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RESEARCH ARTICLE

Higher cutting frequency can restore semi-natural habitat quality on farmland

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Abstract

1. In agricultural landscapes, semi-natural habitats such as field margins play an important role in maintaining biodiversity. However, they are generally highly productive and merely support species-poor vegetation, which may impair their conservation value and ecological functioning.
2. Ecological theory originally predicted that productive habitats cannot support species-rich vegetation; however, more recent studies suggest that regular defoliation of herbaceous vegetation types can maintain species-rich plant communities also under productive conditions. Here we ask whether applying appropriate cutting regimes can restore the species richness of species-poor vegetation even under productive conditions.
3. We carried out a 6-year experiment with three productivity levels induced by artificial fertilizer applications (NPK; equivalent to 0, 55, 110 kg N ha^{-1} $year^{-1}$) and four cutting frequencies (one to four times a year). We examined the response over time of plant species richness and cover of dominant forbs and non-dominant forbs, grasses and Fabaceae species.
4. The negative effects of productivity on plant species richness were moderated by the effects of cutting frequency. At the low productivity level, species richness increased under all cutting frequencies. At the highest productivity level, cutting once or twice per year resulted in a decline in species richness, while cutting three or four times per year produced increases in species richness. The cover of dominant forbs showed a pattern that was largely opposite to that of species richness. After the first year, a clear and consistent negative relationship was observed between plant species richness and dominant forb cover. The non-dominant forbs showed the most pronounced positive response to increasing the cutting frequencies.
5. *Synthesis and applications*. Rather than productivity per se, the cover of dominant plant species drives plant species richness. Breaking the dominance of these species through defoliation can restore the species richness of the vegetation. Because dominant plant species can tolerate more defoliations at higher productivity, the number of times a vegetation needs to be cut to restore and maintain

species-rich vegetation increases with the productivity of the habitat. Our results indicate that the quality of herbaceous vegetation types in semi-natural habitats on farmland can effectively be restored through cutting regimes that are tailored to the productivity levels of the vegetation.

KEYWORDS
biodiversity, defoliation, dominant plants, fertilizer, grassland, landscape features, mowing

1 | INTRODUCTION

In agricultural landscapes, the vegetation of landscape elements such as field boundaries, road verges, hedgerows and railway embankments plays a key role in maintaining biodiversity. In the otherwise highly disturbed agroecosystem, these habitats with permanent semi-natural vegetation represent the last refugia for many species of plants and animals, including rare ones (Li et al., 2020). They nourish, shelter and provide overwintering sites for functionally important species such as pollinators and natural enemies that may support crop yield through pollination and natural pest control (Dainese et al., 2019), thereby facilitating more sustainable forms of farming (Meehan & Gratton, 2015). They can furthermore facilitate the dispersal of species between protected areas, allowing plant and animal species to more easily adapt to climate change (Donald & Evans, 2006). International policies, therefore, target the restoration of these landscape features, with, for example, the EC Biodiversity Strategy for 2030 aiming to recreate at least 10% of agricultural area under high-diversity landscape features (European Commission [EC], 2020). The relationship between the quantity of landscape features and biodiversity and associated ecosystem functioning has been extensively studied (e.g. Dainese et al., 2019; Shackelford et al., 2013). However, interest in the functional importance of the quality of semi-natural landscape features in agricultural landscapes is a relatively recent thing (Cole et al., 2020; Fijen et al., 2025; Mei et al., 2021).

Vegetation diversity is a key determinant of the quality of semi-natural landscape features. Plant species richness is known to promote the diversity and stability of communities at higher trophic levels, such as arthropod herbivores and associated predators (Crutsinger et al., 2006; Haddad et al., 2011). Plant species richness may also facilitate higher animal richness through its effects on vegetation structure and complexity, and may offer animals more niches to coexist (Mei et al., 2021). Currently, the vegetation of landscape features in high-intensity agricultural landscapes is mostly species-poor and dominated by a few tall and fast-growing species, such as *Rubus fruticosus*, *Elymus repens*, *Galium aparine* and *Dactylis glomerata* (Kleijn et al., 1998). As a result, it supports much less biodiversity than is considered potentially possible and desirable (Cole et al., 2020). Insights into how to restore high-diversity features that are regularly exposed to agrochemicals could help operationalize international policy objectives targeting biodiversity in agricultural landscapes.

Originally, ecological theory predicted that plant species richness showed a hump-backed relationship with productivity, with the highest species richness at intermediate disturbance regimes (Grime, 1973). This implies that species-rich communities are restricted to habitats with relatively low nutrient availability, where plants compete for below-ground resources rather than light (Neuenkamp et al., 2013). Because landscape features in agricultural landscapes are directly or indirectly exposed to nutrients from nearby farmland, they often have a high productivity (Kleijn & Verbeek, 2000), which would suggest it to be impossible to maintain or create species-rich vegetation. However, more recent studies suggest that the key driver of plant species richness is not productivity itself, but the ensuing competition for light (Hautier et al., 2009). If competition for light is the primary process that is driving species decline with increasing productivity of habitats, then reducing the dominance of tall-growing species that outcompete many other species could allow more species-rich vegetation types to persist even under more productive conditions (Borer et al., 2014; Hautier et al., 2018).

