RESEARCH PAPER

Grassland plant and invertebrate species richness increases from mowing are mediated by impacts on soil chemistry

Mark A.K. Gillespie[a,*], Hannah L. Buckley[b,c], Leo Condron[d],
Stephen D. Wratten[b,§]

[a]*Department of Science & Engineering, Western Norway University of Applied Sciences, PB 133, 6851 Sogndal, Norway*
[b]*Bio-Protection Research Centre, Lincoln University, PO Box 85084, Lincoln 7647, Canterbury, New Zealand*
[c]*School of Science, Auckland University of Technology, Auckland, New Zealand*
[d]*Faculty of Agriculture and Life Sciences, Lincoln University, PO Box 85084, Lincoln 7647 Canterbury, New Zealand*

Abstract

Pasture and improved grasslands are commonly managed by a combination of artificial fertilisation and biomass removal, but a deeper understanding of how management options interact over the long-term are required to improve sustainability. Studies of multi-trophic responses to these options can provide important insights for biodiversity and soil management, particularly when they cover long time periods. In this study, we provide a novel perspective on long-term experimental field studies of grassland management by examining the direct and indirect effects of N fertilisation and mowing (with biomass retention and removal) on above-ground biodiversity, below-ground soil chemistry and their interactions. Our experimental treatments were applied annually from 1994 in medium to high soil fertility conditions on a non-native pastoral farm in New Zealand, and analysis of data to 2013 show that in general, plants and soil properties did not respond to N fertiliser treatments. In response to mowing regimes, soil properties exhibited subtle, but annually varying changes mostly related to biomass retention or removal, and plant richness was consistently higher under all mowing treatments. The management regime with the greatest gains in diversity also depended on year of study. We further analysed the indirect effects of mowing treatments on plant and arthropod richness via soil properties using structural equation modelling, and found that the impact of mowing is likely to be mediated by soil chemistry changes. In particular, the direct positive impact of mowing on plant richness may be offset by changes to soil properties, depending on whether biomass is retained or removed. We suggest that management regime effects on soil chemistry may limit plant composition changes to those species able to take advantage of altered conditions. These findings suggest that management to improve grassland diversity and soil conditions should consider the abiotic history and conditions of the site.

© 2022 The Author(s). Published by Elsevier GmbH on behalf of Gesellschaft für Ökologie. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/)

Keywords: Nutrient addition; Mulching; Structural diversity; Community; Biodiversity; Plant-soil feedback; Invertebrates; Principal response curves

*Corresponding author
E-mail address:* markg@hvl.no (M.A.K. Gillespie).

§Professor Stephen Wratten co-authors this work posthumously. He died on 8 March 2021 and helped to conceive the idea and experimental design of the project, supervised data collection, and oversaw early drafts of the manuscript.

Introduction

A quarter of global land use is dedicated to permanent pasture and meadows (FAO 2022), with a substantial portion managed intensively to maximise productivity and quality of livestock feed (Bengtsson et al., 2019; Paudel et al., 2021). While such grasslands are managed with a wide range of techniques and are subject to varying local site characteristics and land-use history (Gilhaus et al., 2017), common components are often fertilisation and biomass removal via grazing or mowing (Borer et al., 2014; Gilhaus et al., 2017; Socher et al., 2012). Nutrient addition to grasslands typically increases biomass, but this often occurs at the expense of species diversity due to subsequent increased dominance of competitive species, a reduction in structural diversity and the limited light availability under a dense canopy (Borer et al., 2014; Harpole & Tilman, 2007; Hautier et al., 2009; Leps, 2014). This may be undesirable, especially as farmers are under pressure to help protect biodiversity and other ecosystem services such as soil nutrient cycling (Caradus et al., 2021; Paudel et al., 2021). Species loss is often ameliorated by removal of biomass as this reduces light competition, altering community structure and belowground dynamics (Borer et al., 2014; Yang et al., 2019). Nevertheless, the combined impacts of fertilisation and biomass removal are complex in that they depend on initial species abundance and composition (Avolio et al., 2014; Leps, 2014), on the life-history traits of the species being disturbed (Baer et al., 2020), and on the nature and frequency of the disturbance event (Miller et al., 2011).

In addition to direct impacts on primary production, combined fertilisation and biomass removal can also impact other trophic levels. For example, mechanical turf disturbance and prescribed burning impacted the composition and functional diversity of spider communities in an abandoned Czech pasture (Hamrik & Kosulic, 2021), and large and highly mobile exotic spiders were the first to colonise burnt tussock grassland in New Zealand (Malumbres-Olarte et al., 2014). In addition, over long time periods, plant communities can impact their own productivity and composition through feedbacks with soil biota and abiotic properties (Eisenhauer, 2012; Guerrero-Ramirez et al., 2019; van der Putten et al., 2013). High plant diversity can lead to heterogenous soil microhabitats and diverse soil organisms (Eisenhauer et al., 2012; Hooper et al., 2000), which in turn can feedback to the plant community via resource partitioning and enhancing niche dimensionality (Eisenhauer et al., 2012; Guerrero-Ramirez et al., 2019). The impact of plant-soil feedbacks may be affected by management such as grazing (Chen et al., 2017; Veen et al., 2014), but few experimental field studies consider the effects of manipulation treatments on several trophic levels at the same time, or on the possibility of feedbacks mediating plant diversity changes.

In New Zealand, where 25.5% of land use was under high-productivity grassland management in 2016 (Whitehead et al., 2021), the need to understand the impacts of management are important to balancing productivity with the country's commitments to sustainability (Caradus et al., 2021). In these productive areas, the species pool is typically non-native, consisting of introduced perennial grasses, legumes, herbs and annual forage crops. In particular, the European introduction of cocksfoot (*Dactylis glomerata* L.), perennial rye-grass, and clovers (predominantly white clover, *Trifolium repens* L.) played a large role in the conversion of native forest and other natural habitats to productive grassland in the 1950s and 60 s. These introductions also brought a range of invasive, non-native plant species including hawkweed (*Hieracium*) and thistle (*Cirsium*) species, which today form a part of the seed bank in and around pastoral farms. Generally, while farmers appreciate the benefit of conserving native species in remnants and marginal vegetation (Maseyk et al., 2021), native plants do not contribute to pastoral farming as they are not adapted to ungulate grazing (Caradus et al., 2021). amongst the range of management practices, nitrogen fertiliser application is common, although farmers are being encouraged to reduce this reliance and return to less intensive legume-based pastures (Caradus et al., 2021). In addition, returning plant residues to the soil may benefit important soil micro-organisms and provide nutrients that are otherwise limiting (Adair et al., 2013; Cabon et al., 2021). However, the long-term implications of these combined practices are not well understood.

In this study, we use a long-term pasture management experiment to examine the direct and indirect effects of fertilisation and mowing on above- and below-ground grassland properties. The experimental area was set up in a paddock planted with a typical mixture of non-native species used for New Zealand pastoral grazing. The treatments comprised a combination of urea nitrogen fertiliser and three mowing regimes that varied in terms of regularity and whether or not biomass was retained. The biomass retention treatment was included as an additional alternative management practice to periodically improve nutrient enrichment (e.g., Cabon et al., 2021). We hypothesised that:

a) In line with similar previous studies (Borer et al., 2014; Gaisler et al., 2019; Yang et al., 2019), mowing would positively impact plant diversity, and mediate the negative effect of fertilisation;

b) Plant diversity would also respond positively indirectly to this biomass retention via changes in soil quality. In previous work on these plots, soil properties have responded to the treatment with the biomass retained, because this represents an increase in the litter provided to soil organisms and nutrient cycling (Boitt et al., 2018);

c) Consistent with other long-term grassland experiments, greater plant diversity would accommodate more arthropod diversity (Weisser et al., 2017).

