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Differences in grassland sward biodiversity and management regime lead to mixed effects on ecosystem services

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ABSTRACT

Species rich grasslands provide ecosystem services such as floral and faunal diversity, livestock forage, carbon sequestration and water regulation. However, the best combinations of sward diversity and management intensity to achieve the above-mentioned ecosystem services are not fully known. To address this, we established experimental grasslands with three sward types with varying diversity levels: productive monoculture (PM; perennial ryegrass (*Lolium perenne*)), biodiverse (BD) and productive biodiverse (PBD; i.e., diverse sward with species selected to increase forage quantity and quality) and with a management gradient ranging from extensive (i.e., low input, late mowing) to intensive (i.e., high input, early mowing). After three years, we found successful establishment of biodiverse swards with high forb cover, particularly under extensive management, but changes to meadow bird habitat parameters (i.e., sward height and vertical vegetation density) were negative. Forage dry matter yield was highest in BD and intensively managed swards in 2019 and 2020, but intensively managed swards had higher dry matter yield regardless of sward type in 2020. Forage N concentration was highest in PBD swards and digestible organic matter was highest in PM and PBD swards, indicating the productive plants species added to the PBD swards improved forage quality. Improvements in carbon sequestration and water regulation were minimal. Collectively, diverse swards, different management regimes and their interactions benefit certain ecosystem services, but not all. Taken together, these findings pull focus on the need for careful consideration of sward species composition, management and their interactions in order to maximise specific ecosystem services in young, mown grasslands.

1. Introduction

Grasslands cover *c.* 25–40% of the earth's terrestrial surface (Chapin et al., 2013), upon which the livelihoods of many humans depend (Carlier et al., 2009). Grasslands provide livestock forage, carbon storage, protection and enhancement of soil nutrient cycling, buffering against flooding, erosion and drought, habitat for desirable species and a valuable cultural asset (Zhao et al., 2020). As a result, increasing attention is being paid to how grasslands provide these ecosystem services (Bengtsson et al., 2019; Sollenberger et al., 2019) (http://cices.eu). As human activity continues to degrade global ecosystems (Assessment, 2005), it is imperative to better understand the drivers of grassland ecosystem services (Boyd and Banzhaf, 2007; Carpenter et al., 2009).

There is movement towards agricultural practices that aim to incorporate ecological processes and ecosystem services to create sustainable, robust, biodiverse agrarian systems (Erisman et al., 2016; Schreefel et al., 2020). Typically, this involves a transition from intensive to more extensive management. Intensive grassland management usually involves early, frequent mowing with high levels of chemical N, P and K fertilisation, while extensive management utilises later,

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infrequent mowing and low fertilization levels with organic fertilizers (Marriott et al., 2004), resulting in pros and cons for ecosystem services. For example, mowing can restore plant species biodiversity via the phytoextraction of excessive nutrients (Pecháčková et al., 2010; Timmermans and van Eekeren, 2016) and improve nutrient cycling rates and productivity (Mayel et al., 2021). However, negative effects on the soil such as increased compaction have been observed (Schrama et al., 2013). Choosing to delay mowing can increase plant seed set (Jantunen et al., 2007; Nakahama et al., 2016) and plant species richness (Humbert et al., 2012) and allow meadow birds sufficient time to complete their lifecycles (Broyer et al., 2016; Grüebler et al., 2012; Perlut et al., 2008). However, delayed mowing can reduce forage nutritional values (Zhao et al., 2021) and habitat suitability for certain meadow birds, e.g., swards become too tall or dense (Vickery et al., 2001). Reducing the frequency of mowing can increase carbon sequestration (Li et al., 2017) and increased forage quantity (Ignatavičius et al., 2013). In addition, most forms of fertilisation can increase soil carbon storage (Conant et al., 2017) and aggregate formation (Haynes and Naidu, 1998), but can lead to negative repercussions such as nutrient runoff (Mayel et al., 2021) and reduced plant community diversity (Ignatavičius et al., 2013; van Dobben et al., 2019). Alternatively, the use of farmyard manure can provide additional benefits for targeted conservation animals such as meadow birds by providing nesting material, camouflage and an attractive resource for earthworms and insects (Kruk, 1993).

Plant species diversity plays a role in determining grassland ecosystem services. Plant species diversity is an ecosystem service itself in terms of the provisioning of resources, cultural aesthetics, etc. (Boyd and Banzhaf, 2007; Fisher et al., 2009). Even though monocultures of species such as perennial ryegrass (*Lolium perenne* L.) have high forage yields (Haas et al., 2019), biodiversity is low due to outcompeting of plant species (Fan et al., 2003). Species-rich, intensively managed production grasslands can be less productive than monocultures (Marriott et al., 2004). However, in extensively managed grasslands, a carefully selected diverse mixture of complementary plant species (e.g., *Carum carvi* L., *Cichorium intybus* L., *L. perenne*, *Plantago lanceolata* L., *Trifolium repens* L., *T. pratense* L.) can match or outperform intensively managed monocultures in terms of forage yield (Cong et al., 2016; Finn et al., 2013). However, extensively managed diverse swards often produce forage less suitable for livestock due to lower digestibility (Tallowin and Jefferson, 1999), but with possible benefits for wildlife (Marriott et al., 2004). Positive effects of grassland plant diversity on soil abiotic and biotic properties include increased carbon storage (Cong et al., 2014) and earthworm abundance (Spehn et al., 2000). Diverse grasslands can benefit other species, such as meadow birds, by providing habitat with the appropriate vegetation densities and heights necessary for insect prey development and ease of capture (Devereux et al., 2004; Whittingham and Evans, 2004).

Individually, sward species composition and management play decisive roles in delivering ecosystem services, but these factors interact. For example, frequent early mowing and high nutrient input can reduce plant species biodiversity, leading to dominance of species such as *L. perenne* (van Dobben et al., 2019) and thereby reduce soil functions such as organic matter decomposition and nutrient cycling (van Eekeren et al., 2022). High levels of N fertilisation can reduce plant species diversity, which, counterintuitively, can hinder sward productivity as certain plant species disappear (Isbell et al., 2013). Swards that are species-poor and mowed frequently are especially poor meadow bird habitat, since they offer little in terms of camouflage and food and result in the destruction of nests and young birds, respectively (Vickery et al., 2001).

In order to test the individual and interactive effects of grassland sward species composition and management regime on the provisioning of ecosystem services in young, mown grasslands, we set up an experiment with three sward types (perennial ryegrass (*L. perenne*) productive monoculture (PM), biodiverse (BD), productive biodiverse (PBD)) and four management regimes that ranged from extensive to intensive: low fertilisation, late mowing (LL); medium fertilisation, late mowing (ML); medium fertilisation, early mowing (ME); high fertilisation, early mowing (HE)). We predicted the following effects on selected ecosystem services: 1) Biodiversity: PBD and particularly BD swards and LL

Table 1

A visual representation of the hypotheses to give a conceptual indication of the expected outcomes of the effects of sward types (productive monoculture, biodiverse, productive biodiverse), management regimes (low fertilisation, late mowing (LL); medium fertilisation, late mowing (ML); medium fertilisation, early mowing (ME); high fertilisation, early mowing (HE)) and their interactions on ecosystem services. Colours and + 's indicate a gradient from low (i.e., red, one +) to high (i.e., dark green, five +'s) deliverance of ecosystem services in the respective treatment combinations. Smaller font in parentheses indicates measurements were not carried out in this experiment to test these specific hypotheses.

