

1 **Plant species diversity mediates ecosystem stability of natural dune grasslands in**  
2 **response to drought**

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17 **Abstract**

18 How plant species diversity can mediate the temporal stability of ecosystem functioning  
19 during periods of environmental stress is still a pressing question in ecology, certainly in the  
20 context of predicted increasing frequencies and intensities of climate extremes such as  
21 drought. The vast majority of empirical research in this context is based on relatively small  
22 scaled experiments, where plant species composition is manipulated and ecosystem functions,  
23 such as biomass production, are monitored through time. Results of these studies have  
24 generally shown that ecosystem functioning is more stable in more species-diverse  
25 communities. Yet, there is very little evidence so far that these relations also hold in naturally  
26 assembled plant communities. In this study, we combined historical vegetation and climate  
27 data with time series of remote sensed indicators of aboveground biomass production  
28 (MODIS-NDVI), to quantify how plant species diversity and plant functional diversity  
29 correlate with the temporal stability of biomass production in naturally assembled Dutch dune  
30 grasslands under influence of fluctuating drought. We found that the negative NDVI response  
31 to drought of grasslands with a higher plant species richness and diversity was significantly  
32 lower than the response of less species rich and species diverse grasslands, indicating a  
33 stabilizing role of plant species richness and diversity on biomass production through time.  
34 We found no relation between plant functional diversity and NDVI-response to drought. This  
35 is the first study to generalize experimentally established relations between species diversity  
36 and stability of ecosystem functioning to naturally assembled grasslands across a large spatial  
37 and temporal scale.

38

39 Keywords: Diversity, Stability, Ecosystem functioning, NDVI, remote sensing, Dune  
40 grasslands, drought

41

**42 Introduction**

43 How and to what extent plant species diversity mediates the stability of ecosystem properties  
44 such as biomass production and nutrient cycling, has become one of the most challenging  
45 questions in ecology (Hector and Bagchi, 2007; Naeem et al., 2009; Aerts and Honnay, 2011).  
46 Although work on the relation between ecosystem stability and species diversity goes back to  
47 Elton (1958) and May (1971, 2001), the acknowledgement that the current biodiversity crisis  
48 (Hooper et al., 2005; Butchart et al., 2010) may also have consequences for ecosystem  
49 functioning, and may affect the services that ecosystems provide to humans (Cardinale et al.,  
50 2012), has renewed interest in how plant species richness may buffer ecosystem responses  
51 against disturbances (Roscher et al., 2011; Vogel et al., 2012). This issue has become  
52 especially relevant in an era where external disturbances such as climatic extremes are  
53 expected to become increasingly frequent (Lloret et al., 2012).

54 Central to understanding the mediating effect of plant species richness on temporal ecosystem  
55 stability is the phenomenon of compensatory dynamics (Yachi and Loreau, 1999; Loreau and  
56 de Mazancourt, 2013). Compensatory dynamics occur when a negative change in the level of  
57 functioning of one species is associated with a positive change in the functioning of another  
58 species, driving the stabilization of ecosystem properties, such as biomass production. Three  
59 specific mechanisms have been proposed to explain how biodiversity may stabilise ecosystem  
60 properties through time (Loreau and Mazancourt 2013). The first mechanism implies that  
61 interspecific differences in coping with external disturbances leads to asynchrony in species  
62 responses to environmental change, while the second mechanism addresses the differences in  
63 the speed at which species respond to a changing environment. Both can be regarded as  
64 temporal complementarity. The third mechanism involves a decrease in the relative  
65 importance of interspecific competition, resulting from the complementarity in resource usage  
66 between species. This may cause a relative increase in the biomass production of the species

67 present (overyielding). A decrease in one species' functioning thus may result in the increased  
68 (or compensatory) overyielding of a complementary species, buffering the change in output of  
69 the ecosystem during environmental change (Loreau and Mazancourt, 2013). In this context,  
70 plant functional diversity, rather than taxonomic diversity, may be the key factor driving  
71 ecosystem stabilization. Functional traits, *i.e.* plant properties that impact growth,  
72 reproduction and survival, can be expected to mediate the ability of individuals, populations  
73 and even of entire ecosystems to cope with environmental disturbances.

74 The vast majority of empirical research in the species diversity *versus* ecosystem stability  
75 context so far has been based on relatively small scaled *in situ* and *ex situ* experiments, where  
76 plant species composition is manipulated and ecosystem functions are monitored over time  
77 (Hector et al., 2010; Aerts and Honnay, 2011). Results of these experimental studies have  
78 generally shown that the ecosystem functioning is more stable in more diverse communities  
79 (Cardinale *et al.* 2012). Yet, there is very little evidence that these relations also hold in  
80 naturally assembled plant communities, as it remains a challenge to upscale this experimental  
81 research to larger geographical and temporal scales (Duffy, 2008). Most observational studies  
82 have focussed on forest communities, as tree biomass increase can be readily monitored  
83 through time, and generally, positive relations have been reported between tree diversity and  
84 stability of wood production (DeClerck et al., 2006; Aerts and Honnay, 2011; Paquette and  
85 Messier, 2011). Long term observational studies on natural grassland ecosystems, such as the  
86 one of Bai et al. (2004), often lack the temporal resolution to measure the relation between  
87 ecosystem functioning and environmental change, thus missing the short term effects of the  
88 changing environmental drivers. It remains therefore a huge challenge to make accurate  
89 observations of ecosystem properties across both larger temporal and geographical scales to  
90 test the generality of the experimentally demonstrated diversity-stability relation in naturally  
91 assembled plant communities (Grman et al., 2010; Loreau, 2010). The difficulty lies

92 predominately in obtaining and combining the required data regarding local plant species  
93 composition, plant functional traits, and time series of ecosystem properties.

