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The relative importance of nitrogen deposition and climate change in driving plant diversity decline in roadside grasslands

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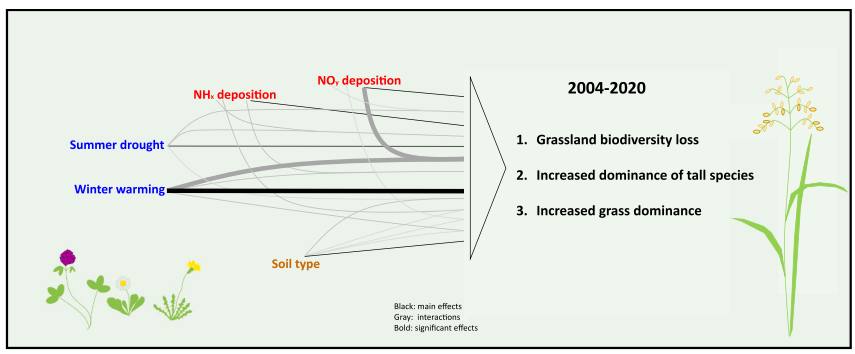
HIGHLIGHTS

- Effects of climate changes, nitrogen deposition and soil type were disentangled.
- Winter warming was associated with biodiversity loss and productivity increase.
- The effects of winter warming were stronger with higher N deposition.
- The effects of winter warming occurred on a wide range of soil types.

GRAPHICAL ABSTRACT



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ABSTRACT

Nitrogen deposition and climate change have been identified as major threats to the biodiversity of semi-natural grasslands. Their relative contribution to recent biodiversity loss is however not fully understood, and may depend on local site conditions such as soil type, which hampers efforts to prevent further decline. We used data from >900 permanent plots in semi-natural grasslands in Dutch roadsides to investigate whether trends in plant diversity and community composition (2004–2020) could be explained by: (1) nitrogen deposition (NH_x and NO_y) and climate change (winter degree days and summer drought), (2) the interactive effect of nitrogen deposition and climate change, and (3) the interactive effect of nitrogen deposition and climate change with soil type. Overall we observed a decline in plant diversity and an increased dominance of tall species and grasses. These changes were linked to winter warming, but not to changes in summer drought and nitrogen deposition. The effect of winter warming was more pronounced in areas with higher NO_y deposition, but was consistent across different soil types. Our results suggest that winter warming will become an important driver of plant diversity loss by altering competitive interactions, which could have major repercussions for other trophic levels and ecosystem services. Future conservation and restoration of grassland biodiversity therefore requires management regimes that are adapted to winter warming.

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1. Introduction

Grasslands cover vast areas of the Earth's surface and play a crucial role in maintaining biodiversity (Bardgett et al., 2021). In Europe, traditional, extensively managed semi-natural grasslands provide habitat for species-rich plants communities (Dengler et al., 2014). These communities, in turn, support diverse communities of other trophic levels including insects and birds (Habel et al., 2013). However, over the last decades plant species richness has declined rapidly in European semi-natural grasslands and many characteristic plant communities are currently under threat (Wesche et al., 2012; Eichenberg et al., 2021). To halt and reverse biodiversity decline in semi-natural grasslands it is imperative to improve our understanding of the drivers of loss (Bardgett et al., 2021).

In addition to habitat fragmentation and changes in land use, the deposition of sulfur (S) and/or nitrogen (N) have proven to be important factors in explaining the decline in biodiversity in grasslands since the 1950s (Stevens et al., 2004; Bobbink et al., 2010). Although S deposition has declined in Europe, N deposition has remained high, especially in areas with a high land use intensity such as the Netherlands. N is deposited in the form of reduced N (NH_x; e.g., ammonia and ammonium) and oxidised N (NO_y; e.g. nitrate and nitrogen oxides). The reduced form is mostly emitted by agricultural sources, while the oxidised form primarily originates from industry and traffic. Both forms have a eutrophying effect, while acidification of the soil is largely associated with deposition in the form of NH_x (Stevens et al., 2011). Acidification and eutrophication lead to a decrease in the number of species characteristic of oligotrophic and mesotrophic conditions and an increase in species characteristic for eutrophic ecosystems, often resulting in a net decline of local biodiversity (Stevens et al., 2004; Bobbink et al., 2010).

In recent decades climate change has emerged as another important potential driver of biodiversity change in semi-natural grasslands (Tilman et al., 1992; Kreyling et al., 2019). For instance, dry summers may affect the species richness of grassland vegetation either positively or negatively depending on the traits of plant species and local environmental conditions. Droughts may favor disturbance-dependent and stress-tolerant species by reducing the vigor of dominant species (Dunnett et al., 1998), but may also cause biodiversity loss due to local extinctions, especially of rare species (Tilman et al., 1992). Sustained alterations in precipitation patterns can also disturb the formation of seed banks for certain species, potentially reducing the capacity to recover after extreme weather events (Basto et al., 2018).

Temperature rise also impacts community composition, and there are some indications that increases in winter temperature can have a more pronounced effect on plant community composition compared to increases in summer temperature (Kreyling and Beier, 2013; Kreyling et al., 2019). In temperate, non-arid regions, warmer winter temperatures cause an extension of the growing season and appear to increase grassland productivity, potentially favoring productive and competitive species (Dunnett et al., 1998; Hutchison and Henry, 2010; Fridley et al., 2016; Kreyling et al., 2019; MacDougall et al., 2024). Restricted vegetation growth due to soil moisture limitations during dry summers could explain the lower sensitivity of biomass production in grasslands to summer warming (Rustad et al., 2001).

While effects of enhanced N availability and climate change on plant diversity have been studied mostly in isolation, the relative importance of both factors in driving biodiversity decline is still largely unknown (Greaver et al., 2016; Borer and Stevens, 2022). Unravelling the individual impacts of climate changes and N deposition proves challenging, as they may exert comparable impacts on vegetation or may counteract each other by affecting vegetation in opposite ways (Weiskopf et al., 2020). For example, winter warming, N deposition and summer precipitation can each lead to increased productivity, potentially favoring competitive species that outcompete others (Grace et al., 2016). Summer drought on the other hand can reduce the competitive vigor of dominant species. The effects of N deposition and climate change may also interact, which further complicates the disentanglement of their individual impacts (Borer and Stevens, 2022). For example, N demand may be higher if productivity can be higher in a warmer climate, leading to a stronger effect of climate warming when more N is available (Tian et al., 2019). N addition however may also increase plant sensitivity to drought (Van Sundert et al., 2021). In addition, local site conditions such as soil type, hydrology or management also influence productivity and species composition, and the impacts of N deposition and climate change can be affected by the prevailing conditions. For example, acidification resulting from N deposition is an important cause of biodiversity decline in grasslands on soils with a low capacity for neutralizing acidity, while N deposition-induced eutrophication particularly affects grasslands characterized by oligotrophic or mesotrophic conditions (Maskell et al., 2010; Bobbink et al., 2022). Furthermore, grasslands on more fertile soils may be more responsive to climatic changes such as winter warming and summer drought (Grime et al., 2000; Chen et al., 2023).