This suggests that repeated defoliations of the mostly species-poor vegetation of productive landscape features in agricultural landscapes, through mowing or grazing, could allow new plant species to colonize these habitats and promote species richness. A meta-analysis by Francksen et al. (2022) indeed found that species loss increased with fertilizer-induced productivity, but that species loss decreased with the number of defoliations per year to the extent that it was effectively neutralized at 2–4 defoliations per year. However, Francksen et al. (2022) could not rule out that this was caused by plant species richness already being reduced at higher defoliation rates as a smaller number of species have their optimum distribution at high cutting frequency than at low frequency (Busch et al., 2019). Furthermore, how frequently the vegetation needs to be removed for species-rich vegetation to develop, after what period of time effects become apparent, and whether that depends on the productivity level is unknown. Additionally, the responses to both productivity and defoliation might differ markedly between plant functional groups. Grasses generally benefit from higher productivity, while legumes generally decline (Humbert et al., 2016).

Here, we address this knowledge gap by testing the effects of changes in plant species richness from four cutting rates at three different productivity levels in a 6-year experiment. We build on a longer-term experiment that examined the effects of exposure to low levels of agrochemicals on field boundary vegetation that was annually cut once at the end of the growing season (Kleijn & Snoeijing, 1997). At the start of the current study, plant species richness was no longer related to the original treatments (Figure S1). The vegetation was

dominated by a small number of tall perennial forbs that had outcompeted most other species, with legumes and rosette-forming forbs being almost completely absent (Table S1), which resembled the typical low-diversity vegetation found in landscape features in agricultural landscapes. Using these relatively homogeneous experimental plots that resembled the typical semi-natural vegetation that can be encountered in agricultural landscapes, we ask (1) How does cutting frequency moderate the impact of productivity on plant species richness and (2) How can shifts in the cover of specific functional groups explain the mechanisms underlying plant species richness responses to cutting frequency and productivity?

2 | MATERIALS AND METHODS

2.1 | Study design

The current study built on an experiment that used low levels of fertilizer and herbicide treatments to study the potential effects of agrochemical drift on plant species richness (Kleijn & Snoeijing, 1997). Briefly, in March 1993, herbaceous vegetation plots had experimentally been established by sowing a seed mixture of 30 forb species on a former arable field on sandy soil in Wageningen, the Netherlands (51.984186° N, 5.654263° E). Because the experiment was carried out on the experimental farm of Wageningen University, no permits were required to carry out the work. The experimental area bordered an arable field on two sides and a regularly cut, grassy farm track on the other two other sides (Figure S2). The study comprised forty-eight 2 × 2 m plots separated by 1 m wide regularly cut perennial ryegrass buffers. The plots were arranged in a randomized complete block design, with three levels of artificial NPK fertilizer application and four levels of broadleaf herbicide application (Starane, active ingredient fluroxypyr), representing respectively 0%, 25% and 50% and 0%, 5%, 10% and 50% of full-field application rates. There were four blocks with all combinations of the different levels of the two treatments. The results of the first 3 years of this study have been reported by Kleijn and Snoeijing (1997). As part of standard management, the plots were cut once a year in September, with cuttings being removed. The study ran until 2000, by which time it was clear that cutting only once a year was driving vegetation succession towards dominance of a few tall species that most successfully competed for light. Between 1996 and 2000, species richness declined by 2.4 species per year on average, and in the Year 2000, the tall forbs *Tanacetum vulgare* and *Centaurea jacea* accounted for almost half of the vegetation biomass, with species composition resembling the ruderal type of vegetation that can be found in many semi-natural habitats in agricultural landscapes. We used these plots to study the effects of cutting frequency at different productivity levels. For the new study, we ceased the herbicide application but kept the fertilizer treatments that experimentally manipulate vegetation productivity. We doubled the original fertilizer application rates (NPK fertilizer [15–12–24] now applied at a rate equivalent to 0, 55 and 110 kg N ha^{-1} $year^{-1}$). In 2001, at the start of the current experiment and prior to the application of the first new experimental treatments, none of our examined response variables were significantly affected by the fertilizer application (Table S2). Fertilizers were applied in two parts: once at the start of the growing season (in the period late April to early May) and once after the second cut of the four-cut treatment (in early June). The herbicide applications were replaced by cutting frequency treatments in such a way that in each of the four blocks, a herbicide treatment was replaced with a different cutting frequency treatment to make sure that cutting treatments were not confounded with possible legacy effects of the herbicide treatments. Cutting treatments were more or less equally distributed over the growing season between early April and early October, when the final harvest took place. The two-cut treatment had three-monthly intervals between cuts, the three-cut treatment had 2-monthly intervals, and the four-cut treatment had 6-weekly intervals. Vegetation was removed from the plots after each cut, and care was taken to avoid seed dispersal between plots.

2.2 | Observations

From 2001 to 2006, vegetation composition was assessed in the central square metre of the plots, leaving a buffer of 0.5 m on all sides between the permanent quadrat and the edge of the plots. Following the 1993 survey protocol, species cover was assessed consistently using a modified Braun–Blanquet scale. However, for the current analyses we converted the cover classes to average cover estimates in percentages: cover class 1—0.05%; 2—0.175%; 3—0.525%; 4—1.65%; 5—3%; 6—8.75%; 7—18.75%; 8—37.5%; and 9—75%. Species cover and richness were assessed between late April and early May, right before the first annual fertilizer application, and treatment effects therefore essentially reflect the cumulative effects of prior years.

Productivity was assessed as dry weight by harvesting all aboveground biomass in a 0.5 × 0.5 m plot in the central square metre and drying for 48 h at 80°C. Harvesting was done simultaneously with the application of the cutting treatments, and for plots with multiple cuts per year, dry weight estimates were summed to achieve a total productivity per year. Productivity estimates were therefore affected by the treatments in the year they were assessed. To be able to compare the treatment effects on vegetation composition and biomass, we used biomass data from the period 2000 to 2005, where 2000 reflects the baseline situation for this study.

