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Species-rich semi-natural grasslands have a higher resistance but a lower resilience than intensively managed agricultural grasslands in response to climate anomalies

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Summary

1. The stable delivery of ecosystem services provided by grasslands is strongly dependent on the stability of grassland ecosystem functions such as biomass production. Biomass production is in turn strongly affected by the frequency and intensity of climate extremes. The aim of this study is to evaluate to what extent species-poor intensively managed agricultural grasslands can maintain their biomass productivity under climate anomalies, as compared to species-rich, semi-natural grasslands. Our hypothesis is that species richness stabilizes biomass production over time.

2. Biomass production stability was assessed in response to drought and temperature anomalies using 14 years of the Normalized Difference Vegetation Index (NDVI), temperature and drought index time series. More specifically, vegetation resistance (i.e. the ability to withstand the climate anomaly) and resilience (i.e. the recovery rate) were derived using an auto-regressive model with external input variables (ARx). The stability metrics for both grasslands were subsequently compared.

3. We found that semi-natural grasslands exhibited a higher resistance but lower resilience than agricultural grasslands in the Netherlands. Furthermore, the difference in stability between semi-natural and agricultural grasslands was dependent on the physical geography: the most significant differences in resistance were observed in coastal dunes and riverine areas, whereas the differences in resilience were the most significant in coastal dunes and fens.

4. *Synthesis and applications*. We conclude that semi-natural grasslands show a higher resistance to drought and temperature anomalies compared to agricultural grasslands. These results underline the need to reassess the ways agricultural practices are performed. More specifically, increasing the plant species richness of agricultural grasslands and lowering their mowing and grazing frequency may contribute to buffer their biomass production stability against climate extremes.

Key-words: biomass stability, grasslands, Normalized Difference Vegetation Index, plant diversity, remote sensing, resilience, resistance, the Netherlands

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Introduction

Grasslands cover 20–40% of the Earth's land surface and provide a range of crucial ecosystem services, including the provisioning of fodder and wildlife habitat, control of soil erosion, preservation of species and genetic diversity, water flow regulation, recreation and buffering of climate change through above- and below-ground carbon fixation (Häyhä & Franzese 2014). The stable delivery of these services is strongly dependent on the stability of grassland ecosystem functions such as nutrient cycling and biomass production, which are in turn affected by the frequency and intensity of external disturbances, such as climate extremes (Harrison *et al*. 2014). The expected world-wide increase in frequency and magnitude of these climate anomalies and extremes (IPCC 2012) therefore urges the need to improve our understanding of the temporal stability of grassland ecosystem functions (Ivits *et al*. 2014).

Throughout human history, most European grasslands have been created and sustained through human intervention, including grazing and cutting, haymaking and burning (Pärtel, Bruun & Sammul 2005). These practices resulted in very biodiverse semi-natural grasslands with a relatively low biomass productivity (Huyghe *et al*. 2014). During the 20th century, agricultural intensification through nitrogen and phosphorous fertilization, and the selection of highly productive grass species, has strongly increased grassland productivity, at the cost of plant species diversity (Wesche *et al*. 2012; Ceulemans *et al*. 2014). Given the expected increase in the frequency and the magnitude of climate anomalies, it is uncertain to what extent these relatively species-poor agricultural grasslands can maintain their long-term productivity. There is growing evidence that plant species richness affects ecosystem response to external disturbances, and in particular, that species-rich grasslands provide a more stable biomass production than species-poor grasslands (Cardinale *et al*. 2012). However, the majority of the evidence regarding the relationship between biomass production stability and species diversity so far is based on relatively small-scale experiments where plant species richness is manipulated and productivity is monitored through time (e.g. Tilman, Wedin & Knops 1996; Van Ruijven & Berendse 2010; Vogel *et al*. 2012). It is currently unknown whether the species diversity effects on biomass production stability also operate at much larger spatial scales, and can be generalized to *in situ* natural and agricultural ecosystems.

A first important hurdle in studying ecosystem response to climate anomalies at large geographical scales is the labour intensity and the invasive character of biomass production quantification through time. Here, remote sensing data offer considerable opportunities. The availability of remote sensing products directly associated with the vegetation state makes them highly valuable for ecosystem monitoring (Lhermitte *et al*. 2010, 2011; De Keersmaecker *et al*. 2014, 2015b). Remote sensing derived indicators include the use of the Leaf Area Index or LAI (e.g. Myneni *et al*. 2002), fraction of photosynthetically active radiation or fPAR (e.g. Myneni *et al*. 2002), net and gross primary productivity or NPP and GPP (e.g. Justice *et al*. 2002) and other descriptors of biomass and greenness of vegetation, such as Normalized Difference Vegetation Index or NDVI (e.g. Tucker *et al*. 2005) and Enhanced Vegetation Index or EVI (e.g. Justice *et al*. 2002). In addition, these indicators exhibit valuable spatio-temporal properties which are very useful in ecological applications (Vern & Paruelo 2010; Pettorelli *et al*. 2014).