To disentangle the effects of N deposition and climate change on grassland biodiversity under different environmental conditions (e.g. soil type), data from large and long-term field observation surveys and in-depth analyses are key. Much of our understanding of the relative and interactive effects of N deposition and climate change on species composition in grassland originates from short-term, small-scale controlled experiments (Borer and Stevens, 2022). While these provide valuable insights, upscaling to encompass larger spatial and temporal scales remains challenging. For example, in a field study, Gaudnik et al. (2011) only found effects of climate change when looking at a larger spatial scale, while the effects of nitrogen deposition were detectable on a smaller spatial scale. Moreover, experiments simulating nitrogen deposition and climate change may yield different effects compared to real-world nitrogen deposition and climate change. Experimental nitrogen addition usually exceeds real world nitrogen deposition, which reduces interpretability (Bebber, 2021). Aboveground biomass is on average twice as much affected by natural droughts as by experimentally imposed drought events, possibly because experiments often only include a reduction in rainfall and not other aspects of drought (Kröel-Dulay et al., 2022). This suggests that experimental findings may underestimate the impacts of climate change, emphasizing the necessity of monitoring the effects of natural climate change events. Furthermore, examining changes in biodiversity indices such as species richness may also cause underestimation of impacts of N deposition and climate change. Given that climate change and N deposition can exert opposing effects on different species groups, the use of biodiversity indices might mask shifts in species composition.

In this paper we use a large-scale and long-term dataset to examine the relative effects of N deposition and climate change on changes in grassland vegetation, and whether and how these effects interact and depend on soil type. The Dutch monitoring network on roadside grassland flora ('Meetnet bermflora') provides a unique dataset for this purpose. It consists of >900 permanent plots across the Netherlands, in which vegetation changes have been monitored since 1999. The plots cover gradients of local N deposition, climate and soil type. All plots were managed similarly (mowing with removal of biomass) and detailed information on soil type, climate and N deposition data was available. We used this dataset to examine 1) whether and how plant diversity, different species groups and environmental indicator values in roadside verges have changed over the period 2004–2020; and 2) whether and how variation in local temporal trends is explained by spatial variation in N deposition (NH_x and NO_y separately), climate change (summer drought and winter warming), the interaction between soil type and the first two factors, and the interaction between climate change and N deposition.

2. Material and methods

2.1. Study system

The Netherlands has a temperate oceanic climate with year-round precipitation, mild winters and relatively cool summers. In the eastern part of the Netherlands, the climate shows a more continental character. Towards the south, the average temperature increases. Over the last decades, the Dutch climate has changed significantly. Temperatures have risen by approximately twice the global average (2.2 °C between 1907 and 2020) both in winter and in summer (CBS et al., 2023). In winter the most prominent change was a decline in the days with temperatures between 0 and 5 °C and an increase in the number of days with temperatures between 5 and 10 °C (Siegmund, 2023). Since 5 °C is the temperature above which vegetation can grow (Hurtado-Uria et al., 2013), this change is ecologically significant. Furthermore, particularly the more inland regions of the Netherlands have experienced more pronounced spring and summer droughts (Philip et al., 2020).

N deposition in the Netherlands remains at a high level (on average 1500 mol N/ha in 2020; deposition is exceeding the critical deposition value in 70 % of Dutch nature areas, van Dobben and Van Hinsberg, 2023) but was even higher in the past (on average 28 kg N/ha in 2000, and above 35 kg N/ha in 1990; Noordijk, 2007). After 1990, NH_x deposition initially declined, but remained relatively stable after 2000 (25 kg N-NH_x/ha in 1990, around 15 kg N-NH_x/ha after 2000; Noordijk, 2007, CBS et al., 2024). NO_y deposition steadily declined since 1990 (around 13 kg N-NO_y/ha in 1990, around 6 kg N-NOy/ha in 2020; Noordijk, 2007, CBS et al., 2024). In road verges the deposition of NO_y is higher than average due to emissions by traffic (Cape et al., 2004).

In this study we used data from a roadside grassland flora monitoring network ('Meetnet bermflora'; CBS, 2003). Dutch road verges mostly consist of semi-natural grasslands and have high potential to contribute to conservation of grassland biodiversity, especially in contemporary fragmented landscapes (Lázaro-Lobo and Ervin, 2019; Phillips et al., 2020). This is because of their large spatial extent (e.g. 1.7 % of the Netherlands is road verge, compared to 4 % unforested natural area; Schaffers, 2000). In addition, road verges harbour a significant degree of biodiversity (Sýkora et al., 1993; Noordijk et al., 2009) and they provide corridors between natural areas (Tikka et al., 2001).

Dutch highway road verges make up about one third of the total road verge area of the Netherlands. The vegetation ranges from very productive to unproductive, and the soil ranges from heavy clay to coarse sand. Since the 1970s, road verges have been ecologically managed through low frequency mowing with hay removal. Until 2013 the majority of productive road verges were mown twice a year, typically in June/July and August/September, however since 2013 they have been mown once a year, in August/September. In contrast, most unproductive road verges have consistently been mown once a year, in August/September (Scherpenisse et al., 2020).

The monitoring network 'Meetnet bermflora' was initiated in 1999. Between 1999 and 2003, about 1600 permanent plots were established, 882 of which in grassland road verges (CBS, 2003). Permanent plots were equally divided over Dutch highway road verges (with approximately equal distance between permanent plots). They were established next to highway location markers to increase the probability of recovery and decrease placement bias. Plots were 3 × 3 m and were mostly located at 7–9 m distance from the traffic (ca 4.5 m from the emergency lane). At this distance, no clear effects of elevated salinity associated with road deicing salt application are present in the plots (Scherpenisse et al., 2020). After 2003, permanent plots were resurveyed every four years (Bakker and Bijkerk, 2008; Boddeke and Japink, 2012; Boddeke et al., 2016; Scherpenisse et al., 2020).

