned meadows (Figure 6B).

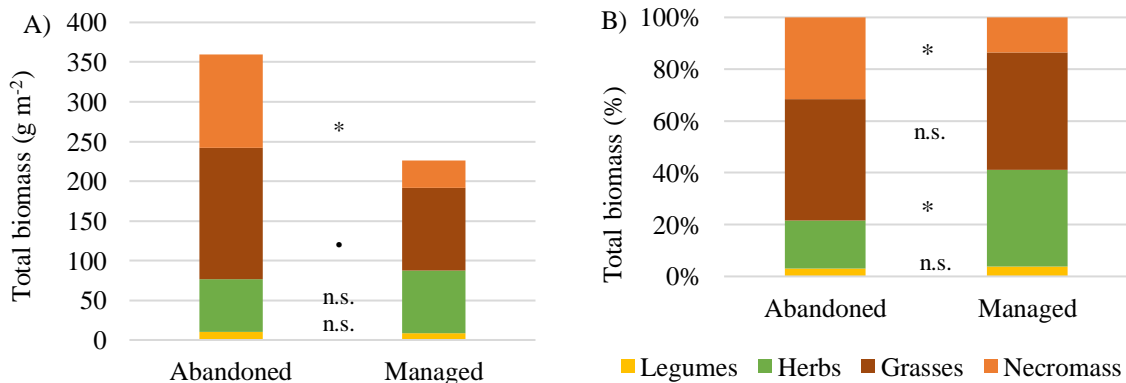


Figure 6: Structure of total biomass (g m^{-2}) (A) and proportion of total biomass (%) (B) in abandoned and managed meadows. * denotes significant difference between management types ($p < 0.05$), * denotes marginal difference ($p < 0.1$), n.s. denotes no significant difference. Mean \pm SD, $n = 4$.

4.1.3 Plant traits

Management had no significant influence on the different measured Ellenberg indicators.

Within the plant strategy types, competitors were predominant in both treatments. Ruderal plants had a significantly higher proportion in managed meadows. The proportion of competitors and stress-tolerators showed no differences between management types (Figure 7A).

The predominant growth-form in both management types was hemi-rosette. In abandoned meadows, significantly more erect growing and less hemi-rosette plant species were found. Proportion of rosette plant species showed no significant difference (Figure 7B).

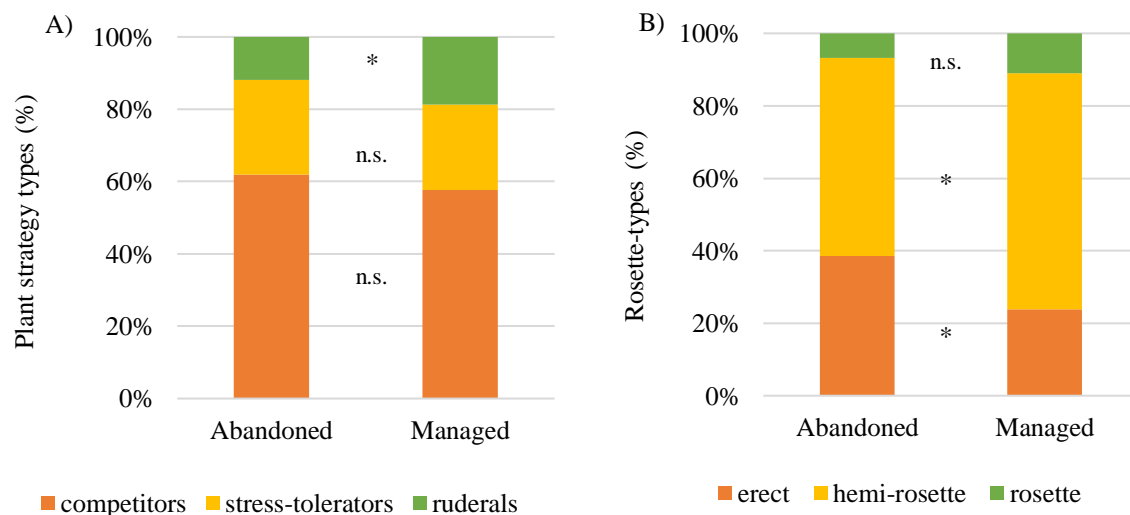


Figure 7: Proportion of plant strategy types (A) and rosette-types (B) in abandoned and managed meadows. * denotes significant difference between management types ($p < 0.05$), n.s. denotes no significant difference. Mean \pm SD, $n = 4$.

4.2 Litter decomposition

In total 80 pairs of tea bags were buried in each meadow. 13 pairs of tea bag in managed and 4 pairs in abandoned meadows could not be found in August or were defect. Decomposition rate k was significantly higher in abandoned meadows (Figure 8A). For stabilisation factor S , no significant difference was found (Figure 8B).

