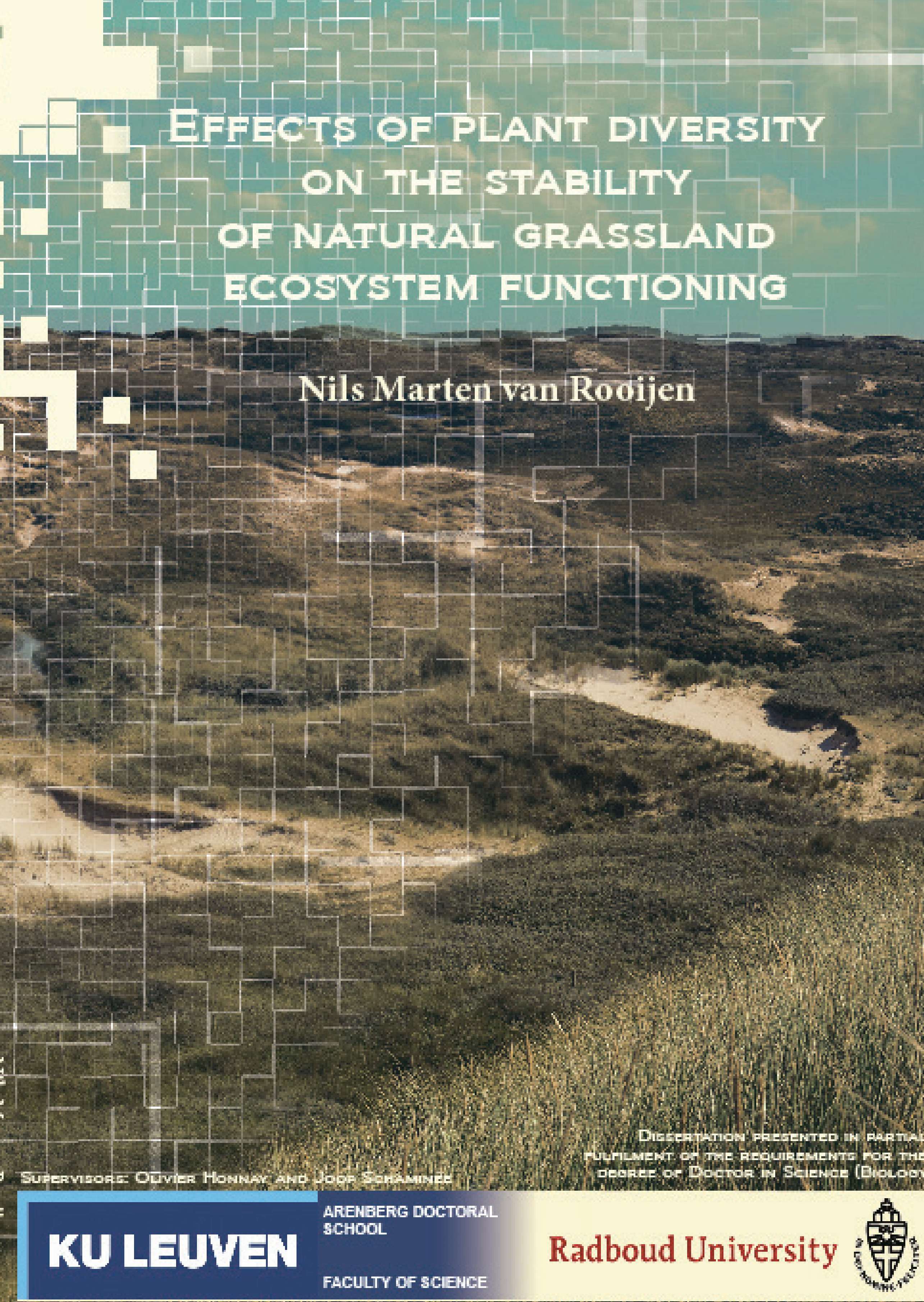

Effects of plant diversity on the stability of natural grassland ecosystem functioning

Nils Marten van Rooijen

Dissertation presented in partia
fulfilment of the requirements for th
degree of Doctor in Science (Biolog

Supervisors: Olivier Honnay and Joop Schaminee

KU LEUVEN

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“Facilius natura intellegiturquam enarratur.”
- Seneca

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Glossary

An overview of commonly used terms and abbreviations in this thesis:

Anomaly- The deviation of a measurement at a certain time and location compared to the long-term average.

ARx– Auto-regressive model with exogenous terms

Biomass production - Above ground biomass production or above-ground primary productivity. The growth of above-ground plant material.

Climate extreme– Extreme weather event (often prolonged) related to climate change, e.g. drought or heavy precipitation

CORINE– Coordination of information on the environment, database on land cover

Diversity– The variety in species or functional traits within a predefined area, in this thesis linked to plants. Expressed as:
- Plant species richness (Nr/R): number of vascular plant species
- Shannon – Wiener Index (H`) : number and relative abundance of vascular plant species
- Evenness (E): distribution of relative abundances
- Functional diversity (FD): number and relative abundance of a predefined selection of functional traits of vascular plant species

Dutch National Vegetation Database (DNDV) – Database containing historical vegetation data of the Netherlands

Ecosystem function – Any measurable output of one or more of the processes present within a predefined ecosystem

Ecosystem service – An ecosystem function of societal relevance

Ellenberg values – Species related ecological indicator values regarding biogeochemical parameters

fPAR– Fraction of Photosynthetic Active Radiation

KNMI– Koninklijk Nederlands Meteorologisch Instituut, Royal Dutch

Meteorological Society. Source for localized environmental, weather and climate data.

LANDSAT– Land satellite, satellite imaging program for earth surface observations

Leaf Area Index (LAI) – Amount of biomass per unit leaf area.

LEDA– European database on plant functional and life-history traits

MODIS– Moderate Resolution Imaging Spectroradiometer, imaging device aboard NASA's AQUA-and TERRA satellites.

NDVI– Normalized Difference Vegetation Index. Index used in remote sensing to assess the photosynthetically active biomass on a surface.

Productivity (Biomass production, primary productivity)– The production of above-ground biomass of plant species

Permanent plot – PQ or Permanent quadrat. A vegetation plot that is repeatedly recorded over time.

Pixel (Px)– Unit of observation in remote sensing approaches. A pixel, as in a photograph, contains the combined or averaged data within that pixel. In our MODIS dataset pixel-sizes cover 250×250 m ground surface.

PQ– Permanent quadrat, permanent plot.

R– Open-source programming language and environment for statistical computing and graphics

Relevé – Vegetation recording including plant species numbers and relative abundance (in relation to the surface of the plot). Often, the Braun-Blanquet scale is used in recording.

Remote Sensing (RS) - Satellite imaging or other aerial measurement or observation techniques

Resilience– The extend and time in which and the ability of an ecosystem or community to recover ecosystem functioning after an environmental perturbation

Resistance (Ω)– The extend and time in which, and the ability, of an ecosystem or community to maintain ecosystem functioning during an environmental perturbation

RMSE– Root-mean-square error. Measure of the difference between model-derived and observational data.

SPEI– Standardized Precipitation and Evapotranspiration Index. Index to calculate the water availability for vegetation.

SPEIbase– Database containing historical data on global SPEI measurement

Stability - The lack of effect of an external pertubation on the functioning of the studied ecosystem. More effect means less stability.

SynBioSys – Syntaxonomical Biological System, information system on syntaxonomy, phytosociology and ecological parameters.

Time-series – Series of observations of the same location but at different times (mostly with standardized intervals).

Trait – Functional trait. Variables in morphology or strategy specific to a plant species, and often its environment, which is functional within the life-history of that species especially linked to, growth, survival, reproduction and dispersal.

TRY– Global database on plant functional and life-history traits

Turboveg– Software program to digitally archive and manage vegetation recordings

Wamelink values – Species related ecological indicator values regarding biogeochemical parameters, specifically derived for plant species in Dutch environmental conditions.

Contents

Viola curtisii

General introduction

The world is changing. Global change, for a large part driven or sped up by human activity, can be recognized in weather, climate, soil and land use, and affects individuals, populations, species, communities and entire ecosystems. Changes can be on a large scale, when climate change shifts the distribution of entire ecosystems up north, or on a small scale, when a local drought withers crops and grassland for a few days. The interaction between short term disturbances, long-term changes and biological and ecological processes is as variable as what drives them and differs with variable scales in time and space. Learning about these interactions and trying to understand processes will become more and more crucial to preserve the earth as our home.

1.1 Global change

Over the past century the environments on earth have been undergoing severe changes. Human activity can be identified as one of the major drivers behind global change and is manifested on many levels. The growth of the human population on earth (from ca. 1.2 billion people in 1850 to almost 7.5 billion people in 2016 (Gerland et al., 2014)) has put pressure on earth's resources and ecosystems, through major changes in land use and over-exploitation. Agriculture, combustion of fossil fuels, water level changes, intensive management, fertilization and pollution are some of the major anthropogenic drivers behind large environmental changes (Ruddiman 2013). Alteration and fragmentation of habitats and the introduction of artificial fertilizers , exotic species and plant diseases have increased the pressure on biodiversity, leading to a unprecedented rapid decline in the number of species on the planet (Butchart et al., 2010, Hodkinson et al., 2011).

Climate change is a major component of the current global change. The increase of atmospheric greenhouse gasses (such as CO2 and CH4) through the combustion of fossil fuels, intensive agriculture, industry and transport and the degeneration of natural sinks greenhouse gasses are causing alteration in our long-term and short-term climate. On the long-term climate change is affecting phenology (Richardson et al., 2013) and disturbs global water- and nutrient cycles. On the short-term global climate change affects weather patterns causing climate extremes. These extreme climate events are predicted to increase in frequency and magnitude in the near-future and may consists of anomalies in temperature and precipitation (Field and Van Aalst 2014, IPCC 2015). High or low temperatures and the occurrences of a surplus of precipitation or severe drought puts the functioning of ecosystems, communities, species, overall biodiversity and their interactions under additional pressure (Peñuelas et al., 2013). Research on the functioning of ecosystems under climate change and the role of biodiversity in those ecosystems is necessary to gain insights in the ecological consequences of global change and how to be able to coop with the earth's biggest threat.

1.2 Biodiversity research: a matter of data

Biodiversity is an complex concept which can be interpreted in many ways and many contexts. In biological sciences, the word has been used for decades to indicate a general overview of the number of species present in a predefined area, mostly only including plant and/or animal species (Gaston and Spicer 2013). In this thesis, biodiversity refers to the diversity of vascular plant species.

Diversity in plants and their relation to their environment has been studied for millennia, dating back to the botanical work of the Greek philosopher Theophrastus (Morton 1981). In order to assess biodiversity, easy observable morphological characteristics were used to make distinction between plant species and families. Recent advances in genetic research expanded the traditional taxonomical classification of species, and phylogenetics became a major determinant in discerning species. These new capabilities led to a broadening of the biodiversity concept by discerning a genetic diversity both on the species level and population level. As a consequence, the concept and context of biodiversity developed, and where taxonomic species were always the main unit in which diversity was explained, biodiversity could now be approached on scales smaller than whole species. On a molecular level, phylogenetic diversity discerns different genetic lineages within populations, resulting in a distinction of new levels of biodiversity within communities, based on the assumption that phylogenetic diversity is reflected in ecological differences (Cadotte et al., 2012). More recently, new methods in describing diversity emerged, not based on a taxonomical or genealogical classification of species. Diversity indices founded on physiological or functional (life-history) traits are an example of a relatively new method in approaching the diversity of an ecosystem, giving information about processes and the environment, independent of taxonomical species composition (Garnier et al., 2016). In the functional approach, diversity is assessed based on a classification of functional traits and functional trait values. Traits are directly linked to a function within a species' life-history, for example biomass production (growth), flowering (reproduction) or seed longevity (dispersal) (Ozinga et al., 2005b). Trait groups and values may overlap on or transcend the species level, giving a new index of biodiversity. Over the years, data concerning a multitude of functional traits and species have been collected around the globe in observational studies as well as in experiments, that are currently accessible via trait databases such as the LEDA (Kleyer et al., 2008) and TRY (Kattge et al., 2011) databases. Such diversity measures are mostly applied to local species diversity (α-diversity). However, the approach may extend to the habitat scale (β-diversity) and the landscape scale (γ-diversity) as well. For the term biodiversity is applied in a in a range biotopes differing in size, it is important to interpret biodiversity measures in the context of the scale and the type of ecosystem in which these are determined.

Over a century ago, phytosociology appeared as a scientific discipline and researchers started to study plant communities and their environment. These studies not only resulted in new insights in ecological relations between species, communities and their environment (in time and space), but also generated an enormous amount of data (Coesèl 2007). Databases were compiled and fairly recently digitalized, making them available for policy-makers, nature managers and researchers. The Dutch National Vegetation Database (Schaminée et al., 2012) and the European Vegetation Archive (EVA) (Dengler et al., 2011, Chytrý et al., 2016), are good examples of modern ways in collecting, storing and distributing historical biodiversity data on plants. Combined with other digitally available data on e.g. Remote sensing, climate, soil and land use, interactions can be studied in novel ways, by using developing techniques in statistics, Geographic information systems (GIS) and eco-informatics. Nowadays, large datasets offers many opportunities to analyse, study, discover and a variety ecological processes such as dynamics in succession, populations and dispersal (Ozinga et al., 2005a, Bekker et al., 2007). Moreover, large amounts of historical data on vegetation and the environment enables the quantifications of changes in the ecosystem over large temporal and spatial scales, in order to unravel the mechanisms behind ecosystem functioning (Michener and Jones 2012).

1.3 Ecosystem functioning and stability: a matter of resistance and resilience

Ecosystem functioning reflects the collective life activities of all organisms within that ecosystem, such as growing, moving, feeding, excreting, as well as the effects of these activities on the physical and chemical environment (Naeem et al., 1999). With regards to ecological research, the measurable output of an ecosystem is often referred to as an ecosystem function (Loreau et al., 2002).

Examples of ecosystem functions are biomass production, chemical fluxes, community composition and the ecosystem output with a societal relevance, known as ecosystem services. The sum of the properties of species and the interactions between the species within the ecosystem are fundamental for the output of the system and thus for the functioning of the ecosystem over time. Furthermore, the interactions between the organisms and their abiotic environment (Fig. 1.1) affects ecosystem functioning continuously (Tilman

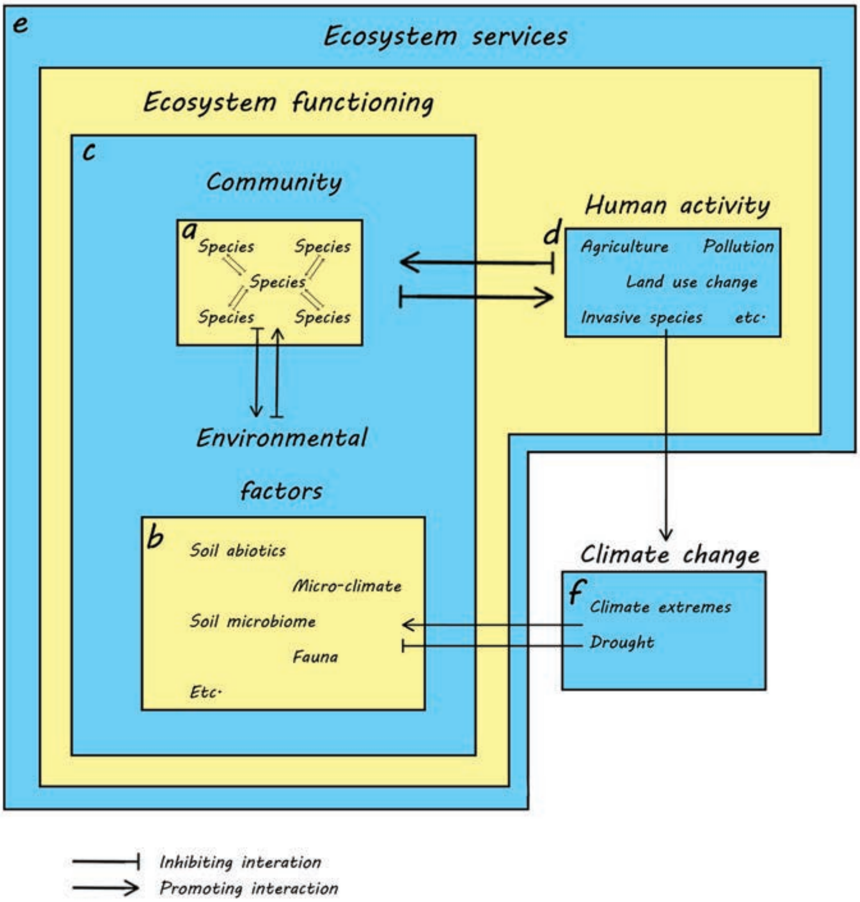


Figure 1.1 A simplified and schematic representation of several promoting and inhibiting interactions on different levels. Species, which interact with other species on a community level (a) are interacting with their environment (b) and form a functioning ecosystem (c). This ecosystem is affected by humans (d) and is utilized as an ecosystem service (e). Human activity causes changes in long-term and short-term climate (f), which causes changes in the environmental factors (b), affecting the entire interaction-cycle.

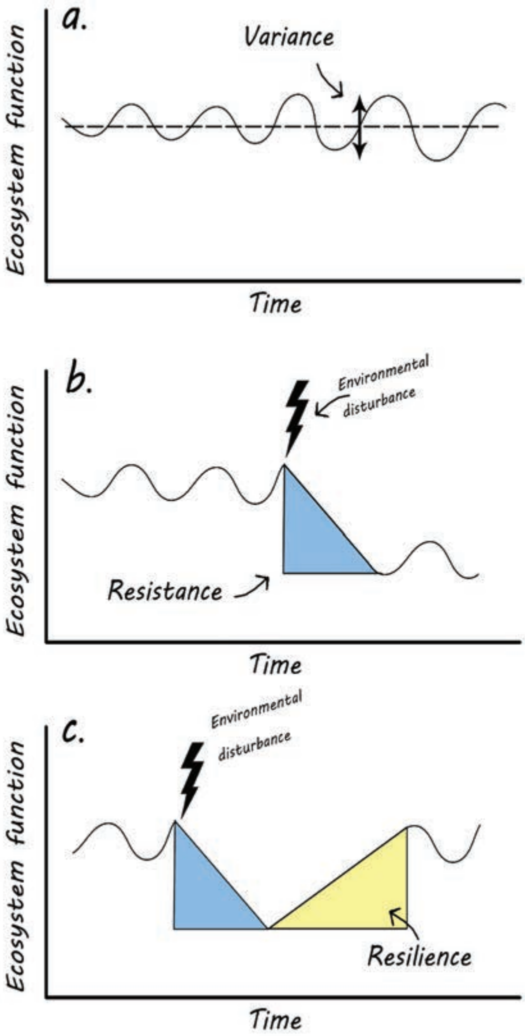


Figure 1.2. A schematic representation of three aspects of the stability of ecosystem functioning that are often referred to: variance, resistance and resilience. a) The natural variance caused by ecosystem related dynamics. b) After an environmental disturbance ecosystem functioning is altered into a different state. The time and magnitude of this induced alteration is referred to as resistance. c) If the environmental perturbation decreases or stops, ecosystem functioning may be restored to the pre-disturbed state of functioning. The time the system takes and to what extent it is able to reach this state is referred to as resilience.

et al., 2014), and may have reversible or irreversible effects on the long-term. The stability of an ecosystem (or of an ecosystem function) is generally expressed by the metrics variance, resistance and resilience (Pimm 1984, Tilman 1996) (Fig. 1.2).

Species are adapted to their environment. Through evolution and selection species acquired specific traits to cope with environmental factors, including biotic and abiotic factors, influencing their fitness. In this way, each species functions optimally in respect to certain environmental conditions and a certain community (Díaz and Cabido 2001). Under natural circumstances, environmental conditions continually change over time under influence of climate, weather, geological and chemical processes, affecting the performance of all species present. Many of these dynamics are ecosystem specific and can be regarded as an integral part of that ecosystem, its species and its functioning. This is reflected in the measures of that ecosystem's function. The variation through time around the long-term average is known as the variance of function (Text box 1).

External disturbances or extremes in dynamics may affect ecosystem functioning, changing the 'stable' state of functioning and causing a deviation from a long-term average. The speed at which an ecosystem deviates from the pre-disturbed state under influence of an external perturbation, is referred to as the resistance of the ecosystem or ecosystem function (Tilman and Downing 1996). Resistance is dependent on numerous ecosystem- and species properties and the individual interactions of these properties with the environment. A low resistance indicates that the function of an ecosystem during a disturbance quickly and/or severely reacts to the disturbance, while a high resistance results in a slow or minor response, given an equal intensity of the stressor.

After a disturbance has ended, an ecosystem has a chance to restore its function and return to the state before the disturbance. To what extent and at what pace this pre-disturbance state is achieved is defined as the resilience of ecosystem functioning (Pimm 1984, Tilman and Downing 1996). Just as resistance, resilience relies on species-specific properties and interactions.

1. 4 Diversity-stability relationships

It has been theorized that diversity has a positive mediating effect on the stability of ecosystem functioning under environmental perturbations. The theories behind these diversity-stability relations in ecosystem functioning are based on functional compensation in which a positive change in the functioning of

Variance, resistance and resilience in a grassland

Variance, resistance and resilience are illustrated by the example of an imaginary grassland ecosystem. The grassland system consists of several species and produces above-ground primary biomass through photosynthesis. This primary production can be regarded as one of the functions of this particular grassland. The interactions between species within this grassland and their dynamics, as well as the soil type, the amount of nutrients, the availability other natural resources and environmental properties, such as management, determine the amount of biomass that is produced. All these environmental conditions vary over time, due to a multitude of causes, including seasonality, and with these, the biomass production varies. Over a long time period, the amount of biomass produced (i.e. the extent to which the ecosystem's function is performed) revolves around an long-term average value (which may be shifting due to successional processes). These internal dynamics are referred to as the natural variance of the grassland ecosystem functioning.

A climate extreme occurs, a severe drought. As the drought perseveres, more and more plants start to show responses to the drought. Primary production declines until plants start to wilt, causing biomass to decrease, resulting in a decline in greenness of the vegetation. Some plants are affected earlier than other and some plants may even a reverse response to the drought, and increase their primary production. The interplay between species determines the resistance of biomass production to drought. Patches of the grassland that prolong to be green, seem to be stable, indicating a high resistance. In other patches of the grassland the withering is more pronounced, indicating a lower resistance in terms of biomass production.

The drought has ended and the vegetation of the grasslands is starting to recover. Overall greenness increases, indicating an increase in primary production. Again, some species show a different recovery after the drought than others. After a couple of days, most of the grassland seems to be recovered into the same condition as before the drought, whereas some patches in the grassland need over a week to recover and to reach the state of greenness before the drought. These latter patches seem to have a lower resilience.