The results of this study will provide important insights into the relationships between biodiversity, soil fertility and management at the higher end of the grassland productivity scale. In addition, it provides an opportunity to evaluate the

impacts of combined management options on non-native species composition in the long-term.

Materials and methods

Study area and experimental design

The study area and experimental design are part of the Long-Term Ecology Trial established at Lincoln University, New Zealand (S 43°38′51, E 172°28′05) in 1994. During the study period, the average summer (Dec-Feb) temperature of 16.6 °C and average rainfall of 123 mm was recorded at Plant & Food Research approximately 2 km away. Details of the site have been described elsewhere (Farrell et al., 2014; Simpson et al., 2012), but we provide a brief outline here. The study area is a lowland agricultural field with a history of mixed cropping prior to establishment of the trial, with Wakanui silt loam soil (Mottled Immature Pallic [NZ]; Udic Ustochrept [USDA]; Soil Survey Staff 1999), and 'medium' (Olsen P: 28 mg P kg^{-1}) soil fertility (Simpson et al., 2012). In 1994, a new mixed grassland was established to simulate the species composition of a typical non-native New Zealand grazing paddock, including red clover (*Trifolium pratense* L. cv. Pawera; sowing rate 10 kg/ha), white clover (*T. repens* L. cv. Tahora; 4 kg/ha), perennial ryegrass (*Lolium perenne* L.; 15 kg/ha) and cocksfoot (*Dactylis glomerata* L. cv. Kahu; 8 kg/ha).

The treatments were established on 5 × 5 m plots arranged in four randomised blocks with eight treatments applied per block (32 plots in total). The eight treatments consisted of four mowing regimes, with and without fertiliser application. The four mowing regimes consisted of:

1) *Unmown*: undisturbed control,
2) *Irregular retained*: irregular mowing with biomass retained on the plot,
3) *Irregular removed*: irregular mowing with biomass removed, and
4) *Regular retained*: regular mowing with biomass retained (Fig. 1).

For the *Irregular* mowing treatment, mowing was applied when the sward reached approximately 30 cm in height. The speed at which this height was reached after each cut varied depending on recent rainfall, resulting in a range of 2 to 5 cuts per year. For the *Regular* mowing treatment, the first cut was applied when the sward reached 30 cm, and subsequent cuts were applied once per month (September to March) resulting in 6 to 7 cuts (depending on the time for the sward to reach 30 cm initially).

Soil analyses carried out in July 1994 revealed that the soil pH was very low (~5) across the trial area, and accordingly lime was applied to the entire trial later in 1994 to increase the soil pH to between 5.5 and 6. The fertiliser was applied in September (spring) each year and was a urea nitrogen fertiliser (50 kg N ha^{-1}), in line with common practice in lowland managed grassland.

Plant and arthropod sampling

The experimental plots were measured annually during most years for plant (1998 to 2013) and invertebrate (2000 to 2010; Appendix A: Table S1) species composition by undergraduate students on an introductory ecology course. To sample the plant community, five 0.25m^2 quadrats were randomly located within each plot. All plant species found within each quadrat were identified and recorded. For the calculation of plant species richness and for multivariate analysis, we only used data on the 11 most common species identified in plots: *Cirsium arvense* (L.)*, Hypochaeris radicata* (L.)*, D. glomerata, Taraxacum officinale* (L.)*, Stellaria media* (L.)*, Rumex obtusifolius* (L.), *Bromus willdenowii* (Kunth.)*, T. repens, T. pratense,* L. *perenne* and *Achillea millefolium* (L.). Other plant species, including one native species, were identified in some years, but these were not recorded often enough to be included in analyses. To account for differences in sampling effort between 2011 and 2013 (five quadrats per plot) and the other years (ten quadrats per plot), we estimated species richness as the number of species from the 11 most common found per quadrat.

As invertebrates are generally difficult for the novice to identify in the field, species were grouped by Order. To collect the invertebrates within each plot, students used a Vortex suction device, with four random samples of five seconds duration per plot. Arthropods were sorted in the field before returning the material to the plot.

Soil sampling

Five soil samples (7.5 cm depth, 3 cm diameter) were taken from each plot of the *Unmown, Irregular retained* and *Irregular removed* treatments each year in July for chemical analyses, including total carbon, total nitrogen, bioavailable phosphorus (Olsen P), exchangeable cations, and pH. The *Regular retained* plots were not included due to limited resources. Methods for soil chemistry characterisation are described in Farrell et al. (2014). Most soil variables were collected only between 2003 and 2013. Although a small number of soil variables were recorded in 1999 and 2002, they have only been included in univariate analysis and not multivariate analysis. Initial soil data for 1994 (before the liming treatment described above) are shown in the Results section.

Data analysis

All data analysis was conducted using the R programming environment (v 3.6.2, R Core (Team, 2021)). Plant species richness and arthropod order richness were analysed with a repeated measures linear mixed model using the *nlme* package (Pinheiro et al., 2020), with Mowing, Fertiliser and Year (as a factor) as fixed effects, together with their interactions,
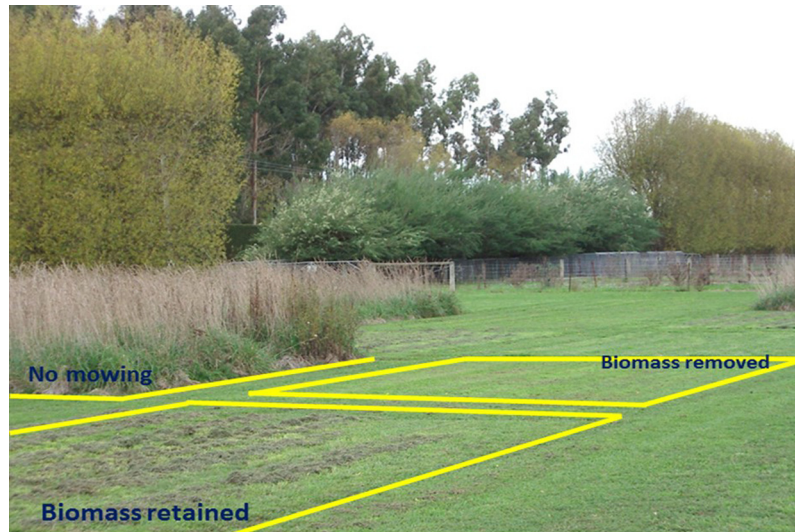
Fig. 1. The Long-Term Ecology Trial at Lincoln University (2017) with three of the four mowing regimes depicted (Photo: L. Condron).

and Plot as the repeated (random) factor. We also initially included Block as a random factor, but this was dropped as it did not improve model fit as measured by AICc (second-order Akaike Information Criterion, corrected for small samples). Where necessary, we used the Constant Variance (VarIdent) function structure to homogenise the variance of residuals. We constructed models using the grouping factors Year, Mowing treatment, and a combination of the two in this function, and selected the most appropriate model based on AICc, and a visual inspection of the residuals. All model residuals were also inspected visually for normality.