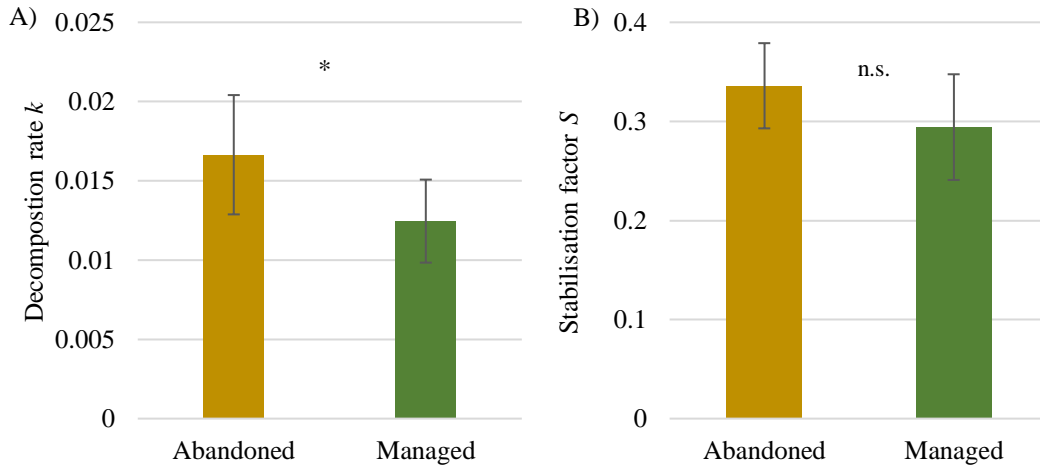


Figure 8: Decomposition rate k (A) and stabilisation factor S (B) measured with tea bag index in abandoned and managed meadows. * denotes significant difference between management types ($p < 0.05$), n.s. denotes no significant difference. Mean \pm SD, $n = 4$.

4.3 Earthworms

In total, seven species were found in all meadows. Ranked, *Aporrectodea rosea* and *Octolasion lacteum* were the most abundant species across management type, followed by *Aporrectodea caliginosa* in abandoned meadows and *Lumbricus rubellus* in managed meadows. Three species were endogeic and three were epigeic. Only one species belonged to the ecological group anecic, with two recorded individuals in managed sites (Table 3). Earthworm assemblages were similar between management types (PERMANOVA, $P = 0.642$; Figure 9A) and time (PERMANOVA, $P = 0.330$; Figure 9B). Additionally, there was no significant management effect, time effect or interaction effect of management and time on species richness (Table 4).

Table 3: Adult earthworm species found in abandoned and managed meadows with mean density of individuals per species in June and August. Mean \pm SD, $n = 8$. Results do not include juvenile species with unclear identification.

Species	Ecological group	Density (earthworms m ⁻²)	
		Abandoned	Managed
<i>Aporrectodea rosea</i>	endogeic	44 \pm 56.57	52 \pm 62.12
<i>Octolasion lacteum</i>	endogeic	20 \pm 22.22	32 \pm 28.36
<i>Aporrectodea caliginosa</i>	endogeic	10 \pm 19.00	0 \pm 0.00
<i>Lumbricus rubellus</i>	epigeic	8 \pm 17.10	18 \pm 28.84
<i>Lumbricus castaneus</i>	epigeic	4 \pm 7.41	0 \pm 0.00
<i>Lumbricus polyphemus</i>	anecic	2 \pm 5.66	0 \pm 0.00
<i>Octolasion cyaneum</i>	endogeic	0 \pm 0.00	2 \pm 5.66

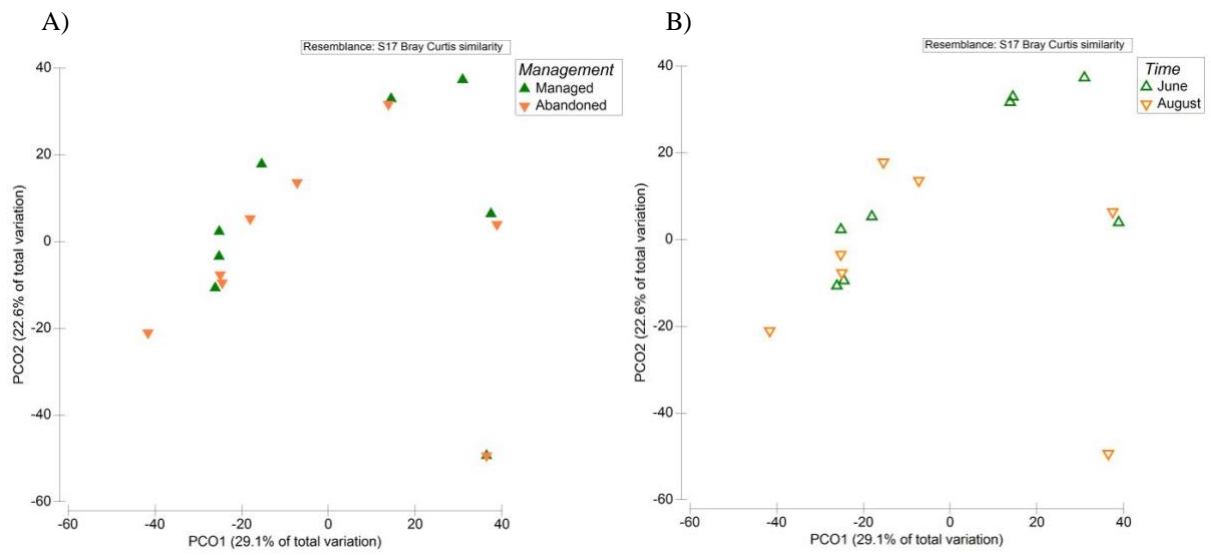


Figure 9: Principal coordinate analysis (PCO) showing the distribution of earthworm species assemblages between managed and abandoned meadows (A), and between June and August (B).

Table 4: Earthworm (EW) parameters in response to meadow management. Means \pm SD, n = 8. GLM and Kruskal-Wallis¹⁾ results showing the effect of management and time on earthworm parameters (df=1,15). GLM and Scheirer-Ray-Hare²⁾ results showing the effect of an interaction between management and time (df=1,15). Values written in bold denote (marginally) significant results. Results include data in June and August.