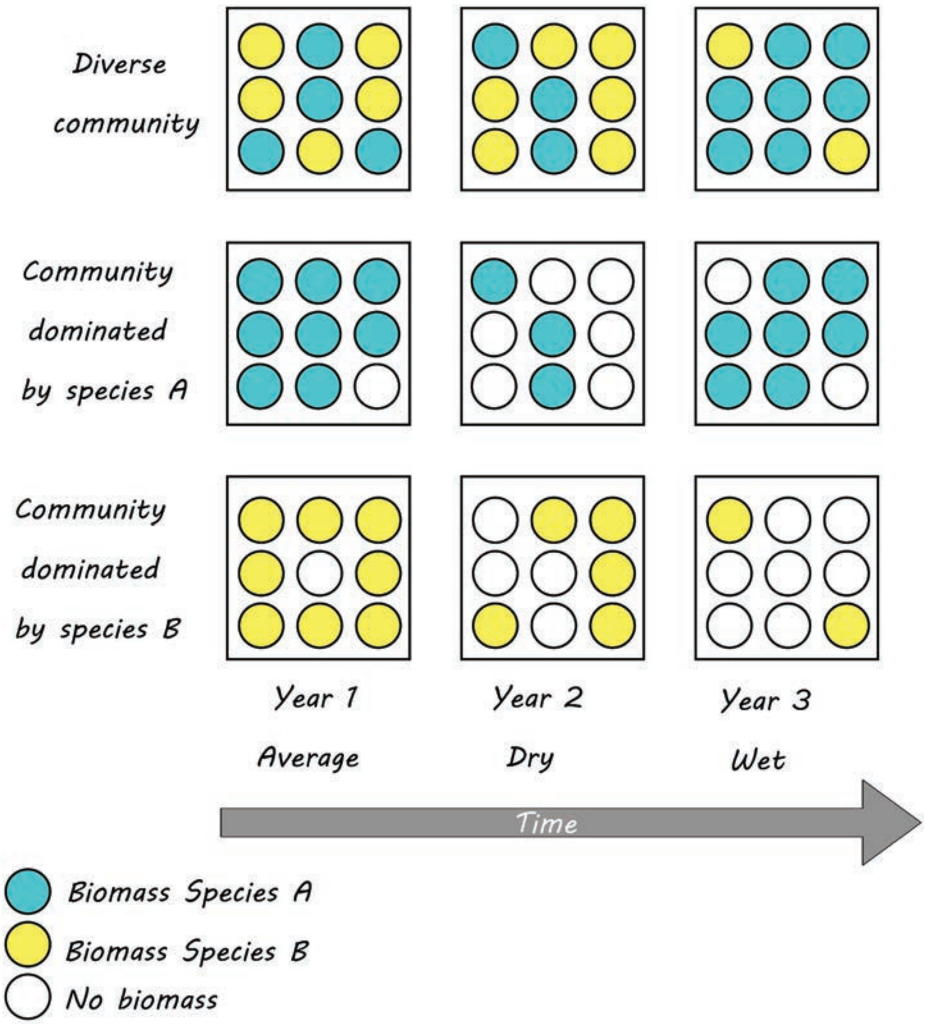


Figure 1.3. A schematic representation of diversity effects under changing climate conditions. Species all react differently under a climate anomaly as represented here by drought. Where the biomass production species A has a strong response to drought, species B responds stronger to wet circumstances. In communities dominated by one of the two species, climate anomalies will have a major effect on the biomass production of the entire community, resulting in a lower output when the climate changes. In a diverse community, where both species A and B are represented, the total biomass remains stable for the response of one species is compensated by the response of the other species. *Adapted from Cleland (2011).*
]

a species is associated with the negative change of the functioning of another species within the same community leading towards a stabilization of the function over time (Loreau et al., 2002, Loreau and Mazancourt 2013). A higher species diversity increases the chance that a species will be present to compensate the functioning of another species, driving the stabilization of over-all ecosystem properties or functions, such as biomass production (Fig. 1.3).

The most widely adopted theory is the ‘insurance hypothesis’, presented by Yashi and Loreau (1999). The theory consists of three specific mechanisms that explain how biodiversity may stabilize ecosystem properties over time. The first mechanism implies that differences in the response of species to environmental disturbances leads to an asynchrony in the response to the disturbance within a community. Different strategies in allocating resources like water and nutrients cause asynchrony in the way plant species within the same community respond to an environmental perturbation. Where some species have a quicker response to an environmental stressor than other species. The second mechanism focusses on the differences in speed at which species performances respond. Combining these mechanisms leads to complementarity in time. The third mechanism implies that an environmental disturbance decreases the resource competition between species, which enables a relative increase in the primary production of the species present, known as overyielding. The decrease in one species’ functioning may thus lead to an increased (or compensatory) overyielding of a complementary species, buffing the overall output of the system during the perturbation.

The differences between plant species which may lead to asynchrony are based on niche-differentiation, species-specific adaptations to their environment, and the interactions with other species within the community. The mechanisms behind the variation in species responses are largely based on functional properties of the species. These functional (life-history) traits of species are directly related to certain functions, such as growth, reproduction and dispersal. The variation in the role of a species in executing a function can be used as a different approach to species diversity: functional diversity, where the taxonomic unit is replaced by a functional unit (Polley et al., 2013). A higher number of species potentially increases the pool of functional traits, but it may also increase the redundancy of species: non-dominant species with a similar functional role in the ecosystem function, which may therefore have no significant effect on ecosystem functioning. Although being redundant on a single function, through other properties, these species may contribute to an asynchronous response to environmental perturbations (Pillar et al., 2013).

1.5 Evidence of the Diversity-stability paradigm

Research on how diversity mediates ecosystem stability and functioning dates back to the 1950's when it was shown that species diverse communities have a higher resistance against invasive species (Elton 1958). Research slowly progressed in the following decades, where May (1971) theorized and modelled the mediating role of species diversity in maintaining ecosystem functions (community related processes like decomposition). Later McNaughton (McNaughton 1977) and others emphasized the need for empirical evidence, and it was demonstrated that experimental species-rich grassland plots had a higher resistance to drought compared to species poor grasslands (Tilman and Downing 1996). Large field experiments, such as the experiments in Cedar Creek (USA), Silwood Park (UK) (Hector et al., 1999) and Jena (Germany) (Weigelt et al., 2010), provided increasing evidence of the important role of plant species richness in ecosystem functioning and provided additional empirical evidence for the diversity-stability hypotheses.

The experiments not only substantiated that a higher diversity, most commonly expressed as plant species richness, increased primary productivity (Tilman et al., 2001), but also that high diversity buffered the effect of imposed drought (Tilman et al., 2006). Meta-analyses of field experiments around the world show that the diversity-productivity and diversity-stability relationships appear to be consistent in different grassland ecosystems under experimental conditions, showing generally less response of above-ground biomass production on drought in species-rich grassland plots compared to species-poor plots (Isbell et al., 2015). This consistency, however, was found when the nature of the disturbance was similar. Changing the nature of the disturbance may result in contrasting relationships. For example, a natural flooding destabilized biomass production more in species-rich grassland plots compared to species-poor grassland plots (Wright et al., 2015). More diverse communities were more capable to take advantage of an increased availability of nutrients after the flooding, resulting in a relatively large increase in production, hence a large deviation from the baseline productivity. Other disturbances, often involving an increase in the resource availability, such as external eutrophication by fertilizers, nitrogen deposition, CO2-enrichment and fire, may also cause a reversed diversity-stability relationship as found in drought experiments (Ojima et al., 1994, Reich et al., 2001, Hautier et al., 2014).

Although there is mounting experimental evidence for the hypothesis that a greater species diversity leads to a greater ecosystem stability, often referred to as the "diversity-stability paradigm" (Naeem 2002), it is still one of the most debated topics in ecology and still leads to new challenges in ecological research (Hector and Bagchi 2007, Aerts and Honnay 2011). Until now, most empirical research on the diversity-stability relationship was performed in relatively small *in situ* field experiments, where species composition was designed and manipulated, and where environmental co-variables were under control. This makes it hard to come to generalizations of the diversity-stability paradigm in more natural, uncontrolled situations, where plant species composition is the result of natural assembly processes. However, there is an increasing need for returning to natural field situation and validate the experimentally derived relationships to policy- and management relevant scales (Cardinale et al., 2012, Tilman et al., 2014). Moreover, observational studies can generate new insight, changing the scales of focus, where the diversity-stability paradigm is put to the test in environments with a generally higher heterogeneity in environmental conditions compared to experimental set-ups. In addition, observational studies may produce new questions which can be returned to experimental research (Hector et al., 2007). Most observational studies on the diversity-stability paradigm have focussed on forest communities, as long-term tree biomass increase can be readily monitored. Positive relationships between production of primary production and the diversity of woodland communities have been found in multiple studies (DeClerck et al., 2008, Aerts and Honnay 2011). The rare studies on diversity-stability mechanisms in natural grassland communities added to the evidence of positive diversity-stability relationships (Tilman and Downing 1996, Bai et al., 2004, Hautier et al., 2014). However, these studies made use of invasive measurement techniques by periodically yielding biomass and thus hampered the long-term monitoring of unmanipulated grassland ecosystems. In addition to that, the plots monitored are relatively small, complicating the extrapolation of the results to ecosystem scales. Also the studies received criticism for not sufficiently incorporating the heterogeneity of the plots and abiotic co-variables within the analyses (McNaughton 1977, Tilman and Downing 1996). Further upscaling observations in time, covering areas of sufficient size to approximate ecosystem processes on ecosystem scales, and conceiving methods in observing these processes without manipulating them is necessary in order to extrapolate experimental findings to nature and to make generalizations applicable in real-world ecosystems.

Global climate change and other anthropogenic influences will continue to cause the loss of species in the near future, deepening the current biodiversity crisis (Butchart et al., 2010). And while it is expected that the amount of environmental and climate related disturbances will increase (Field and Van Aalst 2014) and will jeopardise ecosystem functions and services of societal relevance, there will be a growing interest in the role of species richness in mediating ecosystem responses under environmental disturbances (Roscher et al., 2011, Vogel et al., 2012). The need for understanding ecological stability mechanisms in nature, in order to predict ecosystem responses to climate change and take adequate measures, has never been more important.

1.6 Up-scaling from experiments to natural ecosystems

The main challenges in upscaling research from an experimental set-up to natural ecosystems is lying in collecting sufficient data on local species composition, species dynamics, and acquiring productivity data using a non-invasive method. The previously discussed availability of large databases on plant species composition, plant traits and environmental conditions offer new opportunities to combine sufficient data to do reliable analyses. As an example, Kuiters and colleagues showed an increased stability of the community composition during drought, using long-term historical vegetation data on dune grassland ecosystems (Kuiters et al., 2009) and, in addition, compared contrasting habitats showing consistent correlations (Kuiters 2013). However, these approaches have not yet been applied to study the effects of environmental disturbances on the production as a function of grassland ecosystems.

Remote sensing

Non-invasive remote sensing techniques rapidly develop and offer new approaches for monitoring and measuring ecosystem functions at larger spatial scales, covering large vegetation plots up to entire ecosystems, or even global vegetation dynamics, using satellite observations. Remote sensing techniques offer ways to assess primary production without affecting the measurement though yielding. The most commonly used index for assessing photosynthetically active biomass is the Normalized Difference Vegetation Index (NDVI), that uses the difference between the incoming and the reflected photo-active light (in the red and near infrared light spectrum) on a certain surface (Carlson and Ripley 1997) (Fig. 1.4). The difference in incoming and reflected light caused by absorption reflects the use of light for photosynthesis, hence photosynthetically active biomass, resulting in a proxy for vegetation primary production, calculated as:

$$NDVI = \frac{NIR - VIS}{NIR + VIS}$$

Where NIR is light in the Near-Infrared spectrum and VIS is visible light. Changes in light absorption of the same surface through time can be used to monitor dynamics in biomass production. Commonly used to acquire NDVI measurements are the MODIS (MODerate resolution Imaging and Spectroradiometer) aboard NASA's TERRA- and AQUA-satellites and the LANDSAT satellites, which monitor the earth's surface with different spatial and temporal resolutions. Raw satellite image-products are not correctly interpretable and need to be processed (including for example corrections for latitude, cloud cover, atmosphere, zodiac effects weather conditions and seasonality) to acquire usable and interpretable information (De Keersmaecker et al., 2014). Although NDVI is commonly used to monitor (tropical) forest ecosystems, the technique cannot penetrate through different vegetation layers and is therefore, with regard to forests, mainly applied in observing canopy dynamics. Nonetheless, NDVI is an adequate index to be used in relatively two-dimensional systems such as grasslands.

Combining databases

In order to up-scale research on diversity-stability relationships, both spatially and temporally, large amounts of data are necessary. To attain this data, the rapid increase of digital databases (often freely online accessible) can be exploited. These databases range from databases containing historical measurements or observations of diversity, productivity and climate to databases providing information on land-use or species-specific life-history traits.

To make adequate time-series of climate events, diversity and primary productivity, historical data is required. Meteorological databases provide data on large-scale climate events and weather data, for example precipitation or drought. Local databases such as the database of the Royal Dutch Meteorological Institute (KNMI) presents daily information on multiple variables measured in weather stations across the Netherlands, enabling to calculate relatively local Standardized Precipitation and Evapotranspiration Index (SPEI) values, going back to the 1970's. A more commonly used database on SPEI-data is the SPEIbase which offers grid-based SPEI values dating back to the 1950's (Beguería et al., 2010). In order to attain historical

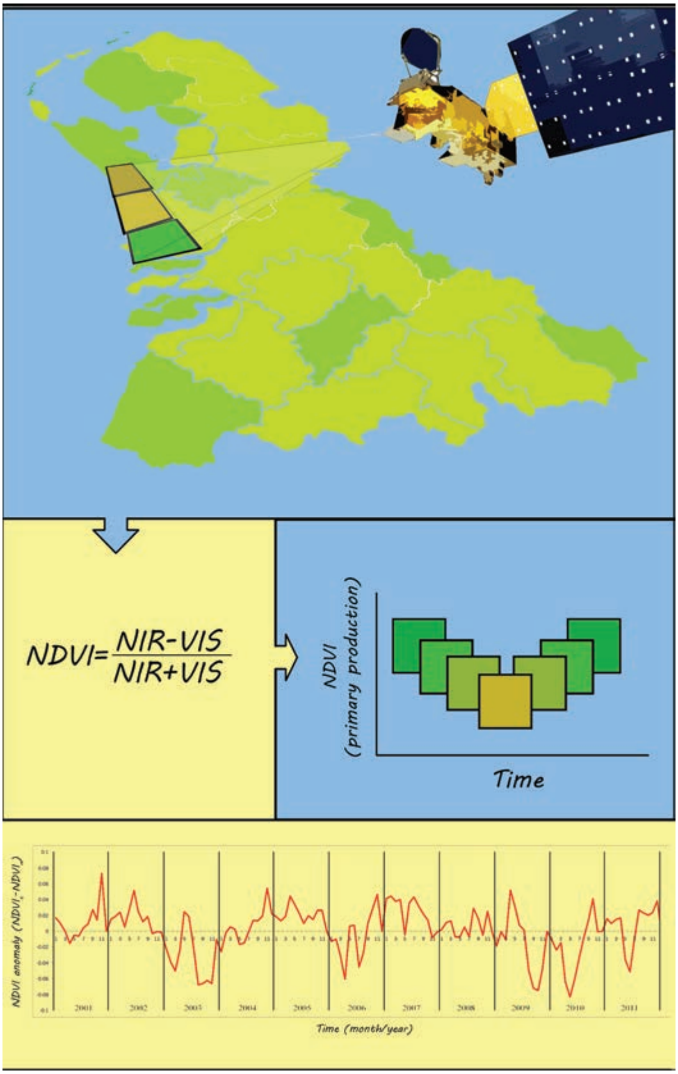
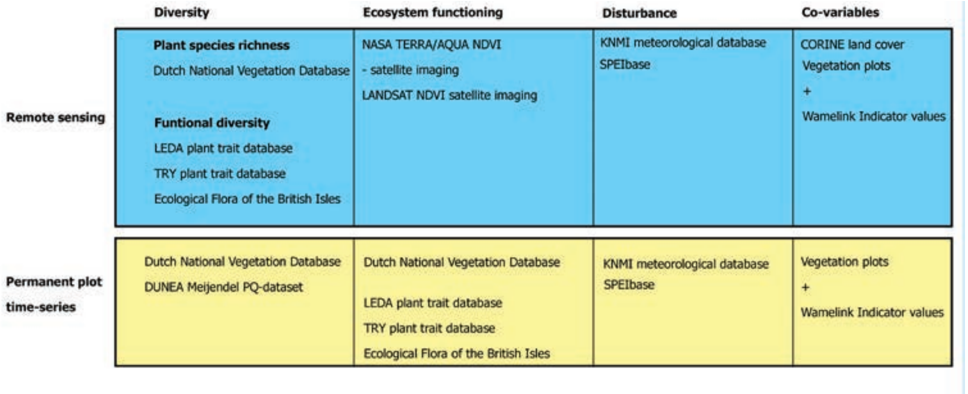


Figure 1.4. A schematic representation of Normalized Difference Vegetation Index (NDVI) satellite imaging. NASA's MODIS (AQUA/TERRA) or LANDSAT satellites monitor the earth surface by registering the Near-Infrared (NIR) and visible (VIS) light spectrum and calculate the NDVI per pixel. Changes in NDVI can be observed by creating a time-series for each pixel. Changes in the NDVI are associated with changes in the on-ground photosynthetic biomass within a pixel. This change in NDVI can be compared with the long-term NDVI measurements in order to calculate an anomaly (or deviation from normal), subtracting the long–term NDVI (NDVIn) from the actual measurement (NDVIe). Subsequentially, time-series of NDVI-measurements can be made using the actual measurement or calculated anomaly.

data on diversity, the above-mentioned Dutch National Vegetation Databases (Schaminée et al., 2012) covers the vegetation across the entire country and dates back to the 1930's, enabling the creation of observational time-series of plant species diversity. In addition to georeferenced information on species and their relative abundance, this database often provides information on site-specific conditions. Once the species composition is known, it is possible to append functional trait data to each species. Although historical data on primary production can be derived from remote sensing databases when satellite imaging is applied, it is not always possible to attain historical measurements of site-specific primary production. In order to assess biomass production, or functional diversity measures, it is possible to attach species-specific trait data to historical observations from a vegetation database. The European LEDA plant trait database (Kleyer et al., 2008), which is currently included in the global TRY database (Kattge et al., 2011), offers trait data of many common species. An additional selection of relevant traits is necessary in order to draw conclusions on the functions studied. The trait databases mainly include information on common species and for many rare species the information is incomplete, causing gaps in the dataset. At the same time, not all traits are well-covered and a selection of data has to be made. It must also be noted that many trait data are collected in different environments and often are measured in ex situ settings, therefore database-derived trait information should only be used as a proxy (Cordlandwehr et al., 2013). This also applies to the use of ecological databases where environmental conditions per plot can be calculated based on species associated ecological indicator values such as the Ellenberg Indicator Values (Ellenberg et al., 1991) and the



	Diversity	Ecosystem functioning	Disturbance	Co-variables
Remote sensing	**Plant species richness** Dutch National Vegetation Database **Funtional diversity** LEDA plant trait database TRY plant trait database Ecological Flora of the British Isles	NASA TERRA/AQUA NDVI - satellite imaging LANDSAT NDVI satellite imaging	KNMI meteorological database SPEIbase	CORINE land cover Vegetation plots + Wamelink Indicator values
Permanent plot time-series	Dutch National Vegetation Database DUNEA Meijendel PQ-dataset	Dutch National Vegetation Database LEDA plant trait database TRY plant trait database Ecological Flora of the British Isles	KNMI meteorological database SPEIbase	Vegetation plots + Wamelink Indicator values

Figure 1.5. An overview of the applied sources providing historical data on diversity, ecosystem functioning, climate and co-variables.

Wamelink Indicator Values (Wamelink et al., 2005). Data on land-use, for example extracted from CORINE land cover database (Büttner et al., 2004), can provide information on additional environmental factors, such as recent and historical land-use, relevant to the vegetation. An overview of the datasets and databases used in this thesis is given in Figure 1.5.

1.7 Grasslands ecosystems in the Netherlands

Most grasslands in Western Europe are semi-natural. Only in relatively extreme environments, such as coastal dunes, grasslands can sustain themselves without human intervention. In less extreme environments, wild herbivores and human activity, such as farming, herding and hay-making, have created and maintained grasslands in a great variety of environments. Grassland ecosystems offer many ecosystem services. Not only are grasslands just related to a wide variety of agricultural uses, grassland ecosystems are essential for global food production, providing a source for edible plant species and providing food and space for cattle and other livestock. Next to food, grassland harbour sources for the production of biofuels. In dune ecosystems, natural grasslands stabilize the soil and, by doing so, maintain the functioning of the dune system for extracting drinking water as well as for coastal defence. In Europe, natural grasslands cover some of the most species-diverse habitats and harbour numerous rare or endangered species (Wilson et al., 2012). Apart from their aesthetic values, promoting tourism, these habitats may play a vital role in conserving and protecting plant species. And while temperate grasslands are some of the ecosystem types most vulnerable for the current climate change (Loarie et al., 2009), unravelling their ecological mechanisms is becoming increasingly urgent. In particular in the Netherlands, given the projected vulnerability of the Netherlands to the increase in frequency and magnitude of weather extremes (Botzen and Van Den Bergh 2008, Field and Van Aalst 2014), gaining more insights in the ecological mechanisms of resistance and resilience adds to designing adaptive and mitigating strategies to cope with global climate change.

In Western Europe, grasslands cover a large part of the land and consist mostly of relatively species-poor agricultural pastures. However, the semi-natural grasslands, which are mostly extensively managed, harbour the most biodiverse communities. The many ecosystem functions and services to society have made grassland ecosystems among the best-studied ecosystems in Europe. In particular in the Netherlands, with over 120.000 grassland recordings available in the Dutch National Vegetation database, covering all habitat types from peat land meadows, limestone grasslands, mesotrophic fen meadows, riverine meadows, mat-grass swards and dune grasslands, a large amount of historical data is available. Especially dune grasslands are well-studied, representing the bulk of grassland relevés (vegetation recordings) in the database, including many permanent plot time-series (Smits et al., 2002). Dune grasslands are the most natural grasslands of the Netherlands and in particular grey dune grasslands are well preserved and protected and are still used for many services relevant for the Dutch society, for example drinking water production and coastal defence, where vegetation still plays a crucial role. Additionally, as most dune grassland are positioned along the borders of densely populated areas, the natural areas also serve an important recreational and aesthetic purpose. Grey dune grasslands form biodiverse communities with an azonal vegetation in mosaic patterns. Grass species, sedges, mosses and herbs characterize the relatively dry vegetation along the western shores, that are classified within the class of Koelerio-Corynephoretea, whereas on the inland Pleistocene sands in the Netherlands, heather and matgrass dominated grasslands of the classes Nardetea can be found on less calcareous soils (Schaminée 1996).

The natural and societal relevance of the Dutch grasslands and the fact that they are relatively well studied and comparable to the grasslands used in the major biodiversity experiments make these grassland communities good subjects to explore the possibilities to upscale research on biodiversity-stability relationships.

1.8 Research Focus

1.8.1 General aim

The general aim of this dissertation is to study diversity-stability relationships in (semi-) natural grassland ecosystems, and to up-scale experimentally substantiated evidence for positive diversity-stability relationships in time and space. Whereas the bulk of research has been performed in relatively small-scaled experiments, where species composition is artificially assembled and manipulated, this study aims to study naturally assembled uncontrolled grassland plant communities across relatively large temporal and spatial scales. To achieve this, new approaches in combining large-scale long-term data of non-invasive measurements of ecosystem functioning with monitoring data on biodiversity and data on climate variability, needed to be developed. Additionally, new approaches were needed to estimate the effect of the possible confounding factors such as environmental abiotic variables, species-specific variation in functioning.

The general aims can be decomposed in four more specific objectives:
Objective 1: Assess and quantify the relationship between plant and trait diversity and ecosystem functioning in natural and semi-natural grassland ecosystems.

Objective 2: Assess and quantify diversity-stability relationships in natural and semi-natural grassland ecosystems under stress of climate variability.

Objective 3: Develop new methods in combining Remote sensing techniques and large vegetation databases to study diversity-stability relationships in natural and semi-natural grassland communities.

Objective 4: Assess whether diversity-stability relationships hold across different grassland ecosystems with different environmental variables.

1.8.2 Dissertation outline

This dissertation comprises two methodologies, each applied at two different spatial scales (Fig 1.6). In the first part, the study focusses on applying remote sensing techniques to quantify ecosystem functioning and stability of ecosystem functioning. First focussing on dune grasslands along the Dutch western coast, and subsequently scaling-up to different grassland ecosystems across the entire Netherlands. In the second part, the focus lies on analysing time-series of permanent plots, repeatedly recorded vegetation surveys on two spatial scales. The dune grassland ecosystems of the Meijendel dunes are focussed upon and subsequently a dataset is used comprising all permanent plot time-series in grassland of the Netherlands. An visual overview of the outline is given in Figure 1.6. Each of the chapters have been published, submitted or are in review in international peer-reviewed scientific journals.