To assess changes over time to the plant community in response to the mowing treatments (fertiliser treatments were left out due to non-significant effects on plant richness), we applied a Principal Response Curve (PRC; Van den Brink & Ter Braak, 1999) with the *vegan* package (Oksanen et al., 2019). We again used abundance data for the eleven plant species listed above and set the *Unmown* treatment as the control benchmark for the PRC. To test the significance of the PRC we performed a permutation test with 499 permutations. To further explore the temporal dynamics and reordering of the most common plant species, we used rank clocks to plot the mean rank order of abundance of key species over time (Collins et al., 2008), using the *codyn* package (Hallett et al., 2016). We also conducted a PRC analysis on the soil properties, to explore the effect of both Mowing and Fertiliser treatments on combined soil characteristics over time. The variables used were those for which most data were available (K, Mg, P, Ca, Total N%, Total C%, C:N ratio and pH), and they were standardised using the *decostand* function of the *vegan* package before conducting the analysis. The Mowing and Fertiliser treatments were combined into one categorical variable for this analysis, as the PRC method only allows for one grouping variable at a time.

Finally, to test the indirect effects of treatments on plants via soil chemistry, we used multigroup piecewise structural equation modelling (SEM) via the *piecewiseSEM* package (Lefcheck, 2016). Full details of this method are given in Appendix A; briefly, this technique allows us to construct separate linear (mixed) models for each response (endogenous) variable, representing paths in a hypothesised network, before piecing them together to test the network of relationships. The multigroup SEM then allows us to test whether the relationships apply to every year, or just certain years (*sensu* Larson & Larson, 2010). For this model, data from 2003 to 2007 and 2011 were used as these were the only years with data for plants, soil and arthropods together, and as soil variables were not measured on the *Regular retained* plots, this treatment is excluded. To condense the correlated soil variables down to fewer components, we conducted Principal Component Analysis (PCA) on the scaled variables and used the first two principal components as "Soil Component" variables. The component linear models of the SEM were constructed as linear mixed models, with the two irregular mowing treatments included as dummy variables where applicable and Plot as random factor in all cases.

Results

Plant species richness

There was a significant effect on plant species richness of Mowing treatment, Year and the interaction between the two (Table 1, Fig. 2). In all cases, Fertiliser and the interactions involving this treatment were not significant. Confidence intervals around mean plant species richness indicate that the differences were predominantly between *Unmown* and the other three mowing regimes, with occasional

Table 1. Type III Analysis of deviance results for repeated measures linear mixed-effects models on the species richness per quadrat.

	df	χ^2	p
Mowing	3	55.7	<0.001
Year	10	20.4	0.026
Fertiliser	1	0.1	0.734
$M \times Y$	30	54.7	0.004
$M \times F$	3	0.9	0.820
$F \times Y$	10	9.6	0.488
$M \times F \times Y$	30	26.2	0.666

differences amongst the latter (Fig. 2). Such patterns are not consistent through time, and indicate frequent reshuffling of species richness ranks amongst the mowing regimes.

Plant community response

The PRC showed a significant difference in species composition between treatments and the unmown control ($p = 0.002$); the first axis explained 41% of the variance in community composition change over time (Fig. 3A). All three of the mowing treatments significantly diverged from the *Unmown* plots in terms of community composition over time. Species weights between −0.5 and 0.5 tend to be considered weak or unrelated to the PRC. Thus, *C. arvense* showed a strong benefit from the *Unmown* treatment, while *H. radicata,* L. *perrene, T. repens, T. pratense, A. millefolium* and *Taraxacum officinale* benefitted from the three other mowing treatments. The rank clocks for these key species show that the *Unmown* treatment had low cover of most species (though it was dominated by *D. glomerata*) and increasing covers of *C. arvense* and *A. millefolium* (Fig. 3B). The latter species had a strong negative species weight in the PRC, suggesting that it benefitted from the

mowing treatments and the rank clocks of these regimes show relatively high covers of the species. In addition, amongst the three treatments with mowing, *T. pratense* was dominant at the beginning of the study period before declining over time, being replaced with increasing covers of the remaining species.

Arthropod richness

For arthropod order richness, the patterns over time were less consistent than for plants. There was a significant effect of Year, Mowing and their interaction (Table 2), but Fertiliser and the interactions involving this treatment were not important. Generally, the *Unmown* treatment tended to have significantly more arthropod groups than did the mown treatments (Fig. 4), but the differences were not as clear in every year as they were for plants.

Soil chemistry properties

Initial and final soil properties are shown in Appendix A: Table S2. The PRC for soil properties was significant (Fig. 5, $p = 0.002$) and the first axis explained 34% of the variance in soil property composition over time. The two irregular mowing treatments showed divergence from the unmown treatment, but this appears more pronounced for *Irregular removed*. By contrast, the *Irregular retained* treatment resembles the *Unmown* in some years. Furthermore, fertiliser only seems to have a consistent effect on soil chemistry in the *Unmown* plots. The soil properties K, P, Mg, Total C and Total N, were all negatively related to the response curve, suggesting that these variables show a strong affinity with the two *Irregular retained* treatments (with and without fertiliser), and that these properties are less characteristic of the *Irregular removed* treatments. Plots of the variables by treatment over time (Appendix A, Fig.
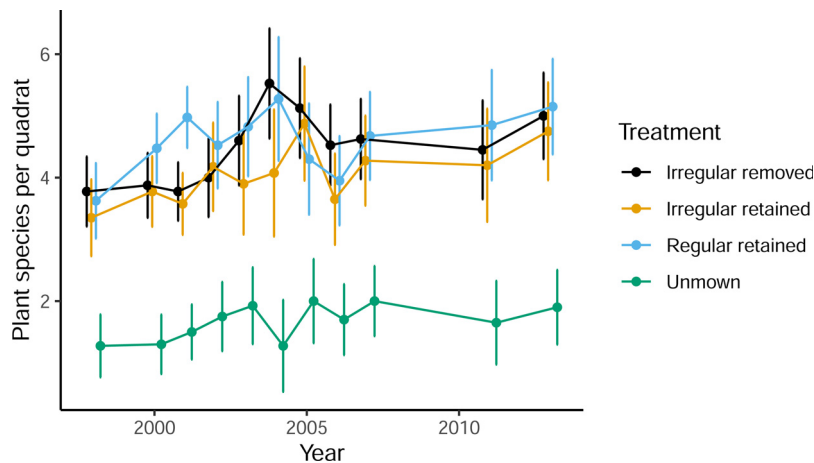