	Productive monoculture				Biodiverse				Productive biodiverse				Hypotheses supported?
	LL	ML	ME	HE	LL	ML	ME	HE	LL	ML	ME	HE	
Biodiversity													
Botanical diversity	+++	++	++	+	+++++	++++	++++	++	++++	+++	+++	++	Yes
% cover forbs	+++	++	++	+	+++++	++++	++++	++	++++	+++	+++	++	Yes
Meadow bird habitat	+++	++	++	+	+++++	++++	++++	++	++++	+++	+++	++	No
Earthworm diversity	+++	(++)	++	(+)	++++	(+++)	+++	(++)	++++	(+++)	+++	(++)	Partial
Forage													
Dry matter yield	+	++++	++++	+++++	++	++	++	+++	++	+++	+++	++++	Partial
Forage quality	+	++++	++++	+++++	++	++	++	+++	++	+++	+++	++++	Partial
Mineral concentration	++	(+)	+	(+)	++++	(+++)	+++	(++)	++++	(+++)	+++	(++)	Partial
Climate regulation													
Soil organic matter	++	++	++	+	++++	+++	+++	++	++++	+++	+++	++	No
Soil structure	++	(++)	++	+	++++	(+++)	+++	++	++++	(+++)	+++	++	No
Soil pores	++	(++)	++	+	++++	(+++)	+++	++	++++	(+++)	+++	++	No

Table 2
Overview of cutting and fertiliser application of the four management regimes.

Management regime				Fertilisation**						
Code	N fertilisation level	Timing of first cut*	# cuts / year	FYM*** (m^3 ha^{-1})	CS (m^3 ha^{-1})	CAN (kg N ha^{-1})	N (kg ha^{-1})	K (kg ha^{-1})	P (kg ha^{-1})	Applied before first cut?
LL	**L**ow	**L**ate	3	18	–	–	115	170	37	Yes
ML	**M**edium	**L**ate	4	–	18	90	162	152	39	No
ME	**M**edium	**E**arly	4	–	18	90	170	149	39	No
HE	**H**igh	**E**arly	4	–	42	180	378	251	57	Yes

CAN = Calcium ammonium nitrate, CS = cattle slurry, FYM = Farmyard manure.
*Late = after the 1st week of June, in line with meadow bird conservation guidelines: 12/6/2018, 20/6/2019, 15/6/2020; Early = 17/5/2018, 16/5/2019, 19/5/2020. In 2018, treatment ML was cut three times instead of four.
**In 2018, no fertiliser was applied before the first cut in any of the treatments. N, K and P application rates are based on the weighted mineral (CAN, potassium sulphate granulate, Triple-Super phosphate), FYM and CS composition of different fertilisation events in 2019 and 2020. Fertiliser levels of HE in 2018 were 18 m^3 ha^{-1} for FYM and 180 kg N ha^{-1} for CAN. See Appendix 4 for details on fertilisation and harvest dates.
***Mean N, K and P concentrations were 4.5, 1.3 and 2.4 g kg^{-1} for CS and 6.4, 1.9 and 5.4 g kg^{-1} for FYM, respectively.

management regimes will have a positive effect on botanical diversity, forb cover, meadow bird habitat quality and earthworm diversity compared to PM swards with the HE management regime; 2) Forage production: Overall, dry matter yield and forage quality (e.g., N concentration, digestible organic matter) will increase with increasing management regime intensity regardless of sward type. However, compared to PM swards with the LL management regime, dry matter yield and quality will be higher in BD and PBD swards under the LL management regime, partially due to inclusion of legumes and other species intended to increase nutritional value and productivity, and PM swards under the HE management regime will have the highest dry matter yield and quality. Forage mineral concentrations will be highest in the BD and PBD swards and under the HE management regime due to higher forb coverage; and 3) Climate and water regulation: there will be higher soil carbon accumulation, improved soil structure and increased density of soil pores (i.e., better water infiltration) in BD and PBD versus PM swards and the LL management regime will enhance this effect. A conceptual visualisation of the hypotheses can be found in Table 1.

2. Material and methods

2.1. Site

The experiment was established in August 2017 at the Dairy Campus Research Facility (Wageningen University and Research) in Leeuwarden, The Netherlands (53° 10' 52.2" N, 5° 45' 24.5" E) on a previously intensively managed permanent production grassland field. The soil is *c.* 13% sand, 38% silt and 39% clay, with 7.7% soil organic matter content, 7.1 pH, 4.2 g total N kg^{-1}, 0.5 mg plant available P kg^{-1}, 90 mg plant available K kg^{-1} (P and K extraction method used $CaCl_2$ according to Houba et al., 2000). Fertilisation regimes were tailored to help alleviate nutrient limitation, in particular P limitation; see Table 2. In 2020, there were 978,000 ha of grassland in The Netherlands, which compromises 54% of agricultural land (https://www.clo.nl/indicatoren/nl211910-agrarisch-grondgebruik). Soils that have a relatively high clay content (such as those used in this experiment) comprise a substantial proportion of Dutch soils (Appendix 1). Temperature and precipitation data can be found in Appendix 2.

2.2. Experimental design

We experimentally established three sward types and four management regimes. In August 2017, the existing grass crop was killed using herbicide, followed by ploughing and seedbed preparation. Seeds were sown at 2–3 cm depth using a pneumatic sowing machine after which the plots were rolled with a Cambridge roll. The following sward types were established: 1) Productive monoculture (PM) sward consisting of *L. perenne* (BG3 commercial mixture of diploid perennial ryegrass cultivars (https://www.barenbrug.nl/bg3-superplus), 30 kg ha^{-1}) (Remmelink et al., 2020) was included as a reference for conventional agricultural practice; 2) Biodiverse (BD) sward (20 kg ha^{-1}) contained species from natural sources aimed at developing a species-rich meadow conducive to meadow bird conservation with an open structure, to allow for easy movement for meadow bird chicks ("Mengsels Voor Agrarische Toepassingen | Biodivers" n.d., www.biodivers.nl) (Geerts et al., 2014); and 3) Productive biodiverse (PBD) sward combining the BD mixture (10 kg ha^{-1}) with additional herbs and grasses aimed at improving production and forage quality (*L. perenne*, cv Barhoney, 7 kg ha^{-1}; *T. repens*, cv Rivendel, 2 kg ha^{-1}, *C. intybus*, 0.5 kg ha^{-1}; *C. carvi*, 1 kg ha^{-1}, *Scorzoneroides autumnalis* L., 0.15 kg ha^{-1}) (Geerts et al., 2014). The seeding density varied between the different sward types in order to most accurately replicate what is currently done in practice in grasslands for forage production (Geerts et al., 2014; Remmelink et al., 2020). In line with current practice, *L. perenne* cultivars varied between the PM and PBD swards (Geerts et al., 2014; Remmelink et al., 2020). Further, it has been shown that varying seeding densities at the start of an experiment does not result in changes to ecosystem function, with total species richness being the stronger driver (Schmitz et al., 2013). This means that variation in seeding densities between the treatments likely played a minimal role in driving the results seen here. Details on the seed mixtures can be found in Appendix 3.

Each sward type was subjected to four management regimes varying in the date of the first harvest, number of cuts and the timing, type and amount of fertiliser applied (Table 2, Appendix 4). The most extensive management regime (LL) followed the recommended management for maintaining species rich swards for meadow bird conservation, which consisted of a low (L) level of fertilisation with farmyard manure only (provides nesting material, camouflage and attracts insects and worms (Kruk, 1993)) combined with a late (L) first cut (after the 1st week of June when most meadow bird chicks are flight-ready (Broyer et al., 2016; Grüebler et al., 2012; Perlut et al., 2008)). The most intensive management regime (HE) had a high (H) level of fertilisation consisting of both mineral fertiliser and cattle slurry combined with an early (E) cutting date for the first cut (mid-May). The intermediate management regimes ML and ME both received moderate (M) rates of organic and mineral fertilizers as determined by Dutch fertilisation rates for dairy farms (www.bemestingsadvies.nl). Although the management techniques used in the intermediate regimes are not typically utilised in practice, the goal here was to determine if maximized deliverance of ecosystem services can be realised when a "middle ground" in terms of management intensity is struck. Plots received no fertiliser until after the first cut in 2018 in order to allow establishment of the plants. However, throughout the experiment, organic and mineral fertilisers were applied on both intermediate management regimes after the first cut to avoid a dense and uniform sward composition, which makes movement and feeding difficult during critical stages in meadow bird chick development (Devereux et al., 2004; Whittingham and Evans, 2004). The difference between management regimes ML and ME was that the ML had a late (L) first cut, whereas the first cut for ME was early (E) (Table 2). In total, this resulted in three sward types × four management regimes × four replicates = 48 plots. Each plot measured 6 m × 10 m and plots were arranged in a randomised block design, with 10 m strips between each of the blocks. To account for a seepage effect (i.e., moisture gradient) that was detected ad hoc, an additional “row” random factor was also included; see *Statistical analyses* Section 2.7 below.