2.2. Vegetation indices

To assess trends in road verge plant communities we derived three types of indices from the species composition of each plot: biodiversity-indices (based on all species), indices of species groups (Table 1) and environmental indicator values (the unweighted mean of the coexisting species, Table 1). We quantified three biodiversity indices: richness (total number of species), evenness, and the Shannon-index. The Shannon-index and evenness can be expressed as:

$$\text{Shannon} - \text{index} = -\sum_{i=1}^{S} p_i \ln p_i \quad (1)$$

$$\text{Evenness} - \text{index} = -\frac{\sum_{i=1}^{S} p_i \ln p_i}{\ln(S)} \quad (2)$$

where S is the species richness and p_i is the relative abundance of each species (as percentage cover). To gain more insight into the plant species that drive changes in vegetation composition we subsequently defined several species groups (Table 1). These species groups were classified (Appendix A) based on the traits canopy height (Kattge et al., 2020; proxy for competitiveness, Keddy et al., 2002), life span (Dijkstra, 2012), and ruderalness (Tamis et al., 2004). Because of the different ecophysiology and the high relevance of forbs for insect biodiversity, we also separated grasses and forbs, resulting in eight unique species groups (Kattge et al., 2020). We additionally examined the grass to forb cover ratio (Table 1). We used this approach instead of the commonly used CSR classification proposed by Grime (1977) or estimates of CSR strategy based on a set of traits (Pierce et al., 2017). Our classification allows for a clear insight in the relation between species traits and species groups, while this is less clear for Grime's CSR classification. There were however similarities between our approach and Grime's CSR classification. The species groups 'annuals' and 'tall annuals' roughly reflect the R-strategy (i.e. a high R-score), and other species groups, especially

Table 1
Overview of indices for biodiversity, species groups and environmental conditions as used in the analysis.

Type	Index	Description
Biodiversity	Richness	Biodiversity index
	Evenness	Biodiversity index
	Shannon diversity	Biodiversity index
Species groups	Grass to forb ratio	Ratio between grasses (including annual grasses) and forbs (including annual forbs) cover.
	Small forbs	Cover of none-annual forbs, ≤50 cm.
	Tall forbs	Cover of none-annual non-ruderal Forbs, >50 cm.
	Ruderal tall forbs	Cover of none-annual ruderal forbs, >50 cm.
	Annuals	Cover of non-ruderal annuals.
	Ruderal tall annuals	Cover of ruderal annuals, >50 cm.
	Small grasses	Cover of none-annual grasses, ≤100 cm.
	Tall grasses	Cover of none-annual grasses, >100 cm.
	Shrubs and trees	Cover of phanerophytes; Seedlings and young specimens included.
Environmental indicator values	Ellenberg nutrients	Estimated nutrient concentration in the soil based on species present
	Ellenberg moisture	Estimated moisture of soil based on species present
	Ellenberg reaction	Estimated pH of the soil based on species present
	Ellenberg light	Estimated light availability based on species present
	Ellenberg Mowing	Estimated sensitivity to mowing of the species present
	Ellenberg Temperature	Estimated temperature based on species present
	Plant height	Estimated competitiveness of vegetation based on average species height
	Life span	Estimated disturbance of vegetation based on the presence of species that depend on open patches for germination

those with taller species roughly reflect more C-dominated strategies in grasslands (Kühn et al., 2004). Our approach did not define S-strategy species groups, but species with S as primary strategy were very rare in permanent plots included in this analysis. Another reason for using our trait-based approach instead of Grime's CSR approach, was that our approach allows for an approximation of competitiveness on a continuous scale (see next section) which the traditional CSR classification does not allow for. As environmental indicator values we used Ellenberg indicator values which reflect niche optima along gradients of key environmental variables (Ellenberg et al., 1992, Briemle et al., 2002; calculated using TURBOVEG, Hennekens and Schaminée, 2001), and the plant traits plant height (as proxy for competitiveness; Kattge et al., 2020) and plant life span (as proxy for disturbance, consistent with Grime, 1977 and Midolo et al., 2023; Dijkstra, 2012). Plot-level means for the indicator values were based on presence/absence of species and not on abundance (Käfer and Witte, 2004).

2.3. Explanatory factors

To estimate the effects of climate change and N deposition on biodiversity and vegetation composition on different soil types, climate variables, N deposition and soil type variables were calculated for every permanent plot (Fig. 1).

As climate variables we used a proxy for summer drought, measured as the precipitation deficit from March to August, and a proxy for the prolonged growing season, calculated as the winter degree days above 5 °C from October to March (Tsum, temperature above which vegetation can grow; Hurtado-Uria et al., 2013). Precipitation deficit was estimated by subtracting the Makkink evaporation (i.e. the potential evaporation taking into account air temperature and sunshine duration; Winter et al., 1995) from the precipitation. Weather data from weather stations with available data for the period 1998–2020 were used to calculate the climate variables (Royal Netherlands Meteorological Institute; KNMI). Data were interpolated according to methodology used by the Royal Netherlands Meteorological Institute (KNMI; Temperature: Universal Kriging using log distance to the shoreline, Precipitation: Ordinary Kriging, Evaporation: Thin plate spline regression; Sluiter, 2012).

Two proxies for N deposition were calculated: Background NH_x-concentrations and NO_y-emissions by traffic. Background NH_x concentration data was used instead of NH_x deposition data, since the NH_x concentration data may be more reliable for local grassland patches. N deposition data was only available at a 1 × 1km resolution nationwide. However, N deposition at plot level can significantly deviate from grid cell nitrogen deposition, because local roughness of the surface may be very different from average surface roughness on the 1 × 1km scale. Local differences are therefore not captured by the national N deposition data. Instead, we assumed that surface roughness length was the same for every plot as all plots are grassland vegetation (Moene and Van Dam, 2014), and used NH_x concentrations as proxy for NH_x depositions. Background NH_x-concentrations (NH_x) were extracted from 1×1km resolution maps (Hoogerbrugge et al., 2024) for the period with sufficiently high-resolution data available (2005–2020). Car traffic emissions were calculated with the AERIUS Connect API (RIVM, 2024), using traffic intensity data (Rijkswaterstaat, 2018), traffic jam data (Rijkswaterstaat, 2015) and speed limit data (Rijkswaterstaat, 2018). Traffic related reactive N emissions could not be converted to traffic related reactive N concentrations with available models, because they cannot accurately convert N emissions to N concentrations within 20 m of the road. However, most permanent plots were at approximately the same distance from traffic (7–9 m), and therefore reactive N emissions should be proportional to N concentrations and depositions (Cape et al., 2004). Our local N emission estimates were correlated with 1×1 km NO_y background concentration data ($r = 0.65$). However, in the vicinity of traffic influence of traffic NO_y emissions on N deposition becomes much more prominent compared to background NO_y deposition (Cape et al., 2004), which is especially the case in the rural environments where the plots included in our analysis are located. Therefore, we assumed that traffic was the major source of NO_y deposition and consequently, background NO_y concentrations were not included in the analysis. NH_x traffic emissions and NO_y traffic emissions were strongly correlated ($r = 0.87$), and therefore we only included one of these variables (NO_y traffic emissions) in the analysis. Traffic NO_y emissions are higher than traffic NH_x emissions, but traffic NH_x deposition probably considerably contributed to plot level traffic N deposition (Cape et al., 2004).