Chapter 2 explores the possibilities to combine large datasets of remote sensing derived NDVI measurements, with vegetation plots and locally attained SPEI-data in dune grasslands in the Netherlands to up-scale diversity-stability of above-ground primary production relationships in natural grasslands during drought. Stability, measured over a period of ten years, is expressed as a resistance term based on the anomaly of (MODIS, 250m) NDVI measurements during a period of drought compared to the long-term average. In addition to diversity indices based on species richness, such as plant species numbers, Shannon-Wiener index and Evenness index, functional diversity (i.e. Rao's Quadratic Entropy) is taken into the analyses, based on five biomass production associated traits, derived from the LEDA plant trait database. Results show, for the first time, a positive significant relationship between the stability of NDVI measurements during drought and both the plant species richness and the Shannon-Wiener index values (both indices predominately based on species numbers). Functional diversity (and Evenness index values) did not show a significant effect on the stability of ecosystem functioning.

Chapter 3 studies the differences in stability between semi-natural and agricultural grasslands. Although the majority of grasslands in the Netherlands are man-made, the extensive management caused grasslands that are highly diverse in species composition and richness. Agricultural intensification through fertilization, hydrological manipulation and continuous disturbances led to productive and relatively species-poor grasslands. As it is expected that the frequency and magnitude of climate anomalies will increase in the near future, it is uncertain to what extend agricultural grasslands can maintain their productivity under climate stress, compared to semi-natural grasslands. According to the diversity-stability paradigm, it is expected that semi-natural grassland, with a higher diversity, should be more stable compared to the low diversity agricultural grasslands. By using 14 years of remote sensing data (500m MODIS, NDVI), combined with climate data, we show that semi-natural grasslands are indeed more resistant to climate variability compared to intensively managed grassland. However intensively managed grassland do recover better and thus show a higher resilience.

Chapter 4 uses a unique dataset of permanent plots in dune grassland ecosystems to assess and quantify the diversity-productivity and diversity-stability relationships under varying drought conditions over a period of sixty years. Where satellite observations are often not detailed enough to distinguish the biodiversity present in the monitored vegetation, applying permanent plot observations gives the advantage of a very high resolution and the ability to study biodiversity over longer time periods. Although no productivity measurements were available, a proxy of above-ground biomass production could be made using the relative abundance to calculate a Leaf Area Index (LAI). Together with the Specific Leaf Area (SLA), biomass could be calculated, comparable to remote sensing derived observations. Significant positive long-term diversity-productivity and diversity-stability relationships were shown. In addition, the effects of abiotic co-variables were added to the analyses, based on species based ecological indicators. Although environmental factors did have a significant effect on productivity, no confounding effects were seen on the diversity-stability of ecosystem functioning relationship in dune grassland ecosystems.

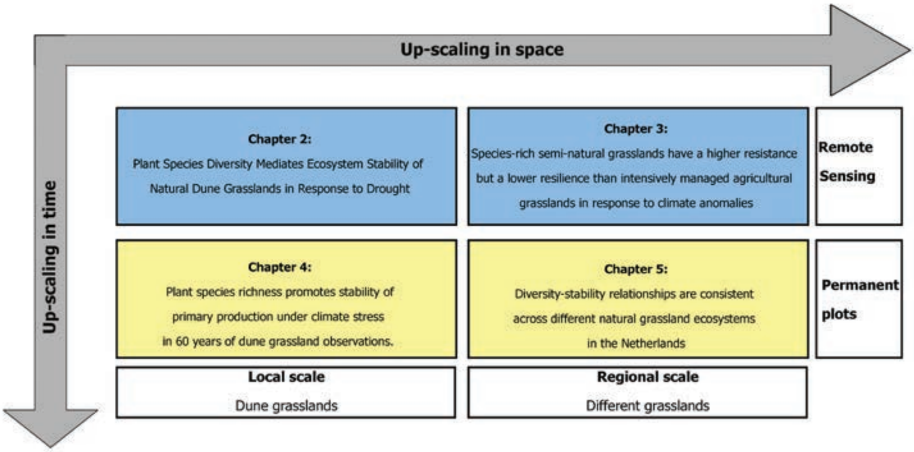


Figure 1.6. A schematic overview of the interrelations between the chapters in this thesis. Chapter 2 and Chapter 3 utilize remote sensing observations over a period of 10 years to study diversity-stability relationships in dune grasslands ecosystems (local scale) and across different grassland habitats (regional scale), while Chapter 4 and Chapter 5 use long-term time-series of permanent plots to study the diversity-stability paradigm in dune grassland on again local scale and different grassland ecosystems on a regional scale.

Chapter 5 focusses on environmental factors which may confound the diversity-stability relationship in grasslands. Whereas chapter IV was limited to dune grassland ecosystems, the study presented in chapter V utilizes the entire database of permanent plots in the Netherlands, covering a period between 1930 and 2012. The dataset included grassland habitats on different soils and under various abiotic conditions, ranging from dry grasslands on poor sandy soils to wet grasslands in nutrient rich clay. Biomass production was estimated per plot, using LAI and SLA. SPEI-data, as a drought indicator, was attained using SPEIbase. Wamelink ecological indicators were used to assess abiotic co-variables per plot, including soil pH, soil moisture and nitrogen and phosphorus content of the soil in addition to soil type and physical geography. In this study, an effect of the abiotic co-variables on biomass production was found at larger spatial scales; however, no significant effect could be observed on the long-term stability of biomass production. This suggest the robustness of diversity-stability relationships in natural ecosystems.

Chapter 6 concludes this dissertation by summarizing the main results and conclusions of each chapter and giving an overview of remaining challenges and recommendations for future research.

1.9 Publications derived from this thesis

- **N.M. van Rooijen**, W. De Keersmaecker, W.A. Ozinga, P. Coppin, S. Hennekens, J.H.J. Schaminée, B. Somers and O. Honnay (2015). Plant Species Diversity Mediates Ecosystem Stability of Natural Dune Grasslands in Response to Drought. Ecosystems 18(8): 1383-1394.
- W. De Keersmaecker W, **N.M. van Rooijen**, S. Lhermitte, L. Tits L, J.H.J. Schaminée, P. Coppin, O. Honnay and B. Somers (2015). Species-rich semi-natural grasslands have a higher resistance but a lower resilience than intensively managed agricultural grasslands in response to climate anomalies, Journal of Applied Ecology 53(2): 430-439

Submitted

- **N.M. van Rooijen,** Thomas M.W.J. van Goethem, Marlijn Vliegenberg, Joop H.J. Schaminée, Wim A. Ozinga, Olivier Honnay (). Diversity-stability relationships are consistent across different natural grassland ecosystems in the Netherlands, Journal of Vegetation Science (*Under review*)

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

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Abstract

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

2.1 Introduction

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

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

Mazancourt, 2013). In this context, plant functional diversity, rather than taxonomic diversity, may be the key factor driving ecosystem stabilization. Functional traits, i.e. plant properties that impact growth, reproduction and survival, can be expected to mediate the ability of individuals, populations and even of entire ecosystems to cope with environmental disturbances.

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

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

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

More specific, the aims of this study were to:

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

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

2.2 Material and Methods

Selection of study sites

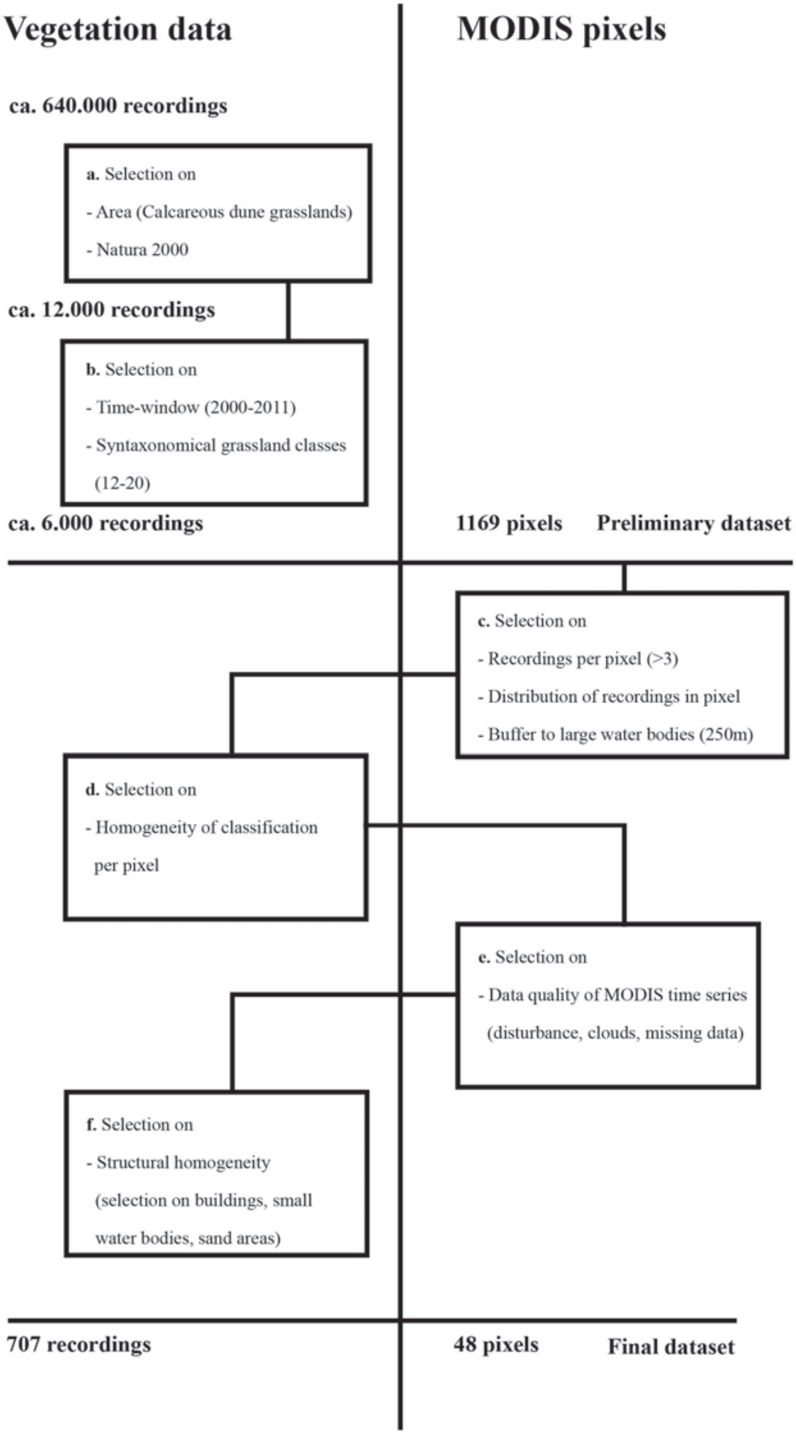
The study focuses on calcareous dune grassland ecosystems in the Netherlands. The Dutch calcareous dune region stretches along the western coast from the Belgian border in the South to the village of Bergen in the North. Phytosociological syntaxonomy classifies these vegetation types predominately into the class of Koelerio-Corynephoretea (Schaminée et al., 1996). All studied grasslands are located in an area under the European 'Natura 2000' legislation. Management consists of seasonal grazing with cattle (Fig. 2.1a).

Selection of remote sensing data

Time-series of the NDVI were used to monitor ecosystem properties through time. NDVI quantifies the amount of greenness of vegetation and can therefore be used to give an approximation of aboveground biomass production (Verbesselt et al., 2010; Zhang et al., 2010; De Keersmaecker et al., 2013). Moderate Resolution Imaging Spectroradiometer (MODIS) NDVI images from the MOD13Q1 and MYD13Q1 product, collected by both the TERRA and AQUA sensor, were obtained from the NASA Land Processes Distributed Active Archive Centre (LP DAAC: http://lpdaac.usgs.gov) (Gu et al., 2013). MODIS NDVI data has a resolution of 250 × 250 meter pixels. Time-series were made from the data covering the time window between the years 2001 and 2012, with an eight daily temporal resolution. A total of 1169 MODIS pixels covered the studied area (Fig. 2.2).

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

> Figure 2.1. Flow chart indicating the steps in selecting MODIS pixels and vegetation relevés to study the effects of species diversity on dune grassland response to drought events.


Vegetation data
MODIS pixels
ca. 640.000 recordings
a. Selection on
- Area (Calcareous dune grasslands)
- Natura 2000
ca. 12.000 recordings
b. Selection on
- Time-window (2000-2011)
- Syntaxonomical grassland classes (12-20)
ca. 6.000 recordings
1169 pixels
Preliminary dataset
c. Selection on
- Recordings per pixel (>3)
- Distribution of recordings in pixel
- Buffer to large water bodies (250m)
d. Selection on
- Homogeneity of classification per pixel
e. Selection on
- Data quality of MODIS time series (disturbance, clouds, missing data)
f. Selection on
- Structural homogeneity (selection on buildings, small water bodies, sand areas)
707 recordings
48 pixels
Final dataset

(Fig. 2.1c).

Selection of vegetation data

Vegetation data from the selected areas were acquired from the Dutch National Vegetation database (DNVD) (Schaminée et al., 2012). An initial dataset of 12,000 records of calcareous dune grasslands was available. All vegetation recordings used to calculate species and functional diversity were made between 1995 and 2000, prior to the start of the NDVI time-series. Records syntaxonomically classified as grasslands were selected, including classes 12 (Plantaginetea majoris - wet meadows) to 20 (Calluno-Ulicetea – arid heath- and grasslands)) (Schaminée et al., 1996) (Fig. 1.1b). Phytosociological classification was performed using ASSOCIA (Tongeren et al., 2008), included in the Turboveg software package (Hennekens and Schaminée, 2001). Species cover abundance in all vegetation records was quantified using the adapted Braun-Blanquet scale in 2×2 meter plots. Subsequently, cover scales were transformed to percentages (Schaminée et al., 2011).

Selection of study pixels

The study pixels were selected, through overlaying the 250x250m MODIS pixels with the vegetation records. Only MODIS pixels including at least three vegetation records, evenly distributed across the pixel area, were selected (Fig. 2.1c). To guarantee homogeneity of the pixels' vegetation, it was verified whether all vegetation records were classified within the same phytosociological class (Fig. 2.1d). To minimize heterogeneity in the selection, only pixels were selected situated within the habitat type of grey dune grasslands. Although all pixels fall in areas with comparable abiotic conditions and similar nature management, including controlled ground water tables, some variation in vegetation types is present. An overview of the occurring vegetation types (phytosociological classes) can be found in Appendix A.

To prevent interference from large water bodies and sandy surfaces (including sea and beach), pixels adjacent to these surfaces were omitted. Additionally, the NDVI time-series of all pixels were manually checked for interference factors and noise. Finally, the structural homogeneity of the vegetation in the selected pixels was verified based on Google earth and/or by visiting the pixels in the field (Fig. 2.1f). This series of selection criteria resulted in a final selection of 48 250×250 m MODIS pixels, containing 707 vegetation records.

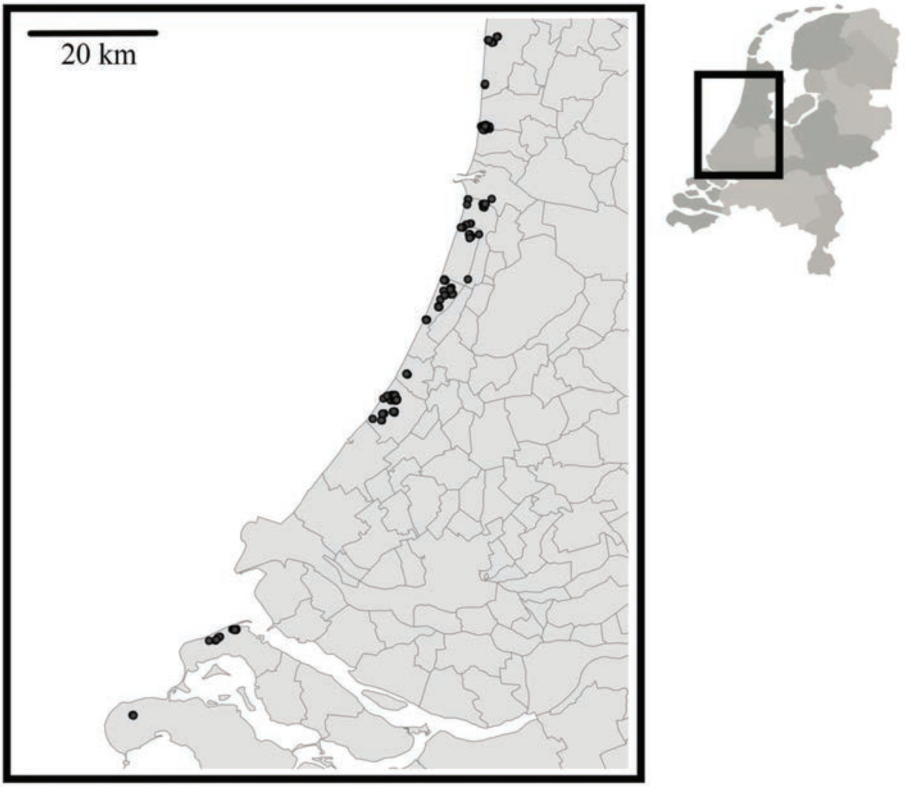


Figure 2.2. Location of the final selection of MODIS pixels in the calcareous dune grasslands at the western coastal area of the Netherlands.

Species diversity indices

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

- Species number (Nr)
- Shannon-Wiener Index (H') following equation 2.1.

$$H' = \sum_{i-1}^{s} P_i \ \ln P_i \qquad \textit{equation 2.1}$$

Where S is the total number of species and Pi is the proportion of the individual species relative to the total cover.

- Evenness (E) following equation 2.2.

$$E_H = \frac{H^{'}}{H^{'}_{max}} = H^{'} / \ln S$$ *equation 2.2*

For each study pixel, also functional diversity was calculated as Rao's quadratic entropy (FD_Q), according to equation 2.3, where d_{ij} is the difference between species i and j as calculated according to equation 2.4 where t is the number of considered traits and X is the trait value of a specific trait k for species i or j (Botta-Dukát, 2005). Functional trait data of the species were retrieved from the trait databases LEDA and the Ecological Flora of the British Isles (Fitter and Peat, 1994; Kleyer et al., 2008). The following plant traits were selected: specific leaf area (SLA), leaf size, leaf dry matter content, leaf mass, root depth and canopy height. These traits can be expected to mediate biomass production in individual plant species and can be related to resource acquisition (Schumacher and Roscher, 2009). Additionally the flowering onset time and length of the flowering period were included in the analysis to reflect temporal variation in phenology of the vegetation. Selection of traits was constrained by the availability of trait data for the complete plant species data set. Therefore FD_Q was based on species occurring in at least 75% of the pixels, to calculate functional diversity. All trait values were quantitative variables and were standardized to values between 0 and 1.

$$FD_Q = \sum_{i=1}^{S-1} \sum_{j=i+1}^{S} d_{ij} P_i P_i$$ *equation 2.3*

$$d_{ij} = \frac{1}{t} \sum_{k=1}^{t} (X_{ik} - X_{jk})$$ *equation 2.4*

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

Meteorological data

Meteorological data were retrieved from the online databases of the Royal Meteorological Society of the Netherlands (KNMI) (2014). Data were acquired from the Vlissingen monitoring station for the time window 2001-2011. This particular monitoring station was chosen for its proximity to the observed dune areas. Data regarding temperature, precipitation and potential evaporation were used for calculating the Standardized Precipitation and Evapotranspiration Index (SPEI) (Vicente-Serrano et al., 2010). The SPEI reflects drought events and the effect on plant life, considering not only precipitation but also the evaporation and transpiration of water from the soil and plant material. A negative SPEI value is associated with the occurrence of drought. Monthly values of SPEI were calculated as measure of drought (Drought indices: C_{SPEI}) taking the previous two months into account. Only SPEI-values during the growth season (March-October) were used between 2001 and 2011 (n=80). Calculations were performed with the R-package SPEI.

Ecosystem drought response: NDVI anomaly

Temporal variation of an NDVI time-series contains (I) a seasonal component (due to phenology), (II) an anomaly due to external environmental factors, (III) noise through atmospheric influences or sensor noise (Lhermitte et al., 2011) and (IV) trends (e.g. due to long term vegetation changes or sensor degradation (Fensholt and Proud, 2012; Wang et al., 2012). These trends can be considered to represent long term changes in the equilibrium state of the grassland, instead of being short term anomalies resulting from climate disturbances. Since it was our aim to quantify short term responses of biomass production to precipitation variability, each NDVI time-series was detrended in case of a significant temporal linear trend. The NDVI-anomaly

(A_{NDVI}) of each pixel was used as an indicator for ecosystem drought response. NDVI values were available in eight day averages. A_{NDVI} was calculated by removing the seasonal component within the NDVI variation. This was done by subtracting the mean eight daily NDVI over all years, from the original NDVI time-series. A monthly NDVI-anomaly was calculated, to match the temporal resolution of the meteorological data. A decrease in NDVI results in a negative NDVI anomaly, thus a decrease of biomass production.

Statistical analyses

Analyses were performed on all selected pixels (n=48). We calculated response coefficients ($P_{response}$) for each pixel (px) as the slopes of the regression lines between A_{NDVI} and C_{SPEI} using Model 2.1.

$$P_{response} = (A_{NDVI} \sim C_{SPEI})_{px} \qquad \textit{model 2.1}$$

The response coefficients were subsequently correlated with the diversity indices (Species richness (Nr), Shannon-Wiener index (H'), Evenness index (E) and the Functional diversity (FD_Q)). A linear regression was then performed to analyse the correlation between the diversity indices and the response coefficients to drought of all pixels (Model 2.2). In this model we also included the phytosociological class (V_{class}, n=5) of the grassland vegetation type as a fixed effect.

$$P_{response} \sim I_{Nr/H'/E_H/FD_Q} * V_{class} \qquad \textit{model. 2.2}$$

The pixels were tested for spatial autocorrelation in A_{NDVI} by computing Moran's I for the residuals of the regression model (Mod. 2.1). Analyses were performed in R including R-packages *FD* (Laliberté and Shipley, 2010), ape (Paradis et al., 2008), lme4 (Bates, 2010) and Vegan (Oksanen et al., 2007).

2.3 Results

No spatial autocorrelation could be detected between the pixels' NDVI anomaly (MORANS's I: I=6.29×10-5, P=0.377). Therefore, all pixels were further considered to be independent observations. Ten years of C_{SPEI} and NDVI anomaly data show high variance (Fig. 2.3), with a strong correlation between both variables β=0.55, P<0.001). C_{SPEI} explained 29% of the variance (P<0.001, R^2=0.291) and significantly predicted the average NDVI-anomaly (β=0.55, P<0.001, Fig. 2.3, Table. 2.1). This positive correlation between both variables indicates a decrease in the NDVI-anomaly with decreasing C_{SPEI} values.

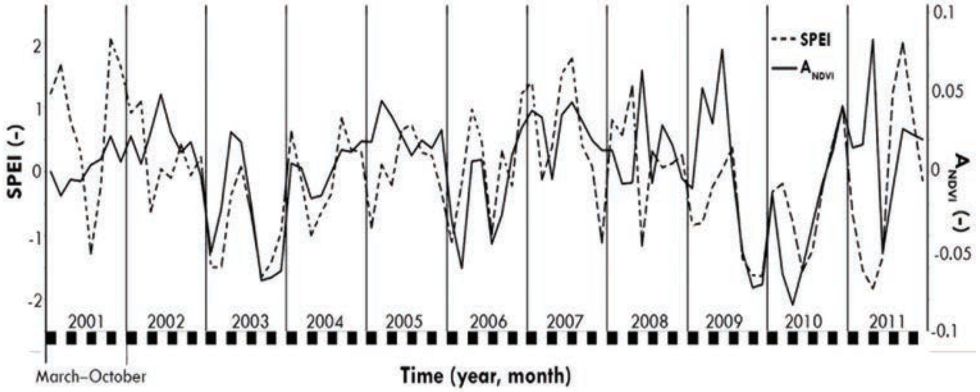


Figure 2.3. Time-series of both the monthly Standardized Precipitation and Evapotranspiration Index (C_{SPEI}; dotted line) and the NDVI-anomaly (average NDVI-anomaly (ANDVI); continuous line). Only the months of the growth season (March-October) are shown.