2.3. Plant community composition and sward structure

The botanical composition was determined in August 2018, 2019 and 2020 using the Braun-Blanquet method (Braun-Blanquet et al., 1932) in two 100 cm × 100 cm quadrats in each plot. Plant species richness and the Shannon-Wiener diversity index (*H*) (Shannon, 1948) were calculated for each plot.

2.4. Sward structure: meadow bird habitat suitability

In mid-May 2019 just before the first early harvest, sward height was determined in all plots by taking 12 measurements with a falling plate metre (tempex plate with 48 cm width). Additionally, in 2019, vertical vegetation density distribution at 10 cm sward height intervals was determined using the white-plate method (Visser et al., 2017). This method is used as a proxy for assessing to what extent high sward density may negatively impact on the ability of meadow bird chicks to forage for insects (Devereux et al., 2004). For this method, a 60 × 60 cm square was cut to 5 cm height using electric secateurs. A white plate of 60 × 60 cm, with 10 cm height intervals indicated by black lines was carefully placed in the sward, at 15 cm from this cut square (creating a 15 × 60 cm wide undisturbed strip with vegetation). A picture was taken at 10 cm height and 75 cm from the white plate. This picture was converted to black and white using ImageJ software (Rasband, 2011) and the percentage vegetation cover for each 10 cm height interval was determined.

2.5. Forage quantity and quality

Plots were harvested three or four times per year (Table 2) using a Haldrup plot harvester (Logstor, Denmark) by cutting a 1.5 × 10 m strip. The fresh weight was recorded, and a sub-sample was taken for dry matter yield (drying at 70 ℃ for 48 h) and chemical analyses.

In 2018 (only dry matter yield), 2019 and 2020, forage productivity was determined for all cuts and treatments at Eurofins Agro (Wageningen, The Netherlands), including crude ash, total nitrogen (Sáez-Plaza et al., 2013) and in vitro organic matter digestibility (Tilley and Terry, 1963). Additionally, in the first cut in 2019 in plots with management regime LL and ME across all swards types, mineral concentrations (i.e., Ca, Cu, K, Mg, Mn, Na, P, S, Zn) were analysed by atomic emission spectrometry with inductively coupled plasma (Lichte et al., 1987).

2.6. Physical, chemical and biotic soil properties

In October 2019, 25 cores were taken in each plot at 0–10 cm depth using a grassland auger with a 2 cm diameter. Soil samples were pooled per plot and sent to Eurofins Agro (Wageningen, The Netherlands) where standard soil abiotic analyses were carried out (Appendix 5).

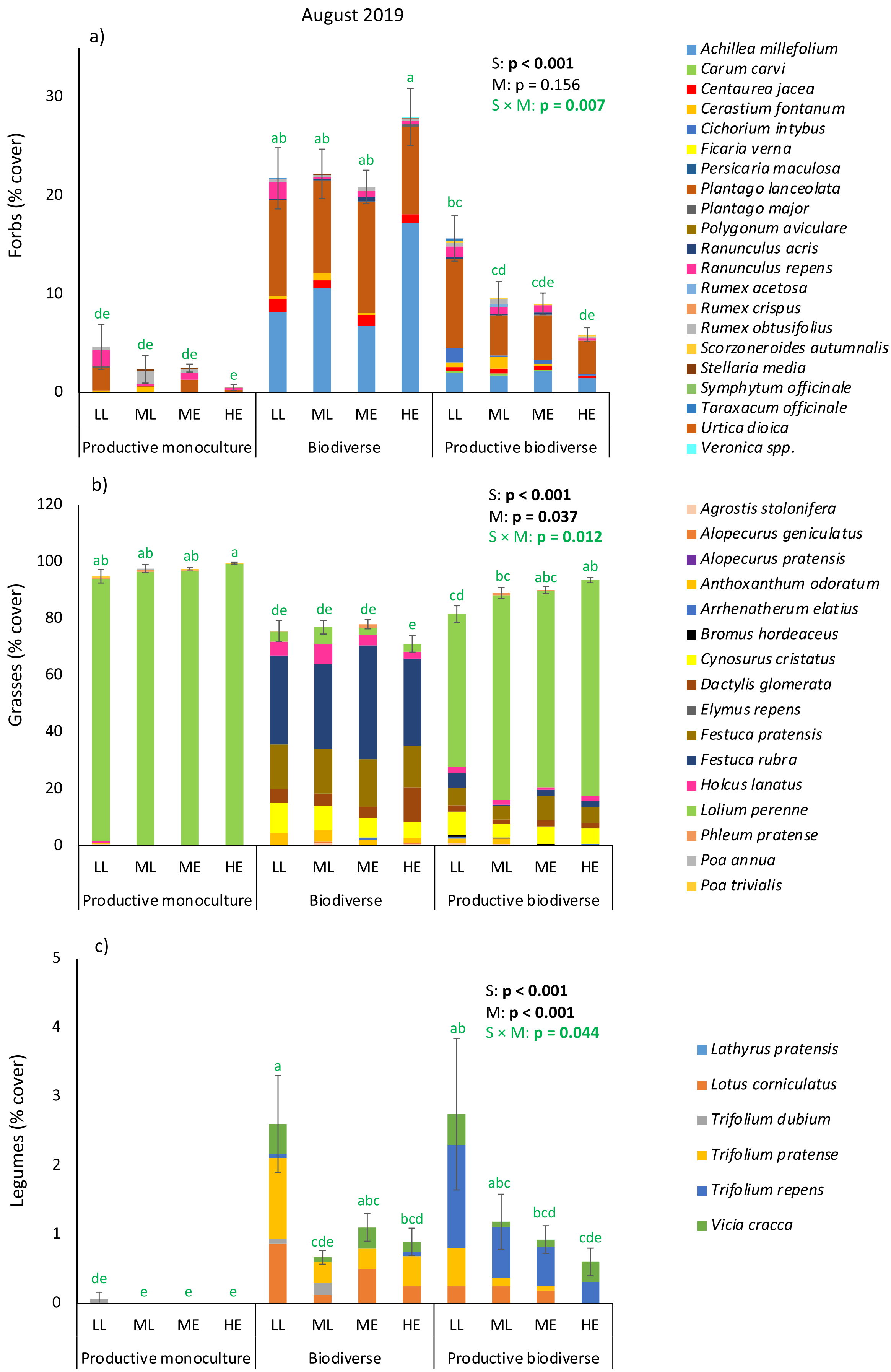
In October 2019, the soil physical and biological measurements described below were carried out in all plots, except those with the ME management regime. Soil penetration resistance was used as a proxy for water infiltration (Iepema et al., 2021). Soil penetration resistance was measured at 0–30 cm depth with a penetrometer (Eikelkamp, Giesbeek, The Netherlands) with a cone diameter of 1 cm and an apex angle of 60°. Ten measurements per plot were taken and then averaged to obtain one value. Visual assessments of soil structure and rooting were conducted on 20 × 20 × 20/25 cm soil cubes from the 0–25 cm and 25–45 cm soil layer. Cubes were dug out with a spade and broken in both horizontal and vertical direction. Soil structure was assessed by estimating the proportion (%) of soil crumbs, sub-angular block elements and angular blocky elements in the cubes, following the method by Peerlkamp (1959) and Shepherd (2000). Rooting score was assessed by scoring visible root density (score 1–10; 1 for no roots and 10 for high root density), with an estimation of the proportion of young roots relative to the total (De Boer et al., 2018). Soil biota activity was assessed by scoring the abundance of soil pores (score 1 – 10; 1 = no visible pores and 10 = above average pore density) (De Boer et al., 2018). Earthworms were sampled on the 4th of November 2019 by digging out a soil block of 20 × 20 × 20 cm from each plot for management regime LL and ME only. Earthworms were hand-sorted, counted, weighed and fixed in 70% ethanol prior to identification. Numbers and biomass were expressed per m^2 (20 cm depth). Worms were classified as adults or juveniles, identified to species and classified into functional groups (epigeic, endogeic and anecic species) (Bouché, 1977).