Dutch highway road verge soils usually match the local natural soil type (Scherpenisse et al., 2020). Soil type of road verges could thus be described using soil maps of natural soils in the Netherlands (Wageningen Environmental Research, 2020). Soil type was described

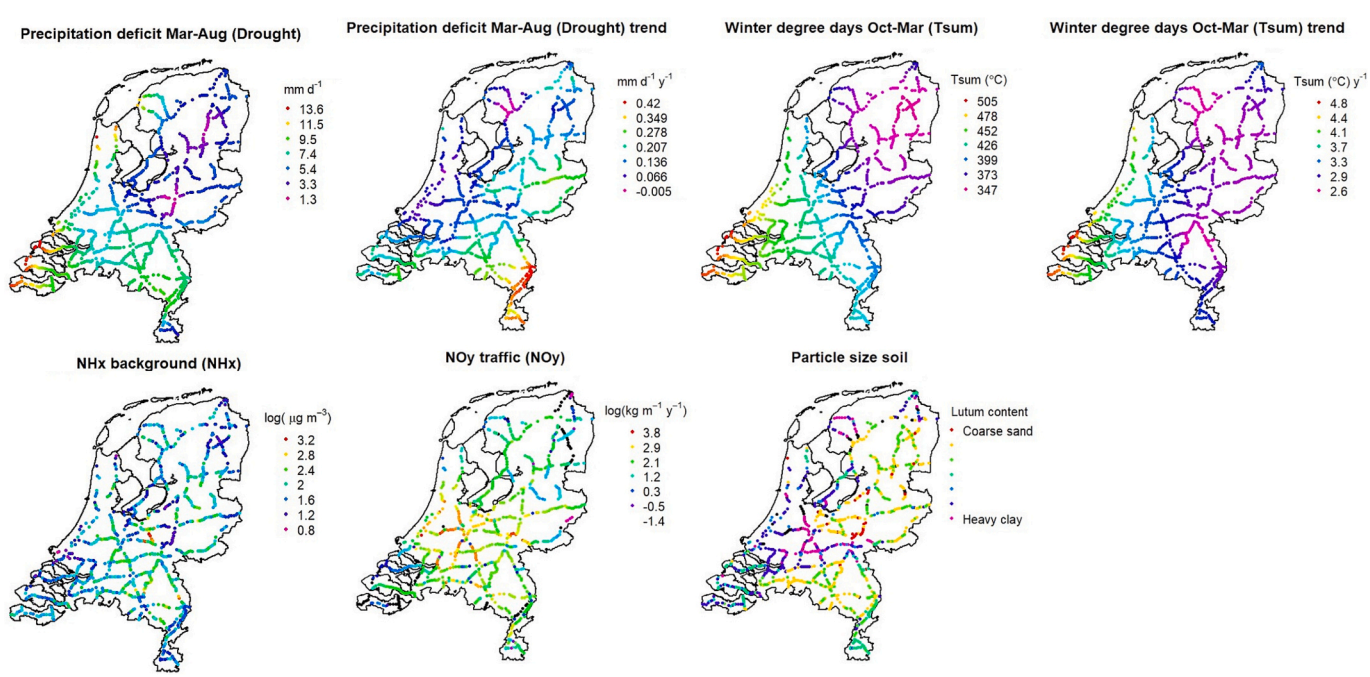

Fig. 1. Plot level climate (1980-2020), climate change (1980-2020), N deposition and soil type. Plots with no data are shown as black dots.

by soil particle size on a scale of one to seven (1. Heavy clay; 2. Clay, heavy silt, and light clay; 3. Silt or Silt mixed with light clay; 4. Light silt and silty loam; 5. Loamy fine sand; 6. Loam poor (fine) sand; 7. Coarse sand; and NA. no mineral soil). In the Netherlands more clayey soils are usually also more nutrient rich and productive than sandy soils. Plots on organic soils were not included in the analyses.

2.4. Analysis

All analyses were performed in R (version 4.3.1, R Core Team, 2023).

The survey data from 2004 to 2020 were selected, because the survey method changed slightly after 2003. To mitigate the risk of species omission or misidentification, surveyors used a species list from earlier surveying rounds, which was not available before 2004. Additionally, permanent plots near gas stations in which frequent mowing was applied instead of extensive management (15 permanent plots) were removed from the analysis.

2.4.1. Trends in biodiversity, species group cover and environmental indicators

Trends in biodiversity, species group cover and environmental indicators were analyzed with linear mixed effect models (Harrison et al., 2018) with year as fixed effect and permanent plot ID as random effect. Model assumptions were checked using the DHARMa package (Hartig, 2018). The index grass:forb ratio was transformed (^2) before applying a linear model with a gaussian distribution, and for the cover of the different species groups a beta distribution with a logit link was used (Douma and Weedon, 2019), with or without a zero-inflation function (~Year; Brooks et al., 2017). For other models, no data transformation was applied, and linear models were used with a gaussian distribution. Regressions were applied with the glmmTMB packgage (Brooks et al., 2017). Significance of the temporal trends was tested by comparing coefficients from permuted models (year variable permuted, 500 times) with coefficients from the non-permuted model.

2.4.2. Relations between trends in biodiversity indices and explanatory factors

For this analysis, permanent plots were selected which had no missing values in explanatory variables and which had at least four repeated measurements. The trend (coefficient) in biodiversity (species richness, Shannon diversity and evenness) was calculated per plot using a simple linear model and subsequently used as response variable in the following analyses.

Summer drought, Tsum, NH_x (background), NO_y (traffic), particle size, interactions between particle size and all other factors, and interactions between NH_x and climate factors, and interactions between NO_y and climate factors were included as explanatory factors in the analysis. Explanatory variables were expected to have cumulative effects throughout the examined time period (De Schrijver et al., 2011). Therefore, climate variables were summed (Tsum: $\sum_{i=a1}^{n=a2} \text{Tsum}_i$, where a1 = Tsum Oct yr1–1 to March yr1, and a2 = Tsum Oct yr2–1 to March yr2; Summer drought: $\sum_{i=y1-1}^{n=y2-1} \text{Summer drought}_i$) corresponding to the survey period (startyear = yr1 to endyear = yr2) for each plot. NH_x concentrations were summed for the years 2005–2020 (no data before 2005) for each plot. Calculated NO_y emissions (based on data from 2015, 2018 & 2019) were assumed to be proportional to the cumulative NO_y emissions, because spatial patterns in traffic hardly changed over the survey period (INWEVA; Rijkswaterstaat, 2021). Cumulative climate variables were subsequently divided by the number of survey-years per plot (because the survey period was not always the same for different permanent plots). Explanatory factors were subsequently standardized (mean centering, divided by 1 SD) to facilitate comparison of effect sizes.

Generalized least squares models including all explanatory variables were used to test for spatial autocorrelation (using an exponential correlation structure; nlme package; Pinheiro et al., 2023). In the next steps, autocorrelation was accounted for if the null hypothesis was rejected (p-value<0.05). Models were checked for variance inflation ($\text{GVIF}^{(1/(2\times \text{Df}))}$-values ≤ 2; car package; Fox and Weisberg, 2019).