2.3 | Analysis

We analysed species richness (m^{-2}), harvested biomass and summed percentage cover of the functional groups dominant forbs, non-dominant forbs, grasses and legumes (Fabaceae). The dominant forbs comprised the species *Tanacetum vulgare*, *Centaurea jacea* and *Saponaria officinalis* that at the start of the experiment were present in almost all plots with high average cover (Table S1). Non-dominant forbs comprise all other forb species excluding Fabaceae.

Data were analysed using a three-way ANOVA with the factors productivity (fertilizer application), cutting frequency, year and all their interactions. Block and, nested within block, plot (to account for repeated measures) were included as blocking factors. We were primarily interested in how the effects of cutting frequency would moderate the effects of productivity and whether this would change over time (i.e. the two-and three-way interactions) and not in which specific combination of treatment levels differed significantly from one another. We therefore did not run post-hoc tests. Normality of error distribution was checked visually using residual plots. Harvested biomass and cover of legumes were log-transformed prior to analysis to improve normality.

Additionally, to test whether dominant forb cover was directly related to plant species richness, we ran a linear mixed model with dominant forb cover, year and their interaction as fixed effects and block and, nested within block, plot as random factors. Analyses were done in Genstat 22nd Edition (VSN International, 2022).

3 | RESULTS

At the start of the experiment, average species richness across all 48 plots was 14.9 species m^{-2} and did not vary much between plots with different treatment combinations (Figure 1). During the experiment, productivity had the expected significant negative overall effect on plant species richness, but this was moderated by significant effects of cutting frequency, which resulted in contrasting trends in plant species richness between productivity levels (significant three-way interaction; Table 1). At the low productivity level, species richness increased under all cutting frequencies, although the increase appeared less pronounced at lower cutting frequencies. At the intermediate productivity level, the overall patterns were similar to the low productivity treatment, but differences between the cutting treatments were more pronounced. At the highest productivity level, cutting once or twice per year resulted in a decline in species richness, while cutting three or four times per year showed increases in species richness (Figure 1). Cutting four times a year seemed to result in species richness levelling off after 3–4 years. The treatment combination that resulted in the highest mean species richness was cutting twice per year at the low productivity level (25.3 species m^{-2} in Year 6).

The effect of fertilizer application on harvested biomass was not moderated by cutting frequency and this furthermore did not change over time (no significant productivity-cutting frequency or three-way interaction; Table 1). In the Year 2000, prior to the first treatment applications, biomass production was around 850 g m^{-2} $year^{-1}$ for all three productivity treatment levels. After the baseline year, the fertilizer treatments resulted in harvested biomass increasing with treatment level (significant productivity-cutting frequency interaction; Table 1; Figure 2a), which indicated the successful creation of different productivity levels. Cutting frequency also significantly affected biomass production after the baseline year (significant productivity-cutting frequency interaction; Table 1; Figure 2b). Cutting twice per year consistently produced the highest mean biomass in all treatment years, with no other consistent differences between other cutting frequencies over the years. Across treatments, after an initial peak during the first treatment year, harvested biomass declined and remained stable at approximately 700 g m^{-2} $year^{-1}$ from the third year onwards.

The cover of dominant forbs was significantly affected by all main factors and all two-way interactions, while the three-way interaction was marginally significant (Table 1). Figure 3 presents the results of the two-way interactions with year. Across all cutting frequencies, at the low productivity level, cover of dominant forbs declined steadily over the years (Figure 3a). At both the intermediate and the high productivity levels, cover of dominant forbs remained more or less stable until the third year of the treatment application, after which they dropped to approximately 60% of their cover at the start of the experiment. Across all productivity levels, cover of dominant forbs remained more or less stable throughout the experiment when plots were cut once per year (Figure 3b). Dominant

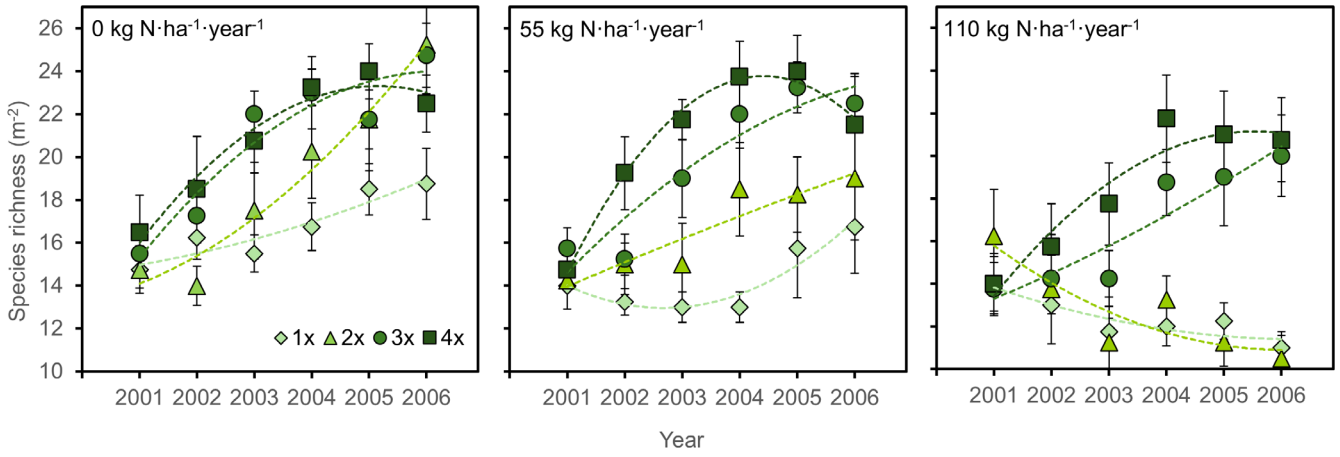

FIGURE 1 Effect of productivity on changes in plant species richness is moderated by cutting frequency. Productivity was experimentally manipulated by annually fertilizing plots with 0, 55 or 110 kg N ha^{-1} $year^{-1}$. Markers indicate means ± standard errors ($n = 4$) of raw data. Dashed lines are visual aids to illustrate trends.