In October 2020, additional soil measurements were carried out in all plots with LL and ME management regimes as part of a national monitoring scheme (www.slimlandgebruik.nl). Forty soil cores were taken in each plot at 0–30 cm depth using a grassland auger with a 2 cm diameter. These samples were analysed for hot water extractable carbon (HWEC) (Ghani et al., 2003), total C (Dumas method; (Bremner and Tabatabai, 1971)) and soil bacterial and fungal biomass (NIRS) (Rinnan and Rinnan, 2007) at Eurofins Agro (Wageningen, The Netherlands). Soil penetration resistance was measured as described above.

2.7. Statistical analyses

The effects of sward type (PM, BD and PBD), management (LL, ML, ME and HE) and their interactions on ecosystem services were determined using general linear mixed effects models. (Note: as indicated above, certain response variables were not measured in all treatment combinations. When this was the case, the appropriate treatment was dropped from the model.) Sward type and management regime were considered fixed factors and block and row were considered random factors. Statistical analyses were performed in R 3.6 (R Core Team, 2020) with the packages lme4/lmerTest (Bates et al., 2015; Kuznetsova et al., 2017). All data were checked for normality, outliers and homoscedasticity to ensure all assumptions for ANOVA were met. Data were transformed as necessary; please see footnotes under the ANOVA tables (located in the Appendices) for details on which variables were transformed and what type of transformations were performed. Significant differences between treatments were assessed using Tukey’s HSD. When significant effects were detected, data were subjected to post hoc tests (Day and Quinn, 1989) using the emmeans/multcomp packages in R (Hothorn et al., 2012; Lenth, 2019) with Tukey HSD adjustment for multiple comparisons.

A principal component analysis (PCA) was performed to explore the relationships between multiple ecosystem services and the different sward type and management regime combinations. A subset of ecosystem services were chosen based on the categories presented in Table 1: botanical biodiversity (i.e., Shannon-Wiener Index, species richness, percentage forb/grass/legume cover, sward height and vertical vegetation density, juvenile/adult/total/total biomass of earthworms), forage quantity and quality (i.e., dry matter yield, digestible organic matter, nitrogen/phosphorus/calcium/potassium concentrations) and carbon sequestration/water regulation (i.e., soil pores/crumbs, soil organic matter, hot water extractable carbon). Certain variables were not measured in every plot (i.e., juvenile/adult/total/total biomass of earthworms, forage phosphorus/calcium/potassium concentrations, soil pores/crumbs, hot water extractable carbon). Values for these missing data points were imputed using the missMDA package (Josse and Husson, 2016). The PCA was then carried out using the FactoMineR package (Lê et al., 2008) and visualised using ggbiplot (Vu, 2016).



(caption on next page)

Fig. 1. The effect of sward type (S: productive monoculture, biodiverse, productive biodiverse), management (M: low fertilisation, late mowing (LL); medium fertilisation, late mowing (ML); medium fertilisation, early mowing (ME); high fertilisation, early mowing (HE)) and their interactions on percentage cover of three plant functional groups (forbs (a), grasses (b), legumes (c)) during August 2019. Data displayed are means ± standard error; n = 4. Within each panel, bars topped with different lowercase letters differed significantly from one another at p < 0.05 (Tukey's HSD). When significant interactions between sward type and management regime were found, only the interactive effect is shown (i.e., no significant individual effects), with different lower case green letters indicating significant differences. Within each bar, species are shown in ascending alphabetical order.

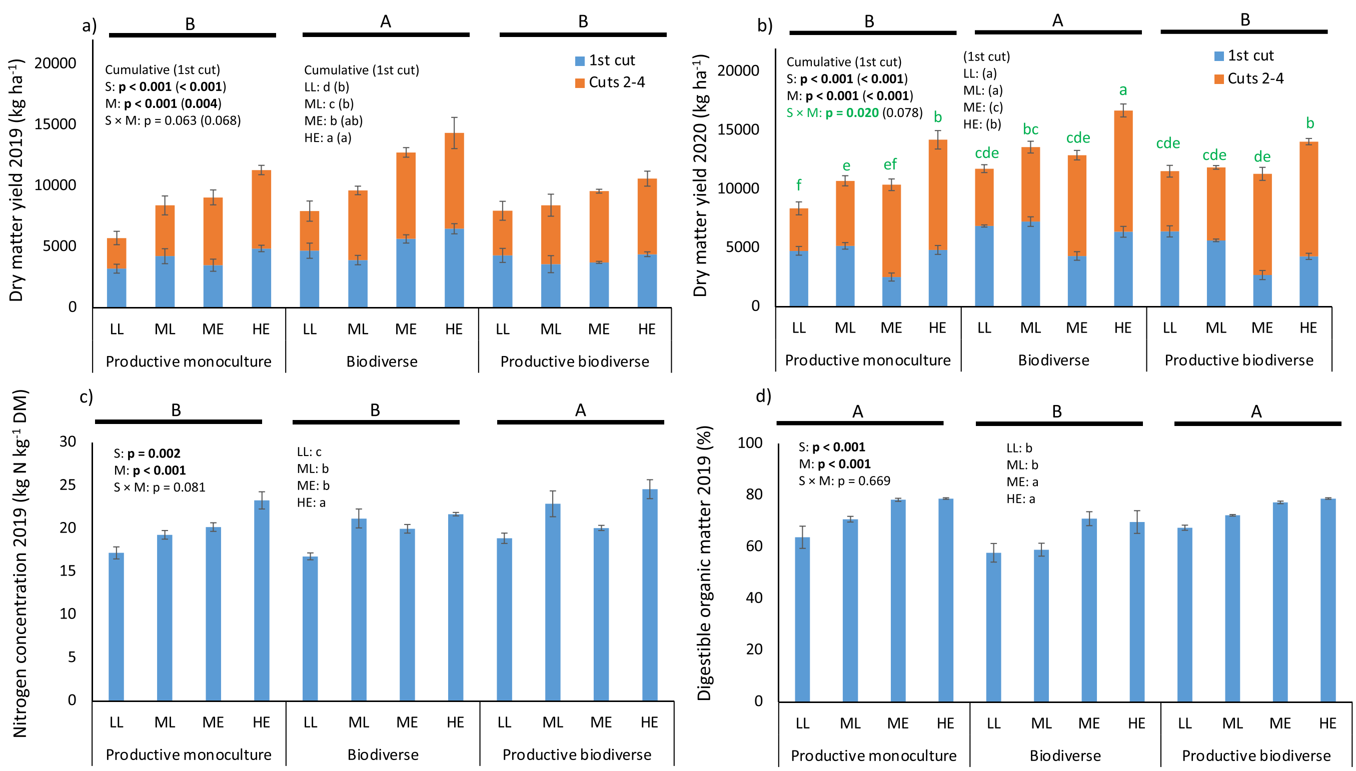


Fig. 2. The effect of sward type (S: productive monoculture, biodiverse, productive biodiverse), management regime (M: low fertilisation, late mowing (LL); medium fertilisation, late mowing (ML); medium fertilisation, early mowing (ME); high fertilisation, early mowing (HE)) and their interactions on dry matter yield in 2019 across the first cut of the season and the cumulative value of cuts (following 2–4 cuts; total 3–4 cuts, depending on treatment) (a), cumulative dry matter yield in 2020 (b), forage nitrogen concentration in 2019 (c) and digestible organic matter in 2019 (d). See Table 2 for more details on specific cutting regimes across different managements. Data displayed are means ± standard error; n = 4; values on top of the 2–4 cuts bars in panels (a) and (b) are the standard error for the cumulative cut value, including cut one. Within each panel, groups of bars topped with different uppercase letters (NB: in the case of panel b, these letters only apply to the first cut, not the cumulative) and inset boxes with management regime treatment codes followed by different lowercase letters differed significantly from one another at p < 0.05 (Tukey's HSD). When significant interactions between sward type and management regime were found, only the interactive effect is shown (i.e., no significant individual effects), with different lower case green letters indicating significant differences.