A second difficulty associated with monitoring vegetation stability at large spatial scales is the spatial variability of the disturbances which complicates the comparison of vegetation property anomalies and ecosystem stability. For example, it is difficult to compare vegetation stability at large spatial scales based on biomass production response alone, because the spatial variability in climate anomalies will also affect the biomass production response. Recent work of De Keersmaecker *et al*. (2015a), however, has provided a methodology to overcome this limitation by taking the magnitude of local climate anomalies explicitly into account when quantifying short-term vegetation stability. Consequently, this methodology facilitates the study of the stability of ecosystem functions at much larger scales than was previously possible. Moreover, as the approach is based on a combination of long-term remote sensing and climate time series on a global scale, it allows assessment of the spatial variability of biomass production response and stability at much larger scales based on multiple observations.

The aim of this study was to evaluate to what extent species-poor, intensively managed agricultural grasslands in the Netherlands maintain their biomass productivity under climate anomalies. Therefore, the biomass production stability of these grasslands was assessed in response to periods of drought and temperature anomalies between 2000 and 2013, using moderate resolution imaging spectroradiometer (MODIS) NDVI time series. More specifically, stability was defined via the resistance and resilience of grasslands, where resistance refers to the ability of vegetation to withstand a perturbation, and resilience expresses the speed at which the system returns to its average state. Production stability of these species-poor agricultural grasslands was then compared with the biomass production stability of relatively species-rich, semi-natural grasslands. Our hypothesis was that species-rich, semi-natural grasslands are more resistant and resilient to drought and temperature extremes than species-poor agricultural grasslands.

Materials and methods

SELECTION OF SEMI-NATURAL AND INTENSIVELY MANAGED AGRICULTURAL GRASSLAND PIXELS

The study focuses on the Netherlands where grasslands cover more than one-third (38%) of the country (Huyghe *et al*. 2014).

The diversity of the Dutch grassland ecosystems covers a wide range, from natural dune grasslands, peat grasslands to grassland swards, heathland and calcareous grasslands. In all areas, both intensively cultivated and semi-natural grasslands are managed in close vicinity. Due to fertilization, hydrological management and the selection of highly productive grass species, intensively managed grasslands are considered to have a lower species diversity when compared to semi-natural grasslands (Wesche *et al.* 2012; Ceulemans *et al.* 2014).

A two-step procedure was followed to discriminate between the species-rich, semi-natural grasslands on the one side and species-poor intensively managed grasslands on the other side. First, all pixels categorized purely in the 100 m 2006 Corine Land Cover data (CLC EEA 2014b) under grassland (i.e. 'Pastures' or 'Natural grasslands') were selected. In order to avoid the selection of grassland pixels which changed from/to another landcover type over the study period, pixels that indicated a change in the CLC 2000–2006 data (EEA 2014a) were removed from the data set. Secondly, intensively managed agricultural grasslands were discriminated from semi-natural grasslands based on their nature conservation status: grassland pixels belonging to a Natura 2000 area (European Commission 2014) were considered as semi-natural or grassland under semi-natural regime, whereas pixels outside these areas were considered as intensively managed agricultural grasslands (Table 1). The Natura 2000 network, which is regulated by European nature and biodiversity policy, aims to assure the long-term survival of threatened species and habitats in Europe. Through the designation of conservation and protection areas, which may also be privately owned, the network aims to ensure sustainable management (European Commission 2014). Intensively managed agricultural grasslands are further referred to as agricultural grasslands.

DATA

In order to quantify biomass production stability of semi-natural and agricultural grasslands, their vegetation response to temperature and drought anomalies was modelled using the vegetation stability approach of De Keersmaecker *et al.* (2015a) which quantifies vegetation resistance and resilience (i.e. the ARx model as explained more thoroughly below). This approach requires data on vegetation response (vegetation biomass) and climate anomalies (drought and temperature).

To assess vegetation response, a biophysical indicator of greenness/biomass based on remote sensing data was used, that is the NDVI (Pettorelli *et al.* 2005; Lhermitte *et al.* 2011; Gu, Wylie & Bliss 2013; Li *et al.* 2013). Eight-daily of bidirectional reflectance distribution function (BRDF) corrected NDVI data (MCD43A4 product; Land Processes Distributed Active Archive Center (LP DAAC) 2014) with a 500 m spatial resolution were obtained over the period 2000–2013. The NDVI data were first spatially reprojected from the MODIS sinusoidal projection to geographic coordinates. High-quality data was ensured by setting data points with a snow-affected BRDF as missing. The eight-daily data were then temporally averaged on a monthly basis to be consistent with the temporal resolution of the meteorological data.

Table 1. General overview of properties of semi-natural and intensively managed agricultural grasslands

Property	Intensively managed agricultural grassland	Semi-natural grassland
Plant species diversity	Low	High
Irrigation	Might be present	Absent
Fertilization	Present	Absent
Mowing/grazing frequency	Mostly high	Low
Management	Mostly intensive	Extensive

The resulting vegetation biomass/greenness time series generally consist of three main parts: (i) the seasonality, which is related to the phenology of the vegetation through time, (ii) trends associated with gradual changes (e.g. long-term vegetation degradation) and (iii) the anomaly which is characterized by the short-term response of vegetation biomass to environmental anomalies such as a drought period and noise (Verbesselt *et al.* 2010a,b). To obtain the anomaly part of the time series, the monthly time series were detrended through the subtraction of significant linear trends (De Keersmaecker *et al.* 2015a). As such, the effect of long-term vegetation changes was minimized. The seasonality, that is the average NDVI for each month over all years, was subsequently subtracted from the detrended NDVI time series to obtain the final NDVI anomaly time series. Hence, positive/negative NDVI anomalies denote a higher/lower vegetation biomass or greenness than average. An illustration of the NDVI anomaly calculation can be found in Fig. S1 (Supporting information).