Parameters	Management				Statistical difference							
	Abandoned		Managed		Management			Time			Management x Time	
	Mean	SD	Mean	SD	Res. Dev.	χ^2	p	Res. Dev.	χ^2	p	Res. Dev.	p
EW species richness	2.25	\pm 1.28	2.13	\pm 1.25	14.18		0.866	12.80		0.240	12.75	0.890
EW density (EW m⁻²)												
total	75.20	\pm 24.37	105.20	\pm 31.61	11150.00		0.052	14606.00		0.716	10033.00	0.302
endogeic	65.20	\pm 23.51	92.80	\pm 35.67	12778.00		0.089	15543.00		0.622	11881.00	0.446
anecic	1.20	\pm 2.38	0.00	\pm 0.00		2.13	0.144 ¹⁾		0.01	0.927 ¹⁾	96.38	0.927 ²⁾
epigeic	8.80	\pm 8.51	12.40	\pm 7.54	904.96		0.386	925.44		0.502	821.76	0.401
juvenile	56.40	\pm 19.80	84.00	\pm 37.70	12691.00		0.088	14074.00		0.219	9950.70	0.277
adult	18.80	\pm 14.76	21.20	\pm 13.35	2772.50		0.738	1966.10		0.029	1940.50	0.902
EW biomass (g m⁻²)												
total	20.04	\pm 6.57	25.87	\pm 13.28	1536.00		0.285	1518.60		0.255	1382.90	0.995
endogeic	15.98	\pm 5.86	20.19	\pm 10.26	976.44		0.331	1003.00		0.445	932.08	0.993
anecic	0.59	\pm 1.16	0.00	\pm 0.00		2.13	0.144 ¹⁾		0.01	0.927 ¹⁾	96.38	0.927 ²⁾
epigeic	3.46	\pm 2.86	5.67	\pm 4.41	193.11		0.254	176.15		0.111	156.51	0.928
juvenile	11.71	\pm 4.60	16.07	\pm 7.76	569.50		0.192	645.19		0.911	566.80	0.836
adult	8.33	\pm 4.99	9.79	\pm 9.19	765.21		0.699	600.87		0.064	590.45	0.847
Specific biomass (g EW⁻¹ m⁻²)												
total	0.29	\pm 0.13	0.27	\pm 0.16	0.29		0.806	0.27		0.331	0.23	0.175
endogeic	0.26	\pm 0.10	0.25	\pm 0.15	0.23		0.941	0.22		0.443	0.18	0.152
anecic	0.04	\pm 0.07	0.00	\pm 0.00		2.13	0.144 ¹⁾		0.01	0.927 ¹⁾	96.38	0.927 ²⁾
epigeic	0.13	\pm 0.14	0.20	\pm 0.16	0.32		0.389	0.29		0.138	0.27	0.619
juvenile	0.23	\pm 0.10	0.21	\pm 0.15	0.21		0.742	0.22		0.852	0.18	0.160
adult	0.24	\pm 0.25	0.31	\pm 0.27		0.14	0.713 ¹⁾		2.83	0.093¹⁾	267.38	0.636 ²⁾

Total earthworm density and endogeic earthworm density were marginally higher in managed compared to abandoned meadows (Figure 10A, B). Further ecological groups (anecic and epigeic) did not significantly differ between meadow types. Marginally more juvenile earthworms were found in managed than in abandoned sites (Figure 10C). Time had a significant effect on the density of adult earthworms, with more adult earthworms in June than in August. Similarly, there was a marginally significant time effect on adult earthworm biomass and adult specific biomass, with higher biomass in June (Table 4).

Soil temperature, soil moisture, electric conductivity (EC) and pH were neither affected by management nor by time. Including interactions between management and time, soil temperature was marginally higher in abandoned meadows in June (Table 5).

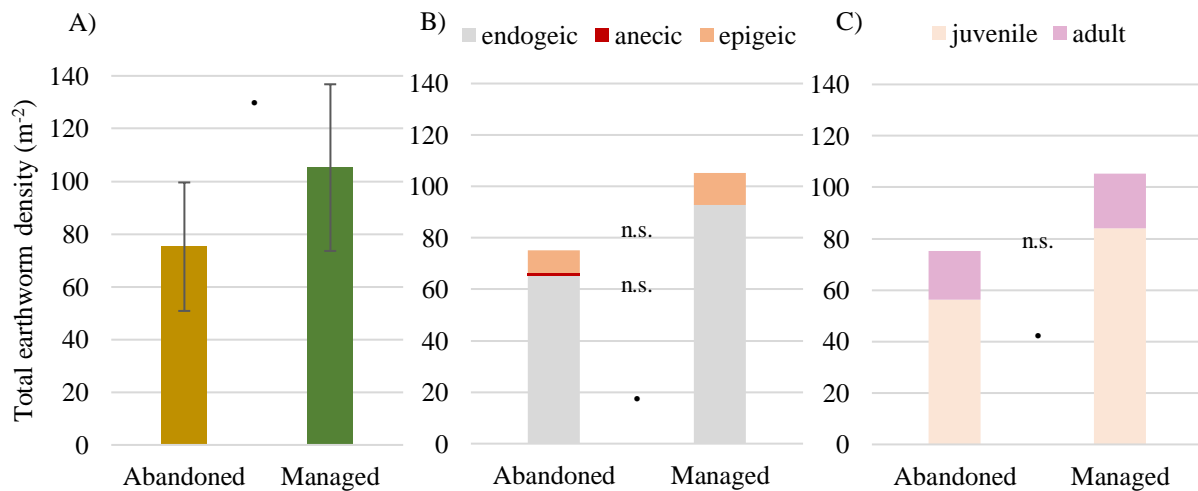


Figure 10: Total earthworm density (A), density of ecological groups (B) and density of age structure (C) in abandoned and managed meadows in June and August. • denotes marginally significant difference between management types ($p < 0.1$), n.s. denotes no significant difference. Mean \pm SD, $n = 8$.