TABLE 1 Results of the ANOVA linking various components of plant species composition to productivity (manipulated by means of fertilizer application) and cutting frequency.

		Species richness		Harvested biomass		Dominant forb cover		Fabaceae cover		Gramineae cover		Non-dom. forb cover	
	df	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Productivity	2, 33	**15.37**	**<0.001**	**20.34**	**<0.001**	**6.65**	**0.004**	**24.94**	**<0.001**	1.42	0.257	1.91	0.164
Cutting frequency	3, 33	**16.41**	**<0.001**	**11.58**	**<0.001**	**56.05**	**<0.001**	**5.39**	**0.004**	**8.21**	**<0.001**	**7.88**	**<0.001**
Prod.×cut. fr.	6, 33	0.60	0.729	1.27	0.3	**2.65**	**0.033**	0.33	0.918	0.99	0.451	0.96	0.465
Year	5, 180	**44.33**	**<0.001**	**84.59**	**<0.001**	**39.80**	**<0.001**	**12.49**	**<0.001**	**32.45**	**<0.001**	1.01	0.415
Year×prod.	10, 180	**5.32**	**<0.001**	**3.58**	**<0.001**	**4.12**	**<0.001**	**2.70**	**0.004**	0.98	0.459	1.63	0.103
Year×cut. fr.	15, 180	**6.27**	**<0.001**	**6.36**	**<0.001**	**11.32**	**<0.001**	**1.89**	**0.026**	**3.81**	**<0.001**	**3.20**	**<0.001**
Year×prod.×cut. fr.	30, 180	**2.41**	**<0.001**	0.98	0.495	1.46	0.069	1.19	0.243	1.14	0.290	0.87	0.667

Note: Species richness and plant cover were estimated from late April to early May before any effects of the treatments of that year could be expected. We therefore compared species richness and cover data (Years 2001–2006) with the cumulative biomass of the Years before (2000–2005). df indicate numerator and denominator degrees of freedom, respectively. Harvested biomass and Fabaceae cover were log-transformed prior to analysis. "Bold values indicate statistical significance $P<0.05$.

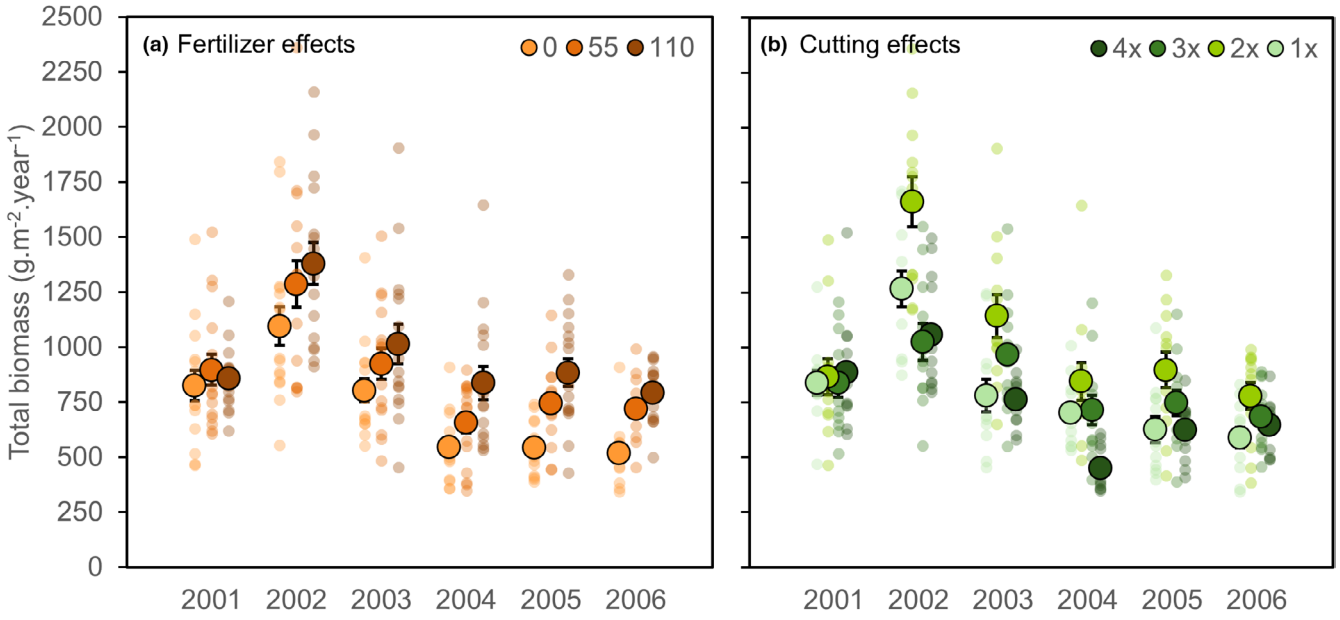

FIGURE 2 Illustrations of the total harvested biomass (dry weight) responses per year in plots with (a) different productivity levels (fertilized with an equivalent of 0, 55 and 110 kg N ha^{-1} $year^{-1}$; $n=16$) and (b) different cutting frequencies ($n=12$). Markers indicate means ± standard error; shaded dots indicate observations. To ease comparison with other figures, the years of the botanical surveys are listed on the *x*-axis as these were annually done prior to the first treatment application and therefore represent the same treatment-year combination. The actual baseline biomass harvests were done in 2000 prior to treatment application, with subsequently five treatment years.