The assessment of climate anomalies during the 2000–2013 period was based on meteorological data, that is temperature anomalies and precipitation deficits. Daily 1000 m temperature and precipitation grids from January 1965 until December 2013 (KNMI 2014) were, respectively, averaged and summed to monthly data. Using these monthly climate grids, a drought index, that is the Standardized Precipitation and Evapotranspiration Index (SPEI; Beguería, Vicente-Serrano & Angulo-Martínez 2010; Vicente-Serrano, Beguería & López-Moreno 2010) with a time scale of 3 months was calculated (including the current and two preceding months). The SPEI is a site-specific drought indicator based on deviations from the average water balance. The latter is calculated as the precipitation minus the potential evapotranspiration over a specified time scale, where the potential evapotranspiration was calculated using the Thornthwaite algorithm (Thornthwaite 1948). The SPEI and temperature grids were subsequently resampled to the MODIS grid. Finally, temperature anomalies were obtained by subtracting the monthly seasonality using the average temperature for each month over all years.

BIOMASS PRODUCTION STABILITY

Vegetation resistance and resilience to climate anomalies were assessed using an ARx model, following the procedure described in De Keersmaecker *et al.* (2015a). This model considers the NDVI anomaly as a linear combination of the temperature anomaly, drought index and lagged NDVI anomaly (eqn 1; De Keersmaecker *et al.* 2015a):

$$\begin{aligned}\mathrm{NDVI}_{\mathrm{anom}}(t) = {} & c + \alpha\,\mathrm{SPEI}(t) + \beta\,T_{\mathrm{anom}}(t) \\ & + \phi\,\mathrm{NDVI}_{\mathrm{anom}}(t-1) + \epsilon(t),\end{aligned} \qquad \text{eqn 1}$$

where $\mathrm{NDVI}_{\mathrm{anom}}(t)$ equals the standardized NDVI anomaly, $\mathrm{SPEI}(t)$ the standardized SPEI index at time t, while $T_{\mathrm{anom}}(t)$ equals the standardized temperature anomaly, $\mathrm{NDVI}_{\mathrm{anom}}(t-1)$ equals the standardized NDVI anomaly at time $t-1$ and $\varepsilon(t)$ the residual term at time t. Each of these model coefficients can be

Table 2. Interpretation of the ARx coefficients [adapted from De Keersmaecker *et al.* (2015a)]

Coefficient	Interpretation magnitude	Interpretation sign
ϕ [coefficient $Y(t-1)$]	Absolute values between 0 and 1 represent systems returning to equilibrium, with large absolute values indicating a slow return to equilibrium	*Positive*: Anomalies are similar to the previous anomaly. In case ϕ is smaller than one, the anomaly gradually diminishes over time *Negative*: Anomalies are similar to the previous anomaly, but with the opposite sign. In case ϕ is larger than -1, the system returns to equilibrium in an oscillating way
α and β [coefficient SPEI(t) and Tanom(t)]	Large absolute values indicate a low resistance to droughts/temperature anomalies, that is a large egetation response to short-term droughts/temperature anomalies	*Positive*: Wetter conditions/higher temperatures than average induce a positive Normalized Difference Vegetation Index (NDVI) response, that is an increase in biomass or vegetation greenness. Dryer conditions/lower temperatures than average induce a negative NDVI response, that is lower biomass or vegetation greenness *Negative*: Wetter conditions/higher temperatures than average induce a negative NDVI response, that is a decrease in biomass or vegetation greenness. Dryer conditions/lower temperatures than average induce a positive NDVI response, that is higher biomass or vegetation greenness

related to vegetation stability metrics, as described in Table 2. α and β are related to the resistance to droughts and temperature anomalies, respectively. If α and β are large in absolute terms, the vegetation biomass anomaly (i.e. NDVI anomaly relative to an average year) responds strongly to climate anomalies, and the vegetation resistance is consequently low. Positive/negative α and β coefficients further denote that the vegetation biomass or greenness (i.e. the NDVI) increases/decreases with higher/lower water availability and temperatures than average. The ϕ coefficient is related to the memory effect (i.e. the dependence of a biomass (i.e. NDVI) anomaly on previous anomalies). In an environment where climate is the major driving factor, this term is associated with the speed of return to average biomass production and could thus be interpreted as a resilience term. However, if the vegetation is managed, anomalies might occur which are not related to climate events. In case these anomalies are persistent during consecutive months, they may also determine the ϕ coefficient.

Pixels might further have an insignificant value for one or more coefficients of the ARx model due to three main reasons. First, vegetation might show a very small response to climate anomalies, leading to insignificant coefficients. This would mean that the percentage of insignificant pixels could be used as a proxy for extreme stability. Secondly, insignificant pixels could be attributed to lack of climatological anomalies. If there are no sufficiently large climate anomalies, the vegetation will not respond to the climate variable and therefore no significant fit can be obtained. Thirdly, if the amount of noise in the data is larger than the response of the vegetation, the fit of the model will be hampered.