Fig. 2. Plant species richness (number of species per quadrat) plotted as predicted means from a linear mixed effect model for each Mowing treatment per year ($n = 8$). Error bars are 95% confidence intervals.
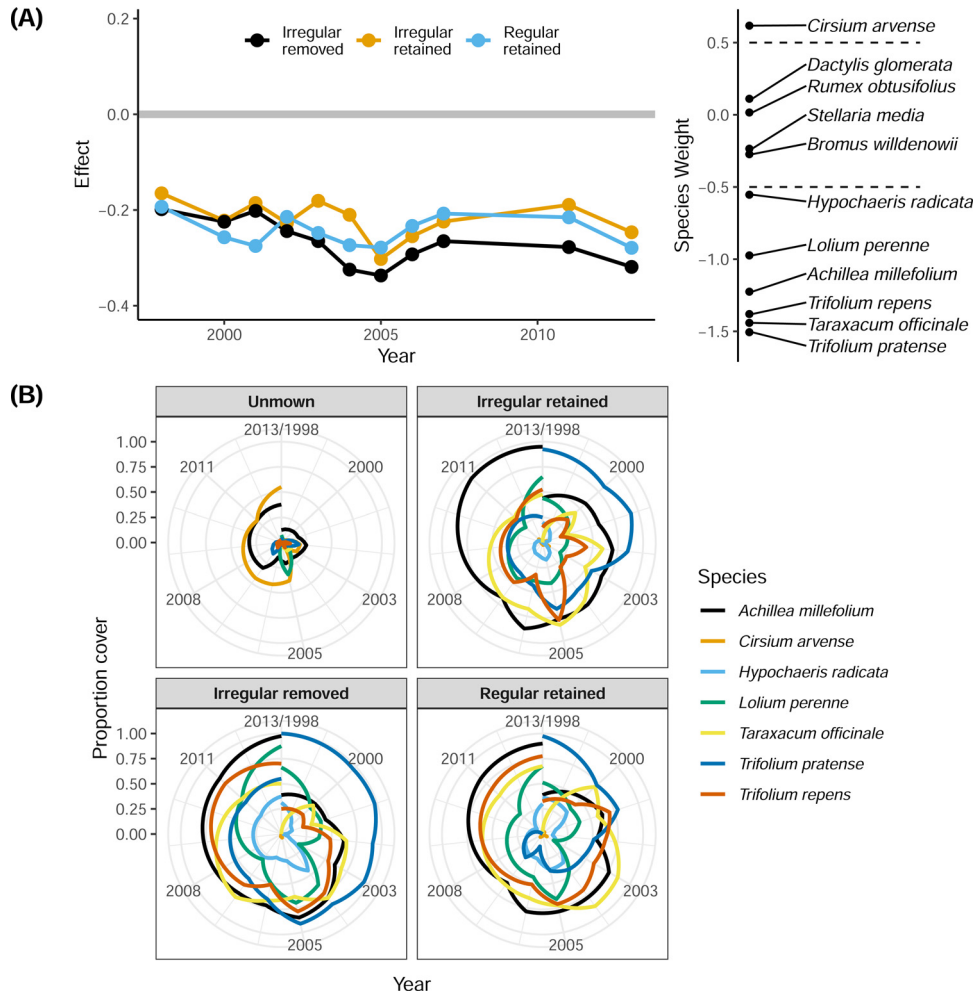
Fig. 3. (A) Principal response curves for plant species composition showing the change in the first PRC axis over time for the Mowing treatments. Treatment effect values are shown in reference to the *Unmown* (control) treatment (grey horizontal line). Species weights are shown to the right representing the affinity of each species with the response shown in the diagram (dashed lines delimit −0.5 and 0.5 species weights). (B) Rank clock plots of the seven plant species with PRC species weights above 0.5 or below −0.5 in the annually treated plots. The vertical grid line shows the starting (and ending) '12 o'clock' position on the rank clock which are the years 1998 and 2013. Species lines towards the outside of the clock indicate high percent covers.

S1) support this, to the extent that these elements differentiate the *Irregular retained* treatment at least from the *Irregular removed* treatment.

Table 2. Type III Analysis of deviance results for Repeated measures linear mixed models on Arthropod order richness.

	df	χ^2	*p*
Mowing	3	8.1	0.044
Year	10	7.5	0.678
Fertiliser	1	0.6	0.434
$M \times Y$	30	48.2	0.019
$M \times F$	3	2.3	0.514
$F \times Y$	10	4.6	0.914
$M \times F \times Y$	30	28.7	0.535

Structural equation model

The PCA of soil properties resulted in the first two principal components that explained 35.4% and 17.4% of the variation in soil variables. Component 1 strongly represents nutrient availability, with high loadings for C and N content, as well as Mg and P, while Component 2 represents a gradient of C/N ratios and Ca availability (Appendix A: Table S3). The two axes also relate to several variables concurrently, such as K and P, reflecting the complexity of the dataset.

The final piecewise SEM was an adequate fit to the data (Fisher's C = 6.92, *p* = 0.328, df = 6; Fig. 6). The majority of pathways in the model were consistent for all years, particularly those contributing to plant species richness. For those not constrained to the global model, the link from the *Irregular removed* treatment to soil component 2 was
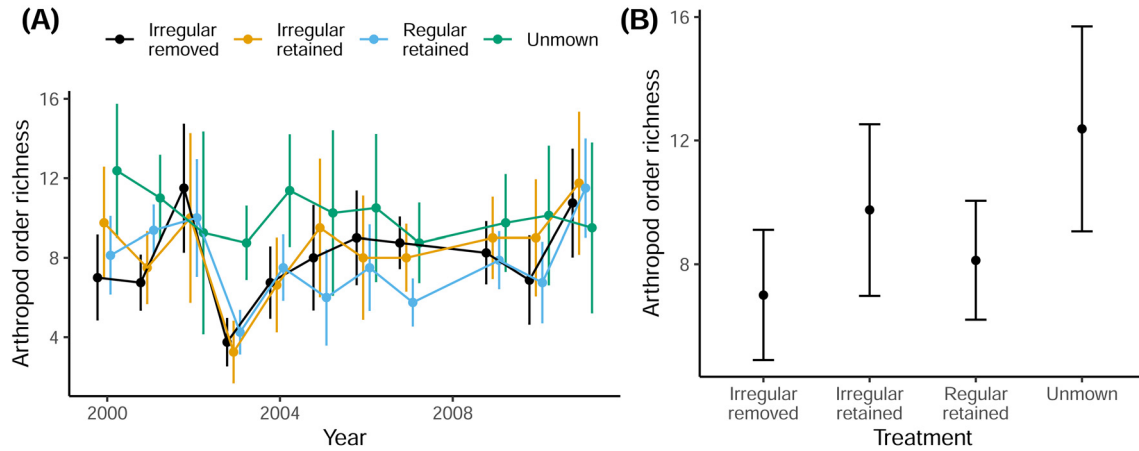
Fig. 4. Predicted mean arthropod order richness from a linear mixed model plotted by a) Treatment and Year; and b) by Treatment only. Error bars are 95% confidence intervals.

significantly positive for all years, but differed in magnitude from year to year (Appendix B). The link from the *Irregular retained* treatment to soil component 1 was positive, but not significant, in 2003, 2005 and 2006. In addition, the negative link between soil component 2 and arthropods was only significant for these same three years, and the negative link between plants and arthropods was only significant in one year (2005). Despite these inconsistencies, the positive effects of the two mowing treatments on soil component 2 suggest that these treatments both led to lower levels of K, P and C/N ratio and higher levels of Ca. To a large extent, this reflects the patterns shown in Fig. S1, although the contrasting effect of the treatments on soil component 1, which also has positive loadings of K, P and Mg, indicates divergence in soil chemistry between the treatments. In addition to the direct impacts of mowing on plant richness, soil component

2 had a consistent negative effect. This effect alone indicates that, all else being equal, plots with higher levels of variables such as K, P, and C/N ratio and low N and Ca tended to have higher plant diversity. However, the impact of mowing on these soil properties suggests that although mowing increases plant diversity directly, this increase is mediated by the negative impact of mowing on certain soil conditions.