forb cover also remained stable during the first three treatment years in twice-cut plots, after which cover dropped rather abruptly. In plots that were cut three and four times per year, dominant forb cover declined steadily to marginal values at the end of the experiment. The graphical illustration of the marginally significant three-way interaction indicated a pattern opposite to that of plant species richness (Figure S3), with, at the low productivity level, general declines in dominant forb cover that became more pronounced with cutting frequency, and, at the high productivity level, approximately stable cover in plots that were cut once or twice per year but strong declines in plots that were cut three or four times annually. The analysis linking dominant forb cover directly to plant species richness showed that in the baseline year no relationship was found, but after one year of treatment application, a clear and consistent negative relationship was observed between species richness and dominant forb cover (Figure 4).

The cover of Fabaceae species was significantly affected by all main factors and all two-way interactions with year (Table 1). Across all cutting frequencies, Fabaceae cover declined consistently with productivity level (Figure 3c). Fabaceae cover tended to show a unimodal relationship with a peak in 2004 in plots that were cut once to thrice a year, while in plots that were cut four

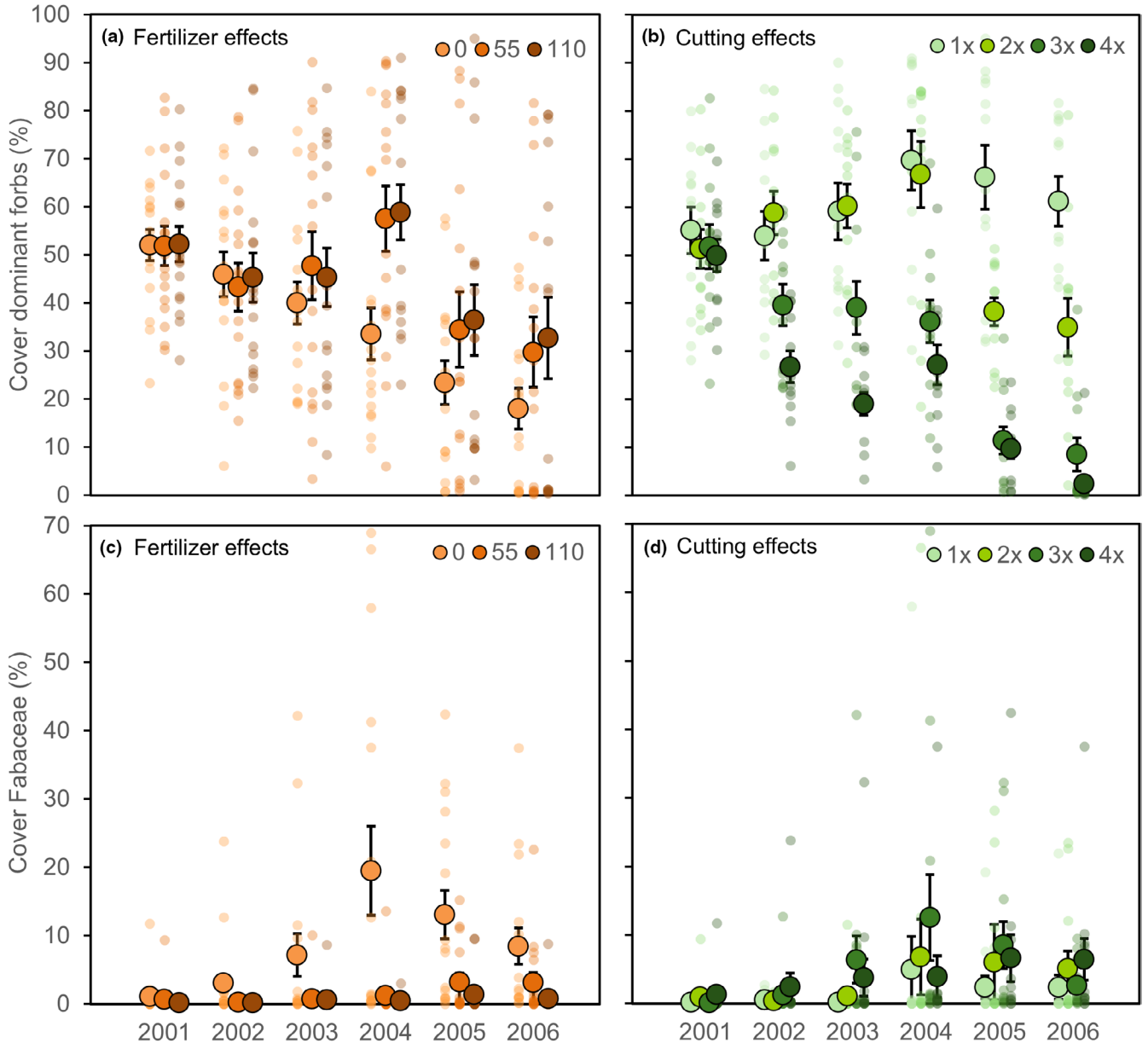

FIGURE 3 Illustration of the effects of different productivity levels on the cover of dominant forbs (a) and Fabaceae (c) and the effects of different cutting frequencies on the cover of dominant forbs (b) and Fabaceae (d). Productivity was experimentally manipulated by annually fertilizing plots with 0, 55 or 110 kg N ha^{-1} $year^{-1}$. Markers indicate means ± standard error with $n = 16$ for productivity treatments and $n = 12$ for cutting treatments. Shaded dots indicate observations. Dominant forbs comprise three species; Fabaceae comprise eight species.