It should finally be noted that – due to the use of the complete time-series period and the standardization of the anomalies – the interpretation of these vegetation biomass stability metrics differs slightly from the metrics that are often derived in experimental studies. The latter studies often focus on one drought period and use resistance metrics that are standardized for grassland biomass (e.g. Tilman 1996). The ARx model uses information of the whole time series period to derive the stability metrics and does not normalize the resistance metrics for grassland biomass, but for the standard deviation of their anomalies.

COMPARING THE STABILITY OF INTENSIVELY MANAGED AGRICULTURAL AND SEMI-NATURAL GRASSLANDS

The mean stability and model error (RMSE) between the selected agricultural and semi-natural grasslands was compared using a mixed model, where the grassland type was the fixed effect. As local environmental conditions might affect differences in stability between semi-natural and agricultural grasslands, phytogeographical regions were taken into account as a random effect. These regions are largely characterized by their potential botanical diversity as derived from similarities of the distribution patterns of plant species, and they can be seen as a good proxy for the local abiotic characteristics (Weeda 1989). These data were obtained using the phytogeographical regions defined in SynBioSys (Schaminée, Hennekens & Ozinga 2007) (Table 3).

To avoid spatial dependency of the stability metrics with respect to management type (adjacent pixels are more likely to have the same metric), we (i) randomly selected one out of each four adjacent pixels, (ii) used a stratified random sampling and (iii) explicitly incorporated a spatial correlation structure in the model. The stratification was based on a clustering of the study area in 10 climatological regions and ensures an equal spread of semi-natural and agricultural pixels across the Netherlands. The model was applied on an equal number of randomly selected pixels for each of both groups of grasslands within each of the strata. This sampling was repeated 100 times, resulting in a distribution of P-values for the fixed effect. This distribution was then summarized by the percentage of resamplings having a significant P-value (i.e. $P < 0{\cdot}05$). The spatial correlation structure was described for each analysis using a linear, Gaussian and spherical semi-variogram. The model having the lowest Akaike Information Criterium (AIC) was finally selected.

Table 3. Overview of the phytogeographical regions

Phyto-geographical region	Characteristics	Dominant soil type	'Semi-natural' grassland types
Coastal dunes (CD)	Calcareous in the south	Sand	Koelerio-Corynephoretea
Hills (Hi)	Calcareous region	Sand, rocky	Festuco-Brometea, Sedo-Scleranthetea
Sandy (Sa)	Pleistocene soils, nutrient poor, high pH	Sand	Nardetea, Calluna-ulicetea
Fen (Fe)	Often below sea level, covered with organic peat and high pH	Peat	Molinio-Arrhenatheretea
Salt water, tidal areas (SW)	Nutrient-rich, high salt content, under influences of regular flooding by salt water	Sand, clay	Saginetea maritima
Sea clay (SC)	At or below sea level, high pH and nutrient-rich	Clay	Molinio-Arrhenatheretea, Plantaginetea majoris
River (Ri)	Layers of clay and salt, high water-table variability	Clay, sand	Plantaginetea majoris, Molinio-Arrhenatheretea

ACCOUNTING FOR PHYSICAL–GEOGRAPHICAL DIFFERENCES

To test whether the phytogeographical regions have a significant effect on the differences in biomass production stability between semi-natural and agricultural grasslands in response to climate anomalies, the interaction between the phytogeographical position and type of grassland (i.e. semi-natural vs. intensively managed) was tested using the model of eqn (2). The spatial correlation structure was also included in this model.

$$\mathrm{STAB}_{\alpha|\beta|\phi|\mathrm{RMSE}} \sim c + \gamma\,\mathrm{VEG} + \eta\,\mathrm{PHYT} + \kappa\,\mathrm{PHYT} * \mathrm{VEG} + \epsilon, \qquad \text{eqn 2}$$

where $\mathrm{STAB}_{\alpha|\beta|\phi|\mathrm{RMSE}}$ equals the resistance to drought, resistance to temperature anomalies, the resilience or the ARx model error; VEG the type of vegetation (i.e. semi-natural vs. agricultural grassland); and PHYT the phytogeographical region. If the interaction term κ PHYT*VEG of eqn (2) is significant, the difference in stability or model error between semi-natural and agricultural grasslands is dependent on the phytogeographical region. In that case, the stability of semi-natural and intensively cultivated grasslands was compared for each phytogeographical region separately, through modelling the stability as a function of the grassland type following the procedure as described above. A flow chart of the methodology can be found in Fig. S4.

Results

The sign of the ARx-based resistance metrics indicates that the grassland vegetation showed an increase in biomass or greenness (i.e. NDVI) with both higher water availability than average and with higher temperatures than average (i.e. positive α and β coefficients, respectively; Fig. 1b,c). Some grassland pixels had an insignificant value for one or more of the ARx-based stability metrics. Most of the pixels (i.e. >99%) showed at least one significant coefficient and had an RMSE $< 0{\cdot}9$, with the resilience term having the largest percentage of pixels with a significant coefficient (99%), followed by resistance to temperature anomalies (91%) and the resistance to drought (65%) (Fig. 1).