The response coefficients ($P_{response}$) of the pixels (i.e. the slopes of the regression line between A_{NDVI} and C_{SPEI} per pixel) were negatively correlated with species richness (P=0.007, R^2=0.11) and Shannon-Wiener diversity (P=0.041, R^2=0.06). Both Evenness (P=0.070, R^2=0.08) and functional diversity (P=0.246) showed no significant correlation with the response coefficient (Table 2.2, Fig. 2.4). There was no significant effect of vegetation type, or of the interaction between vegetation type and the diversity indices, on the response coefficients.

Table 2.1: Direct effects of SPEI on the average NDVI anomaly through linear regression.

NDVI anomaly	Df	Sum Sq ($\times 10^{-3}$)	Mean Sq ($\times 10^{-3}$)	F value	P	β	
C_{SPEI}	1	2.621	2.621	36.748	<0.01	0.55	a
Residuals	86	6.133	0.071				

^{a} indicates P<0.001

Table 2.1: Results from an analysis of variance, comparing two time-series of C_{SPEI} (N=80) and the average NDVI on 48 pixels as given in Fig. 2.3, through linear regression.

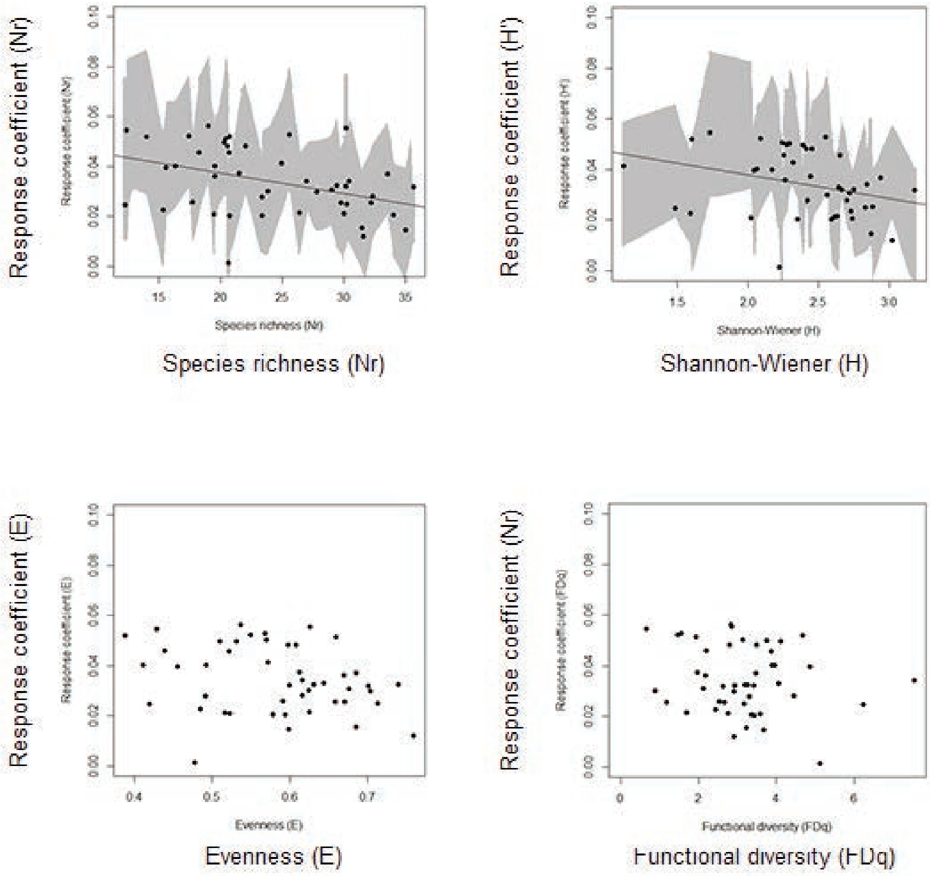


Table 2.2: Linear regression analysis of diversity indices and the response coefficients including the interaction effect with the vegetation type (phytosociological class) as fixed factor (N=48 pixels).

lm(Response~Div*V$_{class}$)

Regression	**df**	**Sum sq (×10^{-3})**	**Mean sq (×10^{-3})**	**F**	**P**	***β***	
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				

^{a} indicates $P<0.05$

Table 2.2: Linear regression analysis of diversity indices and the response coefficients over 10 years (N=48) according to model 2.2.

< Figure 2.4. Linear regression between diversity indices (a: Species richness (Nr), b: Shannon-Wiener (H'); c: Evenness (E); d: Functional diversity (FD$_Q$)) and the respective response coefficients. The 2.5% and 97.5% confidence intervals are given in the shaded area. Significances are indicated in Table 2.2.

2.4 Discussion

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

Overall, we observed a close correlation between the NDVI-anomaly patterns and the patterns of the Standardized Precipitation and Evapotranspiration Index (SPEI)-values derived from the KNMI meteorological database. Although there was a high variation in the response of each pixel, extreme drought events, reflected by SPEI lows occurring in 2003, 2006, 2009, 2010 and 2011 (Fig.2.3), also resulted in extremely negative NDVI anomalies. This is supported by the observed significantly positive correlation between the C_{SPEI}-values and the NDVI-anomaly. These results clearly indicate that variation in water availability in these natural dune grassland ecosystems strongly affect above ground biomass production, as reflected by the NDVI.

Species number, as well as species-based diversity indices, showed a significant interaction with the drought index in its relation with the NDVI-anomaly, and thus mediate the effect of drought on the NDVI response. The immediate effect of drought on the NDVI anomaly was stronger in grasslands with a higher species diversity, indicating an increased resistance against drought of species rich and diverse communities. Plant species richness was a better correlate of grassland ecosystem stability than species diversity, whereas there was no effect of evenness. This indicates that the presence or absence of species is of more importance than their relative abundance. Although no causation can be inferred, our results are in agreement with the findings of many experimental studies, which have reported a stabilizing effect of diversity on a variety of ecosystem functions including biomass production in grassland ecosystems (Ives and Carpenter, 2007). In particular, Gross et al., (2014) demonstrated a stabilizing effect of plant species richness on biomass production at the community level in 16 experimental grassland studies.

Biomass production at the population level, on the other hand, became less stable during environmental disturbances due to asynchronous species responses. As species richness increases in experimental grasslands, also the degree of asynchrony increases, leading to a higher chance of compensatory dynamics, i.e. that declines of some species are compensated by increases of others (Hector et al., 2010; Loreau, 2010; Gross et al., 2014). The net effect is an increased temporal stability of biomass production at the community level. Additionally, also small scale environmental heterogeneity may contribute to increasing stability (Pasari et al., 2013). As dune grassland systems are typically highly variable in water and nutrient availability across small scales (Cain et al., 1999), also spatial heterogeneity, in addition to temporal heterogeneity, may have a role in stabilizing the ecosystems' output. Indeed, a larger local species pool increases the chance of exploiting the variety of available resources, resulting in spatial complementarity (Ozinga et al., 1997; de Mazancourt et al., 2013).

There was no significant effect of plant functional diversity on grassland ecosystem stability. Petchy and Gaston (2002), indicated that in an assemblage with a limited trait dimensionality, the number of traits considered may affect the observed relation between functional diversity, redundancy and stability. Therefore, we cannot exclude that the absence of a significant correlation is related to both the relatively limited number of quantitative traits that could be taken into account and the number of species for which trait values were available (Pakeman, 2014). In addition, it must be noted that the functional data used, were collected for a wide array of applications, mostly others than for this study. However, we believe that the current selection of traits is highly relevant in a context of drought response (Taugourdeau et al., 2014). However, the better correlation of species diversity indices as compared to functional diversity indices is in agreement with the idea that functional redundancy may be of more importance than functional diversity, and that redundancy may limit the influence of functional diversity on the stability of the measured ecosystem function (Pillar et al., 2013). A higher number of species with similar functional trait values, though a differential temporal response to disturbance, increases the probability of functional complementarity, resulting in functional compensation. As dune systems are prone to drought, all species naturally present can be expected to be functionally equipped to cope with this to a certain extent. If this results in a relatively strong convergence in functional traits related to water stress, then individual species have a limited contribution to functional diversity, although they do add to functional redundancy.

Our findings also support Kreyling et al., (2008), who found contrasting effects in different grassland communities, as well as the conclusions of Dalerum et al., (2012),who showed that an increased functional diversity of an assemblage of plant species does not necessarily lead to a higher stability. Although trait databases are already an important source to find such information, many data are lacking or has a high intra-species variability due to trait plasticity or due to different measurement circumstances (Cordlandwehr et al., 2013). Additional extensive measurements of traits in the field are necessary to fill the data gaps and strengthen the outcome of trait-based analyses. This includes collecting trait data on species with low abundance, which may also contribute to biomass stabilization (Walker et al., 1999). Also in situ measurements of trait values of individual species combined with in situ measurements of biomass production data may provide important data . This stresses the continuing importance for the compilation and supplementation of large observational databases containing data on species and functional traits (Cadotte et al., 2009) .

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

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

Acknowledgements

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Luzula campestris

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

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Abstract

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. In this study 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. 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.

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.

3.1 Introduction

Grasslands cover 20 to 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 worldwide 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, hay making 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 (Ceulemans et al., 2014; Wesche et al., 2012). 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 (De Keersmaecker et al., 2014; De Keersmaecker et al., 2015b; Lhermitte et al., 2011; Lhermitte et al., 2010). 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 (Pettorelli et al., 2014; Vern & Paruelo 2010). 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.

3.2 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 (Ceulemans et al., 2014; Wesche et al., 2012).

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. Second, 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 3.1). 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.

Table 3.1: General overview of properties of semi-natural and inte agricultural grasslands

Property	**Intensively managed agricultural grassland**	**Semi/natu**
Plant species diversity	Low	High
Irrigation	Often present	Absent
External fertilization	Present	Absent
Mowing/grazing frequency	Mostly high	Low

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, i.e. the NDVI (Gu, Wylie & Bliss 2013; Lhermitte et al., 2011; Li et al., 2013; Pettorelli et al., 2005). 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 to 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. 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, i.e. 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 B-I of Appendices. The assessment of climate anomalies during the 2000–2013 period was based on meteorological data, i.e. 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, i.e. the Standardized Precipitation and Evapotranspiration Index (SPEI; Beguería, Vicente-Serrano & Angulo-Martínez 2010; Vicente-Serrano, Beguería & López-Moreno 2010) with a time-scale of three 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 (Eq. 3.1;

De Keersmaecker et al., 2015a):

$$\mathrm{NDVI}_{anom}(t) = c + \alpha\,\mathrm{SPEI}(t) + \beta\,T_{anom}(t) + \varphi\,\mathrm{NDVI}_{anom}(t-1) + E(t)$$

equation. 3.1

where $\mathrm{NDVI}_{\mathrm{anom(t)}}$ equals the standardized NDVI anomaly, 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 E(t) the residual term at time t. Each of these model coefficients can be related to vegetation stability metrics, as described in Table 3.2. 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. Second, 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. Third, if the amount of noise in the data is larger than the response of the vegetation, the fit of the model will be hampered.

Table 3.2: 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 zero and one 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 $T_{anom}(t)$)	Large absolute values indicate a low resistance to droughts/temperature anomalies, i.e. a large vegetation response to short-term droughts/ temperature anomalies	**Positive**: Wetter conditions/higher temperatures than average induce a positive NDVI response, i.e. an increase in biomass or vegetation greenness. Dryer conditions/lower temperatures than average induce a negative NDVI response, i.e. lower biomass or vegetation greenness. **Negative**: Wetter conditions/higher temperatures than average induce a negative NDVI response, i.e. a decrease in biomass or vegetation greenness. Dryer conditions/lower temperatures than average induce a positive NDVI response, i.e. higher biomass or vegetation greenness.

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 differ 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 3.3).

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. $p < 0.05$). 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.

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-

Table 3.3 Overview of the phytogeographical regions

Phytogeographical region	Characteristics	Dominant soil type	Dominant Phytosociological classification
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 peat and high pH	Peat	Molinio-Arrhenatheretea
Salt water, tidal area (SW)	Nutrient-rich, high salt content, under influence regular flooding by sea 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 sand, high water table variability	Clay, sand	Plantaginetea majoris, Molinio-Arrhenatheretea

natural versus intensively managed) was tested using the model of Eq. 3.2. The spatial correlation structure was also included in this model.

$$STAB_{\alpha|\beta|\varphi|RMSE} \sim c + \gamma VEG + \eta PHYT + \kappa PHYT * VEG + E$$

equation 3.2

where $STAB_{\alpha|\beta|\varphi|RMSE}$ 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 versus agricultural grassland); and PHYT the phytogeographical region. If the interaction term κPHYT × VEG of Eq. 3.2 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 Appendix B-IV in the Appendices.

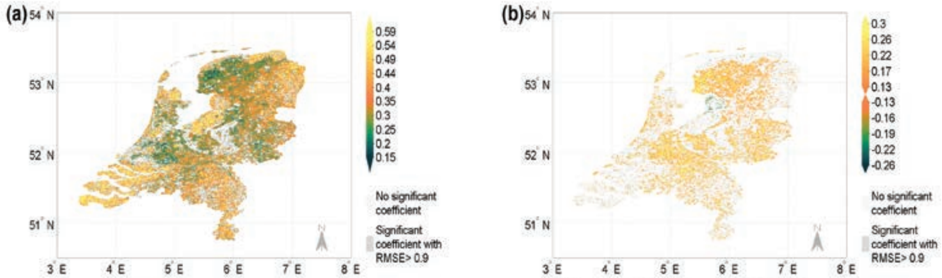
3.3 Results

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. 3.1b,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 < 0.9, 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. 3.1).

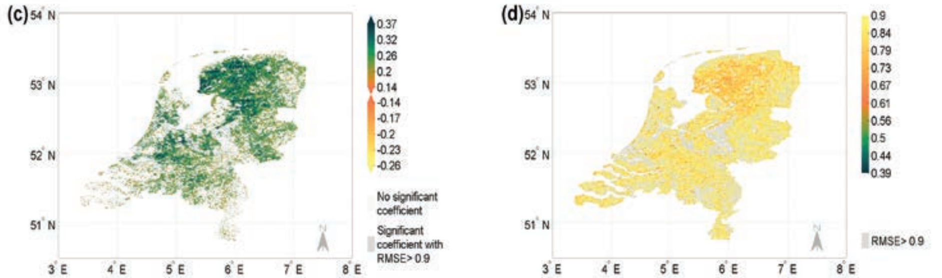
The percentage of pixels having a significant ARx model-based stability metric further differed between semi-natural and agricultural grasslands: the fraction of significant coefficients was much lower for semi-natural grasslands (i.e. 1, 16 and 20% lower for the resilience, resistance to drought and resistance to temperature anomalies, respectively) (Fig. 3.2). 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. 3.3). 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.

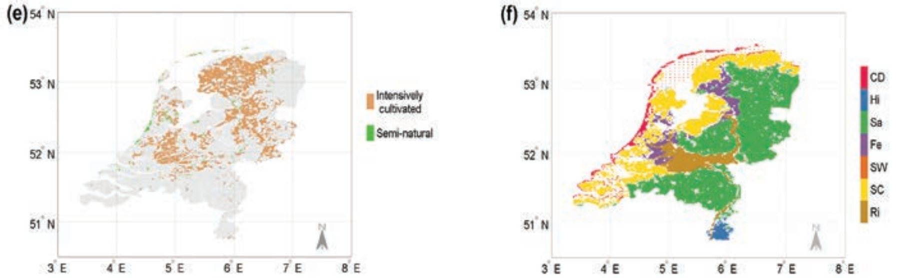
Comparison of the stability metrics and the ARx model error (RMSE) between



(a) φ coefficient of N DV I (t − 1) (b) α coefficient of SP EI (t)



(c) β coefficient of Tanom (t) (d) RMSE



(e) Grasslands (f) Phytogeographical regions

Figure 3.1: Spatial overview of vegetation resilience (φ coefficient of NDV I(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 subfigures 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.

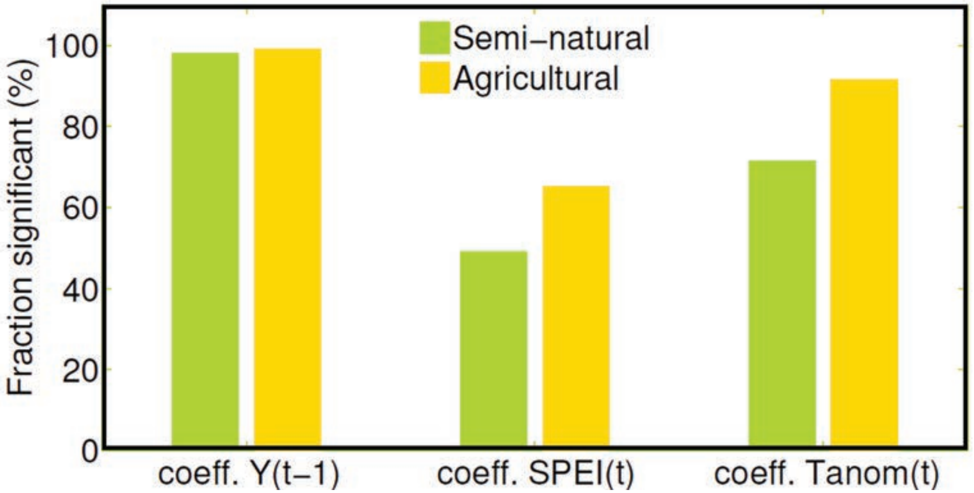


Figure 3.2: The fraction of significant coefficients for semi-natural and intensively managed agricultural grasslands for each of the three stability metrics: the resilience (φ coefficient of NDVI (t-1)), the resistance against drought (α coefficient of SPEI (t)) and the resistance against temperature anomalies (β coefficient of Tanom (t)).

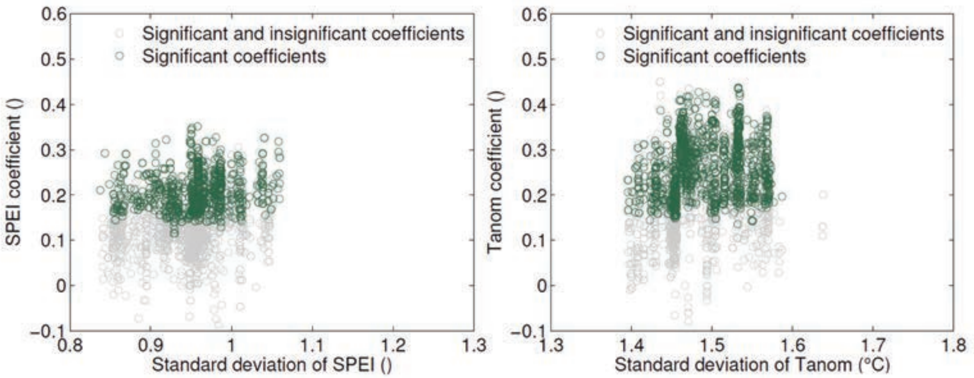
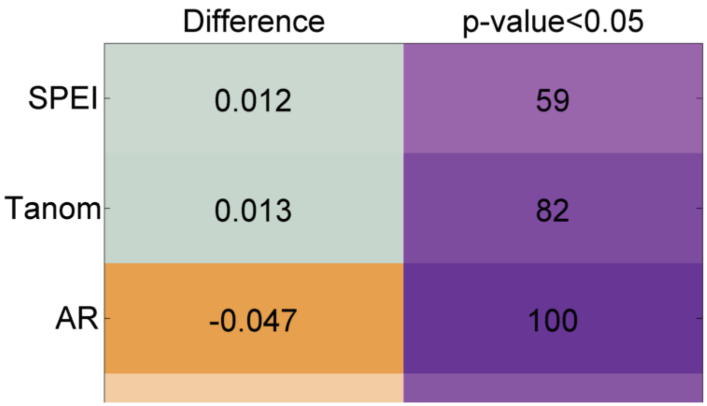


Figure 3.3: The values of the significant and insignificant Standardised Precipitation and Evaporation (SPEI) (a) and temperature anomaly (Tanom) (b) coefficients as a function of the standard deviation of the SPEI and temperature anomaly time-series, respectively.

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. 3.4). 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 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 Appendix B-II & B-III in the Appendices.

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. 3.5). 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.

Based on the test for each of the phytogeographical regions separately (Fig. 3.6), 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.

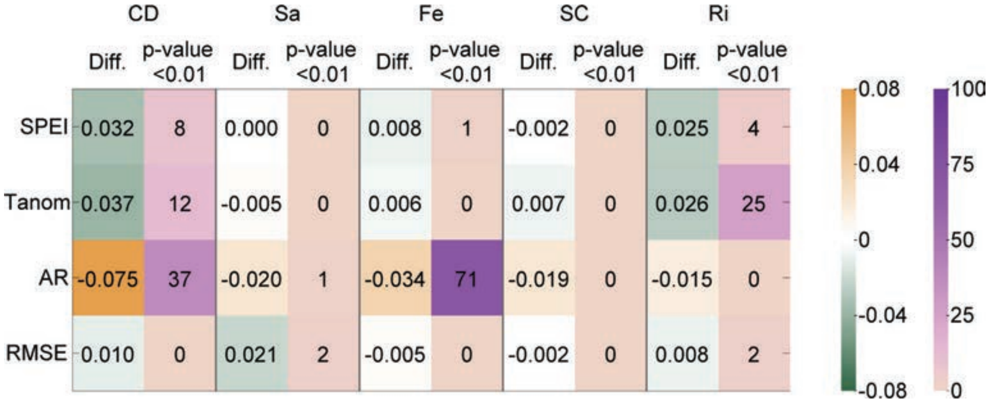


	Difference	p-value<0.05
SPEI	0.012	59
Tanom	0.013	82
AR	-0.047	100

Figure 3.4: 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 NDV I(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 $P < 0.05$ 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.

	Phyt.	Grassland	Phyt.*Grsslnd
SPEI	99	12	48
Tanom	100	100	66
AR	100	87	99
RMSE	100	33	2

Figure 3.5: The number of repetitions having a $P < 0.05$ 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 (Eq. 3.2).



	CD		Sa		Fe		SC		Ri	
	Diff.	p-value <0.01	Diff.	p-value <0.01	Diff.	p-value <0.01	Diff.	p-value <0.01	Diff.	p-value <0.01
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

Figure 3.6: 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<0.01 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 less than 10 pixels are not represented (grey colour) and phytogeographical regions without results are omitted from the table.

3.4 Discussion

In this study, we compared the biomass production stability, i.e. 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 (Ceulemans et al., 2013; Wesche et al., 2012), 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 (Loreau & Hector 2001; Tilman, Lehman & Thomson 1997). As a multitude of different species with a high functional trait diversity likely have a complementary effect during different types of disturbances, e.g. 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). Second, 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, i.e. species differ spatially and temporally in resource and habitat use and requirements, or they benefit from interspecific 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). As these mediating processes may be working simultaneously, more research is needed to disentangle them.

In contrast with vegetation resistance, the test on the resilience metric indicated that semi-natural grasslands were less resilient than agricultural grasslands, i.e. 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 approximately 48–99% of the resamplings the interaction factor between the grassland type (semi-natural vs. agricultural) and phytogeographical 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. Grasslands utilized for intensive agricultural use are situated in landscape positions that are better suited or their environmental conditions were optimized, e.g. 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 & 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.

Acknowledgements

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Gentiana cruciata

Biodiversity and stability in natural dune grassland ecosystems: a two-scales approach.

