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Soil and Vegetation Characteristics of Grassland Have a Greater Influence on the Abundance and Diversity of Earthworms than the Mowing Intensity in a Managed Nature Reserve

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Abstract: Effects of mowing on vegetation parameters have been well studied. However, less is known about mowing effects on soil fauna and if soil properties alter this. We investigated earthworm communities in a long-term experiment 14 years after its establishment in 5 dry, fresh and moist grassland plots located in the Natura 2000 site Lainzer Tiergarten near Vienna, Austria (238–402 m a.s.l., 48°10′ N, 16°12′ E). The grasslands were either mowed once a year or every second year, or not mowed since being established. Earthworms were assessed using the non-destructive octet electroshocking method. Additionally, vegetation composition, soil conductivity, temperature and moisture were assessed. We found 13 earthworm species across all treatments, although their abundance was generally low with 6.1 ± 4.7 worms m^{-2}. The total earthworm abundance and species diversity was higher in dry compared to fresh and moist grasslands but was not affected by mowing frequency. Endogeic earthworms (*Aporrectodea caliginosa*, *Aporrectodea rosea*) and epigeics (*Lumbricus rubellus*) were more tolerant to mowing than anecics (*Lumbricus terrestris*, *Allolobophora longa*). Since plant species richness was highest in annually mown grasslands and earthworm species richness was positively related to plant species numbers, we recommend regular, low-input management to promote above- and belowground biodiversity in these grasslands.

Keywords: grassland management; nature conservation; soil fauna; plant diversity; earthworm diversity; abandonment; mowing

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1. Introduction

Grassland covers 40% of the Earth's land surface and is of high value for the conservation of biodiversity, the provision of forage for livestock and the high carbon storage in soils [1]. Grassland management in mountainous regions of Europe has changed considerably in recent decades due to socio-economic developments, industrialization and agri-environmental policies [2–4]. Two main trends can be observed in grassland management: grassland in easily accessible areas with favorable soil conditions has been intensified, while other sites have been abandoned [5]. When grassland is no longer managed, it tends to revert to a more natural state, with substantial changes in plant and aboveground animal communities [6,7], but also in terms of soil biodiversity and ecosystem functioning [8–11]. However, while the effects of grassland management on vegetation parameters [12–14] and aboveground faunal communities [15–17] are well documented, much less is known about the potential effects on soil organisms such as earthworms [18,19].

In general, invertebrates are the main component of faunal diversity in grasslands and play an important role in ecosystem processes, including nutrient cycling. Compared to other temperate ecosystems, earthworms are generally more abundant and diverse in grasslands [20–22], especially in areas with higher organic matter content and nitrogen mineralization rates [23]. Earthworm diversity is mainly influenced by agricultural management [24], which affects soil fertility, organic matter dynamics, water infiltration and soil erosion [25–27]. Earthworms, in turn, are themselves influenced by soil moisture, organic matter, texture and pH [27]. Commonly, earthworms are categorized into three main ecological groups: epigeic, endogeic and anecic species [28]. Epigeic species are mainly found in the upper organic layers and feed mainly on litter material, while endogeic species are soil-dwelling and live in the upper mineral soil layers. Anecic species form vertical burrows and feed on litter at the soil surface, which they drag into deeper soil layers. Earthworms have been shown to affect plant growth [29–33] and alter the diversity of plant communities [34,35].

Earthworms have been shown to respond to grassland abandonment, reaching the highest densities as early as the fourth year of abandonment, with more endogeic species occurring, but there is no difference with longer abandonment [36]. Similar trends were observed with earthworm communities during the afforestation of grassland in Normandy, France [37]. Other studies found lower earthworm abundances in older successional grasslands compared to newly abandoned areas [38,39]. Extensively managed mountain meadows showed higher earthworm densities and greater plant species diversity than abandoned meadows [18]. With a higher degree of abandonment, plant species richness was also lower [40–42], and studies in experimental plant communities found a positive relationship between plant species richness, earthworm activity and biomass [31,35,43]. However, it is unclear, whether such a relationship exists for native grasslands and whether it depends on soil conditions.

The aim of the present study was to assess the response of earthworms to mowing regimes in grasslands of a nature reserve and to determine to what extent vegetation types with dry, fresh or moist soil conditions alter these relationships. Specifically, it was investigated whether (i) abandonment of mowing has an effect on earthworms and whether this is associated with effects on plant species richness, and (ii) earthworm response is influenced by soil properties of the grassland. These hypotheses were tested in a long-term field experiment established 14 years prior to this assessment.