The percentage of pixels having a significant ARx model-based stability metric further differed between semi-natural and agricultural grasslands: the fraction of significant coefficients was much lower for semi-natural grasslands (i.e. 1%, 16% and 20% lower for the resilience, resistance to drought and resistance to temperature anomalies, respectively) (Fig. 2). This result suggests that semi-natural grasslands are more often highly resistant than agricultural grasslands because the ARx model coefficients become very small and insignificant when the vegetation does not react to environmental perturbations. However, coefficients might also become insignificant if environmental perturbations are mild and do not occur frequently, or if the signal-to-noise ratio of the data is too low to measure vegetation response. To examine the influence of within-pixel climate variability, the magnitude of the significant and insignificant coefficients was plotted against the standard deviation of SPEI and temperature anomalies (Fig. 3). Although significant coefficients were generally larger neither the magnitude of the coefficients nor the separation between significant and insignificant coefficients was related to climate variability. This suggests that climate variability is not an important factor to explain the variability in stability metrics in the Netherlands over the 2000–2013 period.

Comparison of the stability metrics and the ARx model error (RMSE) between semi-natural and agricultural pixels using the repeated spatial resampling procedure revealed that the two grassland types differed significantly for 59–100% of the repeated tests (Fig. 4). Semi-natural grasslands were more resistant to droughts and temperature anomalies, but they were also less resilient when compared to agricultural grasslands. It should also be noted that in 71% of the resamplings, the error of the ARx model fit was significantly larger for agricultural grasslands than for semi-natural grasslands, suggesting that the

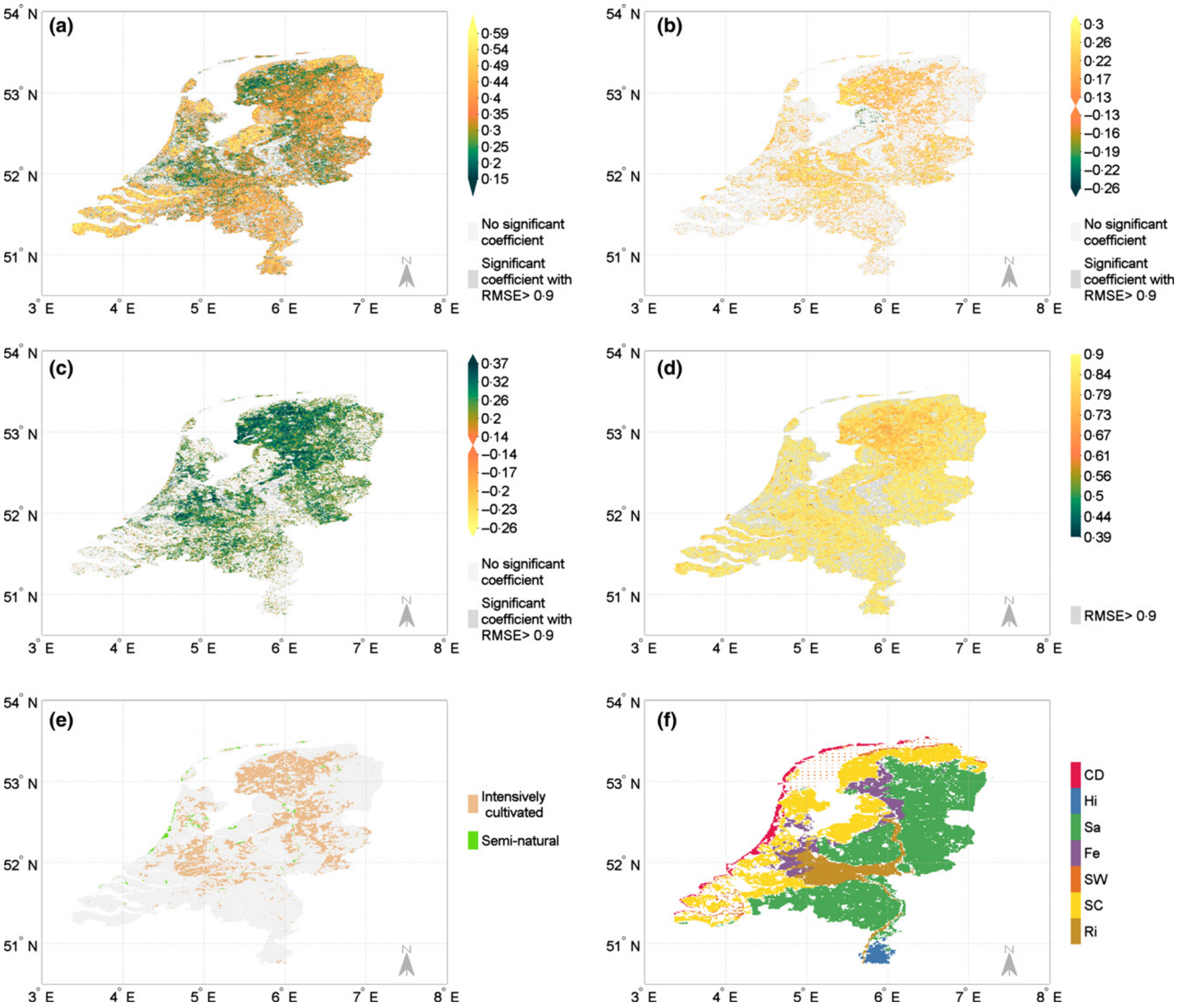


Fig. 1. Spatial overview of vegetation resilience [ϕ coefficient of NDVI($t-1$)] (a), vegetation resistance against drought [α coefficient of SPEI(t)] (b) and vegetation resistance against temperature anomalies [β coefficient of Tanom(t)] (c) the root-mean-squared error (RMSE) of the model (d), the location of semi-natural and intensively managed agricultural pixels (e) and phytogeographical regions (f). Only pixels with a RMSE < 0·9 are represented in subfigure (a) to (d). CD stands for coastal dunes, Hi for hills, Sa for sandy areas, Fe for fens, SW for salt water tide, SC for sea clay and Ri for rivers. NDVI, Normalized Difference Vegetation Index.