times a year a slower but continuous increase in cover could be observed (Figure 3d, interaction between cutting frequency and year). The cover of Gramineae species was significantly affected by the year-cutting frequency treatment. After the initial baseline year, Gramineae cover generally seemed to increase with cutting frequency, although differences between the four treatment levels varied between years (Figure 5a). Non-dominant forb cover was likewise significantly affected by the year-cutting frequency treatment and increased with increasing cutting frequency; a pattern that became steadily more pronounced over the years of the experiment (Figure 5b).

4 | DISCUSSION

The importance of productivity and cutting or grazing for maintaining species-rich herbaceous vegetation is well established (Chen et al., 2021; Parr & Way, 1988). However, how cutting frequency interacts with the generally negative effects of habitat productivity on plant species richness remains poorly understood. Our results suggest that, rather than productivity per se, the cover of dominant plant species drives the number of species that can persist. Effects of productivity on plant species richness mainly occur through allowing a small number of plant species to attain dominance. Breaking the

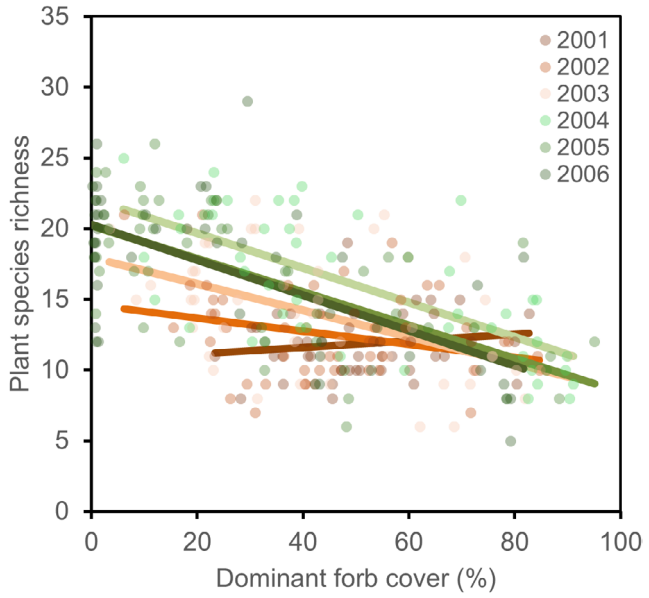

FIGURE 4 Relationship between dominant forb cover and plant species richness (excluding dominant forbs) becomes more apparent with the number of years the cutting and fertilization treatments have been applied. Dominant forb cover–year interaction: $F_{5,232.7}=3.48$, $p=0.005$, Marginal R^2: 0.35, Conditional R^2: 0.69.

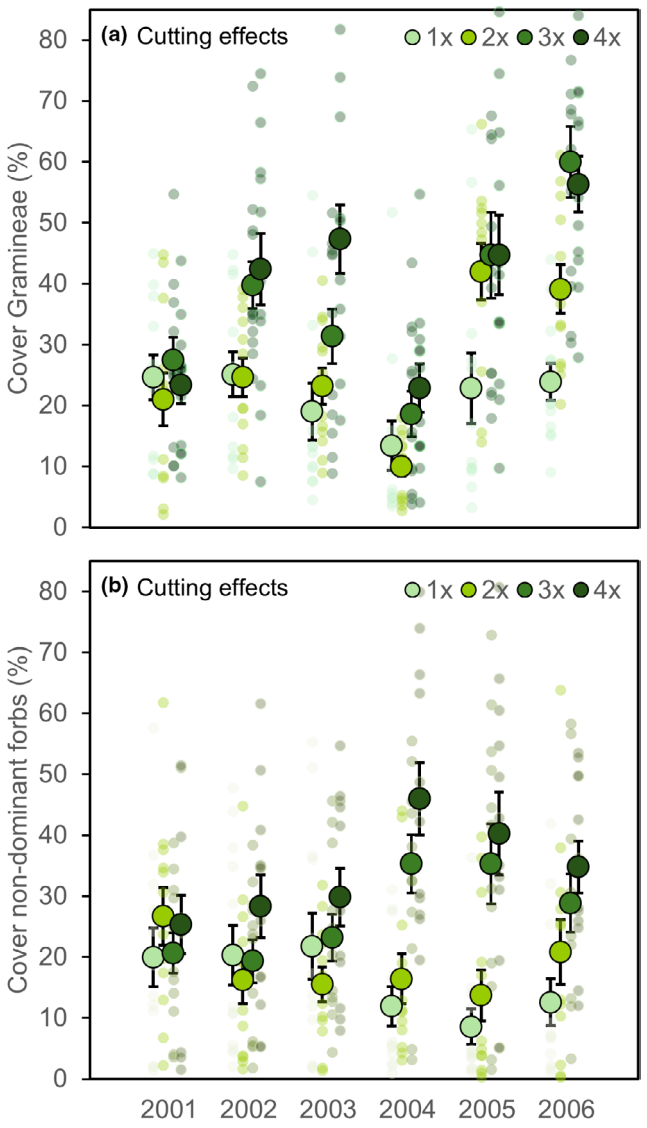

FIGURE 5 Illustration of the effects of different cutting frequencies on (a) cover of Gramineae species and (b) cover of non-dominant forbs. Markers indicate means ± standard errors, $n=12$; shaded dots indicate observations. Gramineae comprise 13 species, non-dominant forbs comprise 45 species.