Table 5: Soil parameters in response to meadow management. Means \pm SD, n = 8. GLM and Kruskal-Wallis¹⁾ results showing the effect of management and time on soil parameters (df=1,15). GLM and Scheirer-Ray-Hare²⁾ results showing the effect of an interaction between management and time (df=1,15). Values written in bold denote marginally significant results. Results include data in June and August.

Parameters	Management				Statistical difference							
	Abandoned		Managed		Management			Time			Management x Time	
	Mean	SD	Mean	SD	Res. Dev.	χ^2	p	Res. Dev.	χ^2	p	Res. Dev.	p
Soil temperature (°C)	23.36	\pm 4.65	22.89	\pm 5.73	380.73		0.858	360.23		0.377	266.15	0.063
Soil moisture (%)	33.48	\pm 7.96	34.63	\pm 5.48	653.50		0.742	608.24		0.299	602.85	0.959
Electric conductivity (EC) (dS m ⁻¹)	1.38	\pm 0.44	1.64	\pm 0.46	2.86		0.276	3.11		0.815	2.84	0.962
pH	7.26	\pm 0.08	7.08	\pm 0.40		0.18	0.673 ¹⁾		0.00	1.000 ¹⁾	332.00	1.000 ²⁾

4.4 Correlations

Table 6 represents various relations between vegetation parameters, soil parameters, earthworm parameters and litter decomposition for data in June. The results indicate a positive relation between total earthworm density and pH ($p = 0.029$). Juvenile earthworm density and juvenile biomass correlated marginally positive with pH ($p = 0.06$; $p = 0.069$). Earthworm density parameters were not significantly related to any soil parameters, vegetation parameters or litter decomposition.

Total earthworm biomass and adult earthworm biomass responded positively to higher biomass of herbs ($p = 0.025$; $p < 0.001$). No further significances could be found for parameters regarding the biomass of earthworms.

Further, total specific earthworm biomass correlated significantly positive, and adult specific biomass marginally positive with higher plant cover ($p = 0.037$; $p = 0.069$). Other relations regarding the specific biomass of earthworms were not significant.

Plant species richness decreased with increasing necromass ($p = 0.019$), as well as with higher decomposition rate ($p = 0.007$) and stabilization factor ($p = 0.032$). While the stabilization factor showed no further significant correlation, decomposition rate was significantly higher in the presence of higher necromass ($p = 0.004$) and higher biomass of grasses ($p = 0.014$).

Table 6: Correlations between earthworm (EW) parameters, soil parameters, vegetation parameters and litter decomposition in June. The table shows Pearson and Spearman¹⁾ correlation coefficients. Values written in bold denote (marginally) significant results.

Parameters	Soil parameters				Litter decomposition		Vegetation parameters							
	Temp (°C)	Mois (%)	EC (dS m ⁻¹)	pH ¹⁾	<i>k</i>	<i>S</i>	Plant species richness	Plant cover (%) ¹⁾	Total biomass (g m ⁻²)	Living biomass (g m ⁻²)	Necromass (g m ⁻²)	Legumes (g m ⁻²)	Herbs (g m ⁻²)	Grasses (g m ⁻²)
Earthworms														
EW species richness	0.034	-0.439	-0.390	0.026	0.275	-0.390	0.021	-0.039	-0.098	-0.265	0.066	-0.206	-0.401	-0.029
EW density (EW m⁻²)														
total	-0.323	0.025	0.224	*0.759	-0.360	0.240	0.200	-0.048	-0.379	-0.449	-0.280	-0.587	0.283	-0.500
juvenile	-0.248	-0.036	0.200	*0.687	-0.413	0.287	0.140	0.398	-0.363	-0.384	-0.312	-0.393	0.332	-0.487
adult	-0.245	0.107	0.127	0.228	-0.059	0.021	0.174	-0.571	-0.175	-0.280	-0.062	-0.537	0.035	-0.218
EW biomass (g m⁻²)														
total	-0.385	0.044	0.039	0.524	-0.540	0.034	0.262	0.571	-0.228	-0.133	-0.298	-0.419	*0.771	-0.459
juvenile	-0.113	-0.007	0.056	*0.690	-0.414	0.090	0.227	0.524	-0.329	-0.300	-0.327	-0.362	0.367	-0.427
adult	-0.582	0.095	-0.005	-0.024	-0.448	-0.064	0.180	-0.119	0.032	0.176	-0.105	-0.288	**0.963	-0.273
Specific biomass (g EW⁻¹ m⁻²)														
total	0.157	0.099	-0.010	0.381	-0.312	-0.053	0.220	*0.762	-0.173	-0.066	-0.257	-0.062	0.258	-0.185
juvenile	0.159	0.043	0.029	0.548	-0.198	0.063	0.173	0.619	-0.317	-0.337	-0.271	-0.279	-0.008	-0.287
adult ¹⁾	0.071	-0.143	-0.310	-0.167	-0.250	-0.299	0.216	*0.690	-0.024	0.024	-0.048	0.262	0.286	-0.071
Vegetation														
Plant species richness								0.263		-0.553	*-0.793			
Litter decomposition														
Decomposition rate <i>k</i>	-0.178	-0.269	-0.420	0.050			** -0.853	-0.551		0.560	** 0.880	0.170	-0.581	*0.813
Stabilisation factor <i>S</i>	-0.110	0.427	0.481	0.096			*-0.751	-0.036		0.085	0.263	0.250	-0.187	0.143