94 Because remote sensing techniques allow the production of ecologically relevant time series  
95 of measures indicative for ecosystem functioning, they offer promising avenues for upscaling  
96 the current levels of observation in species diversity *versus* ecosystem stability research.  
97 Remote sensing through satellites enables systematic monitoring of the earth's surface cover  
98 with temporal intervals using reflectance measurements. Numerous remote sensing studies  
99 have provided insight into global spatio-temporal patterns of ecosystem properties, including  
100 aboveground biomass production through greenness measurements (Zhang et al., 2003;  
101 Formica et al., 2004; Fraser et al., 2011). The most widely used proxy for ecosystem  
102 productivity is the Normalized Difference Vegetation Index (NDVI) (Rouse et al., 1973; Beck  
103 et al., 2011). NDVI gives an indication of how much light is used for photosynthetic activity,  
104 and it approximates ecosystem properties such as photosynthetic active biomass and biomass  
105 production (Lloret et al., 2007).

106 The general aim of this study was to quantify how plant species diversity and plant functional  
107 diversity correlate with the stability of aboveground biomass production in naturally  
108 assembled dune grassland ecosystems under influence of fluctuating drought. We exploit the  
109 unique Dutch National Vegetation Database consisting of over 640,000 vegetation plots  
110 (relevés) (Schaminée et al., 2012), and combine available historical vegetation data and  
111 climate data with remote sensed indicators of stability in biomass production. Therefore we  
112 used Moderate Resolution Imaging Spectroradiometer (MODIS) NDVI images at a 250m  
113 resolution. To examine ecosystem responses, two widely used measures of ecosystem stability  
114 are used: the variance, *i.e.* the long term variability of ecosystem properties; and resistance,  
115 *i.e.* the degree of immediate response on a changing environmental factor (Van Ruijven and  
116 Berendse, 2010; De Keersmaecker et al., 2013).

117

118 More specific, the aims of this study were to:

119 1) Combine long term climate data and MODIS satellite images to quantify effects of  
120 drought in calcareous dune grasslands in the Netherlands and to correlate precipitation  
121 changes with variance in biomass production.

122 2) Quantify how (i) plant species richness and diversity, and (ii) plant functional diversity  
123 of natural dune grassland ecosystems mediate biomass production in response to  
124 drought events.

125

126 **Material and Methods**127 *Selection of study sites*

128 The study focuses on calcareous dune grassland ecosystems in the Netherlands. The Dutch  
129 calcareous dune region stretches along the western coast from the Belgian border in the South  
130 to the village of Bergen in the North. Phytosociological syntaxonomy classifies these  
131 vegetation types predominately into the class of *Koelerio-Corynephoretea* (Schaminée et al.,  
132 1996). All studied grasslands are located in an area under the European ‘Natura 2000’  
133 legislation. Management consists of seasonal grazing with cattle (Fig. 1a).

134 *Selection of remote sensing data*

135 Time series of the NDVI were used to monitor ecosystem properties through time. NDVI  
136 quantifies the amount of greenness of vegetation and can therefore be used to give an  
137 approximation of aboveground biomass production (Verbesselt et al., 2010; Zhang et al.,  
138 2010; De Keersmaecker et al., 2013). Moderate Resolution Imaging Spectroradiometer  
139 (MODIS) NDVI images from the MOD13Q1 and MYD13Q1 product, collected by both the  
140 TERRA and AQUA sensor, were obtained from the NASA Land Processes Distributed Active  
141 Archive Centre (LP DAAC: <http://lpdaac.usgs.gov>) (Gu et al., 2013). MODIS NDVI data has  
142 a resolution of 250 × 250 meter pixels. Time series were made from the data covering the  
143 time window between the years 2001 and 2012, with an eight daily temporal resolution. A  
144 total of 1169 MODIS pixels covered the studied area (Fig. 2).

145 Low quality MODIS data were removed based on their associated quality flag, *i.e.* flags  
146 indicating the presence of adjacent water bodies, clouds, shadows or aerosols. In order to  
147 remove residual noise, the data were smoothed using the Savitzky Golay filter of the  
148 TIMESAT software with a window size of 7 (Jonsson and Eklundh, 2002; Jönsson and  
149 Eklundh, 2004; Moreno et al., 2014) (Fig. 1c).

150 *Selection of vegetation data*

151 Vegetation data from the selected areas were acquired from the Dutch National Vegetation  
152 database (NVD) (Schaminée et al., 2012). An initial dataset of 12,000 records of calcareous  
153 dune grasslands was available. All vegetation recordings used to calculate species and  
154 functional diversity were made between 1995 and 2000, prior to the start of the NDVI time  
155 series. Records syntaxonically classified as grasslands were selected, including classes 12  
156 (*Plantaginetea majoris* - wet meadows) to 20 (*Calluno-Ulicetea* – arid heath- and grasslands)  
157 (Schaminée et al., 1996) (Fig. 1b). Phytosociological classification was performed using  
158 ASSOCIA (Tongeren et al., 2008), included in the Turboveg software package (Hennekens  
159 and Schaminée, 2001). Species cover abundance in all vegetation records was quantified  
160 using the adapted Braun-Blanquet scale in 2×2 meter plots. Subsequently, cover scales were  
161 transformed to percentages (Schaminée et al., 2011).

162 *Selection of study pixels*

163 The study pixels were selected, through overlaying the 250x250m MODIS pixels with the  
164 vegetation records. Only MODIS pixels including at least three vegetation records, evenly  
165 distributed across the pixel area, were selected (Fig. 1c). To guarantee homogeneity of the  
166 pixels' vegetation, it was verified whether all vegetation records were classified within the  
167 same phytosociological class (Fig. 1d). To minimize heterogeneity in the selection, only  
168 pixels were selected situated within the habitat type of grey dune grasslands. Although all  
169 pixels fall in areas with comparable abiotic conditions and similar nature management,  
170 including controlled ground water tables, some variation in vegetation types is present. An  
171 overview of the occurring vegetation types (phytosociological classes) can be found in  
172 Supplement I.