Subsequently, to assess the relation between the trend in biodiversity and explanatory factors, model selection and averaging was applied (MuMIn package; Bartoń, 2023). First, models with all possible combinations of explanatory factors, including an intercept only model were constructed and compared using an information theoretic approach. The resulting 92 models were sorted based on their Akaike information criterion corrected for small sample size (AICc) (Appendix C. table C1-C3). We restricted our candidate model set to models with Δ AICc <4. For these models, the Akaike weights (ωm) were calculated, which represent the relative likelihood of models. Then, model averaging was applied (MuMIn package; Bartoń, 2023) to calculated full-model averaged coefficient estimates for each explanatory variable in the candidate model set. For each explanatory variable we calculated the sum of model weights over all models including that variable (ωp) as a measure of variable importance.

2.4.3. Relations between trends in species groups and explanatory factors, and between trends in environmental indicators and explanatory factors

The multivariate method redundancy analysis (RDA, Legendre and Legendre, 2012; vegan package, Oksanen et al., 2022) was used to visualize and assess the relation between other vegetation indices and explanatory factors, focusing on trends in changes in cover of species groups and environmental indicator values in relation to explanatory variables.

Trends and explanatory variables were calculated as described in the previous section. Species group data were logit transformed (Warton and Hui, 2011). Variable selection was applied using Monte Carlo permutation (vegan package, Oksanen et al., 2022).

Constrained ordinations, such as RDA can give misleading results if important environmental variables are missing. We therefore also used an unconstrained ordination method (Principal Component Analysis) to ensure we did not overlook a significant portion of the compositional variation. This supplementary method yielded similar patterns (PCA-plots are shown in Appendix C: Fig. C3).

3. Results

3.1. Trend in biodiversity, species groups and environmental indicators

Substantial changes in species richness and vegetation composition were found between 2004 and 2020 (Table 2). Plot level biodiversity summarized as Shannon diversity and evenness decreased with 11 % ($p < 0.01$) and 8 % ($p < 0.01$), respectively. Species richness decreased with 7 % but this change was not significant ($p = 0.11$). Different patterns in vegetation cover were observed for different species groups: Species groups composed of small none-grass-species declined strongly (small forbs and annuals declined with >25 % in cover), whereas species groups composed of tall species (tall forbs and tall ruderal forbs) remained stable, varied strongly (tall ruderal annuals) or increased strongly (cover of tall grasses increased with about 65 %, $p < 0.01$; and shrubs/ trees -seedlings and young specimens included- increased with >100 %, $p < 0.001$). Species within their respective species groups followed the trends observed for species group cover (Appendix B). Environmental indicator values also changed. Ellenberg moisture and Ellenberg pH significantly increased, while Ellenberg mowing showed a significant decline. Plant height and life span increased significantly. No changes were observed for Ellenberg nutrient values.

3.2. Relation between explanatory factors and biodiversity indices

Model averaging revealed that trends in biodiversity were best explained by winter degree days (Tsum; $\beta = -0.24$, $\omega p = 1$; $\beta = -0.22$,

Table 2
Changes in biodiversity, species group cover and environmental indicator values between 2004 and 2020.

Index	Model coefficient	CI 2.5 % permuted	CI 97.5 % permuted	p-Value
Species richness	−0.420	−0.521	0.538	0.1137
Shannon diversity	−0.073	−0.051	0.051	**0.0049**
Evenness	−0.019	−0.013	0.014	**0.0059**
Ellenberg N	0.006	−0.013	0.012	0.3752
Ellenberg pH	0.039	−0.025	0.027	**0.0034**
Ellenberg Moisture	0.035	−0.030	0.033	**0.0415**
Ellenberg Light	0.001	−0.009	0.010	0.7435
Ellenberg Mowing	−0.057	−0.036	0.038	**0.0030**
Ellenberg Temperature	−0.002	−0.016	0.016	0.8202
Life span	0.011	−0.009	0.010	**0.0384**
Height	0.016	−0.009	0.009	**0.0005**
Forb small	−0.107	−0.062	0.070	**0.0028**
Forb tall	0.028	−0.052	0.051	0.2687
Forb tall ruderal	0.025	−0.063	0.057	0.4104
Grass small	−0.046	−0.078	0.077	0.2150
Grass tall	0.150	−0.098	0.089	**0.0021**
Grass:Forb ratio	0.021	−0.018	0.018	**0.0261**
Annual	−0.101	−0.075	0.077	**0.0094**
Annual tall ruderal	0.061	−0.063	0.061	**0.0480**
Shrub/Tree	0.251	−0.114	0.122	**0.0001**

Significant p-values ($p < 0.05$) are indicated with bold text.

ωp = 1; β = −0.14, ωp = 1; for species richness, Shannon diversity and evenness respectively; Figs. 2–3, Appendix C: tables C1-C3). The trend in biodiversity was more negative with higher Tsum. Particle size was also related to the trend in evenness and Shannon diversity but not to species richness (β =0.01, ωp = 0.56; β =0.13, ωp = 1; β =0.15, ωp = 1; for species richness, Shannon diversity and evenness respectively). For coarser grained (i.e., more sandy) soils, the trend in Shannon diversity and evenness was more positive. The interaction between traffic NO_y deposition and Tsum contributed to model fit for Shannon diversity and species richness, but not for evenness (β = −0.15, ωp = 0.94; β = −0.18, ωp = 1; β = −0.07, ωp = 0.59; for species richness, Shannon diversity and evenness respectively; Figs. 2–3). The negative relation between Tsum and species richness and Shannon diversity was more negative with higher NO_y deposition. For the interaction between NO_y deposition and particle size (ωp = 0.38, 0.98 and 0.50 for species richness, Shannon diversity and evenness respectively), and NH_x deposition and summer drought (ωp = 0.02, 0.67 and 0.99 for species richness, Shannon diversity and evenness respectively), variable importance was only high (ωp > 0.7) for only one of the indices and effect sizes were relatively small (abs(β) ≤0.13).

Together, Tsum, Particle size and Tsum:NO_y only explained a small portion of variation (R^2adj 3.4 %, 6.1 %, and 4.7 % for species richness, Shannon diversity and evenness respectively). Even though the explained variation was small, the trend in regions with low Tsum was considerably less negative compared to those with high Tsum (Fig. 3 and Appendix C: Fig. C1).

Changes in biodiversity were not explained by N (both NH_x and NO_y) deposition and summer drought main effects.