Symbols before values denote significant correlations: p < 0.01: **; p < 0.05: *; p < 0.1: ·

Regarding results for June and August in total (Table 7), total earthworm density was marginally higher in the presence of a higher pH ($p = 0.061$). Furthermore, total earthworm biomass and juvenile biomass showed a positive significant relation with pH ($p = 0.016$; $p = 0.003$). Other parameters revealed no significant correlations.

Table 7: Correlations between earthworm (EW) parameters and soil parameters in June and August. The table shows Pearson and Spearman¹⁾ correlation coefficients. Values written in bold denote (marginally) significant results.

Parameters	Soil parameters			
	Temperature (°C)	Moisture (%)	EC (dS m ⁻¹)	pH ¹⁾
EW species richness	-0.064	-0.161	0.060	-0.006
EW density (EW m⁻²)				
total	-0.108	0.317	0.398	*0.478
juvenile	-0.069	0.350	0.309	0.380
adult	-0.085	-0.103	0.180	0.066
EW biomass (g m⁻²)				
total	-0.214	0.152	0.307	* 0.592
juvenile	-0.017	0.291	0.307	** 0.692
adult	-0.299	-0.042	0.170	0.021
Specific biomass (g EW⁻¹ m⁻²)				
total	0.031	0.202	0.058	-0.207
juvenile	0.152	0.216	0.177	-0.172
adult	-0.027	0.009	0.222	-0.038

Symbols before values denote significant correlations: $p < 0.01$: **; $p < 0.05$: *; $p < 0.1$: °

5 Discussion

5.1 Vegetation

5.1.1 Plant species

An average of 54 plant species per m² in managed and 38 species per m² in abandoned meadows (see Figure 4A) is representative to semi-dry grasslands of the Central Ennstal (Bohner et al. 2003). Likewise, the Shannon index was higher and plant species were more equally distributed in managed meadows (see Figure 4B, C). This confirms other findings, which detected a diversity loss of vascular plant species due to abandonment (Tasser & Tappeiner 2002, Jacquemyn et al. 2003, Niederist et al. 2009, Fontana et al. 2014). Regular management and nutrient poor, semi-dry conditions lead to a lower plant biomass production. Thus, the higher light availability enables many meso- and xerophilic, light-demanding species to co-exist, which results in a higher species richness (Bohner et al. 2003). Additionally, disturbances reduce the competitive ability of dominant plant species and create gaps for the establishment of many other species (Jacquemyn et al. 2003).

Pavlů et al. (2011) argue that the principal effect of abandonment on plant species composition is a change in the abundance of some dominant species. In abandoned meadows, some species become dominant forcing other species to decline (Niederist et al. 2009). This shift of species can also be seen in the present results with a decline of *B. erectus* (cover of 8.88 % in managed and 0.14 % in abandoned meadows) and an increase of *B. pinnatum* (cover of 0.98 % in managed and 31.84 % in abandoned meadows) in abandoned sites (see Table 1). Köhler et al. (2005) observed a negative effect of abandonment on the tufts of *B. erectus*, whereas *B. pinnatum* increases with ongoing abandonment due to benefits via rhizomatous growth. Bobbink & Willems (1987) related the dominance of *B. pinnatum* to its high growth form, and Willems (1983) argued with its ability to produce many tiller. The change in species richness is also linked to a higher above-ground biomass, hindering seedlings establishment due to reduced light intensity under the canopy (Bakker et al. 1980, Willems 1983). In addition, shade tolerate species like *L. latifolium* and *G. album* were more abundant in abandoned sites. In accordance with Bohner et al. (2012), *C. vulgare* increased in cover due to abandonment, and the cover of woody plants were relatively low within abandoned plots. Furthermore, a positive effect of cutting on *F. rubra rubra* were also documented by Pavlů et al. (2011).

Regarding total plant cover, Kelemen et al. (2014) detected decreasing plant cover due to abandonment. However, differences in plant cover were not observed in this study (see Table 2).

5.1.2 Plant biomass

The present study showed an accumulation of necromass/litter in abandoned meadows, and accordingly higher total biomass in these sites (see Figure 6A, B). Kelemen et al. (2014) pointed out that cessation of mowing leads to a higher amount of litter and a decline of plant species diversity. Previously, however, Kelemen et al. (2013) found even positive effects of litter on plant species richness in grassland with low biomass production. The slightly increase of litter can promote germination and establishment of many plant species. Furthermore, litter accumulation can mitigate extremities in radiation, lower fluctuations in temperature and evaporation and thereby creates a more humid microclimate. However, at a high level of biomass the relationship between litter accumulation and plant species richness becomes negative, e.g. due to reduced solar irradiation on the surface, hindering germination and establishment of seedlings (Kelemen et al. 2013). Xiong & Nilsson (1999) concluded in a meta-analysis that the negative effects generally outweigh the positive effects of litter accumulation. Carson & Peterson (1990) defined high amount of litter at 900 g m^{-2} , whereas Kelemen et al. (2013) reported a negative litter effect at lower litter amounts (400 g m^{-2}). Although the amount of necromass was much lower in the current study (117.57 g m^{-2} in abandoned meadows), a negative relationship between plant species richness and necromass was detected, too.