173 To prevent interference from large water bodies and sandy surfaces (including sea and beach),  
 174 pixels adjacent to these surfaces were omitted. Additionally, the NDVI time series of all  
 175 pixels were manually checked for interference factors and noise. Finally, the structural  
 176 homogeneity of the vegetation in the selected pixels was verified based on *Google earth*  
 177 and/or by visiting the pixels in the field (Fig. 1f). This series of selection criteria resulted in a  
 178 final selection of 48 250×250 m MODIS pixels, containing 707 vegetation records.

### 179 *Species diversity indices*

180 Based on the vegetation data, species diversity indices were calculated for each of the 48  
 181 pixels, using the average value of the combined vegetation records present in a particular  
 182 pixel. Indices were calculated using the JUICE software package (Tichý, 2002). We  
 183 calculated

- 184 - Species number ( $Nr$ )
- 185 - Shannon-Wiener Index ( $H'$ ) following Equation 1.

$$186 \quad H' = \sum_{i=1}^S P_i \ln P_i \quad (\text{Eq. 1})$$

187 Where  $S$  is the total number of species and  $P_i$  is the proportion of the individual species  
 188 relative to the total cover.

- 189 - Evenness ( $E$ ) following Equation 2.

190

$$191 \quad E_H = \frac{H'}{H'_{max}} = H' / \ln S \quad (\text{Eq. 2})$$

192 For each study pixel, also functional diversity was calculated as Rao's quadratic entropy  
 193 ( $FD_Q$ ), according to Equation 3, where  $d_{ij}$  is the difference between species  $i$  and  $j$  as  
 194 calculated according to equation 4 where  $t$  is the number of considered traits and  $X$  is the trait

195 value of a specific trait  $k$  for species  $i$  or  $j$  (Botta-Dukát, 2005). Functional trait data of the  
 196 species were retrieved from the trait databases LEDA and the *Ecological Flora of the British*  
 197 *Isles* (Fitter and Peat, 1994; Kleyer et al., 2008). The following plant traits were selected:  
 198 specific leaf area (SLA), leaf size, leaf dry matter content, leaf mass, root depth and canopy  
 199 height. These traits can be expected to mediate biomass production in individual plant species  
 200 and can be related to resource acquisition (Schumacher and Roscher, 2009). Additionally the  
 201 flowering onset time and length of the flowering period were included in the analysis to  
 202 reflect temporal variation in phenology of the vegetation. Selection of traits was constrained  
 203 by the availability of trait data for the complete plant species data set. Therefore  $FD_Q$  was  
 204 based on species occurring in at least 75% of the pixels, to calculate functional diversity. All  
 205 trait values were quantitative variables and were standardized to values between 0 and 1.

206

$$207 \quad FD_Q = \sum_{i=1}^{S-1} \sum_{j=i+1}^S d_{ij} P_i P_j \quad (\text{Eq. 3})$$

$$208 \quad d_{ij} = \frac{1}{t} \sum_{k=1}^t (X_{ik} - X_{jk}) \quad (\text{Eq. 4})$$

209 As the species and functional diversity measures were based on vegetation recordings that  
 210 were made before the NDVI time series, we implicitly assumed that species and functional  
 211 diversity did not significantly change within the 2001-2011 time window. This assumption  
 212 was tested by using long term permanent plot data. Five dune grassland permanent plots were  
 213 yearly monitored during 24 years. Both species richness (Nr) and Shannon-Wiener index (H)  
 214 did not change during this time window (Friedman test,  $P_{nr}=0.867$ ,  $P_H=0.899$ ).

#### 215 *Meteorological data*

216 Meteorological data were retrieved from the online databases of the Royal Meteorological  
 217 Society of the Netherlands (KNMI) (2014). Data were acquired from the Vlissingen  
 218 monitoring station for the time window 2001-2011. This particular monitoring station was

219 chosen for its proximity to the observed dune areas. Data regarding temperature, precipitation  
220 and potential evaporation were used for calculating the Standardized Precipitation and  
221 Evapotranspiration Index (SPEI) (Vicente-Serrano et al. 2010). The SPEI reflects drought  
222 events and the effect on plant life, considering not only precipitation but also the evaporation  
223 and transpiration of water from the soil and plant material. A negative SPEI value is  
224 associated with the occurrence of drought. Monthly values of SPEI were calculated as  
225 measure of drought (Drought indices:  $C_{SPEI}$ ) taking the previous two months into account.  
226 Only SPEI-values during the growth season (March-October) were used between 2001 and  
227 2011 (n=80). Calculations were performed with the R-package *SPEI*.

#### 228 *Ecosystem drought response: NDVI anomaly*

229 Temporal variation of an NDVI time series contains (I) a seasonal component (due to  
230 phenology), (II) an anomaly due to external environmental factors, (III) noise through  
231 atmospheric influences or sensor noise (Lhermitte et al., 2011) and (IV) trends (e.g. due to  
232 long term vegetation changes or sensor degradation (Fensholt and Proud, 2012; Wang et al.,  
233 2012). These trends can be considered to represent long term changes in the equilibrium state  
234 of the grassland, instead of being short term anomalies resulting from climate disturbances.  
235 Since it was our aim to quantify short term responses of biomass production to precipitation  
236 variability, each NDVI time series was detrended in case of a significant temporal linear  
237 trend. The NDVI-anomaly ( $A_{NDVI}$ ) of each pixel was used as an indicator for ecosystem  
238 drought response. NDVI values were available in eight day averages.  $A_{NDVI}$  was calculated by  
239 removing the seasonal component within the NDVI variation. This was done by subtracting  
240 the mean eight daily NDVI over all years, from the original NDVI time series. A monthly  
241 NDVI-anomaly was calculated, to match the temporal resolution of the meteorological data.  
242 A decrease in NDVI results in a negative NDVI anomaly, thus a decrease of biomass  
243 production.