dominance of these species through defoliation allows sub-dominant species, that often have lower stature or are more slow-growing, to recolonize the habitat, thus enhancing the species richness of the vegetation. At higher productivity, dominant plant species can tolerate more defoliations, presumably because this allows them to regrow faster and replenish their reserves more rapidly. The number of times a vegetation needs to be cut to restore and maintain species-rich vegetation therefore increases with the productivity of the habitat (Francksen et al., 2022).

The mechanism underlying the observed relationship between the cover of dominant forbs and total plant species richness (Figure 4) is most likely competition for light (Borer et al., 2014; Hautier et al., 2009). The vegetation in the experimental plots had been cut once a year at the end of the growing season for 8 years, prior to the start of this study. Except for very low-productive habitats, this type of management is generally too extensive to support species-rich vegetation types as it allows tall species to attain dominance and subsequently outshade other species (Parr & Way, 1988; Pavlu et al., 2016). Indeed, the original once-a-year cutting regime had led most low-statured species (e.g. *Hypochaeris radicata*, *Campanula rotundifolia* and *Pimpinella saxifraga*) and species with a rosette stage (e.g. *Daucus carota* and *Picris hieracioides*) to become extremely rare in the experimental plots (Table S1). It was this group of non-dominant forb species that benefited most from the introduction of the cutting treatments (in the final years, three- to fourfold increase in cover from one to four cuts per year; Figure 5b), most likely because it at least partially released them from competition for light with the dominant species.

The effect of cutting frequency on trends in plant species richness depended on the productivity level (significant productivity-cutting frequency interaction, Table 1; Figure 1). Cutting removes a larger proportion of above-ground biomass from tall dominant plants than from shorter non-dominant plants (Klimeš & Klimešová, 2001). Cutting more frequently results in lower resource levels in storage organs of dominant plant species (Klimeš & Klimešová, 2001), and depletion of stored resources has been found to be more pronounced in faster-growing species than in slower-growing species, presumably because they use stored resources for rapid regrowth (Atkinson et al., 2014). Thus, to maintain the same level of cover over time, after each cut, dominant plant species need more resources than non-dominant species to replace above-ground foliage. This may explain why, in our study, the dominant forbs were able to maintain their dominance in twice cut plots under high-productivity but not under low-productivity conditions (Erbilgin et al., 2014; Figure S3).

Note that in this study, cover estimates were made at the start of the growing season, so lower cover estimates were not the direct result of cutting but indicative of lower dominance. Our results suggest that the ultimate effects of productivity and cutting on plant species richness depend on the dynamic balance between the amount of biomass removed by the cutting, the length of the interval between two cuts, the speed of regrowth as a function of the availability of stored resources, and habitat productivity determining the possibility to replenish resources. If the vegetation is cut before low stature plants are being outshaded by the dominants, a species-rich vegetation can be maintained even in highly productive habitats. Because regrowth is faster in high-productivity than in low-productivity habitats, here the vegetation needs to be cut more frequently to get the same result.

Across treatments, total biomass production showed a pronounced peak in productivity the first year the experimental treatments had been applied (shown as 2002 in Figure 2). This may have been an overcompensation growth response following defoliations (Hawkes & Sullivan, 2001) facilitated by the use of excess resources in belowground storage organs. Depletion of stored resources in the two to four cutting frequency treatments may have made it impossible for the plants to maintain this overcompensation response in the following years. During the final four years, biomass production consistently showed a unimodal relationship with cutting frequency, going up from one to two cuts and then declining again. Across all treatments, the two-monthly intervals of the twice-a-year cutting treatment may have been long enough to restore full assimilative power of the vegetation and overcompensate for the lack of assimilative apparatus right after the cut. Cutting more frequently may have left the vegetation with insufficient time to maximize assimilation. However, note that the biomass from the different cutting treatments, even when they were similar in quantity, was almost certainly different in composition and therefore quality. The digestibility of old growth vegetation is lower than that of early growth vegetation, and applying fertilizer advances the date when the nutrient concentration in vegetation peaks (Kirkham & Tallowin, 1995). Cutting the vegetation of productive habitats more frequently is therefore not only expected to increase the species richness but also improves the quality of the cuttings, which can then be used for other purposes, such as organic amendments on arable fields (van der Sloot et al., 2025).