While living biomass was not sensitive to management types (see Table 2), management caused differences in the structure of functional groups (see Figure 6A, B). Grasses exhibited a marginally higher weight in abandoned sites while herbs and legumes were similar within management types. Comparing the proportion of the biomass between mown and abandoned meadows, herbs were the only functional group presenting significant differences, with a higher proportion in managed meadows. Grasses are known to be more dominant because of their growth form (Bobbink & Willems 1986). Moreover, the germination of grasses is less hindered by litter (Xiong & Nilsson 1999), which makes them more resistant to cessation of management. Maurer (2005) explored increasing grass cover and decreasing cover of herbs and legumes due to abandonment. Herbs benefit from decreasing biomass of grasses in managed meadows through reduced competition for light and nutrients, as grasses are known to be also superior competitors for nutrients (Del-Val & Crawley 2005). Although Rudmann-Maurer et

al. (2008) discovered declining legume cover due to abandonment, the biomass of legumes was not sensitive to management in this study.

Earthworms are supposed to influence the plant community, by affecting certain plant functional groups (Eisenhauer et al. 2009). Wurst et al. (2005) and Eisenhauer & Scheu (2008) explored earthworms to increase the soil nitrogen uptake by plants and thereby increasing the competitive strength of grasses. Eisenhauer et al. (2009) found legumes to benefit from the presence of earthworms. However, within this study earthworm-grass-interaction or earthworm-legumes-interaction may have occurred to a lesser extent, as more earthworms were found in managed meadows where biomass of grasses was lower than in abandoned meadows and legumes showed no differences.

5.1.3 Plant traits

No differences of Ellenberg indicators were found in the meadows (see Table 2). In contrast, Bohner et al. (2012) found clear tendency towards lower light availability indicator values in abandoned sites. Additionally, Neuenkamp et al. (2016) indicates the competition for light as the predominant process structuring plant communities in abandoned semi-natural dry grassland. Higher values of soil moisture are related to managed meadows, which is due to a decrease in water uptake by plants which underwent defoliation via mowing (Pruchniewicz 2017). The lack of defoliation in abandoned meadows results in an efficient and intensive water economy, which leads to a decrease of water in soil. Furthermore, Pruchniewicz (2017) found a higher nitrogen availability in abandoned meadows, explained due to higher litter accumulation and its mineralization. However, the similar Ellenberg values in this study were not surprising, as e.g. soil parameters (pH, moisture, temperature and electric conductivity), were not different within the management types (see Table 5).

In the context of plant strategy types, ruderals were more abundant on managed than on abandoned meadows, while competitors and stress-tolerators were similar between management types (see Figure 7A). The decline of ruderals during succession is in line with findings by Prévosto et al. (2011), who related the shift in strategy types to the change of disturbances after the abandonment of land use. Ruderal plants have a rapid growth rate and a high annual seed production allowing them to establish in frequently disturbed areas. As access to light is essential, the abilities to grow fast and rapidly occupy open habitats are important to maximize their light acquisition during succession (Neuenkamp et al. 2016). In contrast, competitors are more abundant in conditions where disturbances and stress are minimal (Wilson & Keddy 1986).

Disturbances cause a shift in the structure of plant growth form. In the present study, tall erect growing species increased and short hemi-rosette species decreased during succession (see Figure 7B). According to Huhta et al. (2001) and Neuenkamp et al. (2016), short plants benefit from frequent disturbances because of their high light requirement, the release from competition pressure, higher opportunities to colonise open space, and they are usually less harmed by mowing. In contrast, abandonment promotes tall species which are strong competitors. This happens at the expense of small slow-growing species in the lower canopy layers, which decline due to shading (Pavlů et al. 2011).

5.2 Litter decomposition

Litter decomposition is affected by various factors, such as physical (climate), chemical (decomposing resource quality) and biological determinants (micro- and macro-organism communities) (Lavelle & Spain 2001). Decomposition rate was higher in abandoned than in managed meadows (see Figure 8A) and correlated positively with increasing necromass (see Table 6). The thick layer of necromass may alter the microenvironment conditions (Facelli & Pickett 1991), and thereby influencing decomposition rate. Additionally, Liu et al. (2009) found out that increasing litter quantity influences soil carbon and nitrogen cycles.

Meier & Bowman (2008) showed that the composition and diversity of chemical compounds within plant litter mixtures have important effects on decomposition. Additionally, Scherer-Lorenzen (2008) found decomposition to increase with higher plant functional diversity, while plant species diversity has rather low effects on decomposition. Legumes enhance decomposition via effects on litter quality and on the decomposition microenvironment. This is also in line with Milcu et al. (2008), who highlighted legumes as very important in grassland decomposition processes. While missing effect of plant species richness can be confirmed in this study, no relation between decomposition and legumes was evident. However, in the present results a higher biomass of grasses seemed to increase the decomposition rate (see Table 6). Groffman et al. (1996), who investigated the effects of grass species on microbial biomass, suggested that different grass species may influence the microbial activity, but to a lesser extent than soil type, which is a more important controller of microbial biomass and activity. Nevertheless, effects of soil parameters (pH, moisture and temperature) on decomposition seem unlikely in this study, as they were not affected by management (see Table 5) and no correlations were found (see Table 6). One explanation for missing correlations could be that soil parameters were sampled at a certain time (June and August), whereas decomposition rate

was measured over a consecutive period from June to August, underlying different climatic conditions during the decomposition process.