ARx model had more difficulties assessing vegetation response of agricultural grasslands. The distribution of mean values and p-values of the tests can be found in Fig. S2.

The difference in the stability between semi-natural and agricultural grasslands depended on the phytogeographical region for all stability metrics, but to a lesser extent for the resistance to drought (Fig. 5). For the latter, only 48% of the resamplings showed a significant interaction between grassland and the phytogeographical region, while a larger fraction of interaction terms were significant for the resistance to temperature anomalies (66%) and for the resilience term (99%). Consequently, it was important to assess the difference between semi-natural and agricultural grasslands for each phytogeographical region separately.

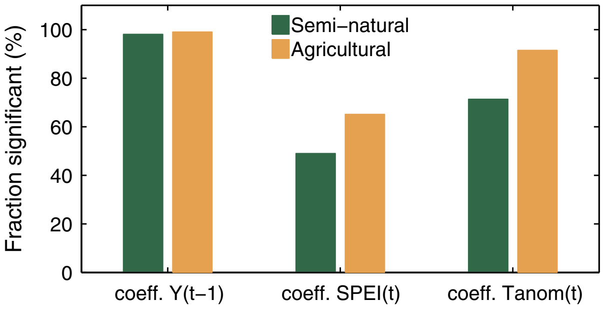


Fig. 2. The fraction of significant coefficients for semi-natural and intensively managed agricultural grasslands for each of the three stability metrics: the resilience [ϕ coefficient of NDVI($t-1$)], the resistance against drought [α coefficient of SPEI(t)] and the resistance against temperature anomalies [β coefficient of Tanom (t)]. NDVI, Normalized Difference Vegetation Index.

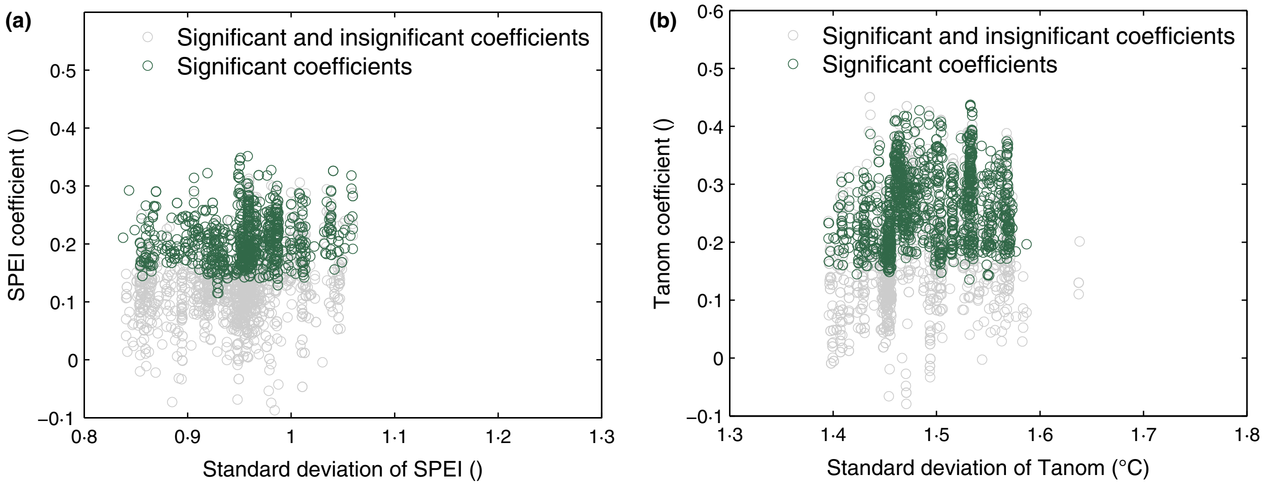


Fig. 3. The values of the significant and insignificant Standardized Precipitation and Evaporation Index (SPEI) (a) and temperature anomaly (Tanom) (b) coefficients as a function of the standard deviation of the SPEI and temperature anomaly time series, respectively.

Based on the test for each of the phytogeographical regions separately (Fig. 6), the magnitude and significance level of the difference in stability of semi-natural and agricultural grasslands differed between phytogeographical regions. Coastal dunes and grasslands associated with river landscapes showed the largest difference in resistance between semi-natural and agricultural grasslands, while for sandy soils, fens and sea clay the difference became insignificant. For the resilience, the difference between semi-natural and agricultural grasslands was the largest for coastal dunes, and fens, while grasslands associated with sea clay, sandy areas and river areas showed an insignificant difference.

Discussion

In this study, we compared the biomass production stability, that is resistance and resilience, of semi-natural and agricultural grasslands of the Netherlands using MODIS NDVI and climate time series. The most important overall result of our study is that semi-natural grasslands show a higher resistance to drought and temperature anomalies when compared to agricultural grasslands. These results strongly suggest that plant species diversity has a role in mitigating vegetation response to disturbances (Wesche *et al.* 2012; Ceulemans *et al.* 2013), which confirms the results of earlier small-scale experimental studies (Tilman & Downing 1994; Tilman, Wedin & Knops 1996).