2. Materials and Methods

2.1. Study Site

This study was conducted in 2013 as part of a long-term experiment established in 1999 by G. Karrer examining the effect of meadow management on plant species richness [40]. The study site is located within the nature conservation area Lainzer Tiergarten (http://www.lainzer-tiergarten.at, accessed on 6 May 2024) in the south-eastern part of Vienna, Austria (238–402 m a.s.l., 48°10′ N, 16°12′ E). The Lainzer Tiergarten has a total area of 2450 ha of which 1945 ha consists of forests and 505 ha of grassland interspersed within the forest. The Lainzer Tiergarten is part of the Wienerwald (Vienna Woods), which are forested highlands that form the northeastern foothills of the Northern Limestone Alps in the states of Lower Austria and Vienna. The entire area is designated as a European Union Natura 2000 nature protection area and comprises a broad range of endangered traditionally managed extensive hay meadows [44]. Geologically, the Lainzer Tiergarten is located in the Flysch zone consisting of sandstone and marl with argillaceous and heavy soils. The mean annual precipitation of the area is 750 mm and the annual mean temperature is 9 °C.

2.2. Experimental Design

The study site consisted of 15 experimental blocks, each 12 m × 12 m (144 m^2), which were fenced off in 1999 to exclude the impact of wild boar, deer, mouflons or red deer. The study sites were arranged in a two-factorial design with the factors of vegetation type (three levels) and mowing regime (three levels); each treatment was replicated five times (i.e., a total of forty-five study plots).

The factors of vegetation type consisted of five blocks as follows:

- Fresh, fertile meadows dominated by *Festuca pratensis* and *Trisetum flavescens* (further called "fresh vegetation type");
- Dry, low-fertile meadows dominated by *Bromus erectus* and *Brachypodium pinnatum* ("dry");
- Moist meadows dominated by *Molinia caerulea* agg. ("moist").

Within these blocks, 3 mowing regimes were established on 3.5 m × 5 m experimental plots. In addition, a control plot was also considered within each block (Figure 1):

- Mowing once a year ("R", regular mowing);
- Mowing once every second year ("C", change);
- Abandonment ("A", no mowing since 2000).

Regular mowing follows the nature conservation management plan for the meadows in the area in order to conserve the high botanical diversity. The meadows were mowed with a power scythe at the beginning of July (fresh meadows) or at the beginning of August (dry and moist meadows) according to the management plan of the corresponding nature conservation agency. Cutting was always removed from the plots. More details on the experimental design can be found in Angeringer and Karrer [40].

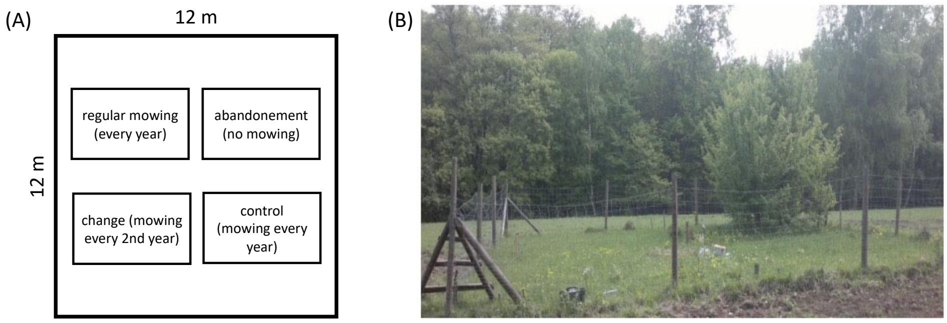

Figure 1. Schematic overview of the experimental design for this study (**A**). Image (**B**) shows a fenced-off experimental block in a fresh meadow, bushes in the right corner in the back of the block are the results of 14 years of abandonment (copyright: G. Kerschbaumer).

2.3. Earthworm Sampling

Earthworms in each plot were extracted in May 2013 using the electro-sampling method [45]. This non-destructive sampling method has yielded comparable estimates of earthworm community size [46] and composition [35,47] than more traditional methods.