3. Results

Throughout this section, percentage differences between treatment means given are rounded to the nearest whole number. When interactions between sward and management regime were significant, the main effects are not described. Means ± standard errors can be found in the Appendices referred to after the description of each response variable.

3.1. Plant community composition and diversity

The plant community composition was affected by sward type, management regime and/or their interactions (Appendices 6–8). In August 2019, forb cover was 168% higher in PBD swards with LL versus HE management regimes and grass cover was 15% higher in PBD swards with HE versus LL management, but differences between management regimes disappeared in the PM and BD swards (sward × management regime interaction; Fig. 1a, b). Legume cover was 238% higher in BD swards with LL versus ML and HE management regimes and 350% higher in PBD swards with LL versus HE management regimes, but there were no differences between management regimes in PM swards (sward × management regime interaction; Fig. 1c). Richness was highest in BD and PBD (*c.* 16) and lowest in PM swards (*c.* 5), while LL managed plots had on average three and five more species compared to both ML and ME versus HE plots, respectively. The Shannon-Wiener Index was ten and 1.5 times higher in BD versus PM and PBD swards, respectively and *c.* 1.3 times higher in LL versus all other management regimes. Botanical data from 2018 and 2020 is provided in Appendix 8 as a reference.

3.2. Sward structure

Sward structure parameters were affected by sward type and management regime (Appendices 9–10). In May 2019, sward height and vertical vegetation density (20–30 cm) were 38% and 36% higher in BD versus PM and PBD swards, respectively. Sward height was 17% higher in HE versus LL, ML and ME plots, and largely followed trends in dry matter yield. Non-significant parameters are not shown.

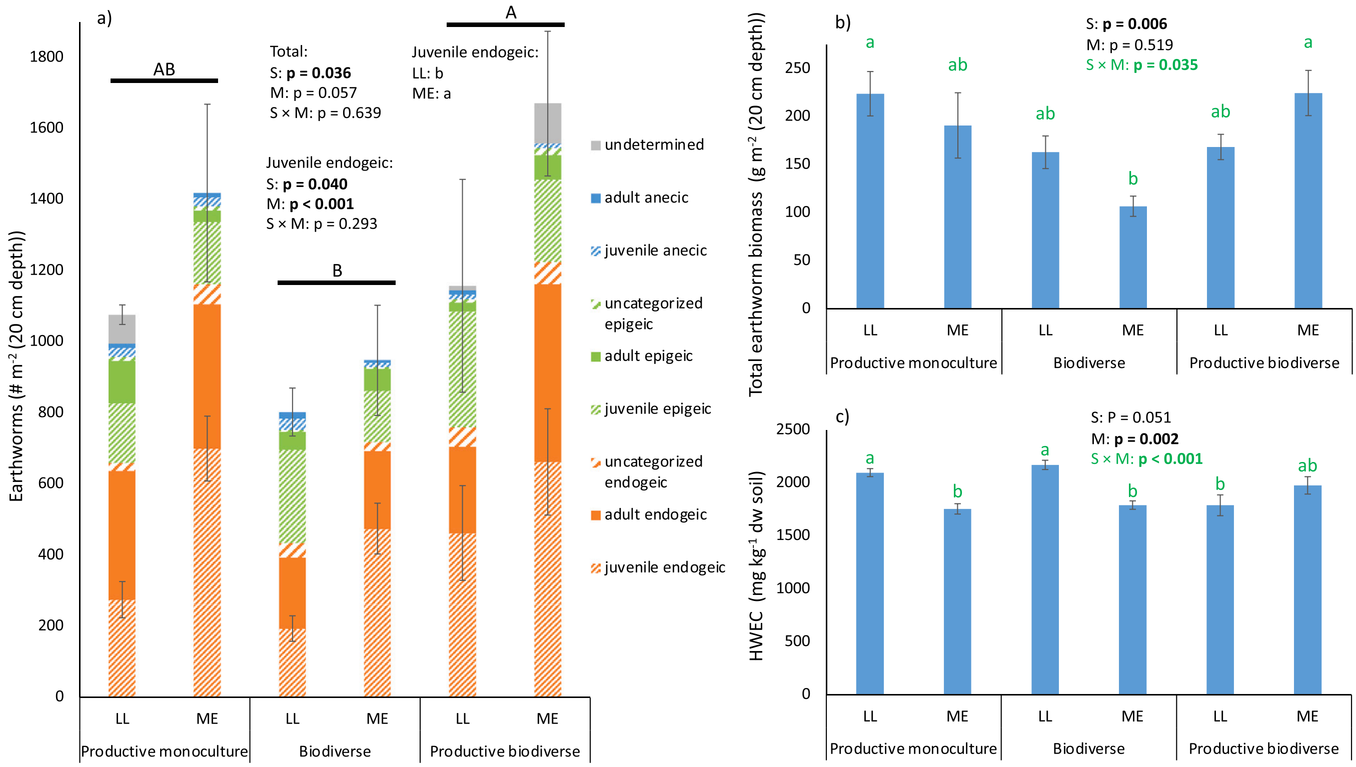


Fig. 3. The effect of sward type (S: productive monoculture, biodiverse, productive biodiverse), management regime (M: low fertilisation, late mowing (LL); medium fertilisation, early mowing (ME)) and their interactions on total number of earthworms (divided into functional groups; uncategorized within a functional group = could not determine adult versus juvenile; undetermined = functional group could not be determined) (a), total earthworm biomass (b) and hot water extractable carbon (HWEC) (c) from soil samples taken in 2019. Data displayed are means ± standard error; n = 4; standard errors at the top of bars in panel (a) were calculated for the total earthworms across all functional groups and standard errors in the middle of the columns were calculated for the total juvenile endogeic earthworms only. Within each panel, groups of bars topped with different uppercase letters and inset boxes with management regime treatment codes followed by different lowercase letters differed significantly from one another at $p < 0.05$ (Tukey's HSD). When significant interactions between sward type and management regime were found, only the interactive effect is shown (i.e., no significant main effects), with different lower case green letters indicating significant differences. NB: Post-hoc results for differences between sward type were the same for total earthworm and juvenile endogeic earthworms and therefore differences for both groups are represented by capital letters above the groups of bars.

3.3. Forage quantity and quality

Nearly all forage nutritional quantity and quality parameters were affected by sward type, management regime and/or their interactions (Appendices 11–14). Here, we present the results of the more critical parameters: dry matter yield (2019–2020 only; 2018 omitted for brevity and to highlight patterns after sufficient sward development), total nitrogen concentration, digestible organic matter and the mineral concentrations. All results can be found in Appendices 11–14.

In 2019, dry matter yield was 23% and 19% higher in the first cut and cumulatively for all cuts over the season, respectively, in the BD swards compared to the PM and PBD (Fig. 2a). In the first cut, the HE management regime had a 24% higher dry matter yield compared to LL and ML management regimes, but cumulatively, HE managed plots had a dry matter yield 12%, 26% and 39% higher compared to ME, ML and LL managed plots, respectively (Fig. 2a). In 2020, dry matter yield in the first cut was 27% higher in BD versus PM and PBD swards and 47% and 14% higher in LL and ML swards versus ME and HE managed plots, respectively (Fig. 2b). Compared to all other management regimes, the 2020 cumulative dry matter yield was consistently higher in HE managed plots across all swards, while dry matter yield was 22% higher in ML versus LL plots in PM swards, but this difference disappeared in BD and PBD swards (sward × management regime interaction; Fig. 2b). Forage nitrogen concentration in 2019 was 7% higher in PBD versus PM and BD swards and HE managed plots had values 12% higher versus ML and ME and 25% higher versus LL swards (Fig. 2c). Digestible organic matter was 11% higher in PM and PBD swards compared to BD and overall 14% higher in ME and HE versus ML and LL swards (Fig. 2d).