Seeber et al. (2006) and Milcu et al. (2008) described macro-decomposers, e.g. earthworms, as important factor for decomposition. Earthworms influence soil microbial communities and as a result effect microbial processes of soil organic matter and nutrient dynamics (Lavelle et al. 1998). Indeed, Lubbers et al. (2017) found earthworm to stimulate the decomposition of freshly added and older organic material rather than they stabilize carbon inside biogenic aggregates. However, the abundance of earthworms cannot be clearly related to a higher decomposition in this study. Firstly, earthworm cannot pass through the mesh of the tea bags, thus only the influence of microorganisms can be measured with this method. Still, there is an indirect effect of earthworms, as they alter the soil microflora and fauna populations (Brown 1995). Secondly, more earthworms were present in managed meadows (see Figure 10A), where decomposition was lower than in abandoned meadows (see Figure 8A). Additionally, there were no correlations between decomposition and earthworms (see Table 6).

Overall, however, no clear pattern based on the current results could fully explain the higher decomposition in abandoned meadows

5.3 Earthworms

In general, species richness of earthworms is remarkably consistent among different habitats and geographic regions. Number of species ranges from 1 to 15 species, with mostly about 3 to 6 species within an earthworm community (Edwards & Bohlen 1996). In the present study, 7 species were found in the eight meadows studied, which is in line with other studies in grassland (Zaller & Arnone III 1999a, Cluzeau et al. 2012) (see Table 3). Based on a long-term field experiment, Pop (1997) concluded that there should be 2 to 4 endogeic, 0 to 2 anecic and 1 to 2 epigeic species in mountain woody and grassland ecosystems. This conclusion is in line with the distribution of ecological groups in the present study (3 endogeic, 1 anecic and 3 epigeic species, see Table 3).

In this study, earthworm species richness and species assemblages remained unaffected by abandonment (see Table 4 and Figure 9A). Indeed, Decaëns et al. (1997) detected no changes in species richness during succession of a grazed chalk grassland over 44 years. In the present study, the most common species in both meadow types were *A. rosea* and *O. lacteum*, followed by *A. caliginosa* in abandoned sites and *L. rubellus* in managed sites (see Table 3). In line with the species assemblages in this study, Didden (2001) found *A. caliginosa* and *L. rubellus* to be the most abundant species in grassland, and Pop (1997) described the earthworm species

assemblage of mountain grassland listing the same species complemented by *O. lacteum*. According to Ivask et al. (2007), *A. rosea* and *L. rubellus* are quite tolerant to disturbances, while *L. castaneus* is a more sensitive species. Indeed, *L. castaneus* was only present in abandoned sites in this study. On the contrary, the stress-tolerate species *A. caliginosa* was not found in the studied extensively managed meadows (see Table 3).

With an average of 75.2 ± 24.37 worms per m^2 (abandoned) and 105.2 ± 31.61 worms per m^2 (managed) the total earthworm density was in accordance with Zaller & Arnone III (1999a) in calcareous grassland communities, but rather low compared to other studies in grasslands (Didden 2001, Cluzeau et al. 2012, Seeber et al. 2005) (see Table 4). In general, earthworm density is heterogeneous at regional scales, influenced by soil type, vegetation type, as well as land-use type and land-use intensity (Lavelle et al. 1997, Smith et al. 2008), e.g. reaching from 32 to 1332 worms per m^2 in managed (Cluzeau et al. 2012) and 5 to 420 worms per m^2 in abandoned grasslands (Decaëns et al. 1997). Grasslands tend to have a higher earthworm density and biomass than forest and annual cropping systems (Lavelle et al. 1997, Rozen et al. 2013). It must be noted, that comparisons of earthworm biomass with other works were not done, as the procedure of weighing was different to other studies, and would lead to incorrect conclusions. Earthworm biomass is mostly expressed in live weight or dry weight (Edwards & Bohlen 1996), while in this study earthworms were stored in a solution of formalin and were not dried.

Regarding this study, abandonment had a negative influence on earthworm density, as managed meadows showed a marginally higher total earthworm density (see Table 4 and Figure 10A). Concurrently, Pižl (1992) and Decaëns et al. (1997) found decreasing earthworm density due to abandonment. Earthworm abundance may be reduced via a decrease in nutrient supply and primary production due to changes in the floral composition (Scheu 1992). However, Scheu (1992), Pižl (1992) and Decaëns et al. (1997) reported a further increase of earthworm density with ongoing succession, explained by the favourable microclimate and a carbon-rich mineral soil during formation of forest (Scheu 1992).

The distribution of ecological groups in this study was in accordance with other published results (Zaller & Arnone III 1999a, Didden 2001, Ivask et al. 2012), who also detected more endogeic and less epigeic and anecic earthworms (density and biomass) in grasslands (see Figure 10B and Table 4). Density of endogeic earthworms was marginally higher in managed meadows, which may primarily reflect the trend in total earthworm density, because most earthworms belonged to the ecological group endogeic. However, Ponge et al. (2013) found endogeic earthworms as K-selected species to be better adapted to disturbances than r-selected

anecic species with a higher sensitivity. This may emphasize the marginally higher density of endogeic earthworms in managed sites, where disturbances are caused by mowing. Additionally, Ivask et al. (2012) found the earthworm community in long-term managed meadows to be dominated by endogeic earthworms, whereas only few epigeic earthworms were observed. Decaëns et al. (1997) discovered an increase of epigeic earthworms during abandonment. The formation of a specific habitat similar to a forest, where meadows became overgrown with deciduous shrubs, is prevailed by typical forest epigeic species (Ivask et al. 2012). However, the increase of epigeic earthworms due to abandonment cannot be confirmed by this study (see Figure 10B and Table 4).