244 *Statistical analyses*

245 Analyses were performed on all selected pixels (n=48). We calculated response coefficients  
 246 ( $P_{response}$ ) for each pixel ( $px$ ) as the slopes of the regression lines between  $A_{NDVI}$  and  $C_{SPEI}$   
 247 using Model 1.

$$248 \quad P_{response} = (A_{NDVI} \sim C_{SPEI})_{px} \quad (\text{Mod. 1})$$

249

250 The response coefficients were subsequently correlated with the diversity indices (Species  
 251 richness (Nr), Shannon-Wiener index ( $H'$ ), Evenness index ( $E_H$ ) and the Functional diversity  
 252 ( $FD_Q$ )). A linear regression was then performed to analyse the correlation between the  
 253 diversity indices and the response coefficients to drought of all pixels (Model 2). In this  
 254 model we also included the phytosociological class ( $V_{class}$ , n=5) of the grassland vegetation  
 255 type as a fixed effect.

$$256 \quad P_{response} \sim I_{Nr/H'/E_H/FD_Q} * V_{class} \quad (\text{Mod. 2})$$

257 The pixels were tested for spatial autocorrelation in  $A_{NDVI}$  by computing Moran's I for the  
 258 residuals of the regression model (Mod. 1). Analyses were performed in *R* including R-  
 259 packages *FD* (Laliberté and Shipley, 2010), *ape* (Paradis et al., 2008), *lme4* (Bates, 2010) and  
 260 *Vegan* (Oksanen et al., 2007).

261

262 **Results**

263 No spatial autocorrelation could be detected between the pixels' NDVI anomaly (MORANS's  
264 I:  $I=6.29 \times 10^{-5}$ ,  $P=0.377$ ). Therefore, all pixels were further considered to be independent  
265 observations.. Ten years of  $C_{SPEI}$  and NDVI anomaly data show high variance (Fig. 3), with a  
266 strong correlation between both variables ( $\beta=0.55$ ,  $P<0.001$ ).  $C_{SPEI}$  explained 29% of the  
267 variance ( $P<0.001$ ,  $r^2=0.291$ ) and significantly predicted the average NDVI-anomaly ( $\beta=0.55$ ,  
268  $P<0.001$ , Fig. 3, Table. 1). This positive correlation between both variables indicates a  
269 decrease in the NDVI-anomaly with decreasing  $C_{SPEI}$  values.

270 The response coefficients ( $P_{response}$ ) of the pixels (*i.e.* the slopes of the regression line between  
271  $A_{NDVI}$  and  $C_{SPEI}$  per pixel) were negatively correlated with species richness ( $P=0.007$ ,  
272  $r^2=0.11$ ) and Shannon-Wiener diversity ( $P=0.041$ ,  $r^2=0.06$ ). Both Evenness ( $P=0.070$ ,  
273  $r^2=0.08$ ) and functional diversity ( $P=0.246$ ) showed no significant correlation with the  
274 response coefficient (Table 2, Fig. 4). There was no significant effect of vegetation type, or of  
275 the interaction between vegetation type and the diversity indices, on the response coefficients.

276

277 **Discussion**

278 The general aim of this study was to upscale the experimentally established positive relations  
279 between plant species diversity and the stability of aboveground biomass production in  
280 natural systems in both time and space, using remote sensing techniques. A stable primary  
281 production is regarded as one of the major ecosystem functions (Loreau, 2010; Isbell et al.,  
282 2011). As far as we know this is the first study that reports a positive relation between species  
283 diversity and biomass production stability in naturally assembled grasslands at a regional  
284 scale.

285 Overall, we observed a close correlation between the NDVI-anomaly patterns and the patterns  
286 of the Standardized Precipitation and Evapotranspiration Index (SPEI)-values derived from  
287 the KNMI meteorological database. Although there was a high variation in the response of  
288 each pixel, extreme drought events, reflected by SPEI lows occurring in 2003, 2006, 2009,  
289 2010 and 2011 (Fig.3), also resulted in extremely negative NDVI anomalies. This is  
290 supported by the observed significantly positive correlation between the  $C_{SPEI}$ -values and the  
291 NDVI-anomaly. These results clearly indicate that variation in water availability in these  
292 natural dune grassland ecosystems strongly affect above ground biomass production, as  
293 reflected by the NDVI.

294 Species number, as well as species-based diversity indices, showed a significant interaction  
295 with the drought index in its relation with the NDVI-anomaly, and thus mediate the effect of  
296 drought on the NDVI response. The immediate effect of drought on the NDVI anomaly was  
297 stronger in grasslands with a higher species diversity, indicating an increased resistance  
298 against drought of species rich and diverse communities. Plant species richness was a better  
299 correlate of grassland ecosystem stability than species diversity, whereas there was no effect  
300 of evenness. This indicates that the presence or absence of species is of more importance than