Discussion

We observed a generally positive effect of all forms of mowing on plant diversity, but no effect of fertiliser addition, and the management regime with the greatest gains in diversity depended on the year of study. While the interannual effects may have resulted from the way the data were
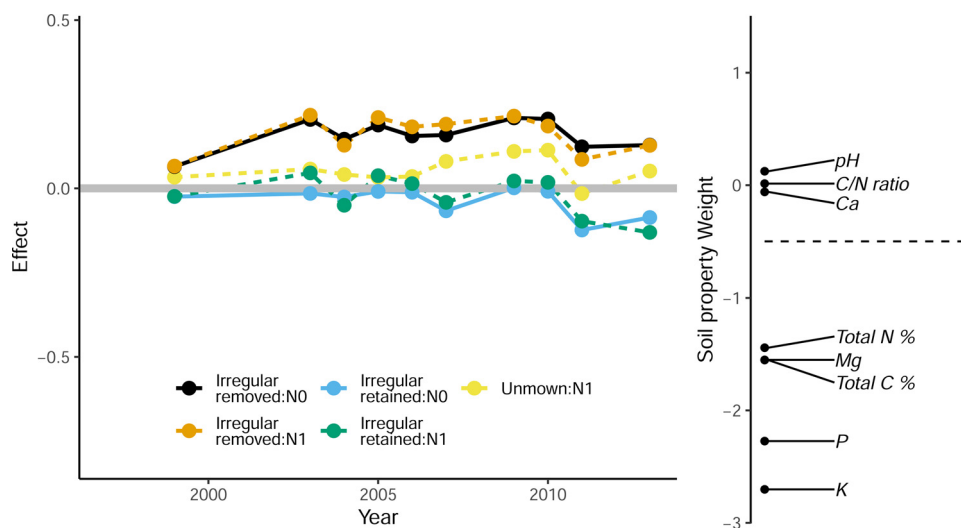

Fig. 5. Principal response curves for soil variables showing the change in the first PRC axis over time for the mowing and fertiliser treatments. Treatment effect values are shown in reference to *Unmown*, no fertiliser (control) treatment (grey horizontal line). Treatment codes: N0 = No fertiliser applied; N1 = Fertiliser applied. Soil property weights are shown to the right representing the affinity of each variable with the response shown in the diagram (dashed lines delimits −0.5 property weight).
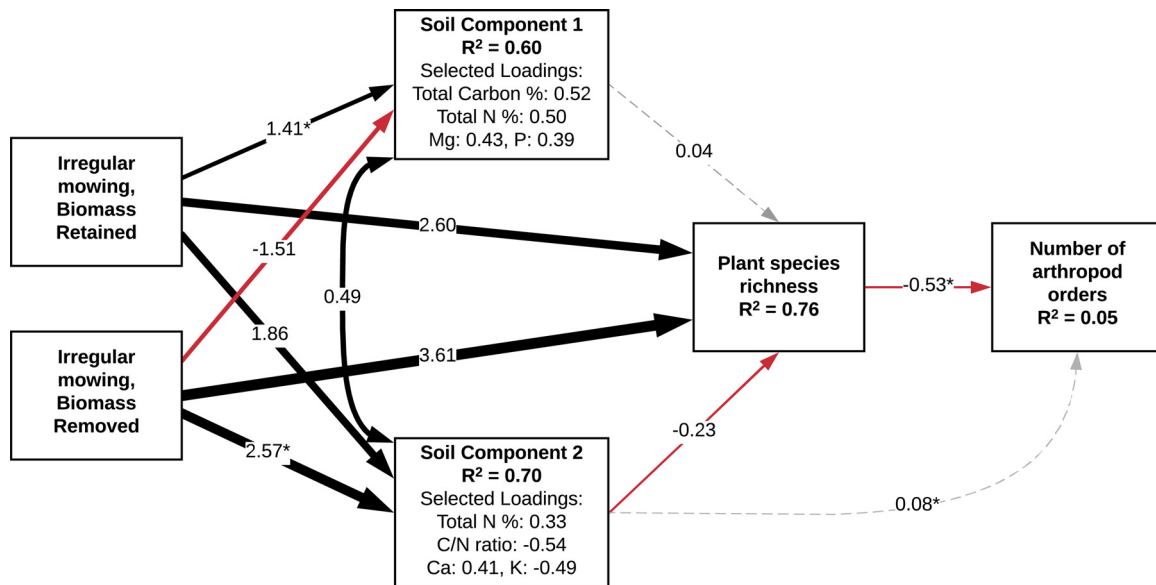
Fig. 6. Global path model for multigroup piecewiseSEM analysis using data from 2003 to 2007 and 2011. Unstandardised coefficients are given as labels on each arrow and the thickness of the line represents the size of the standardised coefficients. An asterisk symbol next to a coefficient denotes that the link was not constrained to the global model, and could differ in magnitude and significance from year to year (See Appendix B). Solid lines are significant pathways at the $p < 0.05$ level. Black lines are positive effects, red lines are negative effects. Soil Components represent the first two axes of a PCA. Full soil component loadings are given in Appendix A: Table S3.

collected, the consistent and long-term impact of mowing is clear. Conversely, arthropod richness was negatively impacted by management, and our SEM results suggest that this is due to the indirect effect of mowing on plant community diversity and composition. We suggest that the impact of the different management options is likely to have been mediated by impacts on soil properties.

Plant community structure

The lack of fertiliser effect on plant richness was surprising because N addition is known to impact graminoid cover, increasing biomass, reducing available space and light leading to reductions in taxonomic diversity (Harpole et al., 2016; Hautier et al., 2009; Titera et al., 2020). However, the impact of the addition of nutrients depends on current nutrient availability (Stiles et al., 2017). Our paddock has a medium-high level of fertility and soil organic matter is relatively low, suggesting that N was not limited in our unfertilised plots. Responses to nutrient enrichment are also species specific (Henrys et al., 2011), and the non-native species pool at this experimental farm may already be depleted of N-sensitive species. While some less common species were recorded in some years in our plots, we lacked the data to test whether they responded to treatments. As the number of plant species with cover of <1% can impact the results of grassland experiments (Gaisler et al., 2019), the lack of fertilisation effect may be explained by our concentration on non-native species, or because our species richness measure was insensitive to small changes in diversity. Nevertheless,

a lack of fertilisation effect has been demonstrated elsewhere. Li et al., and Gibson (2020) found a neutral effect of nutrient addition in an Illinois old field system, suggesting that plant community assembly processes play a greater role than nutrient limitation, or that nutrients were not the main limiting resource.

By contrast, all three mowing treatments were significantly different in diversity from the *Unmown* control. Positive effects of management such as cutting and mulching on species richness have been demonstrated for other grassland management situations (Gaisler et al., 2019; Leps, 2014; Li et al., 2020; Yang et al., 2019), due to the opening of the canopy, reduction in dominant species biomass and the decrease in light competition. Clear effects can also be attributed to the high productivity of our site where high growth rates of the non-native ruderal species found in our plots ensure rapid colonisation, and repeated mowing prevents competitive exclusion (Huston, 2014; Kershaw & Mallik, 2013). Many of the invasive and weedy forb species colonising our mown plots are known to be well adapted to regularly-mown lawn communities, with high seedbank densities (Fitter & Peat, 1994), and such local non-native species pools are more likely to show positive effects of mowing (Kershaw et al. 2013). Our focus on common non-native species may have affected these results in that unmeasured responses of native or rare species may have contributed some differences. However, native species tend to be poor competitors with non-native grasses and require protection from disturbance (Douglas et al., 2007), suggesting that their influence would have been negligible here. The lack of clear difference in richness or community composition

between the two mowing frequencies and biomass retention/removal was likely due to our limited taxonomic range, and/or because our levels of mowing were not distinct enough. Nevertheless, our SEM results, discussed below, suggest that the differences in plot conditions may have been more nuanced than could be detected by species richness alone.