Several processes may explain the mediating role of grassland plant species diversity with respect to biomass production stability. First, a larger number of plant species in a grassland increases the probability that one or more species are present that are more resistant to a disturbance such as drought. This process is based on the *sampling effect* theory (Tilman, Lehman & Thomson 1997; Loreau & Hector 2001). As a multitude of different species with a high functional trait diversity likely has a complementary effect during different types of distur-

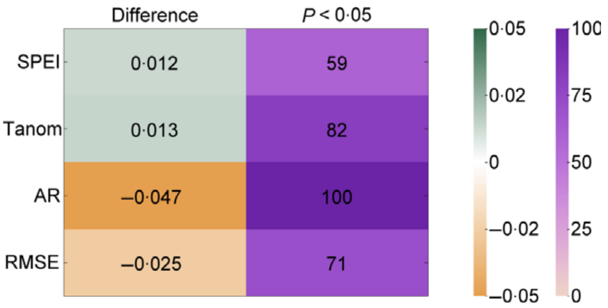


Fig. 4. The mean difference between the stability metrics [i.e. the resistance against drought (α coefficient of SPEI(t)), the resistance against temperature anomalies (β coefficient of Tanom(t)) and the resilience (ϕ coefficient of NDVI($t-1$) or AR)] and the root-mean-squared error (RMSE) of intensively managed agricultural and semi-natural grasslands and the number of repetitions having an associated $P < 0{\cdot}05$ for the grassland type effect of the mixed model. Negative differences indicate that the intensively managed agricultural system is more stable than the semi-natural, while the opposite is true for positive values. NDVI, Normalized Difference Vegetation Index.

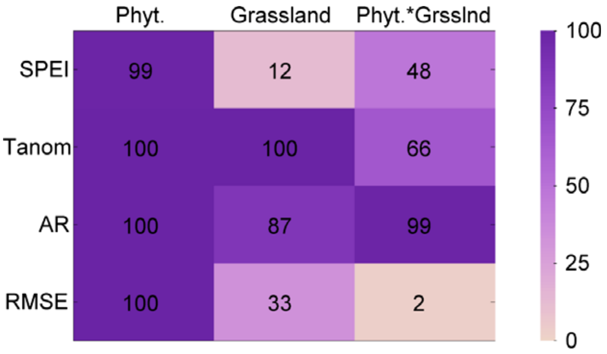
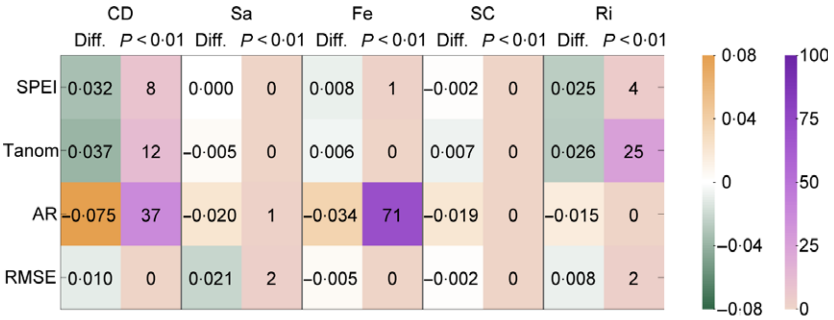


Fig. 5. The number of repetitions having a $P < 0{\cdot}05$ for each of the coefficients [i.e. the resistance against drought (α coefficient of SPEI(t)), the resistance against temperature anomalies (β coefficient of Tanom(t)) and the resilience (ϕ coefficient of NDVI($t-1$) or AR)] and the root-mean-squared error (RMSE) for the interaction model (2). NDVI, Normalized Difference Vegetation Index.



	CD		Sa		Fe		SC		Ri	
	Diff.	$P < 0{\cdot}01$	Diff.	$P < 0{\cdot}01$	Diff.	$P < 0{\cdot}01$	Diff.	$P < 0{\cdot}01$	Diff.	$P < 0{\cdot}01$
SPEI	0·032	8	0·000	0	0·008	1	−0·002	0	0·025	4
Tanom	0·037	12	−0·005	0	0·006	0	0·007	0	0·026	25
AR	−0·075	37	−0·020	1	−0·034	71	−0·019	0	−0·015	0
RMSE	0·010	0	0·021	2	−0·005	0	−0·002	0	0·008	2

Fig. 6. The mean difference (Diff.) for the stability metrics [i.e. the resistance against drought (α coefficient of SPEI(t)), the resistance against temperature anomalies (β coefficient of Tanom(t)) and the resilience (ϕ coefficient of NDVI($t-1$) or AR)] and the root-mean-squared error (RMSE) of intensively managed agricultural and semi-natural grasslands and the number of repetitions having an associated $P < 0{\cdot}01$ for the comparisons per phytogeographical region (CD stands for coastal dunes, Hi for hills, Sa for sandy areas, Fe for fens, SW for salt water tide, SC for sea clay and Ri for rivers). Negative differences indicate that the intensively managed agricultural system is more stable than the semi-natural, while the opposite is true for positive values. Results with <10 pixels are not represented (grey colour) and phytogeographical regions without results are omitted from the table. NDVI, Normalized Difference Vegetation Index.