301 their relative abundance. Although no causation can be inferred, our results are in agreement  
302 with the findings of many experimental studies, which have reported a stabilizing effect of  
303 diversity on a variety of ecosystem functions including biomass production in grassland  
304 ecosystems (Ives and Carpenter, 2007). In particular, Gross et al. (2014) demonstrated a  
305 stabilizing effect of plant species richness on biomass production at the community level in 16  
306 experimental grassland studies. Biomass production at the population level, on the other hand,  
307 became less stable during environmental disturbances due to asynchronous species responses.  
308 As species richness increases in experimental grasslands, also the degree of asynchrony  
309 increases, leading to a higher chance of compensatory dynamics, *i.e.* that declines of some  
310 species are compensated by increases of others (Hector et al., 2010; Loreau, 2010; Gross et  
311 al., 2014). The net effect is an increased temporal stability of biomass production at the  
312 community level. Additionally, also small scale environmental heterogeneity may contribute  
313 to increasing stability (Pasari et al., 2013). As dune grassland systems are typically highly  
314 variable in water and nutrient availability across small scales (Cain et al., 1999), also spatial  
315 heterogeneity, in addition to temporal heterogeneity, may have a role in stabilizing the  
316 ecosystems' output. Indeed, a larger local species pool increases the chance of exploiting the  
317 variety of available resources, resulting in spatial complementarity (Ozinga et al., 1997; de  
318 Mazancourt et al., 2013).

319 There was no significant effect of plant functional diversity on grassland ecosystem stability.  
320 Petchy and Gaston (2002), indicated that in an assemblage with a limited trait dimensionality,  
321 the number of traits considered may affect the observed relation between functional diversity,  
322 redundancy and stability. Therefore, we cannot exclude that the absence of a significant  
323 correlation is related to both the relatively limited number of quantitative traits that could be  
324 taken into account and the number of species for which trait values were available (Pakeman,  
325 2014). In addition, it must be noted that the functional data used, were collected for a wide

326 array of applications, mostly others than for this study. However, we believe that the current  
327 selection of traits is highly relevant in a context of drought response (Taugourdeau et al.,  
328 2014). However, the better correlation of species diversity indices as compared to functional  
329 diversity indices is in agreement with the idea that functional redundancy may be of more  
330 importance than functional diversity, and that redundancy may limit the influence of  
331 functional diversity on the stability of the measured ecosystem function (Pillar et al., 2013). A  
332 higher number of species with similar functional trait values, though a differential temporal  
333 response to disturbance, increases the probability of functional complementarity, resulting in  
334 functional compensation. As dune systems are prone to drought, all species naturally present  
335 can be expected to be functionally equipped to cope with this to a certain extent. If this results  
336 in a relatively strong convergence in functional traits related to water stress, then individual  
337 species have a limited contribution to functional diversity, although they do add to functional  
338 redundancy.

339 Our findings also support Kreyling et al. (2008), who found contrasting effects in different  
340 grassland communities, as well as the conclusions of Dalerum et al. (2012), who showed that  
341 an increased functional diversity of an assemblage of plant species does not necessarily lead  
342 to a higher stability. Although trait databases are already an important source to find such  
343 information, many data are lacking or has a high intra-species variability due to trait plasticity  
344 or due to different measurement circumstances (Cordlandwehr et al., 2013). Additional  
345 extensive measurements of traits in the field are necessary to fill the data gaps and strengthen  
346 the outcome of trait-based analyses. This includes collecting trait data on species with low  
347 abundance, which may also contribute to biomass stabilization (Walker et al., 1999). Also *in*  
348 *situ* measurements of trait values of individual species combined with *in situ* measurements of  
349 biomass production data may provide important data . This stresses the continuing importance



350 for the compilation and supplementation of large observational databases containing data on  
351 species and functional traits (Cadotte et al., 2009) .

352 Our assumption that species richness and diversity in the studied dune grasslands, remained  
353 stable during the observed time window was supported by the analysis of species diversity in  
354 permanent quadrants, which showed no significant changes in both species numbers and  
355 diversity over a period of 25 years. This was not unexpected, given the constant management  
356 regime of the grasslands. Using permanent plots along a water stress gradient, Isermann  
357 (2011) showed that plant species diversity was highest and most stable at intermediate levels  
358 of water stress, while at the same time these plots showed a high turn-over in species  
359 composition. This is consistent with our interpretation that a stabilizing effect of biodiversity  
360 mainly occurs through compensatory dynamics.

361 It is predicted that climate change will increase the frequency and intensity of ecosystem  
362 disturbances (Turner, 2010; Dawson et al., 2011). At the same time, habitat loss,  
363 fragmentation and other anthropogenic activities may decrease plant species diversity (Grimm  
364 et al., 2013). Although we cannot claim causation based on our analyses, the correlations  
365 found in this study strongly suggest that declines in species diversity also decrease the ability  
366 of ecosystems to maintain their functioning in an environment which becomes more prone to  
367 climate extremes (Cardinale et al., 2012). It is therefore of utmost importance to conserve  
368 plant diversity to guarantee the provisioning of ecosystem service.