The composition of the disturbed communities was influenced by the originally seeded forbs as well as the non-native rosette-forming species *T. officinale* and *H. radicata*. These low-growing species were able to take advantage of new spatial niches and lower competition for light, as in many previous studies (Gaisler et al., 2019; Tardella et al., 2020). Conversely, the only originally-seeded species to remain competitive on control plots was the grass *D. glomerata*, which maintained a high level of cover on all plots. This tall graminoid is resistant to a range of management treatments (Gaisler et al., 2019), and its fast growth and tussock forming strategies are likely to have excluded the colonisation by other species of the *Unmown* plots. The noxious weed *C. arvense*, also characteristic of *Unmown* plots, is a highly competitive species favouring decreasing levels of management intensity (Gaisler et al., 2019). It also noteworthy that the prevalence of the leguminous clover species *T. pratense* tended to decline over time in all treatments, but *T. repens* increased in all mowing treatments. Grassland managers in New Zealand are encouraged to return pastures to legume-based systems (Caradus et al., 2021), and our results suggest that while *T. repens* is resilient to mowing, enhancing clover diversity will require further management. In general, the variability in species composition over time is a common finding for long-term grassland experiments (Gaisler et al., 2019; Leps, 2014), and it is also likely that interannual weather variability played a role in the temporal dynamics (Herben et al., 1995; Titera et al., 2020). Nevertheless, the importance of continuous long-term data collection is demonstrated here. Similarly, finer taxonomic resolution data would help to elucidate any impacts of treatments on native and rare species.

Arthropod community structure

The finding that arthropod diversity was greatest in the undisturbed treatment is probably related to the relatively stable micro-habitat structure in the *Unmown* plots (Wratten et al., 2012). The taller vegetation would have provided more shelter and diverse niche space for a greater range of species than the plots with repeated mowing. The negative effect of plant richness was only strongly apparent in one year, so the plant composition may have been more important. In particular, the control plots were probably structurally diverse, dominated by the tall-growing tussock forming graminoid, *D. glomerata*, while the disturbed plots contained more low-growing and rosette-forming species, which would have maintained a certain level of openness in the plot micro-habitat.

These results are partly consistent with findings in other agricultural settings that promote agri-environmental features such as vegetative buffers, strips of unmown vegetation at field margins to promote insect and plant diversity (Case et al., 2020; Landis et al., 2005; Olson & Wackers, 2007). In such studies, high densities and diversity of invertebrates are found in field margins due to protection from disturbance, but also due to high plant diversity compared to the agricultural matrix. In our study, the protection from disturbance appears to be a greater relative driver of arthropod diversity than plant diversity. However, the greater arthropod richness of the undisturbed areas may not imply a preferred management option for maximising species diversity and ecosystem function. Previous work on field margins and undisturbed grassland plots has shown that generalist species tend to benefit (Hamrik et al. 2021), and functional diversity has been found to decrease with disturbance (Gerisch et al., 2012). Our measure of arthropod diversity was rather crude, but may also represent a form of functional diversity. In this case, while mowing as an environmental filter acts to favour more competitive and fast-growing plant species, it may act to reduce the functional diversity of the arthropod community as only generalist species are able to tolerate the disturbed conditions (Devictor et al., 2008).

Indirect impact of soil chemistry

The SEM model and soil analysis were consistent in that mowing affected soil chemistry in complex ways. *Irregular retained* tended to feature higher total N and C content, probably due to the increase in organic matter via the addition of mown plant litter (Boitt et al., 2018). These plots, and the *Unmown,* also had consistently higher levels of Mg, K and P relative to the *Irregular removed* plots, which we attribute to nutrient depletion following continued biomass removal (Boitt et al., 2018; Simpson et al., 2012). The differential impact of the two mowing treatments on soil component 1 (high N, C, Mg and P) supports the key role of biomass retention or removal on soil chemistry, although this soil component was not important in later stages of the model. By contrast, mowing positively impacted soil component 2 (low C:N ratios, low K, and high Ca), and the impact of biomass removal on this was variable, but greater in magnitude every year. As component 2 only explained a small amount of the variation in soil properties, this variable reflects finer differences in soil chemistry, and the subsequent negative link to plant richness implies a mediating role of these properties. For example, the strong direct increase in plant richness of *Irregular removed* to maximise the competitive release effect appears to be offset by a negative impact of slight reductions in C:N ratio and K in this treatment. Similarly, retaining biomass reduced both of the direct and indirect impacts on plant richness, resulting in relatively similar plant richness overall. The SEM result could

also suggest a pathway for interannual variation in richness. For example, when species richness was at its most different in 2004 between the two irregular mowing treatments, the effect of *Irregular removed* on soil component 2 was at its lowest and most similar to *Irregular retained* (Unstandardised coefficients 1.86 and 1.92).

In general, the effects of mowing on soil chemistry may have limited the competitive release effect to those species able to take advantage of both the altered soil and light conditions. Plant species colonising the mown plots could be considered to pass through several environmental filters (Baer et al., 2020), rather than a simplified single mowing filter. Species such as *T. repens, T. pratense,* L. *perenne* and *H. radicata* that can quickly colonise newly opened areas, also exhibit traits that enable them to establish better when competition is low. Conversely, *C. arvense* the dominant species in *Unmown* treatments is a slower-growing, longer-lived and highly competitive perennial. This perhaps reflects a trade-off between nutrient and light availability, which is an important mechanism in grassland plant diversity (Ward et al., 2020), and supports the suggestion that heterogeneity in soil resources are likely to be key to diverse grassland communities (Baer et al., 2020).

The above- and below-ground dynamics are likely to be more complicated than we have been able to test. In our SEM, we specified the path to point from soil conditions to plant diversity, but it could be argued that the arrow should point in the other direction. For example, Teixeira et al., and Peña-Claros (2021) built their SEM with plant diversity positively impacting a soil chemistry and biology gradient together with a direct negative management effect. Similarly, the long-term Jena grassland experiment has demonstrated that plant species richness has significant consequences for soil processes (Weisser et al., 2017), via the availability of water and organic resources (Lange et al., 2014). However, plant-soil feedback mechanisms are probably reciprocal: plots with a history of accommodating fast-growing species are likely to have higher nutrient turnover rates (Wright et al., 2004; Reich, 2014), promoting a positive feedback to the same plant species due to increased nutrient availability. Furthermore, high diversity plant communities may facilitate future growth through diversifying the biotic and abiotic resources in the soil (Eisenhauer, 2012; Guerrero-Ramirez et al., 2019). Many other mechanisms may also be involved and environmental conditions are also likely to be key to the nature of plant and soil interactions (Guerrero-Ramirez et al., 2019). We should also note that our low taxonomic resolution and focus on common non-native plants may have affected our species richness results here, and further study is required to confirm the pathways hypothesised by our SEM. Nevertheless, we recommend that future long-term studies of grassland management incorporate dynamic SEM models that allow the researcher to explore plant-soil and soil-plant feedbacks from year to year.

Conclusions

We have shown that in medium to high soil fertility conditions, in lowland pastures consisting of non-native species pools, the long-term application of grassland management has some predictable but annually varying outcomes. Fertiliser application did not produce a biotic response that we could measure, but mowing increased plant species richness via competitive release, and reduced arthropod order richness through structural disturbance, regardless of cutting frequency. Interannual variation in richness and soil chemistry are likely to be influenced by local climate, but we have also demonstrated that changes to soil chemistry can play a subtle mediating role in distinguishing effects between management options. These findings require more in depth study, but support a recommendation that management to improve diversity and soil conditions should consider the history and abiotic conditions of the site.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2022.06.010.