Therefore, 1 sampling was carried out per experimental plot by pushing 17 steel rod electrodes 60 cm into the ground. On a square of 1 × 1 m situated in the center of each experimental plot, 1 electrode was inserted in the middle (common pole) and 4 electrodes along the 4 sides of the area. We used a custom-made electro-sampling device (RWF 1, ETS, Darmstadt, Germany) powered by a 12 V, 70 Ah car battery. Triggered with a foot pedal, the electric currency alternates with the adjustment of the length of the impulse and the length of the breaks from the outer electrodes to the center electrode. For this study, an impulse length of 3 s and 2 s of impulse-break was chosen. Each plot was sampled for 30 min, increasing the voltage every 10 min from 100 V to a maximum of 300 V. All earthworms coming to the soil surface were collected and transferred into plastic boxes containing moist field soil until species identification and weighing took place in the laboratory. We identified live earthworms using the glass-tube method in which earthworms were fixed in glass tubes of different widths and identified under a dissecting microscope [48]. We used specific earthworm identification keys for Austria [49,50]. Juvenile earthworms without a clitellum are not identifiable at the species level but were considered in calculating the mean density and biomass. Earthworm fresh mass and density are given per m^2. Earthworm fauna was further characterized by age structure (proportion of juveniles and adults) and density and proportion of epigeics, anecics and endogeics [51].

In addition to earthworm sampling, the soil electrical conductivity, soil temperature and soil moisture of the plots were measured in the earthworm sampling area using time domain reflectometry (TRIME®-PICO 64/32, HD2, IMKO Micromodultechnik GMBH, Ettlingen, Germany). Precipitation and air temperature during the sampling period (4–12 May 2013) are shown in Figure 2.

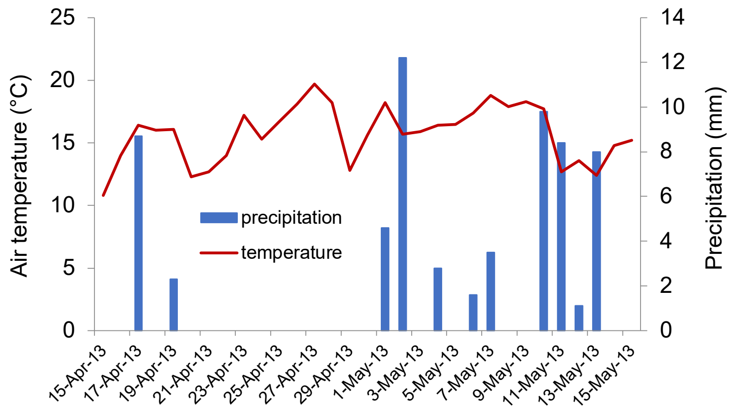

Figure 2. Mean air temperature and precipitation amount around the study period at Vienna-Mariabrunn weather station (225 m a.s.l., 48°7′ N, 16°8′ E) near the study area (data from ZAMG, Vienna). Earthworm sampling took place between 3 and 13 May 2013.

2.4. Vegetation Measurements

Since the establishment of the experiment in 1999, the plant community composition was recorded every year for each plot [40]. Relevés were conducted by G. Karrer using the cover-abundance values of Braun-Blanquet [52], advanced to a 17-digit scale [14]. For the current study, the most recent vegetation data available from 2007 were used.

2.5. Data Analysis

Using the software package SPSS Statistics (vers. 22.0, IBM Corp., Armonk, NY, USA), a two-way General Linear Model analysis of variance (ANOVA) was used with factor vegetation type (3 levels, df = 2), factor mowing (3 levels, df = 2) and their interaction (df = 4). Dependent parameters were earthworm densities, biomass, number of species, contribution of ecological groups, age classes and the Shannon index. The Shannon index of diversity H is a measure of species diversity in a community [53]. Mean comparisons were conducted using Tukey's post hoc tests. When tests of normality with the Kolmogorov–Smirnoff test showed a non-normal distribution, a log transformation gained normality. Percentage data such as proportion of ecological groups, community structure and age classes were arcsine transformed. The homogeneity of variances was tested with Levene's test. Pearson correlations were used to test for relationships between earthworm and vegetation parameters. All results are shown as arithmetic means ± standard deviation (±SD). The significance of all tests was accepted at $p < 0.05$.

3. Results

3.1. Earthworm Density, Biomass

Across treatments, we found a total of 13 different earthworm species out of 5 genera (Table 1). Across vegetation types, epigeic species *Lumbricus rubellus* were most often found, followed by the endogeic species *Aporrectodea caliginosa*, *Octolasion lacteum* and *Aporrectodea rosea* (Table 1).

The vegetation type significantly affected earthworm biomass, species numbers and Shannon diversity, whereas the mowing regime or the interaction of vegetation type and mowing regime showed no effect on these parameters (Figure 3, Table 2). Mean earthworm density across treatments was 6.1 ± 4.7 individuals m^{-2} and was neither affected by vegetation type or mowing treatment or their interaction (Table 2, Figure 3A).