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Abstract

There is increasing experimental evidence that biodiversity stabilizes ecosystem productivity under climate extremes, which are expected to become more frequent worldwide Here we show that the results of these experiments, where species compositions are manipulated, hold across larger temporal scales in real-world unmanipulated ecosystems, even when environmental variation across sites is taken into account. Based on long-term species composition and remote sensing data, we show that over years with climate extremes, ecosystem productivity of dry dune grassland communities was significantly more stable with higher plant species richness. Our results suggest that experimentally determined diversity-stability relationships hold in large scale naturally assembled plant communities in the long term, underscoring the importance of biodiversity in natural ecosystems.

As global change drives climate change and increases the frequency of the occurrence of climate extremes, there is increasing interest in the mediating role of biodiversity in the stability of ecosystem functioning (Field & Van Aalst 2014). Where climate extremes such as extreme droughts may not only affect ecosystem functioning in general but also jeopardizes ecosystem services (e.g. food- and energy provision, carbon cycling and coastal defence), the global decrease in biodiversity may increase the risk of failing ecosystem services in the near future (Butchart et al., 2010). Ecosystem productivity, in particular, is generally considered as a good indicator for ecosystem functioning. Where primary productivity is associated with growth and survival of plants, on a community level it is directly linked to many ecosystem services.

There is increasing experimental evidence that biodiversity stabilizes ecosystem productivity under climate extremes. Work dating back to research of Elton (1958) and May (1971), formed the basis of the theory that a higher biodiversity promotes a higher stability during environmental disturbances. The realisation that biodiversity is decreasing globally and that this may have consequences for a range of ecosystem services of societal importance has increased the interest in studies on diversity-stability relationships (Cardinale et al., 2012).

The insurance hypothesis, proposed by Yachi and Loreau in 1999, infers that the mediating effect of plant species diversity on the temporal stability of ecosystem functioning is largely based on the phenomenon of compensatory dynamics. In this hypothesis, a negative change in the functioning of one species, for example caused by a disturbance, is compensated by a positive change in functioning in another species, resulting in an overall stabilization of ecosystem functions such as biomass production. An asynchronous response of different species within a community to different disturbances, driven by interspecific variation in ecological strategies and temporal discrepancy, leads to temporal complementarity. Moreover, while the importance of interspecific competition for resources decreases, the compensatory dynamics of some species may result in a temporary overyielding (an increased biomass production of a species in a mixed-culture compared to the biomass production of that species grown in mono-culture), buffering the general output of the community (Loreau & Mazancourt 2013).

Experimental work, in which plant species richness could be manipulated in artificial grassland plots, provided evidence for this hypothesis, showing both a positive diversity-productivity as well as a positive diversity-stability relationship under influence of environmental drought (Tilman & Downing 1996; Tilman et al., 2001; Gross et al., 2014). Isbell et al., (2015) substantiated this consistent diversity-stability relationship in their recent meta-analysis of 46 experiments, demonstrating that the productivity of species-rich grasslands generally has a higher resistance to climate anomalies than species-poor grasslands. However, there is little evidence that these relationships hold in naturally assembled plant communities. For experimental studies are all relatively small-scaled and ex situ, it is hard to extrapolate the results to scales relevant for management and policy (Hector et al., 2010). In order to make reliable estimations of diversity and stability measures in field situations, large amounts of observational data are indispensable. It remains a challenge to obtain sufficient data both on large spatial and temporal scales (Grman et al., 2010). In order to measure biomass production as an ecosystem function, remote sensing techniques are capable to cover large spatial scales, using satellite imaging derived Normalised Difference Vegetation Index (NDVI) values, but still lack the spatial resolution to accurately measure biodiversity. Van Rooijen et al., (2015) showed a positive diversity-stability relationship in natural dune grassland ecosystems using remote sensing derived data on ecosystem functioning and approximations on diversity derived from vegetation databases. Due to the restricted availability of remote sensing data, time-series were limited to a length of ca. 10 years. In order to increase the precision of diversity assessments and up-scale observations in time, series of permanent vegetation plots may be applied. Time-series of repeatedly recorded vegetation plots can provide accurate measurements of plant species-richness and provide insight in vegetation development over time (Kuiters et al., 2009).

In this study we aim to test whether the experimentally established relationships between resistance of aboveground productivity to climate anomalies and plant species richness hold in naturally assembled grassland communities over larger temporal scales, using time-series of permanent vegetation surveys in order to accurately determine plant species-richness and assess ecosystem functioning during drought variability over time. We exploit the Dutch National Vegetation Database which contains a large amount of permanent plot series including a dataset of 57 time-series of permanent plots made between 1953 and 2012, distributed over 900 ha of dry dune grassland (Schaminée et al., 2012). In order to assess environmental drought, georeferenced historical meteorological data can be derived from SPEIbase (Beguería et al., 2010). In addition indicators of abiotic site conditions are calculated to control for the effects of environmental heterogeneity across sites.

4.2 Methods

A dataset was compiled of 29 vegetation plots (relevés of 8×4m) that were repeatedly recorded (approximately every 4 years between 1953-2012). Proxies for productivity were used to calculate a resistance indicator *sensu* Isbell et al. (2015). The effect of diversity on resistance under climate extremes (SPEI-3 data) was tested and site-specific Wamelink indicator values were used to correct for environmental co-variables. In order to compare permanent plot measurement and remote sensing derived data, an additional dataset was compiled including the sum of 16-day NDVI-data of 22 selected MOD13Q1v6 pixels (250×250m) (Didan 2015) during the growth season (2000-2014). Resistance was calculated as the response-coefficient of ΔNDVI ~ SPEI-values (van Rooijen et al., 2015). The effect of diversity on resistance was tested together with Wamelink environmental indicators.

Selection of study sites

This study focuses on calcareous dune grassland ecosystems of the Meijendel dune area, near Wassenaar and The Hague, covering an area of approximately 2000 ha along the south-western coast of the Netherlands (N52,8, E40,2, Figure 4.1)). Syntaxonomically, the vegetation types incorporated in the dataset are classified predominately as Koelerio-Corynephoretea. All permanent plots are located in an area which falls under Natura 2000 legislation and is extensively managed by seasonal grazing with cattle. The area is managed and exploited for tap water by a drinking water company (Fig. 4.1).

Community leaf biomass, a proxy for plot productivity (P_n) was calculated using equation 4.1 where SLA is the Specific Leaf Area ($mm^2.mg^{-1}$) per species (s) and Leaf Area Index (LAI) as the leaf area per unit ground surface area per species ($mm^2.mm^{-2}$). LAI is often used as an indication for aboveground productivity and is associated with optical remote sensing products such as NDVI (Carlson & Ripley 1997; Rocchini et al., 2015) and give reasonably high correlations to measured biomass in grassland vegetation when compared with NDVI ($R^2 \approx 0.6-0.75$) (Dusseux et al., 2015). Species-specific SLA values were derived measurements included in the LEDA functional trait database (Kleyer et al., 2008).

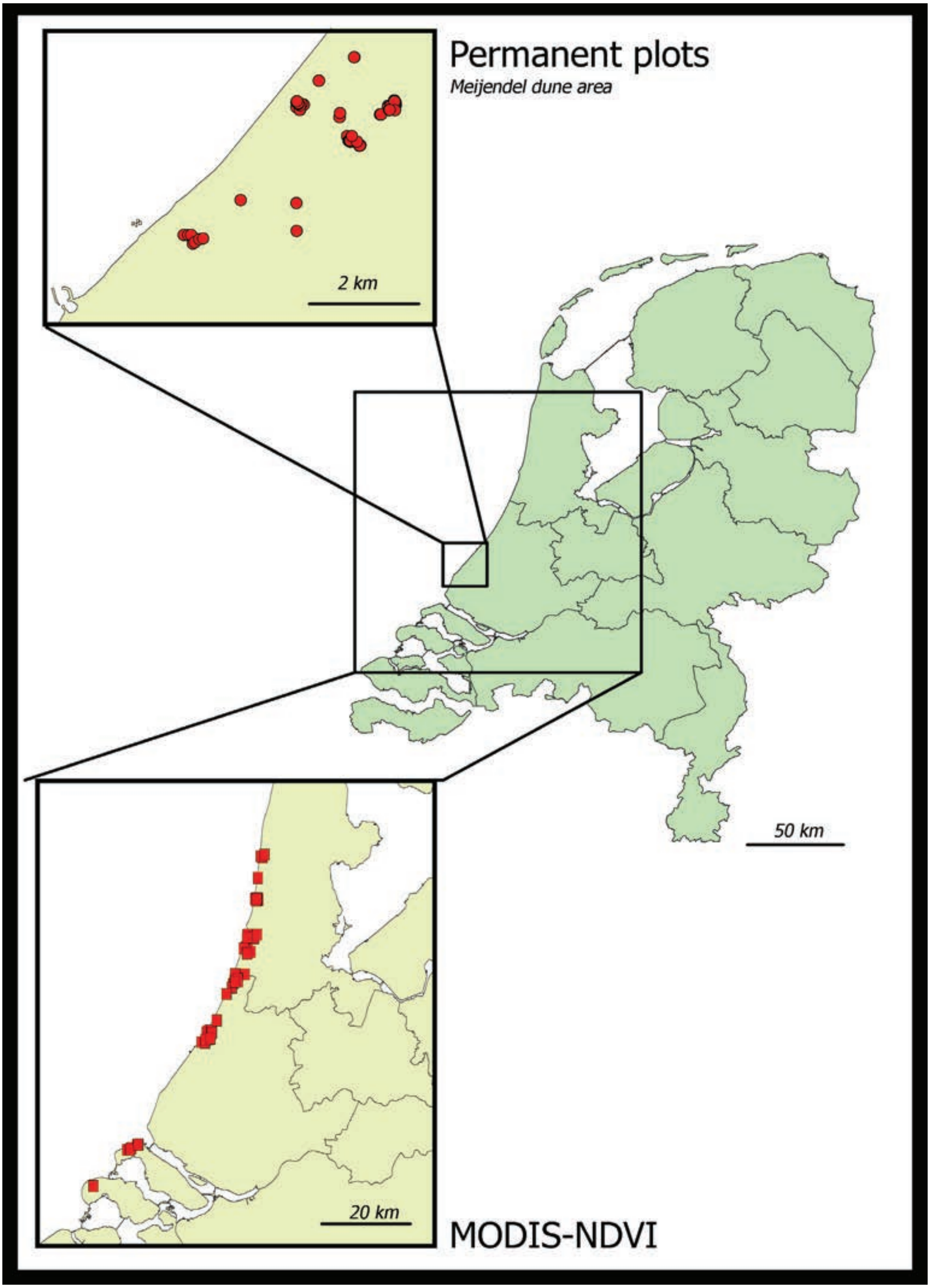


Figure 4.1. Location of the final selection of permanent plot surveys and the MODIS NDVI pixels at the western coastal area of the Netherlands.

$$\mathrm{P_e} = \sum\left(\frac{\mathrm{LAI_s}}{\mathrm{SLA}_s}\right) \qquad \textit{equation. 4.1}$$

Long term average of P_n (P_e) was used to calculate an indication for resistance (Ω) for each permanent plot (pq), following equation 4.2.

$$\Omega_{pq} = \frac{\mathrm{P_n}}{|\mathrm{P_e} - \mathrm{P_n}|} \qquad \textit{equation. 4.2}$$

The effect of plant species richness (R) on the productivity (P_e) was tested according to model 1 adding climate (C_{Dir}.: wet or dry, and Intensity C_{Int}.: absolute 3-SPEI-values) as fixed factor. The effect of plant species richness (R) on the resistance (Ω_{pq}) was tested according to model 2. In both models abiotic co-variables were included.

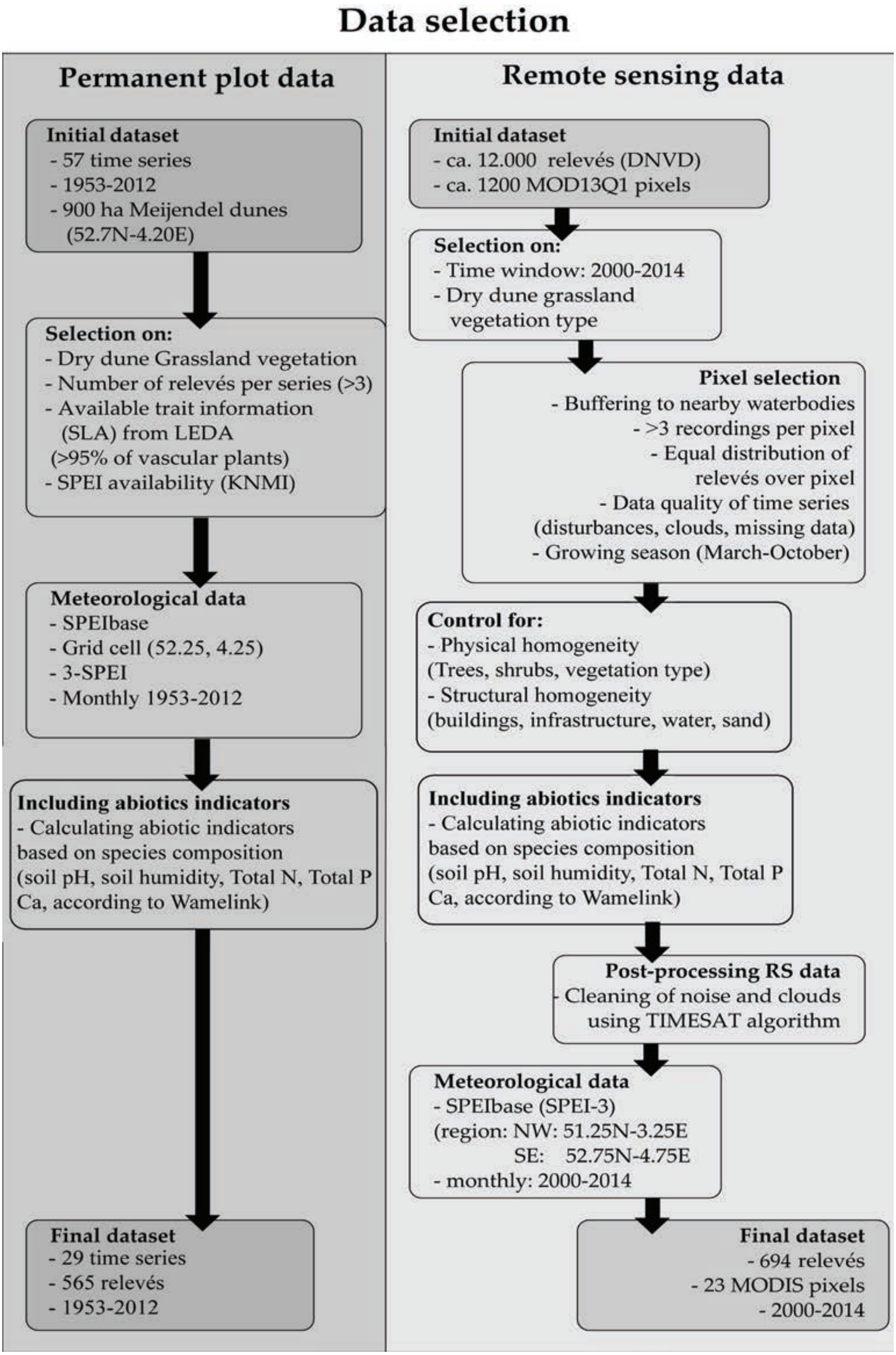
$$P_e \sim R_{pq} \times C_{Dir} \times C_{Int} + V_{pH/H/N/p/Ca} \qquad \textit{model 4.1}$$

$$\Omega_{pq} \sim R_{pq} \times C_{Dir} \times C_{Int} + V_{pH/H/N/p/Ca} \qquad \textit{model 4.2}$$

Remote sensing data set

All observations in the remote sensing dataset were obtained via NASA's TERRA/AQUA satellite observation program (Didan 2015). The selected pixels were situated in natural calcareous dune grasslands along the western coast of the Netherlands (Fig. 4.1). All available observations fell in years with climate extremes in the study area (an average deviation of the SPEI-value from zero to 0.35 (σ=0.35) during growth seasons) and therefore, in contrast to the permanent plot dataset, no reliable resistance measure could

> Figure 4.2. Flowchart indicating the steps made in selecting both the permanent plot dataset and the remote sensing dataset. Both subsets of data were checked for homogeneity of the vegetation using ground based vegetation recordings (relevés). Large physical disturbances which may have an effect on NDVI measurements (i.e. large unvegetated areas, infrastructure, buildings or water) in the landscape were excluded from the final selection.


Data selection
Permanent plot data
Initial dataset
- 57 time series
- 1953-2012
- 900 ha Meijendel dunes
(52.7N-4.20E)
Selection on:
- Dry dune Grassland vegetation
- Number of relevés per series (>3)
- Available trait information
(SLA) from LEDA
(>95% of vascular plants)
- SPEI availability (KNMI)
Meteorological data
- SPEIbase
- Grid cell (52.25, 4.25)
- 3-SPEI
- Monthly 1953-2012
Including abiotics indicators
- Calculating abiotic indicators
based on species composition
(soil pH, soil humidity, Total N, Total P
Ca, according to Wamelink)
Final dataset
- 29 time series
- 565 relevés
- 1953-2012
Remote sensing data
Initial dataset
- ca. 12.000 relevés (DNVD)
- ca. 1200 MOD13Q1 pixels
Selection on:
- Time window: 2000-2014
- Dry dune grassland
vegetation type
Pixel selection
- Buffering to nearby waterbodies
- >3 recordings per pixel
- Equal distribution of
relevés over pixel
- Data quality of time series
(disturbances, clouds, missing data)
- Growing season (March-October)
Control for:
- Physical homogeneity
(Trees, shrubs, vegetation type)
- Structural homogeneity
(buildings, infrastructure, water, sand)
Including abiotics indicators
- Calculating abiotic indicators
based on species composition
(soil pH, soil humidity, Total N, Total P
Ca, according to Wamelink)
Post-processing RS data
- Cleaning of noise and clouds
using TIMESAT algorithm
Meteorological data
- SPEIbase (SPEI-3)
(region: NW: 51.25N-3.25E
SE: 52.75N-4.75E
- monthly: 2000-2014
Final dataset
- 694 relevés
- 23 MODIS pixels
- 2000-2014

be calculated. Instead, a resistance indicator (Ω_{px}) was calculated using the inverse response coefficient of each MODIS-pixel to 3-SPEI-values (equation 4.3). The advantage of this approach is that the resistance measure is not calibrated on the average productivity measure affected by climate anomalies, but on relative changes in productivity in relation to a change in the climate measure. Diversity (R_{px}) was calculated as the average of the time-series. Diversity-productivity relations were tested using model 4.3, where P is an indicator for primary productivity (P) based on the monthly sum of NDVI-observations per MODIS-pixel. To correct for phenological effects, the month (T_m) of observation was added as a fixed effect. The response coefficient was calculated using a linear regression model (model 4.2) where ΔP_{px} is the change in NDVI (P) values during the average monthly 3-SPEI value (C_{SPEI}) during the growth season (March-October) of each year (2000-2014). Again, to take phenology into account, the month (T_m) of observation was added as a fixed effect.

$$P_{px} \sim R_{px} + T_m \qquad \textit{model 4.3}$$

$$\Delta P_{px} \sim C_{SPEI} + T_m \qquad \textit{model 4.4}$$

$$\Omega_{px} = -|\delta y/\delta x| = -|\, \delta(P_{px}) / \, \delta(C_{SPEI} + T_m)| \qquad \textit{equation 4.3}$$

The effect of pixel plant species richness R_{px} on resistance (Ω_{px}) was tested using model 4.5.

$$\Omega_{px} \sim R_{px} + V_{pH/H/N/p/Ca} \qquad \textit{model 4.5}$$

Abiotic co-variables

To limit the potential effect of confounding environmental variables, pixels and vegetation recordings were carefully selected (Fig. 4.1). However, as environmental conditions may still vary and affect productivity and resistance measures (Rammig & Mahecha 2015). To test the effect of abiotic indicator values were calculated for each permanent plot (pq) or MODIS-pixel (px) by using independent species-specific Wamelink indicator values (Wamelink et al., 2002; Wamelink et al., 2005) for some major environmental factors: soil pH, soil moisture (H), Calcium content (Ca), and soil total Nitrogen content (N) and soil total Phosphorus content (p) as nutrient indicators. The weighted average of these values gives reliable proxies for site-specific environmental conditions associated with biomass productivity and environmental drought (van Goethem et al., 2015). Average plot and pixel indicator values were calculated based the relative species composition per plot. To correct for their effects abiotic co-variables (V) were added as fixed factors to the models.

4.3 Results

The results based on linear regression analyses on data derived from the permanent plot observations as well as the results of the analyses based on remote sensing data, both show a significant positive correlation between plant species richness and the resistance (Fig 4.3). In the permanent plot dataset the direction (dry or wet, negative versus positive SPEI-values) did result in the same relationship (Fig 4.3a).

Table 4.1 presents the results of linear regression analyses where environmental co-variables were included. In addition to the results resulting in the correlation depicted in Figure 4.3, also the relationship between diversity and productivity are showed, including the environmental co-variables. Productivity was significantly correlated with climate co-variables. The intensity of the SPEI was strongly correlated with productivity and direction (dry or wet) was significantly related to productivity in the permanent plot observations. Although only soil moisture showed a significant effect on the diversity-productivity relationship in permanent plots, in the remote sensed observations nitrogen, pH, soil type, moisture and calcium-content did significantly affected that relationship (Table 4.1).

When looked at resistance as a measure for stability, the results show no significant effect of environmental co-variables. Climate co-variables did not significantly affect the diversity-stability relation in permanent plot time-series, irrespective of the intensity and direction of the SPEI-values. Because these climate co-variables were included in the resistance-measurement for the remote sensing derived dataset, this was not included in the results. In both approaches, the soil-related co-variables did not significantly interact with the diversity-stability relationship (Table 4.1).

Table 4.1 | Results of linear regression models testing the relation between plant species richness and climate (SPEI) for productivity and resistance of both the permanent plot time series and the time series of remote sensed (RS) (NDVI-MODIS) pixels. In addition of effects environmental co-variables are tested.

	Permanent plots			**Remote sensing**		
Productivity						
D	$F_{(1,83)}$=	134.100	***	$F_{(1,1666)}$=	14.060	***
Dir	$F_{(1,83)}$=	2.518	n.s	$F_{(1,1666)}$=	0.282	n.s.
Int	$F_{(1,83)}$=	14.830	***	$F_{(1,1666)}$=	19.634	***
D × Int	$F_{(1,83)}$=	1.052	n.s	$F_{(1,1666)}$=	0.504	n.s.
D × Dir	$F_{(1,83)}$=	3.891	*	$F_{(1,1666)}$=	1.244	n.s.
N	$F_{(1,83)}$=	1.258	n.s.	$F_{(1,1666)}$=	14.450	***
P	$F_{(1,83)}$=	2.621	n.s.	$F_{(1,1666)}$=	0.920	n.s.
pH	$F_{(1,83)}$=	0.297	n.s.	$F_{(1,1666)}$=	20.670	***
Moisture	$F_{(1,83)}$=	7.273	**	$F_{(1,1666)}$=	28.435	***
Ca	$F_{(1,83)}$=	0.541	n.s.	$F_{(1,1666)}$=	10.2405	**
Resistance						
D	$F_{(1,77)}$=	4.066	**	$F_{(1,13)}$=	7.926	**
Dir	$F_{(1,77)}$=	0.098	n.s.		-	
Int	$F_{(1,77)}$=	1.080	n.s.		-	
D × Int	$F_{(1,77)}$=	0.121	n.s.		-	
D × Dir	$F_{(1,77)}$=	0.073	n.s.		-	
N	$F_{(1,77)}$=	1.502	n.s.	$F_{(1,13)}$=	0.008	n.s.
P	$F_{(1,77)}$=	0.647	n.s.	$F_{(1,13)}$=	0.456	n.s.
pH	$F_{(1,77)}$=	0.488	n.s.	$F_{(1,13)}$=	1.608	n.s.
Moisture	$F_{(1,77)}$=	0.060	n.s.	$F_{(1,13)}$=	0.120	n.s.
Ca	$F_{(1,77)}$=	0.055	n.s.	$F_{(1,13)}$=	0.456	n.s.