Forage mineral concentrations of K, Zn and Cu were generally higher in BD compared to PM swards. Additionally, Mg, Ca, Zn and Cu concentrations were higher for management regime LL compared to ME (Appendices 13–14).

3.4. Physical, chemical and biotic soil properties

Of the soil property measurements taken in 2019, several of the physical, chemical and biotic properties were affected by sward type, management regime and/or their interactions (Appendices 15–19). Penetration resistance in the top 0–10 and 10–20 cm was 15% and 11% higher in BD versus PBD swards, respectively. Penetration resistance at the 20–30 depth was not affected by any of the treatment combinations. Rooting scores were higher in BD versus PM and PBD swards. The percentage of young roots was 39% higher in LL versus ME and HE managed swards. Soil K was the only soil chemical property affected, with the highest overall values occurring in the LL managed soils (35% higher than the other management regimes; data for soil chemical properties not shown).

Total earthworm abundance was 38% higher in PBD versus BD swards (Fig. 3a). Total abundance of juvenile earthworms was 25% higher in ME versus LL managed swards. Total earthworm biomass was 52% higher in ME managed PBD swards and LL managed PM swards compared to ME managed BD swards (sward × management regime interaction; Fig. 3b). Individual earthworm biomass was 35% higher in LL versus ME managed swards. The proportion of juvenile earthworms

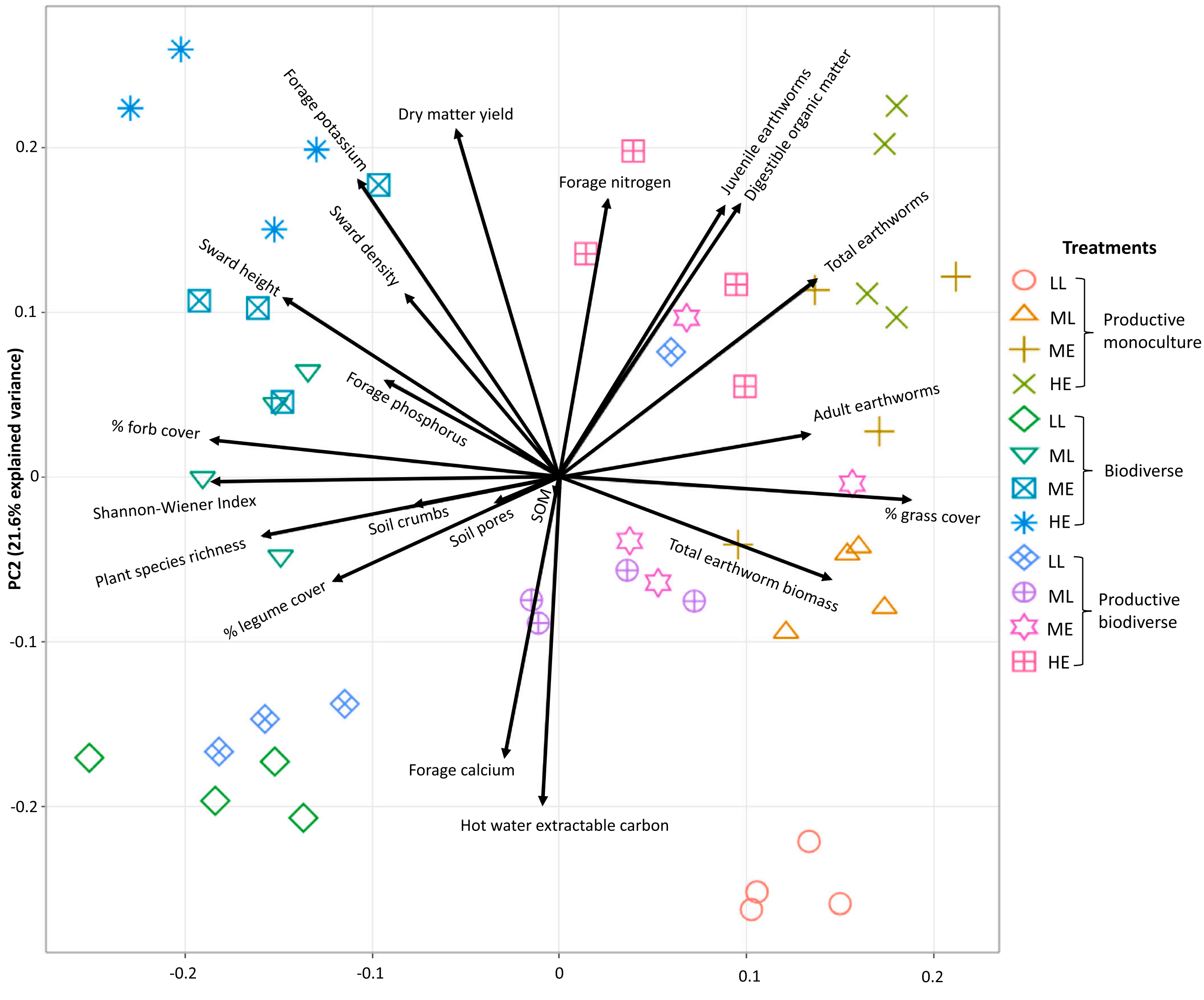


Fig. 4. Visual representation of a principal component analysis (PCA) showing the relationships between selected ecosystem services measured in plots with different sward types (productive monoculture, biodiverse, productive biodiverse) and management regimes (low fertilisation, late mowing (LL); medium fertilisation, late mowing (ML); medium fertilisation, early mowing (ME); high fertilisation, early mowing (HE)). Ecosystem services are grouped under the categories biodiversity (i.e., botanical Shannon-Wiener Index, plant species richness, percentage forb/grass/legume cover, sward height and vertical vegetation density, juvenile/adult/total/total biomass of earthworms), forage quantity and quality (i.e., dry matter yield, digestible organic matter, nitrogen/phosphorus/calcium/potassium concentrations) and carbon sequestration/water regulation (i.e., soil pores/crumbs, soil organic matter (SOM), hot water extractable carbon).

was significantly affected by interactions between sward and management regime, but post hocs revealed no true significant differences. The number of juvenile endogeic earthworms was 41% higher in the PBD compared to the BD swards and 49% higher in ME versus LL managed swards (Fig. 3a).

Finally, of the soil property measurements taken in 2020, several were affected by sward type, management regime and/or their interactions. Hot water extractable carbon was 20% higher in swards with the LL versus ME management regime in both PM and BD swards, but this difference disappeared in PBD swards (sward × management regime interaction; Fig. 3c). The fungal to bacterial ratio was 21% higher in BD versus PM and PBD swards. Penetration resistance was 29% higher in LL versus ME swards.

3.5. Principal component analysis

A principal component analysis revealed relationships between the selected ecosystem services and the sward and management regimes (Fig. 4). The first principal component was driven primarily by botanical variables and earthworm parameters. All botanical variables (i.e., Shannon-Wiener index, forb and legume cover, species richness, sward height and vertical vegetation density) (except grass cover) were strongly correlated with one another, as well as forage potassium and phosphorus, and tended to be associated with BD swards regardless of management regime. Most soil parameters related to C storage and soil structure (i.e., soil organic matter, soil pores and crumbs) were weakly associated with botanical variables (except grass cover). Earthworm adults, total number, total biomass were correlated with grass cover and were generally associated with PM and some of the PBD swards. The second principal component was driven mainly by dry matter yield, DOM and forage nitrogen and calcium, as well as hot water extractable carbon and juvenile earthworms. The dry matter yield was associated with PD swards with the HE management regime, forage nitrogen, DOM and juvenile earthworms with PBD and PM swards with HE. Forage calcium and hot water extractable carbon were associated with PD ML swards.

4. Discussion

In this study, we applied different management regimes to swards with contrasting botanical compositions to assess impacts on ecosystem services: biodiversity, forage quantity and quality, carbon sequestration and water infiltration. Below we discuss the implications of our findings for land management to promote ecosystem services.