Table 1. Earthworm species and density per m^2 collected on dry, fresh and moist grasslands either regularly mown (R), mown every second year (C) or abandoned (A). Species numbers do not include juvenile specimens because of unclear identification.

Taxa	Dry			Fresh			Moist			Total
	R	C	A	R	C	A	R	C	A	
Aporrectodea rosea (Savigny, 1826)	0	3	7	9	6	5	0	1	2	33
Aporrectodea caliginosa (Savigny, 1826)	6	11	8	0	2	2	0	2	7	38
Allolobophora chlorotica (Savigny, 1826)	0	1	0	0	0	0	0	0	0	1
Allolobophora longa (Ude, 1886)	5	1	0	0	1	0	0	0	0	7
Allolobophora georgii (Michaelsen, 1890)	0	1	0	0	1	0	0	0	2	4
Lumbricus rubellus (Hoffmeister, 1843)	10	2	9	2	8	7	1	0	2	41
Lumbricus castaneus (Savigny, 1826)	1	0	1	0	2	2	3	1	0	10
Lumbricus terrestris (Linnaeus, 1758)	0	1	1	3	1	0	0	0	0	6
Lumbricus polyphemus (Fitzinger, 1833)	0	0	0	0	0	2	0	0	0	2
Octolasion lacteum (Örley, 1885)	4	3	8	8	0	1	5	5	0	34
Octolasion cyaneum (Savigny, 1826)	0	0	2	0	0	0	0	0	1	3
Dendrobaena platyura depressa (Rosa, 1893)	5	2	6	1	3	0	1	2	0	20
Dendrobaena octaedra (Savigny, 1826)	1	0	3	0	0	0	0	6	8	18
Juvenile *Allolobophora* sp.	5	0	9	3	3	4	4	3	3	34
Juvenile *Lumbricus* sp.	1	1	1	1	0	2	0	1	0	7
Juvenile *Dendrobaena* sp.	2	1	0	0	0	0	2	2	1	8
Juvenile *Octolasion* sp.	0	0	0	1	2	0	1	1	0	5
Total earthworm density m^{-2}	40	27	55	28	29	25	17	24	26	271
Number of species	7	9	9	5	8	6	4	6	6	13

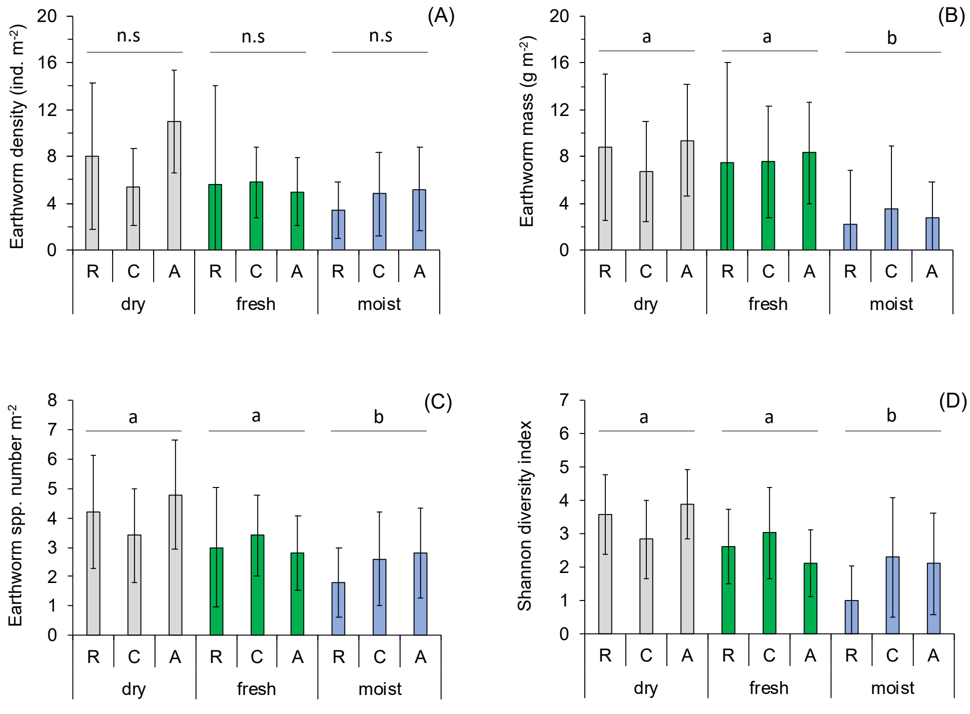

Figure 3. Mean earthworm density (**A**), biomass (**B**), number of species (**C**) and Shannon diversity index (**D**) in dry, fresh and moist grasslands under regular mowing once a year (R), mowing every second year (C) and abandonment (A). Mean ± SD, n = 5. Letters denote significant differences between grassland types; n.s. not significant at α = 0.05.