(P<0.1), **(P<0.01), *(P<0.001), $^{n..s}$ (non-significant)*

Results of linear regression models. a). Permanent plot dataset: N=29, 1953-2012 (per measurement period) , according to model 4.1; b) Remote sensing dataset: N=23, 2000-2014 (monthly), according to model 4.2. D: Plant Species richness, Dir: Wet, Dry, Int: Intensity (absolute SPEI), pH: Soil pH, H: Soil moisture, Ca:Calcium content, N: Total Nitrogen content, P: Total Phosphorus content. All variables were calculated according to Wamelink Indicator values and were log-transformed. SPEI values during growth season. Remote Sensing resistance measure includes climate variables which are excluded from further testing.

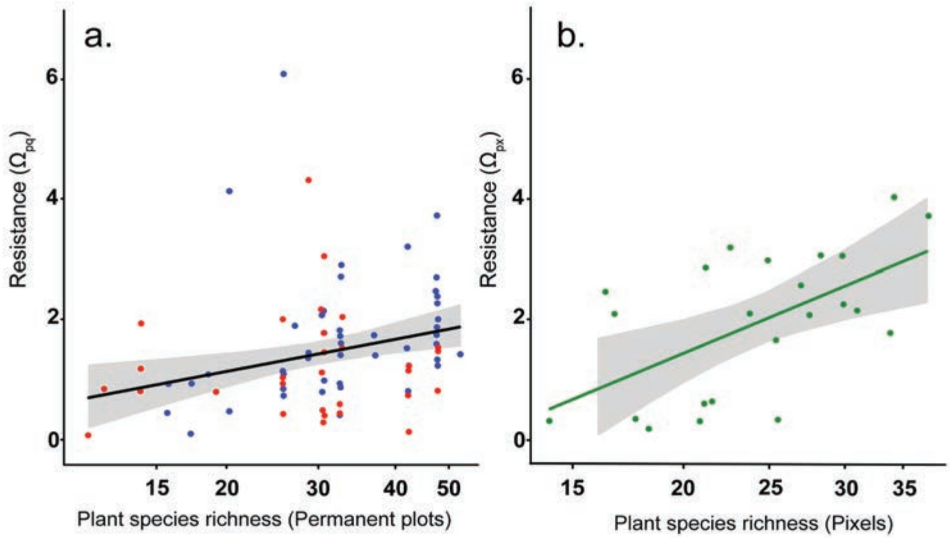


Figure 4.3| Linear regressions between plant species richness and the resistance (unitless values) of biomass indicators of permanent plot series (a) and remote sensing pixels (b). Plant species richness was assessed using (a) the long-term average of each permanent plot time-series (an indicator for long-term plant species richness (r=0.85, P<0.001)) and (b) by matching georeferenced vegetation recordings made prior to the start of the remote sensing observations of the MODIS pixels. Species richness within the MODIS pixels did not significantly change over time. In a, colours indicate drought (red: SPEI<0.) and wet conditions (blue: SPEI>0). Shaded area's show 95% confidence levels. Axes are logarithmic. Significances are indicated in Table 4.1.

< Results of linear regression models. a). Permanent plot dataset: N=29, 1953-2012 (per measurement period) , according to model 4.1; b) Remote sensing dataset: N=23, 2000-2014 (monthly), according to model 4.2. D: Plant Species richness, Dir: Wet, Dry, Int: Intensity (absolute SPEI), pH: Soil pH, H: Soil moisture, Ca:Calcium content, N: Total Nitrogen content, P: Total Phosphorus content. All variables were calculated according to Wamelink Indicator values and were log-transformed. SPEI values during growth season. Remote Sensing resistance measure includes climate variables which are excluded from further testing.

4.4 Discussion

There is convincing experimental evidence that biodiversity can stabilize ecosystem productivity under climate extremes. However experiments are often relatively small-scaled and plant species composition are generally manipulated, hampering the interpretation and extrapolation to real-world ecosystems. The general aim of this study was to test whether experimentally established relationships between resistance of aboveground productivity to climate anomalies and plant species richness hold in naturally assembled grassland communities. We show that the stabilizing effect of species richness on productivity hold across larger temporal scales in real-world unmanipulated dune grasslands, even when environmental variation across sites is taken into account.

Primary productivity of repeatedly recorded permanent plots in natural dune grassland was used as an indicator for ecosystem functioning (Tilman et al., 2014). This measure has previously shown to provide reliable estimates of community leaf biomass and is comparable to measurements derived from optical remote sensing products such as Normalized Difference Vegetation Index (NDVI) (Carlson & Ripley 1997; Running & Zhao 2015), however at a very precise spatial resolution. Subsequently as a productivity resistance indicator was calculated sensu Isbell et al., (2015)), including the proportional changes in primary productivity with the long-term average. As an indicator for the direction and intensity of the climate extremes, the Standardized Precipitation and Evapotranspiration Index (SPEI) values for each period between the recordings was calculated (Isbell et al., 2015), based on georeferenced measurements from SPEIbase (Beguería et al., 2010). Combining these data, a significant positive correlation was found between the resistance of aboveground biomass production and plant species richness (Fig 4.3a, Table 4.1).

Additionally, we used time-series of remote sensing measurements of NDVI values which were used as a proxy for productivity (van Rooijen et al., 2015). When using permanent plot surveys of vegetation, the absence of productivity measurements makes it necessary to calculate a proxy in order to assess productivity. Using remote sensing measurements of primary production via NDVI, productivity can be assessed directly (Keersmaecker et al., 2014). However, data on plant species richness within the unit of remote sensing measurements, pixels, are generally absent. By combining the data of the georeferenced pixels with georeferenced vegetation surveys under strict conditions (Figure 4.2) an assessment of biodiversity is possible (van Rooijen et al., 2015). Again, a significant positive relationship between species richness and resistance was found (Fig. 4.3b, Table 4.1), confirming the relationship found on permanent plots on an extended spatial scale.

In order to distinguish the impact of drought, SPEI-data was divided into a measure for direction (surplus or deficit of precipitation) and the intensity (absolute SPEI value). The effects of weather extremes in particular can clearly be observed when looked at the changes in productivity, showing a consistent significant effect of intensity on biomass production, irrespective of the direction. The effects of drought on stability however were not significant, being largely eliminated by diversity effects. As the stability term of the relatively short term remote sensing derived observations includes SPEI-values, the stability-drought interaction was not tested separately.

Previous studies on the diversity-stability relationship that were conducted in natural communities (McNaughton 1977; Tilman & Downing 1996) did not sufficiently take potential confounding effects (Grman et al., 2010) of differences in environmental conditions into account (Huston 1997). This study attempts to include abiotic environmental conditions into the analyses. Although the selection procedures in compiling the dataset resulted in a dataset as homogenous as possible, dune grasslands are spatially heterogeneously distributed (Assendorp 2010). To correct for abiotic co-effects in our analyses, we derived environmental variables from the actual plant species composition based on species-specific Wamelink indicator values, resembling Ellenberg indicator values (Ellenberg et al., 1991) but specifically developed for the Netherlands by Wamelink et al., (2002). It was shown that the abiotic co-variables affect primary production (Table 4.1). Nitrogen (N) and phosphate (P) indicators were included as a measure for nutrient availability, promoting biomass production (Bloor & Bardgett 2012). Soil calcium (Ca)- content and soil pH have an effect on the nutrient uptake ability of plant species and was therefore added to the analyses (Provoost et al., 2002). Soil moisture affects both the ability of nutrient uptake as the nutrient availability needed for primary production and indicates the buffer capacity of a soil during a precipitation deficit. Moreover, the available soil moisture may have an effect on the impact of drought (Tilman & Downing 1996). Notably, these environmental variables did not interact with plant species diversity as the main factor determining the stability of productivity during drought. These findings were substantiated in analysing the remote sensing dataset. Again, environmental conditions did have an effect on productivity itself, but no significant interaction between environmental conditions and the diversity-stability relationship were found. These corresponding results suggest a dominant role of plant species richness in maintaining ecosystem functioning under environmental disturbances, irrespective of abiotic conditions.

This study explores the potential of combining large datasets with long-term vegetation data derived from natural ecosystems with remote sensing techniques in order to extrapolate the results found in biodiversity experiments to ecosystem functioning in natural communities. The first approach has the advantage of providing detailed information from a specific field site and the possibility of creating time-series of several decades. Remote sensing techniques currently lack the same amount of detail and temporal scales, but can monitor much larger areas with much less effort, We therefore urge the need for more research in combining these techniques. The main difficulty lies in the discrepancy in time and space between the different datasets which therefore need to be adapted to one another. The chance of calculation errors, statistical complexity, and the need to exclude valuable data due to scale mismatches is still challenging the wide application of these large datasets in research (Rocchini et al., 2015). Additionally, the majority of the historical data used in this research was collected with a different objective and often lacks the details needed and therefore the calculation of proxies is required.

Combining different monitoring techniques as done in this project may enhance the predictive power of the results by comparing and verifying the study’s outcome through different approaches. Much can be gained by a more uniform and integral approach of the databases, minimising the amount of missing data. Where remote sensing observations are developing at a rapid pace, field observations of ecosystems and biodiversity are developing less uniformly. Available data is often linked to specific research topics, while general monitoring programs are increasingly abandoned (Chytrý et al., 2014).

We stress the importance of general monitoring of biodiversity, especially regarding the applicability of large data sets of large scale biodiversity over time in predicting and modelling ecosystem responses to large environmental changes. An increasing availability of more data including a range of environmental conditions and ecosystems at high spatial and temporal resolutions offers new opportunities in understanding ecosystem response mechanisms during climate events and global change and may help to develop strategies to maintain ecosystem services (Grimm et al., 2013).

Conclusions

Current climate models predict an increase in the frequency and magnitude of ecosystem disturbances. In addition, a range of anthropogenic activities causes a decrease in species diversity. Meanwhile, the increasing experimental evidence for a positive relationship between diversity and stability of ecosystem functioning, stresses the important role of biodiversity in maintaining ecosystem functioning. While gaining more experimentally derived insight into the ecological mechanisms behind ecosystem stability, there is a growing interest in translating these results to management- and policy-relevant scales (Grace et al., 2016). In this study we demonstrate that the diversity-stability relationship holds in naturally assembled unmanipulated ecosystems.

Both decades of localized species composition data as well as large-scale remote sensing data show that over years with climate extremes, ecosystem productivity of dry dune grassland communities was significantly more stable with a higher plant species richness. A complex of environmental factors determines ecosystem functioning, but by correcting for these factors in our analyses, this study indicates that the role of biodiversity remains vital in stabilizing ecosystem functioning under climate extremes. Our work shows the potential of long-term data series in natural ecosystems in combination with remote sensing techniques for extrapolating experiments on biodiversity and ecosystem functioning to natural communities (Hautier et al., 2015). Moreover, this study confirms the results of biodiversity experiments and underlines the value of species and biodiversity in natural ecosystems.

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Hieracium pilosella

Diversity-stability relationships are consistent across different natural grassland ecosystems in the Netherlands

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Abstract

There is mounting evidence that biodiversity has a mediating effect on the stability of ecosystem functioning under climate variability. However, most studies so far are based on relatively small-scale experiments representing a limited range of different ecosystems, where species composition in artificial communities is manipulated and confounding environmental factors are controlled for. This impedes the generalisation of diversity-stability relationships to management and policy relevant scales in natural ecosystems. This study aims to (1) quantify to what extent plant species-richness mediates stability of above-ground biomass production in different real-world (semi-) natural grassland ecosystems in the Netherlands under influence of fluctuating drought; and (2) quantify the possible effect of environmental co-variables on the diversity-stability relationship in temperate (semi-) natural grasslands across the Netherlands.

Our data set includes 150 time-series of 1,966 grassland vegetation recordings distributed over a range of semi-natural grassland ecosystems varying in plant species-richness and abiotic conditions, recorded across the Netherlands between 1930 and 2012. Stability (resistance) was quantified as the relative change in site-specific above-ground biomass production derived from historic time-series of relative abundance and species-specific biomass traits, relative to drought related climate variability. Drought related climate variability was based on the locally measured Standardized Precipitation and Evapotranspiration Index (SPEI). Environmental co-variables were assessed by using Wamelink Indicator values are based on site-specific vegetation data. Linear mixed-effect models were applied to test the relationship between stability and plant species-richness with relevant environmental co-variables: soil type, soil pH, soil moisture, soil nitrogen and soil phosphorus contents, and the physical geographical position.

Our results show that with as well as without including the set of environmental co-variables, there is a positive relationship between the stability of above-ground biomass production and plant species-richness . In other words, adding the environmental co-variables to the models did not significantly

affect the positive relationship between resistance and plant species-richness, suggesting a consistent diversity-stability relationship across all grassland habitats, irrespective of environmental abiotic conditions.

Plant species-richness is found to be the dominant factor in mediating variation in above-ground biomass production under drought stress. The diversity-stability relationships derived from experimental research is supported by this study in real-world ecosystems, at larger temporal scales and across different grassland habitats. This study underscores the consistent role of biodiversity in maintaining ecosystem functioning under external disturbances.

5.1 Introduction

There is a growing amount of evidence that plant diversity plays a crucial role in ecosystem functioning (Tilman et al., 2014), and that it increases the stability of ecosystem processes over time (Hector et al., 2010; Loreau & Mazancourt 2013; Isbell et al., 2015). These effects of biodiversity on the long-term stability of ecosystem functioning are of particular interest given the current, anthropogenically driven, global environmental change and the predicted increase in frequency and magnitude of climate extremes (Seneviratne et al., 2012). Moreover, if biodiversity generally proves to be critical in maintaining the stability of major ecosystem functions under external disturbances, its current decline (Butchart et al., 2010) may also jeopardize the provision of crucial ecosystem services which depend on these functions (Naeem et al., 2009; Hooper et al., 2012). The diversity-stability relationship reflects the theory of compensatory dynamics (Loreau & de Mazancourt 2013), assuming that a negative change in the functioning of one species is associated with a positive change in the functioning of another species, resulting in an overall stabilizing effect on ecosystem functioning, for example, on biomass production. The theory assumes that species differ in their responses to stress caused by an environmental perturbation. With a higher biodiversity, the asynchrony of species responses increases, as does the chance that a species is present whose positive response can compensate for the negative response of another species (Yachi & Loreau 1999). The intensity of the immediate response of the ecosystem function to an environmental perturbation is generally referred to as its resistance, which has become a commonly used measure of ecosystem stability (Van Ruijven & Berendse 2010; Loreau & de Mazancourt 2013).

The majority of empirical research on diversity-stability relationships in grasslands, so far, has been based on field experiments with a relatively narrow focus on environmental factors. In experimental plots, plant species composition is manipulated and ecosystem functioning is monitored over time (Tilman et al., 2006; Hector et al., 2010; Gross et al., 2014). Vegetation data from plots, available across large spatial and temporal scales, provide the opportunity to validate experimentally based findings in natural ecosystems and at scales unachievable in experiments. Subjecting a wider array of ecosystems to diversity-stability analyses would also allow to test the generality of the relation between species diversity and ecosystem stability. Yet, the evidence that these relationships also hold in naturally assembled plant communities remains scarce (Loreau 2010) and is limited to a relatively small range of different grassland ecosystems, hence hampering the generalisation of the results found to a broader environmental context. One recent study in dune grasslands in the Netherlands has demonstrated that the diversity-stability relationship in naturally assembled communities is indeed consistent with the results of biodiversity experiments (van Rooijen et al., 2015). But, it remains a question how the diversity-stability relationship holds across different (grassland) ecosystems. The complexity of natural assembled communities, where multiple environmental factors may confound with and mask biodiversity effects on ecosystem stability, strongly challenges the extrapolation of experimentally derived biodiversity-stability relationships to unmanipulated field conditions (Huston 1997; Grman et al., 2010).

The contribution of biodiversity in maintaining stability of ecosystem functioning can be expected to depend on both biotic and abiotic contexts in which species are interpreted (Cottingham et al., 2001; Polley et al., 2013). When an external environmental perturbation, such as a climate extreme like drought, disturbs the ecosystem processes, system associated abiotic conditions, for example the availability of water and nutrients, may interact with the stabilizing mechanisms and buffer an ecosystems' response (Tilman et al., 2006; Grman et al., 2010; Lloret et al., 2012). This was supported by recent experimental work of Hautier et al., (2014) in natural communities, showing that anthropogenic eutrophication weakens the diversity-stability relationship. De Keersmaecker et al., (2016) used remote sensing techniques to show that over a range of different habitats, relatively species rich semi-natural grasslands generally have a higher resistance to climate extremes compared to relatively species poor agricultural grasslands. Although this study did not explicitly quantify species-richness of the studied grasslands, the higher grassland stability was contingent upon the physical geography, indicating the mediating role of environmental variables. On the other hand, Kuiters (2013) found consistent diversity-stability relationships in natural grassland communities with contrasting water and nitrogen availabilities. However, this study focussed on ecosystem functioning at the community level, and did not evaluate responses to external perturbations. It therefore remains unknown whether abiotic variability affects the resistance of an ecosystem function such as above-ground biomass production to external disturbances like climate extremes, and this is especially applicable across large spatial and temporal scales.

The aims of this study were to (i) quantify to what extend plant species-richness mediates the stability of above-ground biomass production across grassland ecosystems in the Netherlands under influence of fluctuating drought; and (ii) test whether this diversity stability-relation proves to be consistent across a variety of abiotic conditions. In order to quantify to what extent plant species-richness mediates the stability of above-ground biomass production, a dataset of repeated vegetation surveys, so-called permanent plots including the composition relative abundance of species per plot surface between 1930 and 2012, was compiled (e.g. Smits et al., 2002) and combined with climate data and species-specific trait data. A proxy for the primary productivity of a permanent plot, was calculated to quantify temporal variation in above-ground primary productivity and its response to climate fluctuations, which were based on SPEI-data on drought variability over time. From this relationship, an indicator of resistance of above-ground biomass production was calculated which was used to study diversity stability relationships. In addition, the possible effects of environmental co-variables on the diversity-stability relationships were incorporated. Therefore, site-specific environmental factors were calculated based on indicator values derived from site-specific vegetation data. The study plots were distributed over a range of different grassland habitats in the Netherlands, which enabled the study of diversity-stability relationships under contrasting abiotic variables in terms of soil type, pH, moisture and nutrient contents.

5.2 Methods

Study sites and Vegetation data

A dataset of 150 time-series of permanent plots established in various Dutch grasslands and repeatedly recorded between 1930 and 2012, was compiled, containing 1966 vegetation surveys covering the whole of the Netherlands (Fig. 5.1), and representing six physical geographical regions (Schaminée et al., 2007, Table 5.1). The sizes of the plots varied between 20 m^2 and $100m^2$. All selected plots were made in a homogenous vegetation. Plots used in the dataset were controlled for heterogeneity of vegetation by outselecting plots with deviant species compositions associated with different successional stages or environmental gradients. Time-series were all repeatedly recorded with varying intervals between time-series and sometimes within each time-series (Table 5.1). This dataset is part of the Dutch National Vegetation Database, and each survey consists of the relative abundance (% cover) of all occurring vascular plant species relative to the plot surface (Schaminée et al., 2012) and thus includes stratification in the grassland canopy. All plots were extensively managed in a nature conservation context. The selected plots cover a large range of semi-natural grassland vegetation types in the Netherlands. Vegetation data were compiled using Turboveg v.2.101 (Hennekens & Schaminée 2001).

Meteorological data

Climate data were retrieved from SPEIbase (Beguería & Vicente Serrano 2014, grid cell area UL 50.75-3.25/ LR 53.75-7.25). Monthly averages of the Standardized Precipitation and Evapotranspiration Index, including a three-month legacy of measurements (3-SPEI), were obtained over the period between 1950 and 2012 and used as a general index of short-term drought (Beguerìa et al., 2010). The average SPEI (C_{SPEI}) was calculated for each period to assess drought intensity. A time-series of SPEI-data between 1950 and 2012 with its variability is presented in Fig. C-I in the appendices.

Plant species-richness and environmental variables

Diversity was expressed as plant species-richness of each plot (R) and was calculated as the average number of plant species over the entire time-series. Overall, this average species-richness strongly correlated with the species-

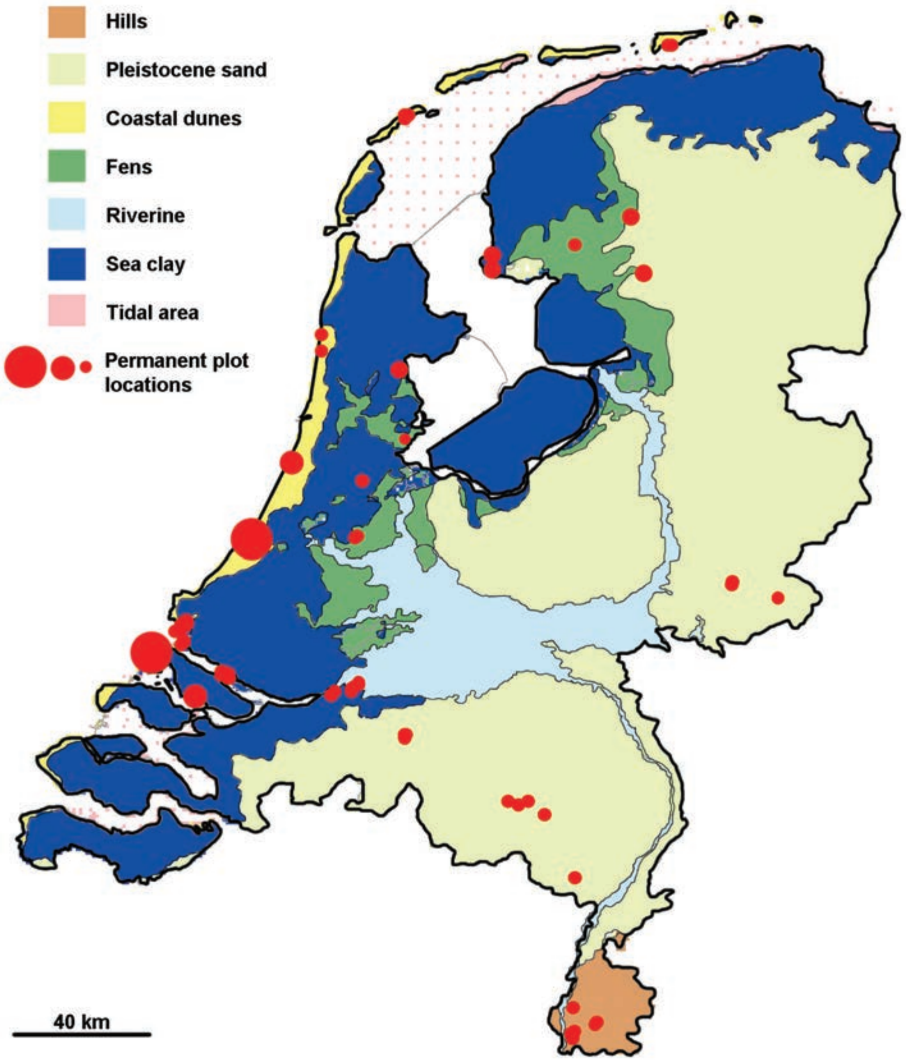

Figure 5.1: Distribution of permanent plot time-series in the Netherlands. The size of the red dots indicates the number of permanent plots per location. Colours show the physical geographical regions as described in Table 5.1.

Table 5.1: Overview of the surveyed grassland habitats, characteristics, dominant soil type and dominant veg physical geographical regions (Schaminée et al. 1996), together with the available time series characteristics.