3.3. Relation between explanatory factors and species groups

Variation in species groups was best explained by the main effects Tsum (F = 4.5) and particle size (F = 2.4; Fig. 4, Appendix C: table C4). The interaction between particle size and NO_y (F = 2.9) also had a significant contribution to model fit (Appendix C: table C4). The best model explained 2.4 % of the variation in the trend in species group cover, 88 % of which by the first two axes. Tsum was associated with a more positive trend in grass:forb ratio, tall grass cover, and shrub and tree cover, and a more negative trend in annuals, tall forbs, and small forbs (Fig. 4). The interaction between soil type and NO_y was explored by performing RDA on two different data-subsets (Appendix C: Fig. C2). One only included soil particle size categories 1–3 (clay) and the other only soil particle size categories 4–7 (loam and sand). The effect of NO_y was stronger on sandy soils (F = 2.4, table sx) than on clay soils (F = 0.8).

The main effect of Tsum (F = 2.5), the interaction between NO_y and Tsum (F = 2.7), and the interaction between NO_y and particle size (F = 2.9) all weakly but significantly contributed to model fit for the environmental indicators RDA. This model explained 1.9 % of the variation in the trend in environmental indicators, 85 % by the first two axes. Plant height and life span showed a more positive trend with a higher Tsum (Fig. 4). The interactions were explored by performing RDA on two different data-subsets (Appendix C: Fig. C2) one only included plots with NO_y deposition that was lower than average, whereas the other included plots with NO_y deposition that was higher than average. These

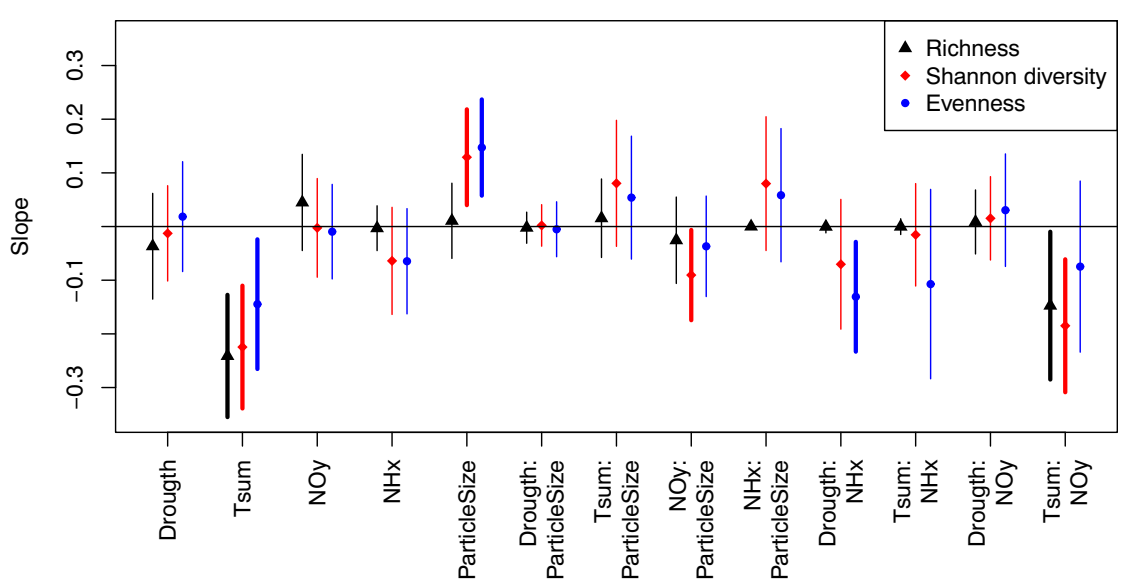

Fig. 2. Relation between the trend in biodiversity (scaled in this figure; richness=black, Shannon=red, evenness=blue) and explanatory variables. The bars show the 95% CI resulting from model averaging. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

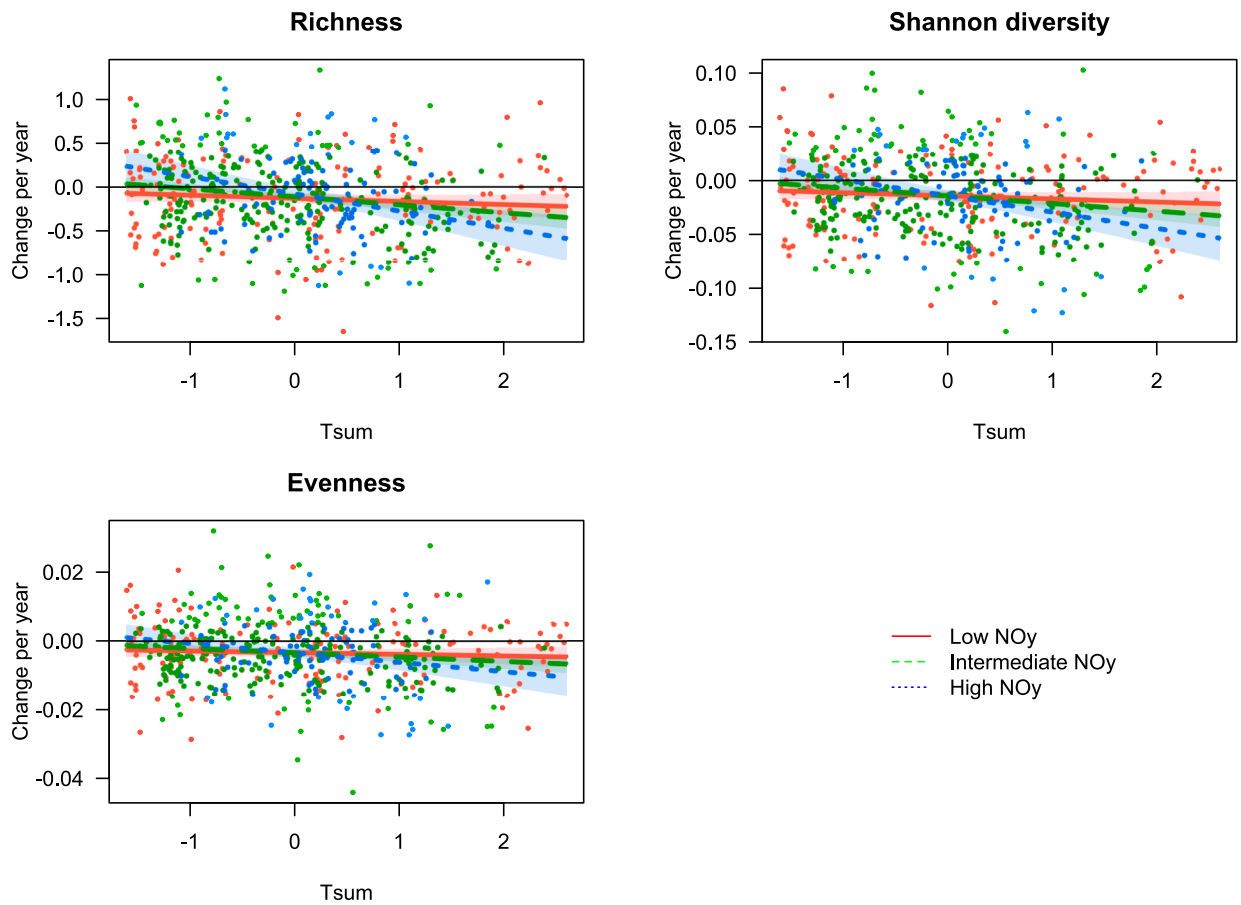

Fig. 3. Plots show the relation between the trend in biodiversity (not scaled in this figure; richness, Shannon diversity, and evenness) and the interactive effect of winter degree days and NOy. Particle size was also included in each model.