Earthworm biomass in moist meadows (2.9 ± 1.4 g m^{-2}) was significantly lower than in fresh (7.8 ± 2.2 g m^{-2}) and dry meadows (8.3 ± 2.9 g m^{-2}; Figure 3B). The number of earthworm species showed a significant difference between the vegetation types with a maximum of 4.1 ± 0.9 spp. m^{-2} in dry meadows and a minimum of 2.4 ± 0.7 spp. m^{-2} in moist meadows (Figure 3C). The Shannon diversity of earthworm communities was similar between dry and fresh, but significantly lower in moist grasslands (Figure 3D).

Table 2. ANOVA results for the effects of vegetation type (dry, fresh and moist grassland) and mowing regime (regular, every second year and abandoned) and their interaction on earthworm (EW) density, mass, number of species, Shannon diversity index and evenness. Soil temperature, moisture and electrical conductivity were included as covariates.

Variable	Vegetation Type		Mowing		Vegetation Type × Mowing	
	F	*p*	F	*p*	F	*p*
EW density (ind. m^{-2})	2.452	0.100	0.265	0.769	1.000	0.713
EW mass (g m^{-2})	4.891	0.013	0.000	0.989	0.000	0.932
EW species numbers	3.891	0.030	0.190	0.828	0.583	0.677
EW Shannon diversity	5.083	0.011	0.288	0.751	0.996	0.423
EW evenness	4.804	0.014	0.224	0.801	1.063	0.389
Soil temperature (°C)	2.150	0.114	2.473	0.077	2.150	0.114
Soil moisture (%)	0.581	0.632	0.440	0.726	0.442	0.725
Soil electrical conductivity (mS m^{-1})	0.480	0.698	0.651	0.587	0.312	0.816

3.2. Earthworm Community Structure

Fresh meadows contained 10 earthworm species with 3 dominant species, namely *Aporrectodea rosea, Lumbricus rubellus* and *Octolasion lacteum* (Table 1). Moist meadows contained nine species with the dominant species *Dendrobaena octaedra, Octolasion lacteum* and *Aporrectodea caliginosa*. Dry meadows contained 12 species with *Aporrectodea rosea, Lumbricus rubellus, Dendrobaena platyra depressa, Octolasion lacteum* and *Aporrectodea rosea* as the dominant species. Seven species were identified in all vegetation types: *Dendrobaena platyra depressa, Octolasion lacteum, Lumbricus castaneus, Lumbricus rubellus, Allolobophora georgii, Aporrectodea caliginosa* and *Aporrectodea rosea*.

Mowing regimes had no effect on earthworm density, mass or species numbers (Table 2).

3.3. Ecological Categories

Almost 46% of the earthworms sampled were endogeics (*Octolasion cyaneum*, *Aporrectodea rosea*, *Aporrectodea caliginosa*, *Allolobophora chlorotica*, *Octolasion lacteum*, *Allolobophora georgii*), 31% were anecics (*Allolobophora longa*, *Lumbricus terrestris*, *Lumbricus polyphemus*, *Dendrobaena platyura depressa*) and 23% were epigeics (*Dendrobaena octaedra*, *Lumbricus rubellus*, *Lumbricus castaneus*) (Figure 4). The most abundant earthworms were *Aporrectodea caliginosa*, *Aporrectodea rosea* and *Octolasion lacteum*.

The vegetation type significantly affected the percentage of anecic species and marginally significantly affected that of endogeic species in earthworm communities (Figure 4, Table 3). The percentage of epigeics was unaffected by vegetation type. Mowing had no effect on the percentage of earthworm functional groups (Table 3).

Table 3. ANOVA results for the effects of vegetation type and mowing regime on ecological groups of earthworms (EW). Soil temperature, moisture and electrical conductivity were used as covariates.