References

Adair, K. L., Wratten, S., & Lear, G. (2013). Soil phosphorus depletion and shifts in plant communities change bacterial community structure in a long-term grassland management trial. *Environmental Microbiology Reports*, 5, 404–413.

Avolio, M. L., Koerner, S. E., La Pierre, K. J., Wilcox, K. R., Wilson, G. W. T., Smith, M. D., et al. (2014). Changes in plant community composition, not diversity, during a decade of

nitrogen and phosphorus additions drive above-ground productivity in a tallgrass prairie. *Journal of Ecology*, *102*, 1649–1660.

Baer, S. G., Adams, T., Scott, D. A., Blair, J. M., & Collins, S. L. (2020). Soil heterogeneity increases plant diversity after 20 years of manipulation during grassland restoration. *Ecological Applications*, *30*, 15.

Bengtsson, J., Bullock, J. M., Egoh, B., Everson, C., Everson, T., O'Connor, T., et al. (2019). Grasslands—More important for ecosystem services than you might think. *Ecosphere*, *10*, e02582.

Boitt, G., Black, A., Wakelin, S. A., McDowell, R. W., & Condron, L. M. (2018). Impacts of long-term plant biomass management on soil phosphorus under temperate grassland. *Plant and Soil*, *427*, 163–174.

Borer, E. T., Seabloom, E. W., Gruner, D. S., Harpole, W. S., Hillebrand, H., Lind, E. M., et al. (2014). Herbivores and nutrients control grassland plant diversity via light limitation. *Nature*, *508*, 517 -+.

Cabon, M., Galvanek, D., Detheridge, A. P., Griffith, G. W., Marakova, S., & Adamcik, S. (2021). Mulching has negative impact on fungal and plant diversity in Slovak oligotrophic grasslands. *Basic and Applied Ecology*, *52*, 24–37.

Caradus, J. R., Goldson, S. L., Moot, D. J., Rowarth, J. S., & Stewart, A. V. (2021). Pastoral agriculture, a significant driver of New Zealand's economy, based on an introduced grassland ecology and technological advances. *Journal of the Royal Society of New Zealand*, 1–45. doi:10.1080/03036758.2021.2008985.

Case, B. S., Pannell, J. L., Stanley, M. C., Norton, D. A., Brugman, A., Funaki, M., et al. (2020). The roles of non-production vegetation in agroecosystems: A research framework for filling process knowledge gaps in a social-ecological context. *People and Nature*, *2*, 292–304.

Chen, T., Christensen, M., Nan, Z. B., & Hou, F. J. (2017). The effects of different intensities of long-term grazing on the direction and strength of plant-soil feedback in a semiarid grassland of Northwest China. *Plant and Soil*, *413*, 303–317.

Collins, S. L., Suding, K. N., Cleland, E. E., Batty, M., Pennings, S. C., Gross, K. L., et al. (2008). Rank clocks and plant community dynamics. *Ecology*, *89*, 3534–3541.

Devictor, V., Julliard, R., Clavel, J., Jiguet, F., Lee, A., & Couvet, D. (2008). Functional biotic homogenization of bird communities in disturbed landscapes. *Global Ecology and Biogeography*, *17*, 252–261.

Douglas, G. B., Dodd, M. B., & Power, I. L. (2007). Potential of direct seeding for establishing native plants into pastoral land in New Zealand. *New Zealand Journal of Ecology*, *31*, 143–153.

Eisenhauer, N. (2012). Aboveground-belowground interactions as a source of complementarity effects in biodiversity experiments. *Plant and Soil*, *351*, 1–22.

Eisenhauer, N., Reich, P. B., & Scheu, S. (2012). Increasing plant diversity effects on productivity with time due to delayed soil biota effects on plants. *Basic and Applied Ecology*, *13*, 571–578.

FAO. (2022). FAOSTAT Online Database.

Farrell, M., Prendergast-Miller, M., Jones, D. L., Hill, P. W., & Condron, L. M. (2014). Soil microbial organic nitrogen uptake is regulated by carbon availability. *Soil Biology and Biochemistry*, *77*, 261–267.

Fitter, A. H., & Peat, H. J. (1994). The Ecological Flora database. *Journal of Ecology*, *82*, 415–425.

Gaisler, J., Pavlu, L., Nwaogu, C., Pavlu, K., Hejcman, M., & Pavlu, V. V. (2019). Long-term effects of mulching, traditional cutting and no management on plant species composition of improved upland grassland in the Czech Republic. *Grass and Forage Science*, *74*, 463–475.

Gerisch, M., Agostinelli, V., Henle, K., & Dziock, F. (2012). More species, but all do the same: Contrasting effects of flood disturbance on ground beetle functional and species diversity. *Oikos*, *121*, 508–515.

Gilhaus, K., Boch, S., Fischer, M., Holzel, N., Kleinebecker, T., Prati, D., et al. (2017). *Grassland Management in Germany: Effects on Plant Diversity and Vegetation Composition*. (pp. 379−397). Tuexenia.

Guerrero-Ramirez, N. R., Reich, P. B., Wagg, C., Ciobanu, M., & Eisenhauer, N. (2019). Diversity-dependent plant-soil feedbacks underlie long-term plan diversity effects on primary productivity. *Ecosphere*, *10*, 14.

Hallett, L. M., Jones, S. K., MacDonald, A. A. M., Jones, M. B., Flynn, D. F. B., Ripplinger, J., et al. (2016). codyn: An R package of community dynamics metrics. *Methods in Ecology and Evolution*, *7*, 1146–1151.

Hamrik, T., & Kosulic, O. (2021). Impact of small-scale conservation management methods on spider assemblages in xeric grassland. *Agriculture Ecosystems & Environment*, *307*, 13.

Harpole, W. S., Sullivan, L. L., Lind, E. M., Firn, J., Adler, P. B., Borer, E. T., et al. (2016). Addition of multiple limiting resources reduces grassland diversity. *Nature*, *537*, 93–96.

Harpole, W. S., & Tilman, D. (2007). Grassland species loss resulting from reduced niche dimension. *Nature*, *446*, 791–793.

Hautier, Y., Niklaus, P. A., & Hector, A. (2009). Competition for light causes plant biodiversity loss after eutrophication. *Science*, *324*, 636–638.

Henrys, P. A., Stevens, C. J., Smart, S. M., Maskell, L. C., Walker, K. J., Preston, C. D., et al. (2011). Impacts of nitrogen deposition on vascular plants in Britain: An analysis of two national observation networks. *Biogeosciences*, *8*, 3501–3518.

Herben, T., Krahulec, F., Hadincova, V., & Pechackova, S. (1995). Climatic variability and grassland community composition over 10 Years: Separating effects on module biomass and number of modules. *Functional Ecology*, *9*, 767–773.

Hooper, D. U., Bignell, D. E., Brown, V. K., Brussaard, L., Dangerfield, J. M., Wall, D. H., et al. (2000). Interactions between aboveground and belowground biodiversity in terrestrial ecosystems: Patterns, mechanisms, and feedbacks. *Bioscience*, *50*, 1049–1061.

Huston, M. A. (2014). Disturbance, productivity, and species diversity: Empiricism vs. logic in ecological theory. *Ecology*, *95*, 2382–2396.