4.1. Biodiversity

4.1.1. Botanical composition

Our first hypothesis was partially supported because plant species-rich sward types, extensive management and their interactions sometimes resulted in higher forb cover and plant biodiversity. Overall, the BD and PBD swards contained higher forb coverage and plant species richness, with forb cover higher in PBD swards with the LL versus HE management regime. Increased forb cover and plant species richness may result in improved ecosystem services (Sollenberger et al., 2019) such as higher forage productivity, when certain forb species are present, e.g., *C. carvi*, *C. intybus*, *P. lanceolata* (Cong et al., 2016; Finn et al., 2013; Weigelt et al., 2009), increased pollinator abundance and diversity (Orford et al., 2016), and improved meadow bird habitat (Gustafson, 2006). However, there was no difference in forb cover between ML and ME plots, indicating a delayed cut may not have led to increased seed set or germination and thereby forb cover (Humbert et al., 2012). This was likely due in part to the short duration of this experiment and the differences in flower and seed set phenology between species. Forb cover and species richness was generally lower in PBD versus BD swards despite five additional species in the PBD mixture. This was likely the result of competitive exclusion by *L. perenne* (Fan et al., 2003) in the PBD swards. In 2019, forb cover was also lower in HE versus LL managed PBD swards, probably due to increased N fertilisation in the HE PBD plots that favoured grass growth (Ignatavičius et al., 2013).

Legume cover declined over time in all plots, likely because the experimental site has a history of high N input and ML, ME and HE managed plots had high rates of N application, which is known to negatively affect grassland legumes (Tognetti et al., 2021). Further, legumes are notorious for their poor persistence in mowed swards (Brophy et al., 2017; Woodcock et al., 2014) and under drought conditions (Nichols et al., 2014) and the dry summer of 2018 may have exacerbated this. However, in 2020, LL managed BD plots supported higher legume cover than all PM and PBD swards with the different management regimes (except ME BD plots). In addition to lower N inputs, the LL managed plots had high concentrations of soil K (due in part to higher K input via farmyard manure), which promotes legumes such as *Trifolium* spp. (Bailey and Laidlaw, 1998) and can increase *T. pratense* competitive ability (Oram et al., 2014), one of the dominant legumes in LL managed BD plots. As was the case with the forbs, superior competitive ability of *L. perenne* may account in part for the low legume cover in LL managed PBD swards (Fan et al., 2003). Legumes foster many ecosystem services (Voisin et al., 2014) such as improved soil N content (Haas et al., 2019; McKenna et al., 2018), increased forage protein content (Hoekstra et al., 2018; Lüscher et al., 2014), contribution to over-yielding in species mixtures (Finn et al., 2012; Nyfeler et al., 2008) and an important food source for both pollinators and by attracting insects for meadow chicks (Wood et al., 2013). Here, simultaneous increases in forb and legume cover were not realised, which may have resulted to suboptimal deliverance of ecosystem services.

4.1.2. Meadow bird habitat parameters

Sward type and management regime altered several parameters related to meadow bird habitat, but not always in the intended manner. Although, as expected, HE managed swards resulted in a taller sward (Chamberlain et al., 2000), in May 2019, the BD swards were the tallest and densest, which is also interesting because the PM swards actually had the highest seeding densities. This may be partially driven by higher percentage cover of the grasses *Festuca pratensis* Huds., which was included in the BD seed mixture, and *Holcus lanatus* L. and *Dactylis glomerata* L., which were not, but emerged from the soil seed bank and seemed to outcompete many other species in the mixture. This was also supported by the relationships between vertical vegetation density and height and BD swards seen in the PCA. Even though sward height and vertical vegetation density were not measured in 2020, the high percentage cover of the aforementioned grasses and high dry matter yield in the first cut in the BD swards indicates that this effect likely continued into 2020, also under extensive management. Delaying the timing of the first cut until after the start of June is important to avoid nest destruction and disturbance and loss of cover for meadow bird chicks (until they can fly), which is a critical factor for chick survival rates (Vickery et al., 2001). However, taller and denser swards increase the time and energy required for meadow bird chicks (e.g., Black-tailed Godwit: *Limosa limosa* L.) to forage for insects, resulting in decreased prey acquisition and thereby lower survival rates (Devereux et al., 2004). It is surprising that the BD swards, with plant species compositions selected specifically to benefit meadow bird chicks, resulted in the habitat of the poorest quality. Transformation of soils with a long history of intensive agricultural management into suitable meadow bird habitat may require extensive management over the long-term. However, the emphasis here was the response of young, productive grasslands.

Further, cutting frequency in general is a disturbing factor for meadow birds (Vickery et al., 2001), however, after the middle of June meadow bird chicks are less affected by cutting (frequency), because the nesting season has (mostly) ended and chicks are more mobile. It should be noted that the cutting frequency in the current experiment was similar across the different treatments and was relatively high (3–4 cuts per year) in comparison to other European extensive grasslands, which are often cut only once or twice per year. However, this management reflects the need for relatively frequent cutting on nutrient-rich soils with a history of intensive management across geographic locations. In addition, total earthworm abundance was higher in PBD versus BD swards and juvenile endogeic were higher in ME versus LL swards. This indicates that PBD and ME swards could provide additional food resources for meadow birds (Vickery et al., 2001), although anecic and epigeic earthworms (i.e., those that frequently emerge at the surface) are more important food sources for meadow birds compared to the ground-dwelling endogeic earthworms (Onrust and Piersma, 2017). However, meadow bird foraging and chick survival were not measured in this experiment, as well as other parameters that affect meadow birds such as the presence of large grazers or mowing versus grazing in general (Whittingham and Devereux, 2008). Nonetheless, these results question whether the prescribed BD sward mixture utilised under these experimental conditions is indeed the most appropriate to improve meadow bird habitat. Future work should explore how grazers, as well as management regime/habitat heterogeneity at the landscape scale, could interact with the BD sward mixture chosen here.

4.2. Forage quantity and quality

4.2.1. Forage quantity

In line with our hypothesis, dry matter yield in 2019 increased with increasing management intensity and in 2020 the highest yield was always in the HE managed plots, likely due to high N fertilisation rates. In 2019 there was a negative effect of delayed mowing on cumulative dry matter yield (i.e., LL and ML had lower dry matter yield versus ME and HE plots). This signals a possible trade-off between sward productivity and allowing plants (Jantunen et al., 2007; Nakahama et al., 2016) and meadow birds (Broyer et al., 2016; Grüebler et al., 2012; Perlut et al., 2008) sufficient time to complete their life cycles (Kragt and Robertson, 2014; Turkelboom et al., 2018). However, differences between ML and ME (delayed and early mowing, respectively) dry matter yield disappeared in 2020, which indicates that this trade-off might abate as swards develop over time, but whether this pattern persists in older or permanent grasslands remains unknown.

In contrast to our hypothesis, BD and PBD swards with LL management did not have higher dry matter yield compared to PM swards with LL management regimes in 2019, but this effect manifested in 2020. Taken collectively, these results suggest that as swards develop, biodiverse swards with extensive management may outperform extensively managed monocultures. This may be attributed to improved resource utilisation via niche differentiation, facilitative interspecific interactions and/or selection effects in biodiverse mixtures versus monocultures (Cardinale et al., 2007; Hooper et al., 2005). Further, PM swards under the HE management regime did not have the highest overall dry matter yield in neither 2019 nor 2020. Instead, in 2020, BD swards with the HE management regime had the overall highest yield. This was surprising, given that swards designed for meadow birds are often less productive compared to *L. perenne*-dominated swards (Haas et al., 2019). This finding indicates that plant species diversity may contribute to superior yield in this young grassland system (Grange et al., 2021). Further, the PCA showed neutral to slightly positive relationships between dry matter yield and most plant diversity metrics, indicating some evidence for concomitant deliverance of high productivity and biodiversity. Importantly, the exceptionally dry summer in 2018 (whose impacts on soil moisture conditions lasted well into 2019) may have affected the results. Finally, the differences in seeding densities between the sward types (i.e., 30 kg ha^{-1} in the PM versus ~20 kg ha^{-1} in BD and PDB) could have influenced forage production. However, given that these seeding densities are in line with those used in practice when creating productive monoculture and diverse grasslands (Geerts et al., 2014; Remmelink et al., 2020), we would argue that this makes these findings of particular relevance to real world application.