Variable	Vegetation Type		Mowing		Vegetation Type × Mowing	
	F	*p*	F	*p*	F	*p*
Proportion endogeic EW (%)	3.140	0.055	0.409	0.667	1.716	0.168
Proportion epigeic EW (%)	1	0.595	1.016	0.372	1.654	0.182
Proportion anecic EW (%)	7.065	0.003	0.563	0.574	0.952	0.446
Soil temperature (°C)	2.532	0.072	1.152	0.341	2.444	0.083
Soil moisture (%)	0.614	0.610	0.243	0.865	0.121	0.947
Soil electrical conduct. (mS m^{-1})	0.933	0.435	1.216	0.318	0.806	0.500

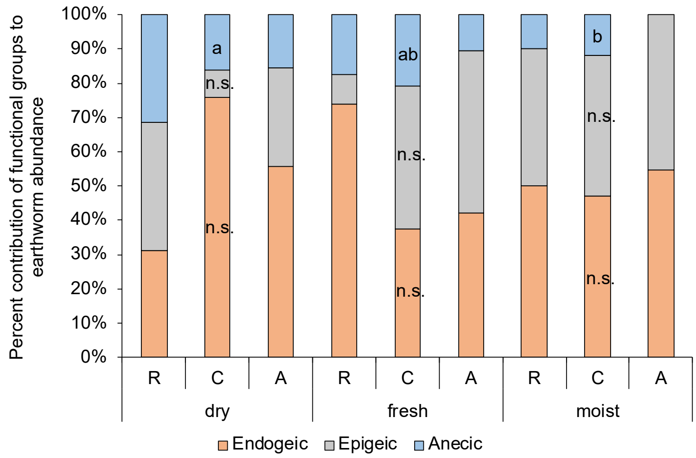

Figure 4. Relative abundance of the earthworm ecological categories epigeics, anecics and endogeics in dry, fresh and moist grasslands under regular mowing (R), mowing every second year (C) and abandonment (A). Letters denote significant differences between grasslands. n.s.: not significant at $\alpha = 0.05$.

3.4. Age Structure

Juvenile earthworms represented 25% of the total earthworm numbers collected in all plots. The highest proportion of juveniles was found in the moist vegetation type and the regular mowing plot (41%) whereas the lowest proportion of juvenile earthworms showed altogether in the dry meadow (19%). The age dispersal of earthworms was neither affected by vegetation type nor the mowing regime or their interaction (Supplementary Table S1).

3.5. Interaction between Plant Species Richness and Earthworms

Plant species richness was significantly affected by vegetation types and mowing regime (Figure 5, Table 4) with the lowest plant species richness in fresh meadows at 57 ± 6.7 spp. and highest in the dry meadows (74 ± 14.7). The plant species number in the moist vegetation type was significantly lower than in dry sites. Across vegetation types, the mean number of plant species decreased from 72 ± 12.9 spp. under regular mowing to 58 ± 13.1 spp. under abandonment. In all three vegetation types, abandonment had significantly lower plant spp. numbers compared to annual and biannual mowing (Figure 5).

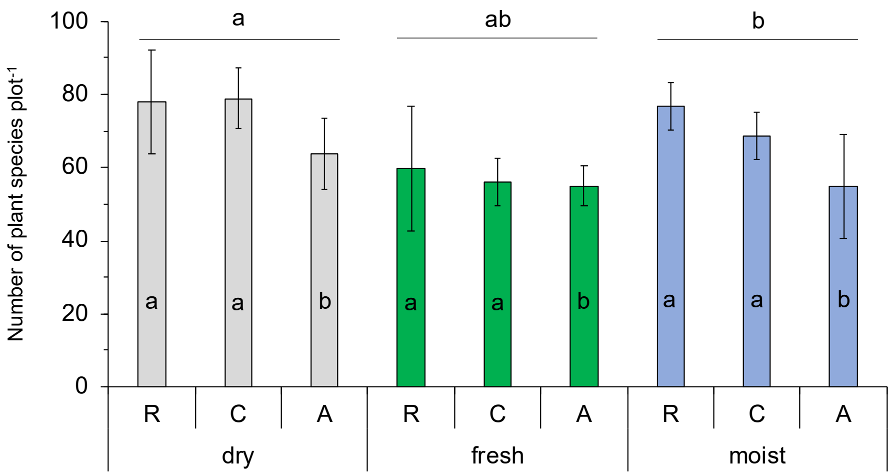

Figure 5. Mean plant species numbers of dry, fresh and moist grasslands under regular mowing (R), mowing every second year (C) and abandonment (A). Different letters above columns refer to significant differences between the mowing regimes within the vegetation types; different letters in columns refer to significant differences between vegetation types at $\alpha = 0.05$. Means ± SD, n = 5.