Kershaw, H. M., & Mallik, A. U. (2013). Predicting plant diversity response to disturbance: Applicability of the intermediate disturbance hypothesis and mass ratio hypothesis. *Critical Reviews in Plant Sciences*, *32*, 383–395.

Landis, D. A., Menalled, F. D., Costamagna, A. C., & Wilkinson, T. K. (2005). Manipulating plant resources to enhance beneficial arthropods in agricultural landscapes. *Weed Science*, *53*, 902–908.

Lange, M., Habekost, M., Eisenhauer, N., Roscher, C., Bessler, H., Engels, C., et al. (2014). Biotic and abiotic properties mediating plant diversity effects on soil microbial communities in an experimental grassland. *Plos One*, *9*(5). doi:10.1371/journal.pone.0096182.

Larson, D. L., & Larson, J. L. (2010). Control of one invasive plant species allows exotic grasses to become dominant in northern Great Plains grasslands. *Biological Conservation*, *143*, 1901–1910.

Lefcheck, J. S. (2016). PIECEWISESEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, *7*, 573–579.

Leps, J. (2014). Scale- and time-dependent effects of fertilization, mowing and dominant removal on a grassland community during a 15-year experiment. *Journal of Applied Ecology*, *51*, 978–987.

Li, G. Y., Barfknecht, D. F., & Gibson, D. J. (2020). Disturbance effects on productivity-plant diversity relationships from a 22-year-old successional field. *Journal of Vegetation Science*, *32*, e12970.

Malumbres-Olarte, J., Barratt, B. I. P., Vink, C. J., Paterson, A. M., Cruickshank, R. H., Ferguson, C. M., et al. (2014). Big and aerial invaders: Dominance of exotic spiders in burned New Zealand tussock grasslands. *Biological Invasions*, *16*, 2311–2322.

Maseyk, F. J. F., Small, B., Henwood, R. J. T., Pannell, J., Buckley, H. L., & Norton, D. A. (2021). Managing and protecting native biodiversity on-farm - what do sheep and beef farmers think? *New Zealand Journal of Ecology*, *45*,(1) 3420.

Miller, A. D., Roxburgh, S. H., & Shea, K. (2011). In *How Frequency and Intensity Shape Diversity-Disturbance Relationships: 108. Proceedings of the National Academy of Sciences of the United States of America* (pp. 5643−5648)*How Frequency and Intensity Shape Diversity-Disturbance Relationships* (pp. 5643−5648).

Oksanen, J., Blanchet, F. G., .Friendly, M., Kindt, R., Legendre, P. & McGlinn, D. et al. (2019). vegan: Community Ecology Package.

Olson, D. M., & Wackers, F. L. (2007). Management of field margins to maximize multiple ecological services. *Journal of Applied Ecology*, *44*, 13–21.

Paudel, S., Cobb, A. B., Boughton, E. H., Spiegal, S., Boughton, R. K., Silveira, M. L., et al. (2021). A framework for sustainable management of ecosystem services and disservices in perennial grassland agroecosystems. *Ecosphere*, *12*, e03837.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & Team, R. C. (2020). *nlme: Linear and Nonlinear Mixed Effects Models: 3* (pp. 1−144). R package version.

Reich, M. C. (2014). The world-wide 'fast−Slow' plant economics spectrum: A traits manifesto. *Journal of Ecology*, *102*(2), 275–301. doi:10.1111/1365-2745.12211.

Simpson, M., McLenaghen, R. D., Chirino-Valle, I., & Condron, L. M. (2012). Effects of long-term grassland management on the chemical nature and bioavailability of soil phosphorus. *Biology and Fertility of Soils*, *48*, 607–611.

Socher, S. A., Prati, D., Boch, S., Müller, J., Klaus, V. H., Hölzel, N., et al. (2012). Direct and productivity-mediated indirect effects of fertilization, mowing and grazing on grassland species richness. *Journal of Ecology*, *100*, 1391–1399.

Soil Survey Staff. (1999). *Soil taxonomy: A basic System of Soil Classification For Making and Interpreting Soil surveys. 2nd Edition*. (p. 436). Natural Resources Conservation Service. U.S. Department of Agriculture Handbook.

Stiles, W. A. V., Rowe, E. C., & Dennis, P. (2017). Long-term nitrogen and phosphorus enrichment alters vegetation species composition and reduces carbon storage in upland soil. *Science of the Total Environment*, *593*, 688–694.

Tardella, F. M., Bricca, A., Goia, I. G., & Catorci, A. (2020). How mowing restores montane Mediterranean grasslands following cessation of traditional livestock grazing. *Agriculture Ecosystems & Environment*, *295*, 106880.

Team, R. C. (2021). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

Teixeira, H. M., Bianchi, F. J. J. A., Cardoso, I. M., Tittonell, P., & Peña-Claros, M. (2021). Impact of agroecological management on plant diversity and soil-based ecosystem services in pasture and coffee systems in the Atlantic forest of Brazil. *Agriculture, Ecosystems & Environment*, *305*, 107171.

Titera, J., Pavlu, V. V., Pavlu, L., Hejcman, M., Gaisler, J., & Schellberg, J. (2020). Response of grassland vegetation composition to different fertilizer treatments recorded over ten years following 64 years of fertilizer applications in the Rengen Grassland Experiment. *Applied Vegetation Science*, *23*, 417–427.

Van den Brink, P. J., & Ter Braak, C. J. F. (1999). Principal response curves: Analysis of time-dependent multivariate responses of biological community to stress. *Environmental Toxicology and Chemistry*, *18*, 138–148.

van der Putten, W. H., Bardgett, R. D., Bever, J. D., Bezemer, T. M., Casper, B. B., Fukami, T., et al. (2013). Plant-soil feedbacks: The past, the present and future challenges. *Journal of Ecology*, *101*, 265–276.

Veen, G. F., de Vries, S., Bakker, E. S., van der Putten, W. H., & Olff, H. (2014). Grazing-induced changes in plant-soil feedback alter plant biomass allocation. *Oikos*, *123*, 800–806.

Ward, D., Kirkman, K. P., Tsvuura, Z., Morris, C., & Fynn, R. W. S. (2020). Are there common assembly rules for different grasslands? Comparisons of long-term data from a subtropical grassland with temperate grasslands. *Journal of Vegetation Science*, *31*, 780–791.

Weisser, W. W., Roscher, C., Meyer, S. T., Ebeling, A., Luo, G. J., Allan, E., et al. (2017). Biodiversity effects on ecosystem functioning in a 15-year grassland experiment: Patterns, mechanisms, and open questions. *Basic and Applied Ecology*, *23*, 1–73.

Whitehead, D., McNeill, S. J. E., & Mudge, P. L. (2021). *Regional and National Changes in Soil Carbon Stocks With Land-Use Change from 1990 to 2016 For New Zealand*. (p. 21). Regional Environmental Change.

Wratten, S. D., Gillespie, M., Decourtye, A., Mader, E., & Desneux, N. (2012). Pollinator habitat enhancement: Benefits to other ecosystem services. *Agriculture Ecosystems & Environment*, *159*, 112–122.

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., et al. (2004). The world-wide leaf economics spectrum. *Nature*, *428*(6985), 821–827. doi:10.1038/nature02403.

Yang, G. J., Lu, X. T., Stevens, C. J., Zhang, G. M., Wang, H. Y., Wang, Z. W., et al. (2019). Mowing mitigates the negative impacts of N addition on plant species diversity. *Oecologia*, *189*, 769–779.