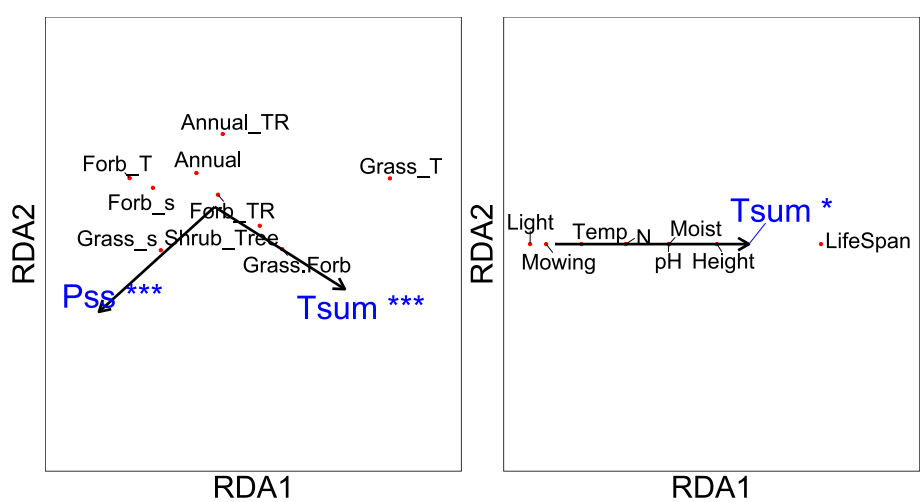

Fig. 4. Redundancy analysis (RDA) of (A) species group cover trends and (B) environmental indicator trends related to main effects of explanatory factors (interactions were excluded here). Figures show the results after model selection. PSS=particle size of the soil. The addition _T stands for Tall, _TR for tall and ruderal, and the addition _s stands for small. Apart from Height and LifeSpan, black text in panel B corresponds to Ellenberg values. p<0.05=*, p<0.01=**, p<0.001=***.

RDA showed that both for high and low NO_y, Tsum was positively related to the trend in plant height and life span. The relation between Tsum and the trend in environmental indices was slightly stronger with higher NO_y (F = 1.9) than with lower NO_y deposition (F = 1.6).

4. Discussion

Our nationwide study showed that between 2004 and 2020 grasslands in Dutch road verges became less diverse and increasingly dominated by tall, competitive species. Climate change -more specifically winter warming- and the interaction between winter warming and N deposition explained part of this degradation. Milder winters were

associated with a more negative trend in biodiversity. In addition, at sites with higher cumulative winter degree days, i.e. milder winters, a more pronounced increase in grass dominance, canopy height and proportion of perennial species was observed, whereas the short-growing species groups (especially forbs) declined significantly more. The detrimental effect of winter warming on biodiversity was stronger with higher N deposition. Interactive effects of soil type and N deposition were found as well; there was a small difference in the effect of N deposition on Shannon diversity and vegetation composition between soil types. In contrast to other studies, the overall effects of N deposition and drought (precipitation deficit) were not observed. Apart from N deposition, there were no significant differences in effects of explanatory factors between soil types. Soil type was however related to changes in Shannon diversity, evenness and species composition, with more positive trends on sandy soils than on clay soils.

N deposition in Dutch road verges exceeds the critical load values for Dutch grasslands (van Dobben and Van Hinsberg, 2023). It is therefore surprising that, although some context-dependent effects of N were observed and we cannot rule out changes in the seed bank related to N deposition (Basto et al., 2015), we found no negative overall effects of N deposition (both in NH_x and NO_y form) on species richness or species community over a period of >15 years. Particularly since other studies have shown strong negative effects of N deposition on grassland biodiversity (Phoenix et al., 2006; Bobbink et al., 2010). A possible explanation for the lack of effect may lie in the exceptionally high N deposition levels in the Netherlands in the period 1970–2000, i.e. before the start of the monitoring, reaching peak levels between 1980 and 1990 (Noordijk, 2007; CBS, PBL, RIVM, WUR, 2024). Species sensitive to N deposition and toxic N concentrations likely went locally extinct during and shortly after this period (i.e. before the start of the monitoring network). Kalwij et al. (2004) support this hypothesis by showing that 22 species characteristic for nutrient poor vegetations (of 45 characteristic species in total) were lost in road verges of Dutch main roads between 1986 and 2001, while only three species established. De Schrijver et al. (2011) also more generally reports for a wider range of vegetation types that species loss occurs faster at lower levels of cumulative N input and subsequently slows down when the cumulative N input gets to higher levels. Moreover, the decrease in N deposition after 1990, especially in traffic NO_y emissions (Noordijk, 2007; Hoogerbrugge et al., 2024), may have stabilized trends of sensitive species. Stabilization and even recovery are possible when nitrogen deposition is reduced after prolonged elevation, although this is severely hampered by legacy effects of a high N accumulation and strong acidification of the soil (Stevens, 2016), slow recolonization of species (Storkey et al., 2015), and depletion of key species in the seed bank (Bossuyt and Honnay, 2008; Basto et al., 2015).

We found a negative relation between winter degree days and biodiversity in semi-natural roadside grasslands, independent of soil type and grassland community, in corroboration with other studies in temperate grasslands (Kreyling, 2010; Dinh et al., 2023). Kreyling et al. (2019) suggested that increased productivity linked with higher winter temperature may be the main driver for the loss of biodiversity. Consistent with this hypothesis, we found a positive association between productivity and winter degree days. Furthermore, we observed a steeper decline in biodiversity related to winter warming at higher NO_y levels. Contrary to our findings, Fay et al. (2015) found weaker effects of nitrogen addition on with higher temperatures. Other studies report no interactive effects (LeBauer and Treseder, 2008) or no interactive effects for biomass but weaker effects of nitrogen addition on plant height with higher temperatures (Fu and Shen, 2016). Antagonistic interactions may be caused by a lower proportion of grasslands with nitrogen limitation at higher mean annual temperatures (Fay et al., 2015). LeBauer and Treseder (2008), Fay et al. (2015) and Fu and Shen (2016) however all include a wide temperature gradient. LeBauer and Treseder (2008) and Fay et al. (2015) include study sites with high mean annual temperatures. High mean annual temperatures can limit biomass production, while in temperate grasslands higher temperatures likely mostly increase biomass production of the vegetation due to an extension of the growing season (Jeong et al., 2011). Fu and Shen (2016) studied alpine grasslands were other limitations may play a role. Studies that simulate realistic warming in temperate grasslands report additive effects (Hutchison and Henry, 2010) or synergistic effects (Grime et al., 2000; Fridley et al., 2016) of warming and nitrogen or nutrient availability. Synergistic effects are also to be expected based on findings indicating higher nutrient demand with warming (Turner and Henry, 2009; Tian et al., 2019), as these demands can be met by more nutrient-rich (or enriched) soils. More synergistic effects may thus be expected with winter temperature increases associated with climate warming in temperate areas.