Table 4. ANOVA results for the effects of vegetation type (dry, fresh and moist) and mowing regime (regular, every second year and abandoned) and their interaction on the number of plant species. Soil temperature, moisture and electrical conductivity were used as covariates.

Variable	Vegetation Type		Mowing		Vegetation Type × Mowing	
	F	*p*	F	*p*	F	*p*
Plant species number (plot^{-1})	6.502	0.004	5.817	0.006	1.006	0.480
Soil temperature (°C)	1.009	0.321	0.229	0.635	0.689	0.412
Soil moisture (%)	0.004	0.952	0.208	0.651	2.560	0.119
Soil electrical conduct. (mS m^{-1})	0.390	0.390	1.146	0.291	1.729	0.198

Earthworm density (Figure 6A), and species numbers (Figure 6C) were significantly positively related to the number of plant species across grasslands. Earthworm mass (Figure 6B) was unrelated to the number of plant species.

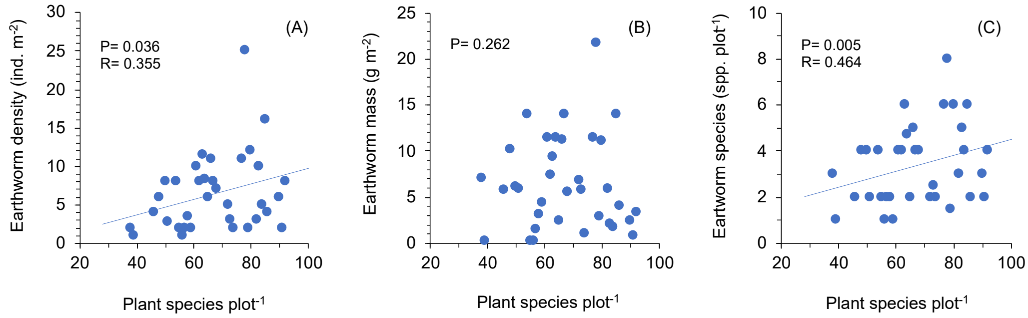

Figure 6. Linear regression between number of plant species and earthworm density (**A**), biomass (**B**) and species numbers (**C**). Trendlines show significant linear relationships.

4. Discussion

4.1. Earthworm Response to Grassland Management

In our study, grassland management had no influence on earthworm densities, biomass and species diversity. This is in contrast to several studies that report lower earthworm densities in managed grassland than in abandoned grassland [25,38,39,54]. However, it is important to note that our study was conducted under very extensive management in a nature reserve, with the highest intensity being mowing once per year. At about 6.1 ± 4.7 worms m^{-2} across all treatments, earthworm density in our grasslands was rather low compared to other studies [29,36,39,55]. In general, earthworm densities in abandoned grassland have been shown to be highly variable and heterogeneous, ranging from 5 to 420 earthworms m^{-2} [37]. Earthworm densities also depend on the efficiency of the sampling method used. However, electro-sampling has been shown to yield similarly high earthworm numbers and biomasses as more conventional methods such as hand digging or formalin extraction [56]. In addition, electro-sampling has the advantage of being non-destructive, which is particularly advisable for long-term monitoring [47]. The low earthworm densities in our grasslands could also be the result of low earthworm populations after a rather dry spring period [57,58].

Despite the low abundance of earthworms, we found a relatively high species richness of 13 species across grasslands, which corresponds to about 22% of the 62 earthworm species described for Austria [50]. According to a long-term field experiment, 2–4 endogeic, 0–2 anecic and 1–2 epigeic species can be expected in mountain forest and grassland ecosystems [59]. Other studies report a total number of 11 species in semi-natural grasslands in Sweden [60], 10 species in grasslands on marine clay soils in the Netherlands [38], 9 species in a calcareous grassland in north-western Switzerland [29], 8 species across Brittany, France [61], 7 species in mountainous grasslands in Austria [18], 5 species across grasslands with different management intensities in Germany [62], and 14 species in a translocated grassland in the UK two decades after restoration [63]. The Shannon diversity of earthworms was significantly higher in the dry and fresh vegetation types than in the moist vegetation type. The soils of the moist sites show strong seasonal fluctuations in soil water content, with full water saturation during the winter period and mesic levels during the vegetation period. Therefore, we explain the lower abundance, biomass and species richness of earthworms in the moist meadows by longer anaerobic periods in these grasslands [64].