Although we did not specifically test for this, our results suggest non-linear plant species richness responses to treatment combinations. In the final year, average species richness in the four-cuts-a-year treatment was consistently lower than the year before (Figure 1). This may have been caused by a number of processes. First, with the higher cutting frequencies suppressing the dominant forbs, grasses may have proliferated, thereby suppressing some of the non-dominant forbs (Figures 3 and 5). Although highly context dependent, dominance of grasses has been known to be a key factor limiting the species richness of herbaceous vegetation in north-western Europe (Piqueray et al., 2019; Schmidt et al., 2020). Second, Fabaceae cover showed a pronounced peak around 2004 in all but the highest cutting frequency treatments. Fabaceae cover was mainly determined by cover of *Trifolium dubium* and, to a lesser extent, *Trifolium pratense*. These are annual or short-lived species that successfully established when cover of the dominant forbs was suppressed and a lot of early-season bare ground was available but that may have failed to successfully regenerate later on due to increased competition from grasses and other species that are well-adapted to higher cutting regimes. This points to the third and potentially most important reason for non-linear species richness trends. Species that regenerate primarily by seed, including annuals, tend to decline when the first cut is too early or intervals between cuts become too short for successful seed production (Kirkham & Tallowin, 1995). After the dominance of dominant plant species is broken, cutting regimes probably need to be relaxed or need to vary between years to allow late flowering species to set seed as well as to prevent grasses from becoming too dominant.

Our experimental results indicate the potential usefulness of cutting management to restore species-rich herbaceous vegetation in disturbed, productive habitats. Because the different treatment plots were located close to one another, colonization of plots by seeds from new species will have been more likely than in real-world semi-natural habitats. This probably also explains why the unfertilized plots that had been cut once a year showed a positive trend (Figure 1) whereas that very same treatment combination showed a negative trend in the previous 8 years. Indeed, especially wind-dispersed species, such as *Hypochaeris radicata*, *Picris hieracioides* and *Jacobaea vulgaris* and grasses such as *Arrhenatherum elatius* contributed to this positive trend in species richness. Under real-world conditions, the availability of seeds (in the seed bank or through dispersal) of species that are currently absent from semi-habitats may limit the restoration of species-rich vegetation, which means that seeds may have to be actively introduced from nearby sources. As this probably does not need to be done every year, this represents a relatively small additional effort for land-owners that are already investing extra resources into increasing the cutting frequency of the herbaceous vegetation of their semi-natural habitats. On the contrary, our experiment may have underestimated the potential of cutting as a management tool for productive landscape features because it maintained productivity at artificially high levels by applying fertilizers each year. For example, in the same general area as the experiment was carried out, average biomass production of conventionally managed field boundary vegetation bordering intensively farmed arable fields was approximately 530 g m^{-2} (Kleijn & Verbeek, 2000); well below the 720 and 792 g m^{-2} of the mid- and high-productivity treatment plots in the final year of the study (Figure 2a). Under real-world conditions, the productivity will most likely go down over time, especially if the vegetation is being removed after cutting. Removal of cuttings is a key driver of the restoration of high-diversity landscape features (Noordijk et al., 2009). Amongst other things, a thick layer of cuttings left on the ground may smother the underlying vegetation, particularly the broadleaved species that do not have a growth habitus allowing them to pierce through this organic layer (Parr & Way, 1988).

With rising concern for sustainably safeguarding food security for a growing world population and with increasing attention for the functional role of biodiversity in supporting agriculture (Kleijn et al., 2019), there is increasing attention for not only enhancing the

quantity of semi-natural habitat in agricultural landscapes but also the quality of these habitats (Cole et al., 2020; Fijen et al., 2025). Our results indicate that the quality of semi-natural landscape features such as field boundaries, roadside verges and extensively managed grasslands that are currently often highly productive and disturbed can be improved by appropriate cutting regimes and removal of the cut material. Here, appropriate means that the cutting frequency needs to ensure that the vegetation is cut before dominant plant species outshade lower statured species. In more productive habitats such as field boundaries, at least initially, higher cutting frequencies need to be applied than in habitats with lower productivity such as roadside verges. Our results indicate that the effects of such management will become apparent within 2–4 years, although the introduction of cuttings from nearby species-rich vegetation may be required to overcome dispersal barriers. The positive effects of cutting are most pronounced on non-dominant forbs, the majority of which produce colourful flowers. Cutting regimes that enhance plant species richness thus most likely also enhance flower diversity and cover (Ebeling et al., 2008). Flowers are generally appreciated by people (Huss et al., 2017) and can be used as widely supported and easily recognizable indicators of management success, even by non-experts such as farmers and members of the general public, which can help achieve much-needed support for biodiversity-friendly management (Kleijn et al., 2020). Furthermore, the diversity of particularly flowering plants has been found to be indicative of improved provision of pollination and pest control services underlying agricultural production (Mei et al., 2021). Since cutting more frequently adds to the maintenance costs of semi-natural habitats, the provision of more public goods such as more wildlife and aesthetically pleasing landscapes may help find societal support for funding it.

AUTHOR CONTRIBUTIONS

David Kleijn conceived the ideas, designed the methodology and collected the data. David Kleijn and Jeroen Scheper analysed the data. David Kleijn led the writing of the manuscript. Jeroen Scheper contributed critically to the drafts. All authors gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available from the Zenodo Digital Repository: https://doi.org/10.5281/zenodo.17053901 (Kleijn & Scheper, 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. The plant species present in May 2001 prior to the first experimental treatments and in May 2006 at the end of the experiment.

Table S2. Results of the ANOVA linking various components of plant species composition to productivity (manipulated by means of fertilizer application) and cutting frequency in May 2001 shortly before the first application of the experimental treatments.

Figure S1. The effects of the original treatments simulating drift of fertilizer (*x*-axis) and herbicide (differently coloured bars) on plant species richness in the Year 2000, 8 years after the start of the experiment.

Figure S2. An overview of the experimental design of the experiment.

Figure S3. The frequency distribution of the annual biomass production per plot in 50 g m^2 classes. Lines illustrate the general trend and represent fifth order polynomials fitted through the data. The years in different colours indicate the peak for each year.

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