bances, for example droughts, temperature anomalies, fire or insect invasions, more plant species-diverse grassland systems will have a higher chance to stabilize biomass production over the long term (Tilman & Downing 1994). Secondly, *niche complementarity* might result in an improved community performance compared to the expected performance from individual species (Loreau & Hector 2001). More specifically, niche complementarity can result from niche differentiation and facilitation, that is species differ spatially and temporally in resource and habitat use and requirements, or they benefit from inter-specific interactions (Tilman *et al.* 2001). For example, De Boeck *et al.* (2006) found that below- and above-ground niche complementarity might increase the water use efficiency of species-diverse grasslands compared to monocultures.

Management may further interact with the effects of species diversity on grassland stability. Although both semi-natural and agricultural grasslands are mown or grazed, the higher mowing and grazing intensity of agricultural grasslands might contribute to lower resistance as more frequent mowing has shown to decrease grassland resistance to drought (Vogel *et al.* 2012). This phenomenon might be related to the addition of a stress factor and growth phenology: grasslands at the regrowth stage are more sensitive to drought due to their lower canopy height and larger soil surface evaporation (Hu *et al.* 2009; Vogel *et al.* 2012). Through a highly intensive mowing regime, the probability to face drought stress during the regrowth stage increases, causing a decreased resistance (Vogel *et al.* 2012).

In contrast with vegetation resistance, the test on the resilience metric indicated that semi-natural grasslands were less resilient than agricultural grasslands, that is semi-natural grasslands tend to return slower to their average state than agricultural grasslands. In agricultural systems, farmers might irrigate the stressed system or adapt ground water levels, potentially enhancing the grassland recovery. Furthermore, as persistent management effects may especially affect the resilience term, the link between resilience and ecological processes should be interpreted with care.

Furthermore, it could be expected that physical geography plays a role in the difference between the stability of semi-natural and agricultural grasslands. Our results indeed indicated that for *c.* 48–99% of the resamplings the interaction factor between the grassland type (semi-natural vs. agricultural) and hytogeographical region was significant. The test per phytogeographical region further revealed that – despite a relatively low percentage of significant tests – coastal dunes and riverine grasslands followed the observed trend, whereas the percentage of significant tests for the resistance terms was the lowest for fens, sea clay and sandy soils. Grasslands situated in fens and sea clay areas typically have a high ground water availability, which may cause only a minor discrepancy between agricultural and semi-natural grasslands during climatic fluctuations. On the contrary, for grasslands located in sandy areas, the water availability is typically much lower due to the low water holding capacity of the soil and their relatively high elevation in the landscape. As such, the conditions during climate anomalies might become so severe that the mediating role of plant diversity may become of minor importance.

Finally, the positioning of the grasslands within the landscape may influence the biomass production stability. Historically, grasslands utilized for agricultural use are situated in landscape positions that are better suited or their environmental conditions were optimized, for example situated on more fertile soils with a better water balance and are as such expected to have a higher productivity. Yet, although these agricultural grasslands are better positioned, the obtained results show that these grasslands tend to be less resistant to droughts and temperature anomalies compared to the semi-natural grasslands. In that sense, the results we obtain are even stronger. Further research may more explicitly account for the landscape position [e.g. quantified through the height above the nearest drainage or HAND (as described in Schietti *et al.* 2014)].

To conclude, climate events or climate extremes such as droughts are expected to become more frequent in the near future and can have severe impact on the environment. The costs of adaptive measures (e.g. irrigation and water-table manipulation) to maintain productivity will consequently rise (Logar & van den Bergh 2013). In order to take mitigating measures, research concerning the functioning of ecosystems and their ability to cope with environmental stressors is crucial. This study suggests that semi-natural grasslands show a higher resistance to drought and temperature anomalies compared to agricultural grasslands. Although the average biomass productivity of agricultural grasslands is higher than that of semi-natural grasslands (i.e. an average NDVI of 0·75 and 0·68 during the growing season for the agricultural and semi-natural grasslands, respectively), these results may underline the need to reassess the ways agricultural practices are performed. More specifically, an altered mowing frequency and the increase of species diversity may contribute to buffer biomass production against climate anomalies.

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Data accessibility

NDVI data: https://lpdaac.usgs.gov/dataset_discovery/modis/modis_products_table/mcd43a4 (Land Processes Distributed Active Archive Center (LP DAAC) 2014).

Climate data: https://data.knmi.nl/portal/KNMI-DataCentre.html#location=nl&tab-detail=quality (KNMI 2014).

Corine Land Cover data: http://www.eea.europa.eu/data-and-maps/data/corine-land-cover-3 (EEA 2014a).

Natura 2000 Network data: http://ec.europa.eu/environment/nature/natura2000/index_en.htm (European Commission 2014).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Data S1. Supporting information.

Fig. S1. Illustration of standardised NDVI anomaly extraction from NDVI time series.

Fig. S2. The histogram of the mean and *P*-value for each of the stability metrics of intensively managed agricultural and semi-natural grasslands.

Fig. S3. The histogram of the *P*-value for each of the coefficients of the interaction model.

Fig. S4. General flow chart of the methodology.