With the exception of *Ocotlasium cyaneum*, *Allolobophora longa* and *Allolobophora chlorotica*, most earthworm species were found in the abandoned grasslands. Species such as *Aporrectodea caliginosa*, *Aporrectodea rosea* and *Lumbricus rubellus* have been shown in other studies to be quite tolerant to disturbance [65,66], and with annual mowing these three species together accounted for 43% of the community, which increased to 57% in the abandoned field. Thus, the abundance of disturbance-tolerant earthworm species increased with less disturbance, reflecting the difficulty in using earthworm species as bioindicators for management [67,68]. Commonly, the occurrence of *Lumbricus terrestris, Allolobophora longa* and *Allolobophora chlorotica* indicates more suitable ecological factors for a habitat [65], but we found more of those species with increasing disturbance. We explain this by the fact that mowing the grass increased the input of organic matter because plant parts remain on the soil surface even when cuttings have been removed [69], or that mowing the grass increased fine-root production, which benefitted earthworms [58].

The changes in density and biomass of anecic and endogeic species during progressed abandonment differed from those of epigeic species, which has also been shown by others [18,19,36,37]. Litter-dwelling epigeic species are mostly smaller earthworms that increase in number during abandonment caused by the formation of the litter layer [18,37]. Indeed, in our study, the three species of epigeic earthworms, *Dendrobaena octaedra Lumbricus rubellus* and *Lumbricus castaneus*, slightly increased in their proportions to the earthworm communities at abandoned sites. Consistent with other studies, endogeics were the dominating species with *Aporrectodea caliginosa* as the most frequent species in grassland studies [64,70]. The number of anecic species also increased slightly with abandonment, which could be due to a denser vegetation structure that provided more surface food and better shelter [71].

Although grassland types that differed in soil hydrology had a significant effect on earthworms, we found no association between earthworms and soil abiotic factors such as electrical conductivity, soil water content or soil temperature. We interpret the absence of such relationships with the fact that most differences in soil parameters were balanced out by the time of sampling and after a rather dry spring period. Others report large fluctuations in earthworm density and diversity in semi-natural grassland areas with increasing soil moisture and fertility in grasslands [60,63].

In addition to mowing, grazing also had an effect on the biomass and species richness of earthworms in a long-term study [19]. These authors concluded that abandoning management does not maintain plant and earthworm diversity, but that extensive grassland management with mowing is a necessary tool for maintaining and improving biodiversity. Previously, no changes in earthworm species richness were observed during the succession of a grazed chalk grassland over 44 years [37].

4.2. Earthworm Response to Vegetation

The plant species richness of grasslands has been shown to be significantly affected by vegetation type and mowing and is lowest in abandoned meadows [12,40–42]. We found earthworm density and species numbers are positively associated with plant diversity, which is consistent with several studies [31,35,43,72]. However, it is also possible that earthworms only correlate with certain plant functional groups, namely legumes [34,73] or with the input of different types of leaf litter [74]. In the current study, a decline in legumes was indeed observed during abandonment [40]. Grasses could reduce the abundance of earthworms mainly due to their dense root system in plant communities [73,75]. Instead, earthworm diversity appears to be concentrated in more productive, grazed grasslands that exhibit high spatial microsite heterogeneity [60].

In addition to earthworms, grassland abandonment has also been shown to affect soil functions, e.g., decomposition [18], an increase in soil microbial biomass, soil organic carbon, C:N ratio and inorganic N supply [12].

While the current study focused on the interactions between plants and earthworms during extensive grassland management, it has been shown that abandonment also has an impact on a variety of aboveground species. The species richness of bumblebees (specifically long-tongued species) [16], the abundance of hoverflies and the abundance of weevils [17] were higher in managed than in abandoned grasslands.

The loss of plant species causes changes in the biomass of the fine root community and negatively affects the food supply for earthworms [35]. However, different earthworm densities in managed and abandoned meadows may also have influenced a feedback process for root growth and aboveground plant production [58].

5. Conclusions

We investigated the effects of low-input meadow management of different grassland types in a Natura 2000 conservation area and found that extensive management consisting of one annual mowing, mowing every second year or abandonment had no effect on earthworm abundance, biomass and species richness. However, a decrease in management reduced the number of plant species, which, together with plant species richness, was positively related to earthworm density, biomass and species diversity. From a nature conservation perspective, yearly mowing can be recommended to maintain a high plant species richness, which in turn also maintains a more diverse earthworm community. As we found no significant interaction between meadow management and vegetation type, this appears to apply to dry, fresh and moist grasslands.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/land13050627/s1.

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