Strong effects of drought on grasslands are often reported (Liu et al., 2023), especially in nutrient-enriched grasslands (Chen et al., 2023). However, apart from a weak interactive effect of summer drought and NH_x deposition for evenness (more positive relation between summer drought and the trend in evenness with lower NH_x), changes in vegetation composition between 2004 and 2020 were not linked to summer drought. The high variability in summer precipitation in combination with a delayed and asynchronous response of many species may explain that no net effect was detected (Hallett et al., 2019). Furthermore, after a dry summer, vegetation biomass and species richness usually recover relatively quickly (Tilman and Downing, 1994), although species composition may change stochastically (Kreyling et al., 2011). Long-term effects of drought were found in other studies (i.e., Basto et al., 2018), although in these cases drought treatments were often more severe as compared to the changes in summer precipitation that were observed in our study. Furthermore, drought can also influence the seed bank differently than the above ground vegetation (Basto et al., 2018, Du et al., 2023), which is something we did not study. This could mean that potential long-term effects of summer droughts are underestimated in our study.

Although we found clear support for winter-warming as driver of decline of road verge biodiversity, as main effect and in interaction with NO_y, the variation explained by the models was relatively low. Part of the unexplained variation in biodiversity trends might be linked to variation in management of the road verges. Plant diversity conservation in semi-natural grasslands requires appropriate management of the vegetation, through e.g. grazing or mowing (Dengler et al., 2014). Dutch road verges are managed by mowing with removal of the cuttings. However, throughout the Netherlands, road verge management is performed by different contractors. Hence, we cannot rule out that subtle, spatiotemporal deviations from the prescribed management, have resulted in unexplained variation in our data. Furthermore, mowing frequency of the productive road verges (usually with clay soil) was lowered from twice a year to once a year around 2013 whereas the frequency of once per year was not changed on unproductive road verges (usually with sandy soils). Earlier studies have shown that mowing twice a year with hay removal is most beneficial for the maintenance of biodiversity in productive semi-natural grasslands and road verges and that lowering this frequency or total abandonment of mowing results in reduced species richness (Tälle et al., 2018; Noordijk et al., 2010). Although it is likely that part of the effects of this management change are explained by the variable 'soil type' (hence the more negative trends in Shannon diversity and evenness on clay soils), it is probably that this change in management accounts for some of the unexplained variation as well.

Our study focused on traditionally managed (semi-natural) grassland in road verges. Dutch road verges cover a wide range of soil types and vegetation types (Sýkora et al., 1993) and there was no convincing indication of differences in effects of N deposition and climate change between soil types. While N deposition is widely known as a global threat to biodiversity (Bobbink et al., 2010; Steffen et al., 2015), our results suggest that winter warming may increasingly become a major threat to diversity especially in areas where N deposition, and hence N

accumulation, has remained at high levels for extended periods of time. Similar effects of winter warming can be expected in other temperate climates(Jeong et al., 2011; Hutchison and Henry, 2010; Kreyling et al., 2019), even if winter warming increases frost damage due to lower snow cover (Kreyling et al., 2019). It is however unclear whether the effects of winter warming are also more strong in nutrient-enriched areas (e.g., those with elevated nitrogen deposition) in other climates. Based on Turner and Henry (2009) and Tian et al. (2019) we generally expect stronger limitation of nutrients on biomass production under warming conditions because of increased nutrient demand in warmer climates. However, studies examining these effects find mixed results. Grime et al. (2000) and Fridley et al. (2016) find synergistic effects of nutrient availability and winter warming effects in a cool oceanic temperate climate (similar climate to our study), Hutchison and Henry (2010) report additive effects in a temperate continental climate, and studies considering a wide temperature gradient often find additive or antagonistic effects of temperature and nitrogen addition (LeBauer and Treseder (2008), Fay et al. (2015), Fu and Shen, 2016). Since plant biodiversity is linked to other trophic levels such as insects, detrimental effects of winter warming on plant communities may cascade through the food web. The more pronounced negative effects of winter warming on forbs than on grasses is particularly concerning in that respect, since declining forb cover reduces floral resource availability for beneficial natural enemies and pollinators. This in turn could have negative consequences for delivery of pest control and pollination services. The increase in biomass related to winter warming may also have direct societal consequences such as increased management costs and an increased fire risk, and an increased fire risk may be further exacerbated by the increased grass dominance (Wragg et al., 2018).

Our study suggests that winter warming is an important driver of plant diversity decline in semi-natural grasslands, and that it causes changes in biotic interactions between competitive, tall growing species and other species in favor of the former. This shows that biotic interactions should not be ignored when predicting future distributions of plants, thereby agreeing with (Lavergne et al., 2010) who report that excluding this factor is a limitation of many contemporary studies. Competitive, tall growing species that appear to benefit from winter warming are generally the same species that also benefit from the contemporary major environmental threat of N eutrophication. Detrimental effects of N deposition can be reduced by changing grassland management (Jones et al., 2017) and we expect that changing the management regime may mitigate the detrimental effects of winter warming on biodiversity as well. To compensate for winter warming induced changes in productivity, increasing the mowing frequency, and changing the mowing timing may be beneficial adaptations. Regardless of adjustments of the mowing regime it is important that management by the contractor is carried out carefully with sufficient removal of biomass (and thereby nutrients; Schaffers et al., 1998, Noordijk et al., 2010). Both increasing the frequency of mowing and changing the timing may however have unwanted side effects on e.g. insect mortality and resource discontinuity (Humbert et al., 2010; Noordijk et al., 2010; Humbert et al., 2012). It is probably challenging to find a proper balance between the beneficial and adverse effects of an increased management intensity (Jones et al., 2017). Therefore, future research is required to study the effects of management regimes in a warmer climate.

CRediT authorship contribution statement

Wiene Bakker: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Toine Morel:** Project administration, Conceptualization. **Wim Ozinga:** Writing – review & editing, Writing – original draft, Methodology, Funding acquisition, Conceptualization. **Jeroen Scheper:** Writing – review & editing, Writing – original draft, Methodology, Funding acquisition, Conceptualization. **Philippine Vergeer:** Writing – review & editing, Writing – original draft, Project administration, Methodology, Funding acquisition, Conceptualization.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.176962.

Data availability

The data and code that support the findings of this study will be openly available in Zenodo at doi:https://doi.org/10.5281/zenodo.12592934.

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