Physical geographical region	Characteristics	Dominant soil type	Grassland vegetation classification	# time-series	Average # surveys/year per time-series
Hills	Calcareous	Sand, Loess, Rocky	Festuco-Brometea, Sedo-Scleranthetea	3	23/28
Pleistocene sandy soils	Relatively dry, relatively acidic, Pleistocene soils,	Sand	Nardetea, Calluna-ulicetea	23	12/20
Coastal dunes	Calcareous in southern regions	Sand	Koelerio-Corynephoretea	107	20/23
Fen	Organic soil, often below sea level	Peat	Molinio-Arrhenatheretea	2	10/21
Riverine	High water table variability	Clay, Sand	Plantaginetea majoris, Molinio-Arrhenatheretea	4	29/36
Sea clay	Below sea level, nutrient rich, high pH	Clay	Molinio-Arrhenatheretea, Plantaginetea majoris	11	16/16

richness per surveyed plot in course of time (r=0.87, P<0.0001). As the plant species-richness does not vary within a time-series, R was added as a nested factor in repeated measure mixed-effect model 1 (see below).

Plot-specific abiotic variables E (Soil moisture, Soil pH, and Soil nutrient contents (total nitrogen content and total phosphorus content)) for each survey were quantified, based on the Wamelink ecological indicator values of the occurring plant species, weighted according to the average abundance of the plant species over time (Wamelink et al., 2002). Ellenberg indicator values (Ellenberg et al., 1992) are often applied in European studies, although they are developed and tested for Central-European conditions, meaning that their usefulness in other European regions may be questioned. For our study, Wamelink indicator values have the advantage of being specifically developed for the Netherlands, giving a better approximation of site-specific abiotic conditions (Wamelink et al., 2002; Wamelink et al., 2005). Additionally, soil texture (sand or clay) of each plot was assessed based on the physical geographical location of the plot or observation attached to the record. Physical geographical data were retrieved from the ecological data available in *SynBioSys* (Schaminée et al., 2007; Bongers et al., 2013).

Primary productivity

To account for the lack of historical measurements of primary production, above-ground biomass production (P_n) was assessed by calculating community leaf biomass for each available vegetation survey. To include species associated variation in productivity, a proxy was calculated according to equation 5.1 (Running & Zhao 2015). Specific Leaf Area ($mm^2.mg^{-1}$, SLA) for all species (s) was retrieved from the LEDA and TRY plant trait database (Kleyer et al., 2008; Kattge et al., 2011) and the Canopy Area Index (CAI) was calculated as the relative area per unit ground (plot) surface area per species in mm^2. CAI-values are based on the combined relative Leaf Area Index (LAI) per species in a plot, which calculates the leaf area per unit surface area, per species in the community present in the survey. This method includes possible stratification of the vegetation canopy, although this is relatively limited in grasslands (Disney et al., 2016).

$$\mathrm{P_n} = \sum(\frac{\mathrm{CAI_S}}{\mathrm{SLA}_S}) \qquad \textit{equation 5.1}$$

The use of LAI and SLA is often applied in remote sensing approaches in combination with the Normalized Difference Vegetation Index (NDVI), to monitor above-ground primary production of both crops and natural vegetation (Lillesand et al., 2014). This approach enables comparisons with studies of diversity-productivity and diversity-resistance relationships which use optical remote sensing techniques such as Van Rooijen et al., (2015); De Keersmaecker et al., (2016) and Wang et al., (2016), where the NDVI is applied to assess long-term primary productivity based on vegetation coverage.

Environmental factors and primary productivity

In order to test whether above-ground primary production was affected by plant species richness and the environmental factors, several linear models were constructed. A linear model, $P_n \sim R$, was applied to assess the direct effect of plant species-richness on biomass production, where Pn is the primary production per survey, calculated using equation 1, and where R is the plant species-richness. Subsequently, the direct effects of individual abiotic environmental factors on primary production were assessed. These factors were tested both combined and separately, according to linear model 5.1, where E are the environmental co-variables (SPEI (C), year of survey (y), physical geographical region (r), soil moisture (h), soil pH, Soil type (sand, peat or clay: s), soil total N-content (n), soil total P-content (f)). The repeated measurements within each time-series were considered by including PQ (Permanent plot number) as a random factor in which the time-series specific plant species richness (R) is nested. The mixed-effect model was build using *R*-package lme4 (Bates et al., 2014).

$$((\mathrm{P}_{\mathrm{n}_t} - \mathrm{P}_{\mathrm{n}_{t-1}}) \sim \frac{\mathrm{C}_{SPEI}}{Y})_{\mathrm{p}} \qquad \textit{model 5.1}$$

Resistance

The relative change in above-ground biomass production ($\mathrm{P_n}$) over an interval between two vegetation surveys was calculated, and an absolute average annual change per interval was determined. This measure was then related with the average SPEI (C_{SPEI}) over that same interval. The response coefficient of all absolute changes in above-ground biomass production related to the drought conditions (C_{SPEI}) resulted in a response coefficient per time-series, based on linear model 5.1. As a stronger response is related to a lower resistance, the inverse response coefficient derived from model 5.2 was then used to quantify the resistance of productivity (Ω) to drought (C_{SPEI}) (equation 5.2) (Van Rooijen et al., 2015). Resistance of productivity is expressed as a unitless measure.

$$\Omega_p \sim R + E_{r/s/h/pH/n/f}$$

model 5.2

$$\Omega = -\frac{C_{SPEI}}{\Delta P_n}$$

equation 5.2

Statistical analysis of resistance

The effect of plant species-richness on the resistance of biomass production (Ω) was tested using a linear model according to model 5.3, using the calculated resistance measure and the diversity measure.

$$P_n \sim E_{C/y/r/s/h/pH/n/f} + (PQ|R)$$

model 5.3

In order to test the effect of the environmental co-variables on the diversity-stability relationship, all environmental co-variables (E) and plant species richness were first simultaneously added to a linear model as fixed factors (Isbell et al., 2015), with resistance of productivity as the dependent variable. In addition, all co-variables were separately added to the model with species richness as the fixed factor, testing both the direct effects of the co-variable on the resistance as well as its interaction with plant species-richness. Environmental co-variables included the soil type (s), soil moisture (h), soil pH (pH), the phytogeographical region (r) and soil total N (n) and P (f) content. Statistical analyses were performed using the car-package in R (Fox et al., 2015).

5.3 Results

The environmental factors, climate variability (SPEI), physical geographical region (region), nutrient content (total N- and P- content), soil type, and soil pH, all had a direct and significant effect ($P<0.05$) on biomass production when tested individually ((Table C-I). In a combined model, including all co-variables only the year of survey, soil pH, and soil moisture were not significantly related ($P>0.05$) with above-ground primary production (Table C-I in the Appendices).

The relationship between the resistance and plant species-richness without including the environmental co-variables, was positive and significant (($F_{(1,148)}=19.33$, $p<0.001$) (Fig. 5. 2). The cloud of data points, each of which represents one time-series, showed a high variation between the time-series.

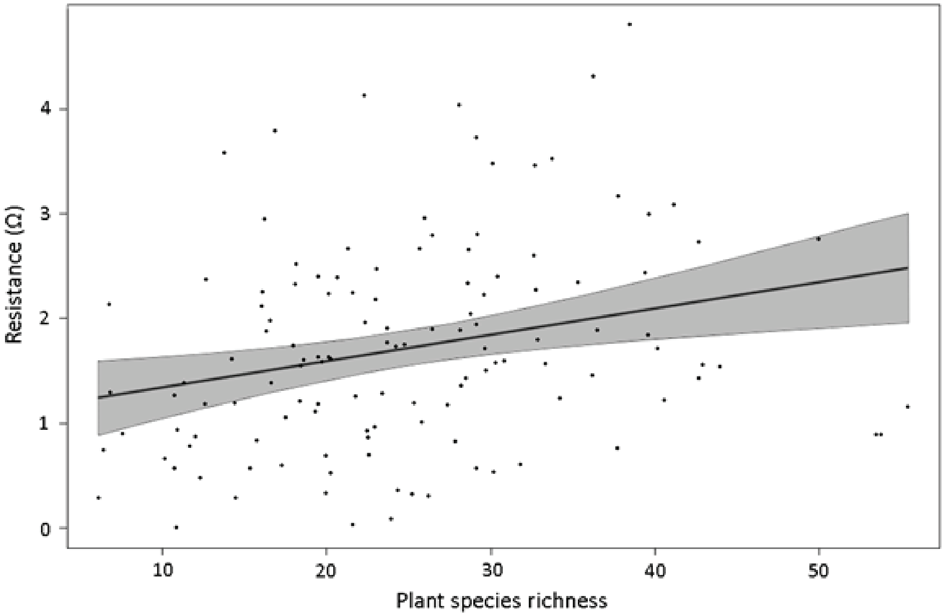

Figure 5.2: Linear regression model between the temporal resistance (Ω) of permanent plot time-series series against drought and their average plant species-richness ($r=0.37$, $p<0.0001$). A 95% confidence interval is indicated in grey. Including environmental co-variables did not change the positive and significant relationship (Table 5.2, Table C-II).

Table 5.2: Results of a general linear model evaluating the combined effects of the environmental co-variables and plant species richness on the resistance of above-ground biomass production against drought conditions.

		F-value	Sign.
Species richness	$F_{(1, 115)}=$	5.07	*
Region	$F_{(3,115)}=$	0.79	$^{n.s}$
Soil Moisture	$F_{(1,115)}=$	0.06	$^{n.s}$
Soil pH	$F_{(1,115)}=$	0.35	$^{n.s}$
Soil type	$F_{(2,115)}=$	0.08	$^{n.s}$
Soil N-content	$F_{(1,115)}=$	<0.01	$^{n.s}$
Soil P-content	$F_{(1,115)}=$	0.09	$^{n.s}$

Significances: *<0.05, n.s.: non-significant

Adding the environmental co-variables and the physical geographical region simultaneously to the model as fixed factors did not change the positive and significant relationship between resistance of above-ground biomass production and plant species-richness, indicating a consistent diversity-stability relationship across the studied environmental gradient (Table 5.2). Also the models, where richness and the separate co-variables were tested with their interaction, showed a consistent significant effect of plant species richness on the resistance of productivity across the environmental gradient, without any of the interactions being significant (Table C-II in the Appendices).

5.4 Discussion

The general aim of this study was to test whether experimentally derived relationships between the resistance of above-ground biomass production and plant species-richness under fluctuating drought conditions are consistent in self-assembled unmanipulated communities of semi-natural grassland ecosystems, covering a wide range of abiotic conditions. Moreover, it was aimed to quantify the effect of different environmental co-variables on the diversity-stability relationship. A unique dataset of long-term permanent plot time-series was used in which plant species composition was repeatedly recorded over time.

Overall, we observed a positive correlation between plant species-richness and the resistance of above-ground biomass production to drought, and this across a wide range of natural grassland habitats. Although there was a high variation between the responses and resistance measures among the different time-series, probably as a result of the variation in ecosystem properties (De Keermaecker et al., 2016), the biomass of permanent plots with high species numbers showed significantly less response to climate fluctuations, as reflected by the drought associated Standardized Precipitation and Evapotranspiration Index (SPEI), resulting in a higher long-term stability. In order to calculate a reliable resistance measure, the response coefficient of each time-series to drought variability was calculated. In contrast to e.g. Isbell et al., (2015), there were no intervals with controlled drought conditions; therefore, all SPEI-measures were included in the resistance measure (model 2). This positive relationship was found irrespectively of the physical geographical region, which reflects a range of environmental conditions operating on a large spatial scale such as, soil type, moisture and geomorphology (Schaminée et al., 2007; De Keersmaecker et al., 2016). Although there was much variation in plot-specific abiotic conditions (soil type, soil moisture, pH and nitrogen and phosphorus availability), and all environmental variables affected primary production of grassland vegetation, no significant effect of abiotic co-variables on the established stability-diversity relationship was found. These results suggest an important and consistent role of plant species-richness in maintaining ecosystem functioning under climatological stress, irrespective of a high variation in environmental conditions.

Studies on diversity-stability relationships performed in natural communities (e.g. (McNaughton 1977; Tilman & Downing 1996) were often criticized for not properly including the variation in resource availability (Huston 1997). As far as we know, this is the first long-term study on diversity-stability relationships in unmanipulated naturally assembled grassland communities that incorporates environmental co-variables. Climate variability, indicated by SPEI-values, does directly interact with soil nutrient mobilisation and availability as well as directly influence plant physiology (Borken & Matzner 2009) and thus affecting primary productivity. Additionally, other major environmental factors as soil nutrient content, soil moisture and pH operate in concert and are associated with resource availability and affect biomass production (Bartelheimer & Poschlod 2014; Roscher et al., 2016). This is in accordance with our results which clearly show a direct effect of all soil and climate associated environmental co-variables on biomass production. The mesocosm experiments of Bloor and Bardgett (2012) showed that although soil nitrogen-content had a positive effect on biomass production in general, N-content had little effect on the short-term stability of productivity and carbon fluxes during extreme droughts in different common grassland communities. Corresponding with their findings, the results presented here suggest no significant effect of soil N- and P-content on the stability of above-ground biomass production nor an effect of other soil associated co-variables such as moisture and pH. Hooper et al., (2005) suggested that species complementarity and an asynchronous response to an environmental stressor such as drought forms the basis for the diversity-stability relationship. This is supported by the recent findings of Hautier and colleagues (Hautier et al., 2014; Hautier et al., 2015), who showed that a decrease in asynchrony caused by fertilization or other anthropogenic changes weakens the diversity-stability relationship, mainly through species diversity. However, the grassland plots in the study presented here were characterized by extensive management throughout the observed time period. Stable plant species-richness over the long-term upholds the asynchrony present, irrespective of the environmental differences between the habitats. This suggests that the diversity-stability relationship is consistent over different habitats as long as the site-specific abiotic conditions within the habitat are stable. The effect of plant species-richness on the temporal stability is more pronounced in homogenous environments such as the surveyed permanent plots in this study. De Keersmaecker et al., (2016) demonstrated that there is high variability in the resistance of grassland vegetation among different ecosystems, which is likely causing the high variation in resistance-measures as depicted in Fig. 2. Real-world ecosystems are affected by a multitude of co-variables working at different temporal and spatial scales. This study attempted to incorporate some major relevant environmental variables. Likely also other variables are at play, causing the high amount of unexplained variation. Whereas an analysis at the meta-community level, considering all different grassland communities and habitats as a single time-series, may present a more noticeable role of abiotic factors on stability-diversity relationships (Wang & Loreau 2016), our study suggests a robust diversity-stability relationship between contrasting grassland ecosystems under climate variability.

In order to upscale experimental research on diversity-stability relationships to real-world situations and to gain more insights in the long-term ecological mechanisms, large data sets are indispensable. The permanent plot data set, which was selected from the Dutch National Vegetation Database, offers many opportunities to study ecological dynamics over time, yet the species compositions and environmental conditions are limited to ecosystems representative for north-western Europe. In addition, observational databases like these are often lacking historical information on environmental measurements forcing the need for proxies.

The proxy for above-ground productivity used in this study was devised to compensate for the lack of historical information on productivity. As the vegetation surveys include information on the coverage of each species relative to the surface area of each plot, and in a homogenous vegetation, this approach is comparable to the estimates given by Leaf Area Index (LAI) values, i.e. leaf cover per unit ground area. The total relative abundance of each species per unit ground surface area, in our method referred to as canopy area index (CAI), can exceed the 100% cover by including multiple layers of vegetation (of the same or different species). To account for interspecific differences in leaf biomass, we included the Specific Leaf Area (SLA)-values in our calculations to take interspecific differences in leaf-biomass into account, in order to increase the predictability of our proxy. This approach is similar to the two-dimensional observations of remote sensing derived methods of monitoring above-ground biomass. These methods have been shown to be more precise at sites with plants with a relatively low LAI (Yan et al., 2016). The grassland vegetation structure of our study plots is characterized by a relatively low LAI (Disney et al., 2016), which adds to the reliability of this proxy.

Another limitation of using large datasets from natural ecosystems, is the lack of the ability to incorporate extremes in the analysis. Since there was a limited range of plant species- richness values within our dataset and as also the encountered variability in SPEI was relatively limited, we cannot draw any conclusions on response of natural ecosystems with extremely low or high richness levels, or on responses to extremely dry or wet periods, which do not naturally occur in the systems studied. Therefore, the linear relationship found cannot be extrapolated to these extremes.

As no historical data on the site-specific abiotic conditions in this study were available, abiotic variables were based on site-specific indicators quantified by species associated Wamelink indicator values. Local species composition is linked to biotic and abiotic factors and is often used to assess these conditions using the ecological amplitude of species occurrence within certain environmental factors, making it possible to use this observational database to calculate a reliable indicator. However, it is highly recommended for future studies to acquire more data and measurements on a wider range of ecosystems and environmental conditions, in order to further generalize and contextualize the results presented in this study, for there is a growing interest in returning to observational studies in real-world natural ecosystems and to scale-up the results from local experiments to scales relevant for managers and policy-makers (Cardinale et al., 2012; Tilman et al., 2014). The use of similar observational databases of vegetation surveys or remote sensed productivity measurements, such as NDVI, offer many opportunities and scales to assess diversity-productivity and diversity-stability relationships and the underlying ecological mechanisms in nature (De Keersmaecker et al., 2014). Although remote sensing imaging enables reliable observations of ecosystem functioning, the method often lacks the spatial resolution to accurately assess biodiversity in grasslands and discern environmental factors at play. Combining remote sensing data with vegetation plot databases may help to overcome this issue. This study proposes an approach which is comparable to remote sensing based methods, where instead of pixels, permanent plots with known plant species composition and co-variables are monitored. The results, showing comparable relationships on a higher resolution, support earlier findings (Van Rooijen et al., 2015) and may add to the interpretation of studies of diversity-stability relationships based on remote sensing observations. Nonetheless, the ability to validate the results with experimental studies, where plant species composition and environmental co-variables can be controlled and structurally monitored, needs to be emphasized. To our opinion the continuous confrontation of experimental findings with field observations as well as the development of new methods in combining large observational databases on vegetation, productivity, plant traits and climate, is essential for the process of extrapolating diversity-stability relationships to real-world settings.

We acknowledge that the demonstrated relationships between plant species-richness and primary productivity are correlational, and that causation cannot be established. However, studies like these provide an opportunity to validate experimental findings in natural ecosystems, at spatial and temporal scales that are unachievable in experiments. Large scale observational studies provide opportunities to test the generality of diversity-stability research in different ecosystems, and at scales that are relevant for nature management and policy decisions.

Climate variability and climate extremes such as drought are expected to occur more frequent in the future and can have major impact on biodiversity and ecosystem services (MacDougall et al., 2013; Hautier et al., 2015). While human activities stress biodiversity globally, regionally and locally, there is an increasing amount of both experiments and field based indications that biodiversity may have a vital role in stabilizing ecosystems and their functioning under environmental perturbations (Hooper et al., 2012). Our results, based on long-term field observations of contrasting grassland habitats in the Netherlands, underline the robustness of this relationship in natural unmanipulated grassland communities and stress the dominant role of species composition in maintaining grassland ecosystem functioning during environmental disturbances irrespective of abiotic conditions. Maintaining and conserving biodiversity on all scales needs therefore be emphasized to insure ecosystem services in the future.

Acknowledgments

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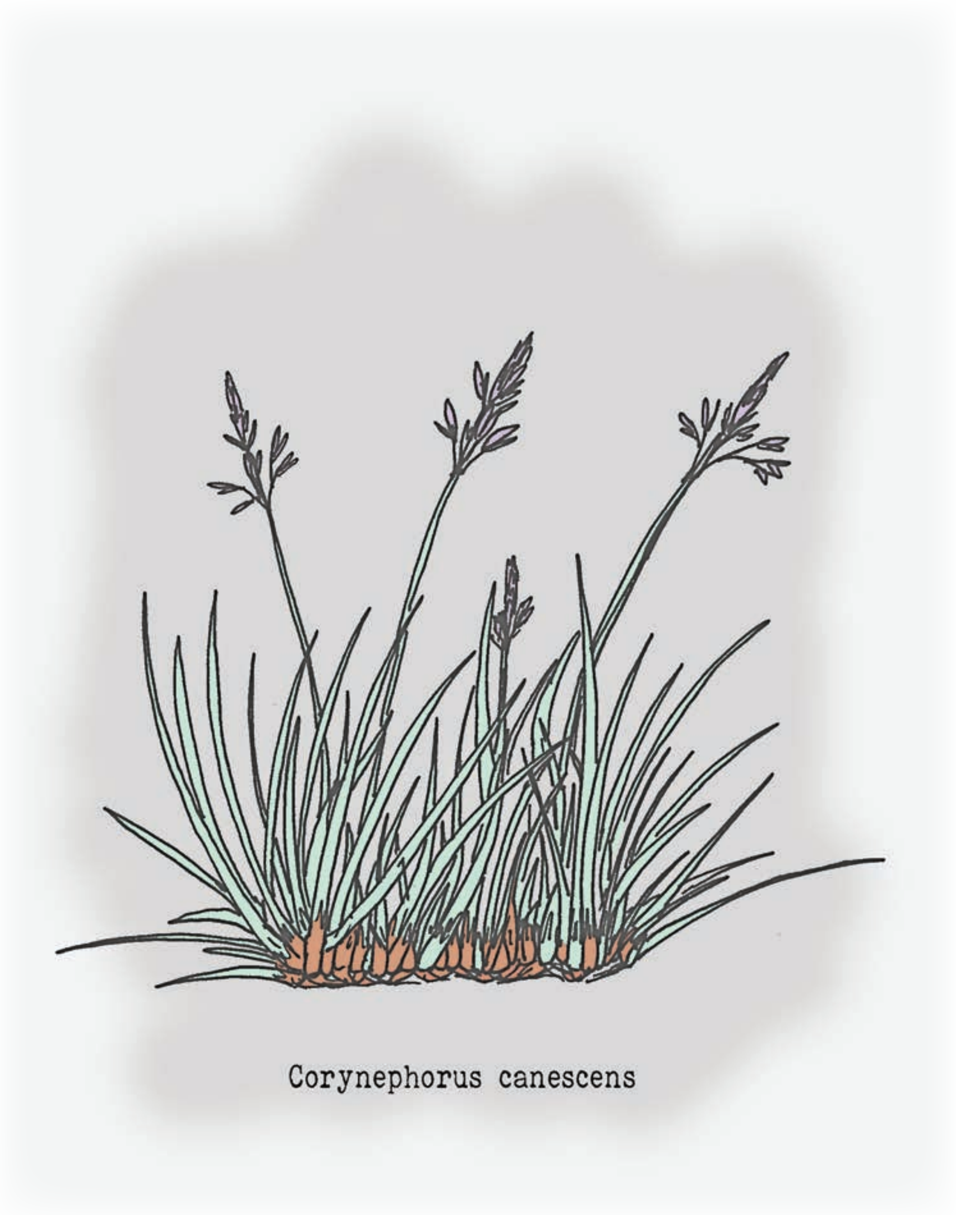
Cerastium semidecandrum

Galium verum

Synthesis



Corynephorus canescens

6.1 Introduction

Global change puts ecosystems under increasing pressure. Biodiversity, ecosystem functioning and the associated ecosystem services are jeopardized through anthropogenically driven causes, such as changes in land use, pollution, disturbed nutrient and water cycles and climate change. As environmental disturbances associated with climate extremes are expected to increase both in frequency and in magnitude in the near future, these may have severe effects on ecosystem functioning across all temporal and spatial scales (Field & Van Aalst 2014). Research on how ecosystems function, and a better understanding of how ecosystems cope with external stress and respond to disturbances is essential for devising adequate adaptive and mitigation strategies in response to global change.