4.2.2. Forage quality

In line with our hypothesis, forage N concentration was higher under the HE management regime versus ML, ME and LL regardless of sward type, probably due to higher N fertilisation. In contrast to our hypotheses, PBD sward forage had higher N concentrations versus BD and PM swards, which may be related to the higher N content in the additional plants added to the PBD such as *T. repens* (Haas et al., 2019) and *C. intybus* (Jan et al., 2011), despite the fact that the percentage cover of these species was quite low (*c.* 0–2.5%). Another contributing factor was likely the inclusion of the *L. perenne* cultivar “Barhoney”, which has a high foliar N concentration. In line with our hypothesis, digestible organic matter was higher in the PM and PBD versus BD swards, likely due to the presence of the highly digestible *L. perenne* in the former two sward types (Bruinenberg et al., 2002). Further, *T. repens,* another highly digestible plant (Haas et al., 2019), was still present in the PBD swards in spring 2019 and this may have contributed to higher DOM. Highly diverse grasslands, such as the BD swards, tend to produce forage with lower digestible organic matter values (Tallowin and Jefferson, 1999), which likely contributed to this result. In partial support of our hypothesis, probably as a result of the delayed mowing in the LL and ML plots, more mature and/or tough forage was harvested in the first cut, resulting in a strong decrease in digestible organic matter compared to ME and HE plots. This decline in digestibility is related to an increase in the proportion of stem material in more mature forage (Terry and Tilley, 1964; Wilman et al., 1977).

4.2.3. Forage mineral concentration

The higher mineral concentrations of K, Zn, P and Cu in the BD swards compared to the PM swards could be correlated to the higher percentage cover of legumes and forbs in May 2019; correlations with cumulative forb and legume cover were: K, r = 0.65; Zn, r = 0.40; P, r = 0.43 and Cu, r = 0.43). Also, forage Ca concentrations showed a positive correlation with the proportion of *T. repens* (r = 0.46) and *C. intybus* (r = 0.44), thereby partially explaining the higher concentrations in PBD. This is in line with the results of Pirhofer-Walzl et al. (2011) that showed higher mineral concentrations of forbs and legumes in comparison to grasses. The relatively high forage Mg, Ca, Zn, and Cu concentrations for the LL versus ME management regimes may have been related to higher application rates of these minerals in farmyard manure compared to cattle slurry (P did not follow this pattern) in combination with the (trend towards) higher proportions of forbs and legumes under LL compared to ME management in August 2019.

4.3. Carbon sequestration and water regulation

We found some support for our third hypothesis as sward diversity and management regime occasionally altered carbon sequestration and water regulation parameters. Percentage forb cover was higher in BD swards, which could lead to increased diversity in rooting strategies between- and within plant functional groups (Gould et al., 2016; Ravenek et al., 2016) and thereby facilitate the build-up of soil organic matter (Chai et al., 2019; Cong et al., 2014) and lead to better water infiltration (Deru et al., 2018).

Further, the fungal to bacterial ratio was higher in BD versus PM and PBD swards. Higher fungal to bacterial ratios are typically associated with dominance of the fungal energy channel, which typically leads to enhanced soil carbon sequestration (Malik et al., 2016). However, there was no concomitant significant increase in soil organic matter and the PCA demonstrated an exceptionally weak relationship between soil organic matter and any treatment. Indeed, significant changes to soil organic matter wrought by grassland restoration (usually increased forb cover) are notoriously unpredictable and when increases are realised, a minimum of 5 years is typically necessary (McLauchlan, 2006). The soil organic matter in these grasslands may be reaching the saturation level for such soils (Iepema et al., 2021). However, the increased rooting score in BD swards may result in increased aggregate stability and resistance to erosion (Reubens et al., 2007). The proportion of young, fine roots was 39% higher in LL versus ME and HE managed swards. In contrast, penetration resistance in 2020 was higher in LL versus ME managed plots across all swards, indicating a potential negative effect of extensive management on water infiltration. Taken together, increases in overall rooting in BD and LL managed swards may lead to enhanced erosion control, water infiltration (Deru et al., 2018) and water retention (Gyssels et al., 2005), with significant effects only realised in older grasslands.

Finally, total earthworm abundance was 38% higher in PBD versus BD swards and this difference was primarily driven by an increase in juvenile endogeic earthworms. Juvenile endogeic earthworms were also more abundant in ME versus the LL management regime, an effect likely driven by higher N fertilisation, including slurry manure, in the former (Corredor et al., 2021). Earthworm activity, particularly those of certain endogeic species, is known to increase soil organic matter build up and foster soil aggregate formation (Pulleman et al., 2005). However, no differences in soil organic matter or aggregate composition were seen between sward types, suggesting potential (endogeic) earthworm effects did not have enough time to manifest. Further, endogeic earthworms are known to have contrasting effects on soil porosity and thereby water infiltration (Blouin et al., 2013), and most earthworm parameters negatively correlated with botanical diversity. Taken together, this suggests simultaneous optimisation of multiple ecosystem services is likely impossible (Kragt and Robertson, 2014; Turkelboom et al., 2018). Collectively, these results suggest that substantial benefits for carbon sequestration and water regulation derived from diverse swards and/or swards with extensive management may only manifest in the long-term. However, these findings must be interpreted cautiously, given that most of these soil parameters were only measured to a depth of 20 cm, with the impact on soil organic matter build up and water infiltration at lower depths remaining unknown.

5. Conclusion

Here, we show that successful establishment of species-rich meadows on clay soils with a history of intensive agricultural management is possible in the short-term. Changes in meadow bird habitat parameters were negative or minimal, indicating long-term, extensive sward management might be necessary. Our findings indicate that different plant functional groups may perform differently in swards with varying diversity levels and management, which pulls focus on the need to consider specific biodiversity/conservation goals when selecting seed mixtures, deciding upon fertilisation regimes and assessing site suitability. Further, dry matter yield was highest in BD and intensively managed swards in 2019 and 2020, but there were strong interactive effects in 2020, with intensively managed swards generally coming out on top. However, forage N concentration was highest in PBD swards and digestible organic matter in PBD swards was on par with PM swards, indicating that the functional plants added to the PBD swards successfully improved forage quality, while maintaining high levels of plant biodiversity. Finally, short term benefits of sward diversity and extensive management for carbon sequestration and water regulation were relatively limited and showed inconsistent relationships between parameters that are expected to be interrelated, again suggesting such benefits may only materialize in older or permanent grasslands. These findings demonstrate that diverse swards, different management regimes and their interactions can benefit certain ecosystem services, while hindering others. Some effects could have been related to the different seeding densities between sward types. However, the seeding densities chosen here to reflect common practice, making these results particularly germane to farmers seeking to create grasslands that maximize ecosystem service. Further, our study did not consider grazing, meaning that these findings are only applicable to mown grasslands. Future research directions should compare short- versus long-term effects of sward composition and management on ecosystem services across multiple sites and soil types, with particular emphasis on teasing apart the effects of particular fertilisation regimes (both quantity and quality) versus mowing timing and frequency, the role of individual plant species and the time needed to realise maximum soil-related ecosystem services.

CRediT authorship contribution statement

Nyncke Hoekstra: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing – original draught, Writing – review & editing. **Jonathan R. De Long**: Conceptualization, Data curation, Formal analysis, Methodology, Validation, Visualization, Writing – original draught, Writing – review & editing. **Anne P. Jansma**: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Resources, Supervision, Validation, Visualization, Writing – review & editing. **Goaitske Iepema**: Conceptualization, Investigation, Methodology, Validation, Writing – review & editing. **Astrid Manhoudt**: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Validation, Writing – review & editing. **Nick van Eekeren**: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing – review & editing.

Declaration of Competing Interest

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Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.eja.2023.126886.

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