In this study, general earthworm population consisted of more juvenile than adult individuals (see Figure 10C and Table 4). A dominance of juvenile earthworms within the earthworm population is also shown in other studies (Pižl 1992, Zaller & Arnone III 1999a). This pattern of age structure is typical for soil-inhabiting invertebrates, having a pyramidal age structure, with more young than adult individuals most of the year (Edwards & Bohlen 1996).

Abandonment seemed to reduce the density of juvenile earthworms, as marginally less of them were found in abandoned meadows. In addition, the higher density, biomass and specific biomass of adult earthworms in June than in August may reflect the annual life cycling of earthworms (see Table 4). However, not much is known about seasonal changes in earthworms age structure, as they differ considerably between different species and findings depend on sampling time, e.g. after breeding periods, there will be a higher proportion of juvenile earthworms and less adult earthworms (Edwards & Bohlen 1996).

In this study, management did not significantly affect soil parameters (moisture, temperature and pH) and electric conductivity. Assuming an interaction between management and time, soil temperature was marginally higher in abandoned meadows in June (see Table 5). Different circumstances (weather, slope, measuring) might lead to this coincidence effect. Specially in the context of weak management effects on earthworms, similar soil properties may have resulted in an absence of clear correlation between earthworms and soil parameters. Results just showed an increase of various earthworm parameters with higher pH (see Table 6 and Table 7). Even though earthworms are very sensitive to pH, the results for pH differed on very small scales (pH 7.26 ± 0.08 in abandoned and 7.08 ± 0.40 in managed meadows) and matched the preferred neutral pH (pH=7) of earthworms (Edwards & Bohlen 1996).

As differences in earthworm parameters within the abandoned and managed meadows cannot be explained by soil properties, characteristics of vegetation may have caused the differences. The higher earthworm density in managed meadows may come along with a higher plant

species richness. Although correlations between plant species and earthworm parameters were not significant (see Table 6), other studies indicate increasing earthworm density and biomass with higher plant species richness (Zaller & Arnone III 1999a, Spehn et al. 2000). A loss of plant species leads to changes in community fine root biomass and negatively affect the food supply for earthworms (Zaller & Arnone III 1999a). Furthermore, Eisenhauer et al. (2009a) found the loss of key plant functional groups to be more important than plant species richness. Indeed, specific plant traits of functional groups appear to have a considerable influence (Piotrowska et al. 2013). For example, Milcu et al. (2008) found legumes to be referenced by earthworms, and detected positive effects of legumes on the density and biomass of earthworms in more diverse plant communities. Earthworms may prefer high-quality legume litter (Gastine et al. 2003). Furthermore, earthworms and legumes benefit from each other, as they form a mutualistic relationship (Eisenhauer et al. 2009). In contrast, grasses may reduce the abundance of earthworms primarily due to their dense root system in plant communities (Eisenhauer et al. 2009a, Piotrowska et al. 2013). However, in this study, correlations between plant functional groups and earthworms were only significant regarding herbs (see Table 6). Leuschner et al. (2013) found root nitrogen concentration to be higher in herb than grass roots, which may explain a preference of herbs by earthworms and the positive correlation within this study. In addition to the impacts of specific traits of plant functional groups, plant cover may also affect earthworms by influencing the microclimatic structure. For example, shading by above-ground plants reduces the water loss from soils through evapotranspiration (Suthar 2011). Although Hlavak & Kopecký (2013) found no effects of plant cover on earthworms, in this study positive effects of a higher plant cover were evident for total specific biomass and the specific biomass of adult earthworms (see Table 6). This might indicate, that higher plant cover leads to bigger earthworms, as it shapes the microclimatic conditions and quality of food availability, favoured by earthworms (Suthar 2011).

6 Conclusion

The results showed that abandonment of nutrient poor mountain meadows changed the vegetation. Abandonment led to a reduction of plant species richness and caused a shift in species composition. This may have been mostly driven by the accumulation of necromass, forcing short and ruderal plant species to decline during succession, while erect growing plant species became more dominant (hypothesis i).

Abandonment also led to a higher decomposition rate. However, no clear pattern based on the current results could fully explain the higher decomposition in abandoned meadows (hypothesis ii). Hence, as decomposition is determined by various factors and interactions, more interdisciplinary research is needed.

Although soil parameters did not differ between management types, earthworms seemed to marginally prefer managed meadows. This may indicate that in equal soil conditions earthworms are determined by food supply (litter quality and quantity), which may be more favourable in managed meadows with a higher plant diversity. However, while more juvenile and endogeic earthworms were present in managed meadows, abandonment had no effect on earthworm species and biomass (hypothesis iii).

It is concluded that management has a strong impact on plants above ground, which subsequently alters microenvironmental conditions and soil community via various complex interactions. Thus, management can also influence the decomposition rate and the earthworm population. In order to sustain plant and earthworm biodiversity in the study region both abandoned and extensively managed meadows matter.

7 References

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Affirmation

I certify, that the master thesis was written by me, not using sources and tools other than quoted and without use of any other illegitimate support.

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Vienna, Mai 2018, Ines Jernej