369

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374

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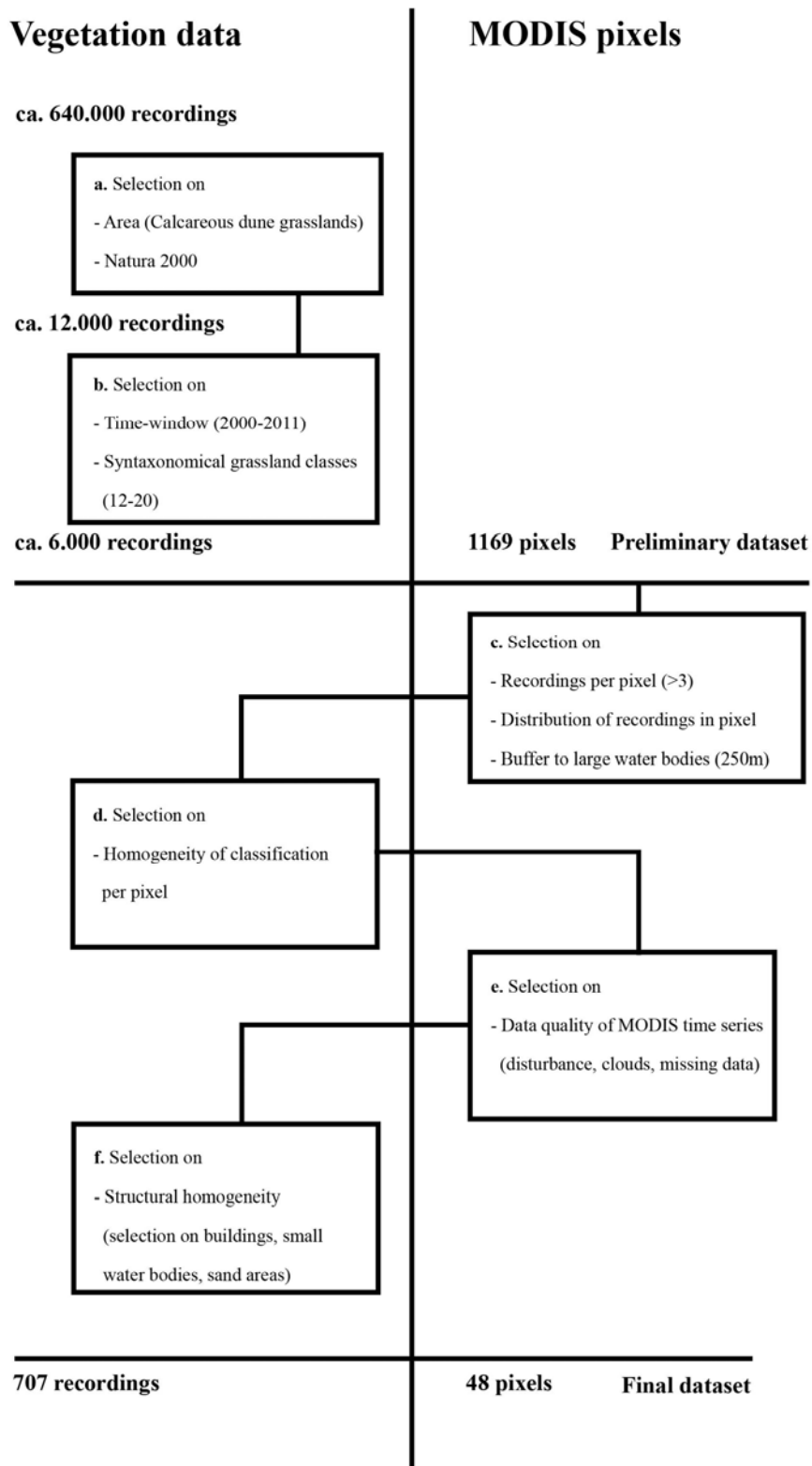
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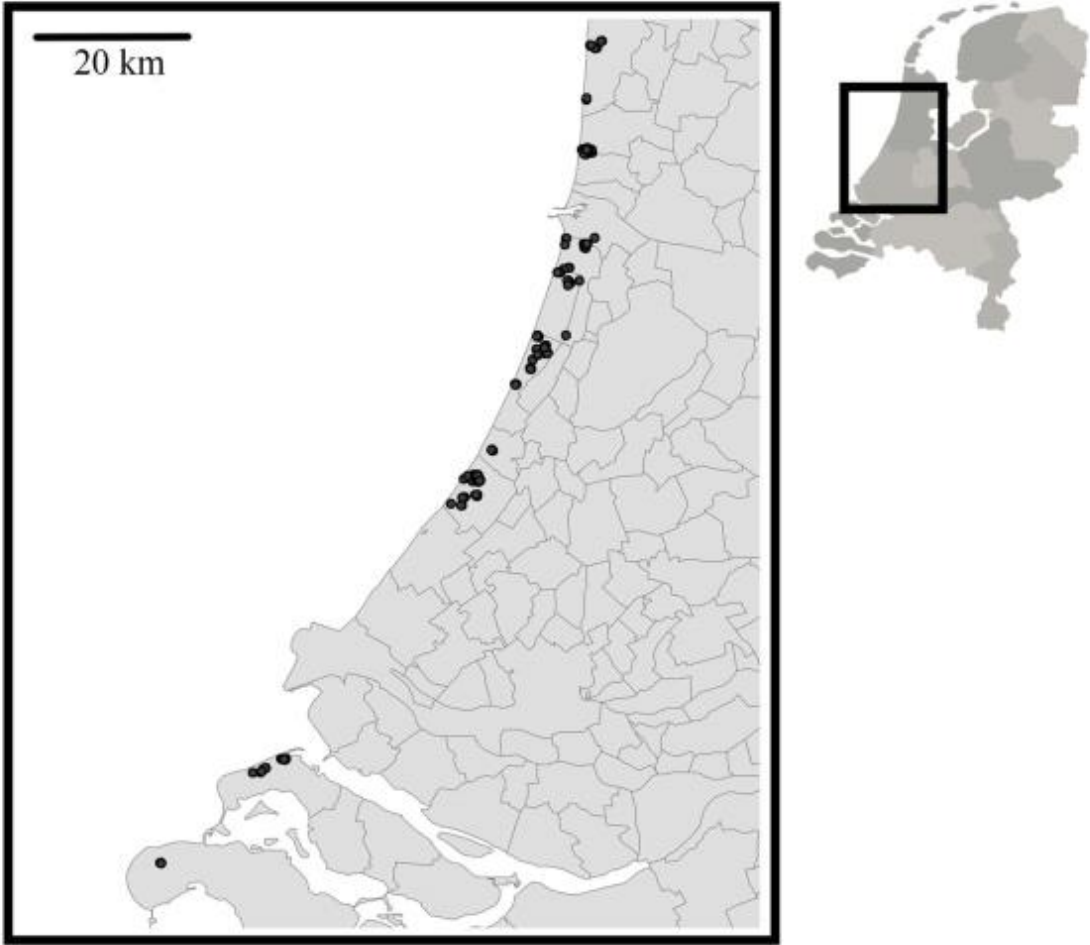
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545 **Figures**



546

547 **Figure 1**

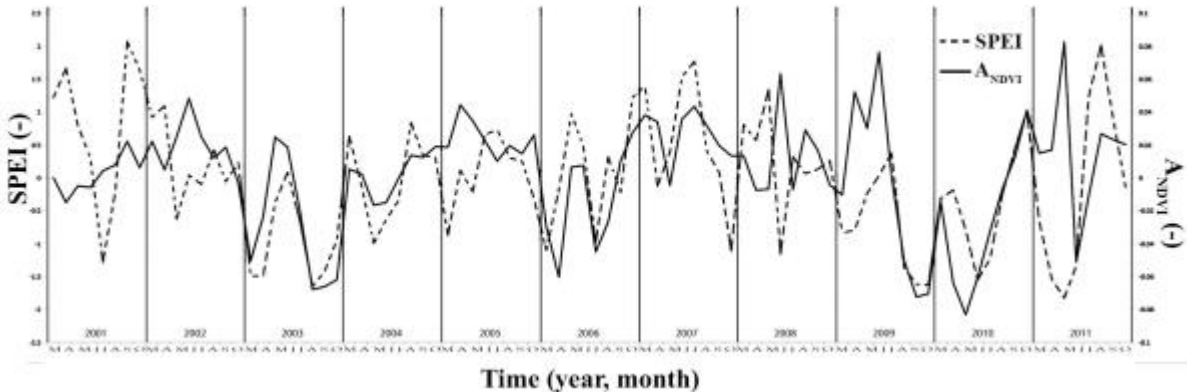


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549 Figure 2

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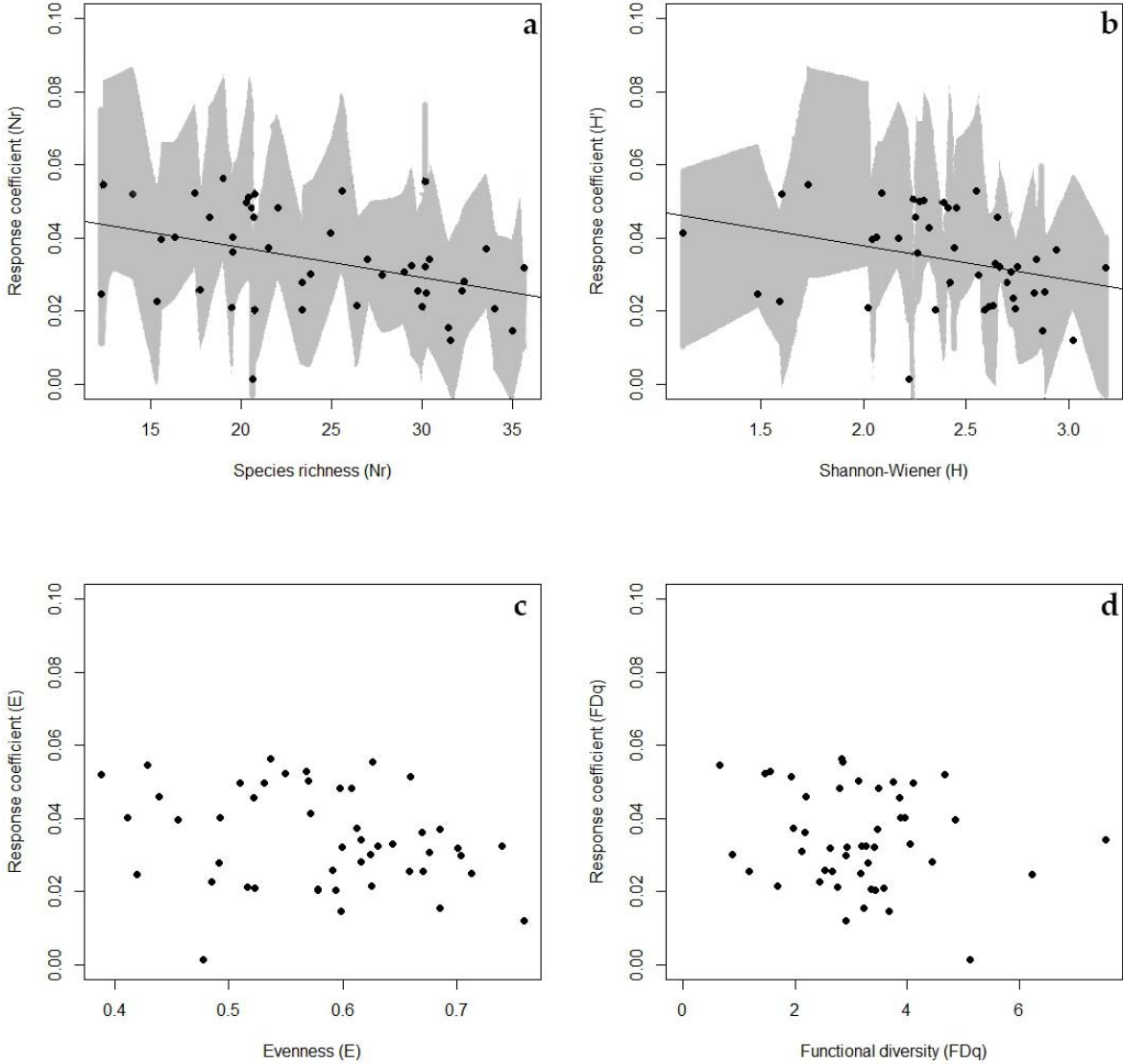
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552 Figure 3

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555

556 Figure 4

557 **Figure legends**

558 **Figure 1.** Flow chart indicating the steps in selecting MODIS pixels and vegetation relevés to  
559 study the effects of species diversity on dune grassland response to drought events.

560 **Figure 2.** Location of the final selection of MODIS pixels in the calcareous dune grasslands  
561 at the western coastal area of the Netherlands.

562 **Figure 3.** Time series of both the monthly Standardized Precipitation and Evapotranspiration  
563 Index ( $C_{SPEI}$ ; dotted line) and the NDVI-anomaly (average NDVI-anomaly ( $A_{NDVI}$ );  
564 continuous line). Only the months of the growth season (March-October) are shown.

565 **Figure 4.** Linear regression between diversity indices (a: Species richness ( $N_r$ ), b: Shannon-  
566 Wiener ( $H'$ ); c: Evenness ( $E$ ); d: Functional diversity ( $FD_Q$ )) and the respective response  
567 coefficients. The 2.5% and 97.5% confidence intervals are given in the shaded area.  
568 Significances are indicated in Table 2.

569

570 **Tables and Table titles**

571 **Table 1: Direct effects of SPEI on the average NDVI anomaly through linear regression.**

<b>NDVI anomaly</b>	<b>Df</b>	<b>Sum Sq</b> ( $\times 10^{-3}$ )	<b>Mean Sq</b> ( $\times 10^{-3}$ )	<b>F value</b>	<b>P</b>	<b><math>\beta</math></b>
C <sub>SPEI</sub>	1	2.621	2.621	36.748	<0.01	0.55 <sup>a</sup>
Residuals	86	6.133	0.071			

<sup>a</sup> indicates P<0.001

572



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573 **Table 2:** Linear regression analysis of diversity indices and the response coefficients  
 574 including the interaction effect with the vegetation type (phytosociological class) as fixed  
 575 factor (N=48 pixels).

<b>lm(Response~Div*V<sub>class</sub>)</b>							
<b>Regression</b>	<b>df</b>	<b>Sum sq</b> <b>(×10<sup>-3</sup>)</b>	<b>Mean sq</b> <b>(×10<sup>-3</sup>)</b>	<b>F</b>	<b>P</b>	<b><i>β</i></b>	
Nr	1	1.244	1.243	7.911	0.007	-0.39	a
Type	1	0.043	0.043	0.270	0.606		
Nr*Type	1	0.064	0.064	0.403	0.528		
Residuals	42	6.700	0.159				
H	1	0.693	0.693	4.490	0.041	-0.32	a
Type	1	0.025	0.025	0.163	0.689		
H*Type	1	0.213	0.213	1.387	0.247		
Residuals	39	6.024	0.154				
E	1	0.579	0.579	3.461	0.070	-0.26	
Type	1	0.135	0.134	0.804	0.375		
E*Type	1	0.184	0.184	1.101	0.300		
Residuals	44	7.356	0.167				
FD	1	0.237	0.237	1.384	0.246	-0.17	
Type	1	0.072	0.072	0.420	0.521		
FD*Type	1	0.354	0.354	2.071	0.157		
Residuals	43	7.356	0.171				

<sup>a</sup> indicates P<0.05

576

577

578

579 **Table legends**

580 **Table 1:** Results from an analysis of variance, comparing two time series of  $C_{SPEI}$  (N=80)  
581 and the average NDVI on 48 pixels as given in Fig. 3, through linear regression.

582 **Table 2:** Linear regression analysis of diversity indices and the response coefficients over 10  
583 years (N=48) according to model 2.

584

585

586 **Appendix**587 **Table Supplement I**

588

# Pixels	V <sub>class</sub>	Dominant vegetation class	% of pixels
3	12	<i>Plantaginetea majoris</i> <sup>1</sup>	6.25
40	14	<i>Koelerio-Corynephoretea</i> <sup>2</sup>	83.33
1	17	<i>Trifolio-Geranietea sanguinei</i> <sup>3</sup>	2.08
3	19	<i>Nardetea</i> <sup>4</sup>	6.25
1	20	<i>Calluno – Ulicetea</i> <sup>5</sup>	2.08

589

590 <sup>1</sup>*Plantaginetea majoris*: a very common vegetation class in the Netherlands, consisting of common  
 591 plant species. This class is often associated with minor disturbance systems due to trampling by large  
 592 grazers.

593 <sup>2</sup>*Koelerio-Corynephoretea* is the dominating vegetation class in the observed dune systems. The  
 594 vegetation can be found on relatively nutrient poor to moderately nutrient rich sandy soils and is  
 595 dominated by grass species and small herbs.

596 <sup>3</sup>*Trifolio-Geranietea sanguinei* is vegetation class mostly found on moderately nutrient rich sandy  
 597 soils and is associated with calcareous conditions. Grass species are dominating this class.

598 <sup>4</sup>*Nardetea* is a grass dominated vegetation class on relatively poor soils and is often associated with  
 599 the presence of cattle.

600 <sup>5</sup>*Calluno – Ulicetea* is a vegetation class associated with dry, relatively nutrient poor sandy soils,  
 601 although some woody heat species may occur, the system is dominated by grass species (e.g. *Festuca*  
 602 and *Deschampsia*). This class is often found near open sandy surfaces and is associated with cattle or  
 603 livestock for grazing.

604 According to (Schaminée et al., 1996)

605