In unravelling how ecosystems function under environmental disturbances, the diversity-stability paradigm (Naeem 2002; Loreau 2010) plays a central role. The theory that higher species diversity increases the stability of ecosystem functioning during or after a disturbance is largely based on complementarity of the species within a community. In this insurance theory (Yachi & Loreau 1999) the negative change of the function of one species is associated with a positive change of that of another species. A higher species richness increases the chance of such a relationship, stabilizing the overall performance of the ecosystem. A growing amount of evidence for this theory is produced by mostly experimental studies, where plant species richness is manipulated and biomass production is monitored over time. The bulk of these studies are however performed ex situ and are relatively small-scaled. This hampers the possibility to extrapolate the results to natural ecosystems on a larger spatial as well as a temporal scale, which is relevant for land- and nature managers and policy makers.

New developing technologies create new possibilities for studying the natural world at different spatial and temporal scales. Monitoring vegetation through remote sensing enables large-scale non-invasive observations over time and can provide time-series on a wide array of ecosystem functions. Databases on vegetation and species-specific plant traits may offer insights into spatial and temporal dynamics in species diversity and ecological processes. Combining these data unlocks numerous opportunities to quantify patterns in ecological systems and enables to interpret, verify and extrapolate ecological mechanisms in real-world systems, which are previously only established in experiments.

In this thesis, we explored some of these opportunities. As the frequency and magnitude of extreme climate events such as drought is expected to increase in the Netherlands due to climate change, it is important to gain insights how natural ecosystems function under such disturbances. Through combining large data sets with Remote Sensing observations, we studied the stability of above-ground primary productivity indices as an ecosystem function in the temperate grassland ecosystems of the Netherlands, across large spatial and temporal scales, with a particular emphasis on calcareous dune grassland ecosystems.

The general aim of this study was to quantify to what extend the diversity-stability paradigm, largely founded on relatively small-scaled experiments, holds in these semi-natural self-assembled grassland habitats and across these relatively large spatial and temporal scales. To achieve this, four separate objectives were put forward: i) to assess and quantify the relationship between biodiversity and ecosystem functioning in semi-natural grassland ecosystems; and ii) to assess and quantify this relationship under climate variability and climate extremes. In order to do this iii) new methods for combining large datasets on vegetation, functional traits and climate with Remote Sensing data; and iv) methods to control for possible confounding environmental variation have been devised.

6.2 An overview of the main results

In chapter 2, we aimed to correlate Remote Sensing observations with climate data to assess the effects of drought on dune grassland vegetation. In addition, we combined these data with vegetation data to quantify the effect of different diversity indices on the relationship between biomass production and climate anomalies. We showed that there is a close correlation between the dynamics of the Standardized Precipitation and Evapotranspiration Index (SPEI), a measure for drought, and the anomalies of the observed Normalized

Difference Vegetation Index (NDVI) values.
A negative change in SPEI correlated with a negative change in NDVI, indicating a decrease in biomass production compared to the expected primary production value. This indicates that drought has indeed an effect on the functioning of dune grassland vegetation. Using the Dutch National Vegetation Database (DNVD) (Schaminée et al., 2012), a diversity index for each observed pixel was calculated, in order to test the relationship between diversity and the extent to which the vegetation within the pixel was affected by the change in SPEI. Plant species-richness was estimated by combining the diversity data of vegetation plots from large databases with the pixels geographic location. This estimation was improved by selecting as many plots as possible, spatially distributed within the pixel. Plant species-richness was strongest correlated with the magnitude of SPEI induced NDVI anomalies. Plots with a low plant species richness showed a stronger response to drought than plots with a high plant species richness, indicating an increased stability of ecosystem functioning under stress with an increased number of species. Looking at functional diversity instead of species richness, according to the insurance theory, it is assumed and substantiated in experiments (Polley et al., 2013a), that a higher functional diversity correlates with a higher stability. Our study, however, did not reveal such a relationship between the stability during drought and functional diversity expressed as Rao's quadratic entropy (Botta-Dukát 2005). No significant relation between stability in primary production and functional diversity could be found for the set of functional traits that was taken into account (van Rooijen et al., 2015). This in accordance with recent findings of Gamfeldt and Roger (2017) where the functional diversity of a system is not directly associated with species-richness within similar conditions, limiting the trait-dimensionality.

Whereas chapter 2 covered the Dutch calcareous dune grassland ecosystems, chapter 3 aimed to up-scale resistance and resilience measures in a wider range of grassland ecosystems, incorporating a larger area and including a greater variety of grassland habitats within several physical geographical regions. The relationship between diversity and stability was investigated, by comparing semi-natural grasslands with intensively managed agricultural grasslands across the Netherlands. For this analysis, the CORINE land use database was used (Büttner et al., 2004). All grasslands were observed applying MODIS NDVI Remote Sensing imaging combined with SPEI as a localized drought indicator. As agricultural grasslands are known to be less plant species diverse compared to more natural and extensively managed grassland vegetation, it was hypothesized, that the resistance of agricultural grasslands would be relatively low. The differences between these management regimes were also tested across different physical geographical regions. It was shown that semi-natural grasslands had a higher resistance to drought compared to agricultural grasslands, while the magnitude of the differences varied between the physical geographical regions, suggesting an effect of environmental factors on the stability mechanisms. Although a higher resistance was found in semi-natural grasslands, these grasslands had a lower resilience to drought compared to agricultural grasslands. The underlying mechanisms could not be identified, but active management techniques, such as irrigation, are likely to contribute to this effect (De Keersmaecker et al., 2016).

In up-scaling diversity-stability studies, Remote Sensing techniques offer large-scale, non-invasive methods of measuring or estimating ecosystem functioning such as primary productivity. However, current satellite observation data are not detailed enough to distinguish between single species in the vegetation observed, obstructing the simultaneous assessment of biodiversity. In chapter 4 and 5, we use permanent plot time-series. The advantage of these permanent plot time-series over Remote Sensing pixels is the ability to use the actual measurements of diversity instead of estimations based on historical data. The DNVD contains a large number of permanent plot series. These plots are geographically fixed and repeatedly recorded over time. The periods between recordings and the length of the time-series differ, as well as the distribution of these permanent plot series across the Netherlands. A unique data subset, included in the DNVD, covers 57 permanent plot time-series in dry dune grasslands in the Meijendel dune area near The Hague (Kuiters et al., 2009), systematically recorded between 1952 and 2012. In chapter 4, we analysed this data set to assess, long-term relationship between species diversity and resistance of biomass production to drought variability. As there were no historical recordings of biomass production, a proxy of primary productivity was calculated by using the relative abundance of species, expressed as the relative area covered by leafs per area of the entire plot, which is similar to the Leaf Area Index (LAI). To account for interspecific differences of biomass allocation between the species, the Specific Leaf Area (SLA; leaf surface area per gram of leaf biomass) was added. This approach results in a measure that resembles productivity assessment by NDVI, and is therefore applicable to verify Remote Sensing studies as described before. A significant relationship was found between productivity and plant species-richness. Moreover, in line with the results of chapter 2 and 4 a significant positive relationship was found between the resistance of biomass production under climate variability and plant species-richness over a time period of sixty years, as such validating our former results across a larger spatial and temporal scale.

Earlier studies of diversity-stability relationships in situ (McNaughton 1977; Tilman & Downing 1996) were often criticized for not considering environmental factors. Therefore, possible confounding effects caused by environmental variation such as soil moisture, nutrient availability or pH could not be identified. In chapter 3, our analyses showed that the difference between the resistance of agricultural and semi-natural were not consistent across the physical geographical regions (De Keersmaecker et al., 2016). In chapter 4 co-variables were added to the analyses to correct for small abiotic differences, which may have been overseen in the selection on environmental heterogeneity on the level of physical geographical regions. Co-variables were calculated by using plant species-based Wamelink ecological indicator values for soil moisture, soil pH, nitrogen, phosphorus and calcium content. No significant effects of these co-variables were detected on the diversity-stability relationship, although biomass production was significantly affected .

In chapter 5, we used permanent plots to upscale our study into the diversity-stability relationship to a larger spatial scale across grassland habitats that differed in a multitude of environmental factors, similar to the Remote Sensing-based study on resistance and resilience in grassland habitats described in chapter 3. To quantify biodiversity and productivity, a dataset was compiled out of the collection of permanent plot time-series of semi-natural grasslands in the Netherlands (Smits et al., 2002). The resulting selection represents a wide variety of grassland vegetation types. As there were no historical records available on abiotic factors, we used Wamelink Indicator values to assess soil pH, soil moisture, soil structure and availability of soil nitrogen and phosphorus (Wamelink et al., 2005). Also the physical geographical region was included to assess the role of more general differences in environment (soil type and geomorphology). Again, we showed a significant relationship between primary productivity and plant species-richness on the one hand, and resistance to climate variability on the other hand. The physical geographical region as well as the abiotic co-variables did not significantly affect the diversity-stability relationship, though, as also found in chapter 4, they did affect primary production itself. These results underline the consistent and robust relationship between plant species-richness and the resistance of biomass production under climate disturbances, and suggest that plant species have a vital role in maintaining and mediating ecosystem functioning under external disturbances. In addition, these observations in natural unmanipulated communities add to the evidence provided by previous experimental work, and allow generalizations to management practices at policy-relevant scales.

6.3 Up-scaling diversity, stability and ecosystem functioning to natural ecosystems

In this thesis we explored new methods and approaches in order to up-scale research in diversity-stability relationships in time and space. Although the results described here often support findings from relatively small-scaled and ex situ experiments, up-scaling research on the diversity-stability paradigm to natural ecosystems comes with new challenges and opportunities. In order to interpret and compare the results derived from experimental and from natural ecosystems, some caution is required.

Up-scaling Biodiversity indices

As biodiversity may be defined and interpreted in multiple ways (DeJong 1975; Magurran 2013), we have to clearly define what is meant by biodiversity on the ecosystem level. In this study, diversity was expressed as plant species-richness, or in other words, as the absolute number of species occurring in the observed plots. The results of chapter 2 showed that plant species-richness was the most determinant measure explaining the stability of ecosystem functioning in response to drought events. The relative abundance of species, reflected in indices such as the Shannon-Wiener index and the Evenness index, affected ecosystem stability to a lesser extent. This is in line with the diversity-stability paradigm, where it has been theorized that the chance on complementary dynamics and asynchrony during an environmental disturbance increases with the number of species present (Yachi & Loreau 1999; Mori et al., 2013). Although Evenness values may be important in maintaining the ecosystem's output, it is no indicator for the number of species capable of compensatory responses to a perturbation. Functional diversity, expressed as Rao's quadratic entropy (Botta-Dukát 2005), did also, surprisingly, not appear to have a mediating effect on stability. Functional traits, associated with plant performances in a certain environment, are hypothetically determinative for species' responses to an environmental stimulus, and a higher functional diversity would therefore result in a broader range of potential responses and thus in asynchrony and possible compensatory effects (Zhang et al., 2015). However, we could not support this theory with our data. A possible explanation is the trait dimensionality in which we tested. Ecosystems under stressful environmental conditions, although characterized by a high species diversity, are subject to a strong filtering of functional traits, resulting in a limited trait dimensionality (Taugourdeau et al., 2014). Increasing the dimensionality, the variation in habitats (in time or space), would increase trait diversity (Petchey & Gaston 2002). Also, the amount of functional traits incorporated in the analysis may have affected functional diversity, as we tested only traits associated with biomass production (Pakeman 2014). Another explanation could be that our results may be influenced by gaps in the available data on relevant functional traits (Pakeman 2014), especially with regard to analyses over larger spatial scales, including many plant species for which the functional trait information is not available. As such, the amount of trait data available for analyses may have been a limiting factor on the results presented. For these reasons, we couldn't draw unambiguous conclusions on the functional diversity-stability relationship at large spatial scales. We therefore underline the need for more research regarding the role of functional diversity in mediating ecosystem stability in grasslands. Acquiring more data by measuring and incorporating more field-based trait measurements in trait databases is essential to achieve this.

Upscaling stability measures using actual measurements and proxies

Temporal variation, resistance and resilience are commonly used measures of stability in ecosystem functioning. In this thesis, we focussed on resistance as a measure for stability of ecosystem functioning. Only in chapter 3, resilience was also included in the analysis, by assessing the recovery of NDVI-measurements in the period after a drought event towards the pre-disturbed state, assuming no additional climate effects after the drought event. Species rich semi-natural grasslands were compared to relatively species-poor agricultural meadows, showing that agricultural grasslands returned to the pre-disturbed state faster than semi-natural grasslands suggesting a higher resilience. However, we did not identify causes for this higher resilience, and anthropogenic interference on the resilience cannot be excluded in these agricultural grasslands. By using climate variability as a driver of primary production, the continuous change of the drought measure SPEI makes it difficult to assess the resilience of primary production, as the pre-disturbed state will never be completely similar. In studying different ecosystem properties, such as community stability, where species composition itself, instead of the functioning of an ecosystem, is followed (e.g. Kuiters et al., (2009), resilience could be determined more easily (Mariotte et al., 2013). However, a high community resilience does not necessarily indicate a higher resilience of ecosystem functioning. The difficulty in establishing resilience measures is especially applicable to recording intervals of multiple years in which climate varies within each period. Therefore, the resistance measure applied in our studies was based on approximations by NDVI-measurements or trait-based proxies, which is a different approach than the general measure of resistance used in experimental set-ups where resistance is directly measured through yielding. It is advised to perform more research on the data behind these proxies in order improve them and increase their spatial and temporal resolution. Additional experimental validation is recommended in order to further develop the reliability of these estimations.

Upscaling ecosystem functioning: linking experiments to field situations

Ecosystem functioning, a collective term to state the measured output of a pre-defined ecosystem, varies over time. Natural phenomena, such as seasonal variation and environmental disturbances, as well as internal factors, such as community interactions, affect to what extent an ecosystem executes its function (Turnbull et al., 2013; Xu et al., 2015). The function that will be studied however, determines the available approaches and methods. In this thesis, above-ground primary production was chosen as the focal ecosystem function. Partly this has a pragmatic background, as it is a commonly measured function in experiments, whereas Remote Sensing techniques are able to accurately monitor above-ground biomass. Moreover, primary production is a function which is closely related to a variety of other plant functions and life-history traits which enables the possibility to estimate plant performances. In addition, biomass production is relevant to multiple ecosystem services important to society, notably in the agro-food sector, production of materials and carbon fluxes. Nevertheless, it must be stressed to be careful with extrapolating the results found with respect to primary productivity to other ecosystem functions, such as gas- and/or nutrient fluxes, where complementary responses and asynchrony need to be addressed differently.

6.4 Up-scaling methods: on Remote Sensing and databases

In order to generalize and extrapolate experimental findings to nature it is essential to up-scale experimental results and validate them at larger spatial and temporal scales. Data sets, covering large geographical areas and/or consisting of long-term time-series are indispensable to perform analyses on relevant scales. Modern monitoring techniques and eco-informatics are continuously developing and are creating new opportunities in collecting, storing and combining data on a variety of ecological, environmental and climate variables.

Remote Sensing

The use of Remote Sensing in monitoring ecosystem functioning of grasslands is continuously developing and the opportunities provided by Remote Sensing observations are constantly growing. Next to the numerous applications of Remote Sensing on monitoring agricultural lands, the bulk of natural vegetation assessments through satellite imaging is performed on forest and woodland vegetation, often to assess production of these ecosystems (Aerts & Honnay 2011). Although some work has been done on grassland vegetation monitoring using aerial photography by aircraft, kite or balloon, and recently by drones, satellite observations provide structural long-term observations over the largest areas (Assendorp 2010). The resolution of the images generated by satellites is determinant for the spatial scale of the analyses and for the precision of the measurements. Currently the MODIS (Moderate Resolution Imaging Spectroradiometer) instrument aboard NASA's AQUA and TERRA satellites and the LANDSAT program provide the best freely available image time-series of productivity indicators for North-Western Europe. However, there is a trade-off between the temporal and the spatial resolution; whereas the MODIS can provide an eight-day average (of two observations per day) on a maximum resolution of 250×250 meter per pixel, LANDSAT offers 30×30 meter pixels however at intervals of 16 days. The temporal change in the ecosystem functioning in response to an environmental stressor, subsequently determines the suitability of the Remote Sensing product. For example, resistance linked to short-term climate extremes may prioritize a high temporal resolution above a high spatial precision. The use of satellite images does require relatively strong selection criteria and data processing (to account for atmospheric disturbances and spatial heterogeneity) before the data can be interpreted, combined with georeferenced data and used for analyses (Keersmaecker et al., 2014). However, the processing methods evolve rapidly and the data-quality and usability increases at similar speed (Turner et al., 2015). As such, there is a growing potential for using Remote Sensing techniques to observe ecological processes and monitor ecosystem functioning over larger spatial scales. And with time, the temporal scale of observation increases, already giving the ability to create time-series of ecosystem functioning for over a decade. Nevertheless, the interpretation of Remote Sensing products remains dependent on the ecological context. Therefore geo-referenced field data of the observation, which can be acquired through databases, is vital for the application of Remote Sensing techniques in ecological research.

Databases

Vegetation - With the emergence of computer technologies and advanced statistics the use of large datasets to monitor and analyse long-term and large-scale ecological processes has become an important aspect of ecological sciences. For this thesis, we exploited the Dutch National Vegetation Database, one of the largest collections of observations of plant species abundances in the world (Schaminée et al., 2012). Since the database includes individual observations as well as time-series of repeatedly recorded vegetation plots dating back to the 1930's and covering vegetation types across the Netherlands, this database offered an enormous amount of data. Yet, as the database is primarily a collection of individually collected observations, selecting data and compiling a usable selection of plots, which could be coupled to other datasets (for example Remote Sensing images) remains a challenge (Chytrý et al., 2014). Although software programs like *Turboveg* (Hennekens & Schaminée 2001) and *Juice* (Tichý 2002) facilitate the usage of the data, the data itself often lacks structure and information. Strong selection criteria and ground validation, if needed, would help to strengthen the dataset. This includes adding data that are collected in a standardized way and repeating measures and observations. A particular section of the vegetation database, as mentioned, refers to permanent plot observations. They are generally surveyed by different people and often for different purposes (Smits et al., 2002). The resulting dataset, with permanent plot time-series of different lengths and with different measurement intervals (sometimes varying within the times series), requires intensive selection procedures and extra processing steps to adjust the data for statistical analyses. The importance of continuing, structuring and unifying the survey of permanent plots should be emphasized. Presently, the majority of permanent plots is no longer recorded, whereas the possibilities to analyse and combine these datasets with other data increases and the need for long-term data sets in investigating long-term ecological processes becomes more apparent (Bekker et al., 2007; Knol 2010).

Climate – The amount of precipitation and groundwater availability have a direct effect on plant performance. Changes in these factors- will therefore have an effect on ecosystem functioning and this will be reflected in primary production. The Standardized Precipitation and Evapotranspiration Index (SPEI) is commonly used as an indicator for drought intensity linked to plant performance. Therefore, the index uses data on temperature, precipitation, wind and geographical position. An advantage of using SPEI over other drought indices is that it includes multiple variables related to plant performance, such as evapotranspiration, air humidity, cloud cover etc., resulting in a better identification of ecological drought-impacts (Vicente-Serrano et al., 2012). By using the freely accessible data of the Royal Netherlands Meteorological Institute (KNMI), which is available per weather station, SPEI-time-series could be calculated for the weather stations closest to the observed vegetation plots. Another source of data that is often exploited is SPEIbase, where global SPEI-observations are calculated in a grid-cell system (Beguería et al., 2010). Although the scale of this drought assessments is relatively coarse, the advantage of using SPEIbase is the ability to easily compare results with international literature and adequate for analyses over regional scales. Grasslands ecosystem functioning of in particular dry grasslands is very responsive to drought (Li et al., 2015) resulting in a close correlation between NDVI and SPEI-dynamics (van Rooijen et al., 2015), resulting not only in a fast changing dynamics through time but also large differences locally (also caused by many environmental conditions related to hydrology). A higher spatial resolution of climate- and drought assessment is therefore recommended for future research.

Functional traits – Functional traits are increasingly applied in studies that are investigating relations between plant species and ecosystem functions (Díaz & Cabido 2001; Mouillot et al., 2013; Polley et al., 2013b). Functional traits associated with primary production may be responsible for the species-specific responses and performances during variable drought or other changing environmental factors and may drive asynchrony and redundancy in plant communities (Hautier et al., 2015). To assess the effects of functional diversity, species-specific trait data were acquired from the LEDA-trait database (Kleyer et al., 2008), now included in the global TRY plant trait database (Kattge et al., 2011). The trait values in these databases are often derived from measurements taken in a range of, often non related, studies. Therefore we used estimations of plant specific trait values associated with the observed plant (Cordlandwehr et al., 2013). Rare species are often not included in the trait databases. This causes gaps in the available information and it therefore remains a challenge to use this trait data in combination with historical vegetation data. In addition, many species occur in a variety of habitats and exhibit a high variation in trait values, adding to the plasticity of trait values in general. This hampers the ability to calculate very reliable proxies for plant traits and plant trait diversity in the field based on information derived from trait databases and forces to make less precise assumptions. As a result no definitive conclusions can be drawn on the effects of trait diversity in the diversity-stability paradigm, as described in chapter 2. In order to It should be stressed that functional trait databases need to be expanded in the near future incorporating more plant species, more populations within species, and more habitat types.

Ecological indicators - Measurements of site-specific environmental factors are often not included in the vegetation databases. However, phytosociological logic states that the plant species composition can be used to assess abiotic factors at play. Ellenberg indicator values are based on that principal and are commonly used in environmental assessments where the vegetation composition is known. Whereas Ellenberg indicator values are originally developed for central-European plant species (Ellenberg et al., 1991), Wamelink developed and validated indicator values specifically for the Netherlands. In this thesis, we therefore applied Wamelink indicator values to asses ecological variables linked to the historical vegetation data (Wamelink et al., 2002; Wamelink et al., 2012). However, independently determined, site- and time-associated measurements of the vegetation plots are preferred (Zelený & Schaffers 2012; Wildi 2016). The need for including and measuring on-site abiotic environmental conditions should be stressed more in vegetation research as well as including this data along with species observations in vegetation databases.

6.5 Implications of this study

This thesis includes some of the first efforts in up-scaling diversity-stability relationships in natural (unmanipulated) ecosystems on larger temporal and spatial scales. The most notable result is the consistency of experimentally determined positive diversity-stability relationships in such ecosystems. The diversity-stability paradigm has been the topic of ecological debate for decades (Elton 1958; McNaughton 1977; Hector et al., 2007; Tilman et al., 2014). Although many experimental studies support the theoretical framework, the extrapolation to other functions and scales remains an enormous challenge.

In this thesis, we tried to up-scale experimental work to a real-world system and explored the possibilities of combining newly available data and information techniques to validate the diversity-stability paradigm in nature. This study, confined to grasslands, may be a first step to provide tools and guidelines to further study diversity-stability relations and the mechanisms behind the insurance hypothesis on larger spatial and temporal scales in real-world ecosystems. Some of our findings suggest an important role for all individual species within their community, as plant species richness was the most important explanatory variable. For this reason, future research on diversity-stability mechanisms should also focus on the performance and role of individual species in the ecosystem's response to a disturbance. Physiological research on plant species and field experiments on the species and the community levels may provide new data which can be incorporated in the available trait information which can be used in large-scale observational studies such as this thesis. By doing this, we want to stress the complementarity of experimental work and observations in natural ecosystems and express the need for a closer collaboration between and combination of these scientific approaches in order to further increase our understanding of the natural world.

This study aimed to upscale diversity-stability research to scales relevant for nature management and nature policy. Data-based knowledge on such a scale may have implications for the way in which we manage and use our ecosystems in a changing world. Chapter 3 provides a good example, showing differences in resistance between semi-natural managed grassland and grassland managed using modern agricultural techniques. As our studies imply, more biodiverse ecosystems, with a higher plant species-richness, have a higher resistance to climate extremes compared to species-poor ecosystems. Although productivity remains higher in agricultural grasslands due to anthropogenic activity, our study suggests that adjusting agricultural management in order to preserve species or utilize a higher biodiversity in agricultural meadows, may result in a more stable productivity during climate extremes. Moreover, fewer measures may have to be taken to ensure a stable productivity when the ecosystem has a high resistance. This does not only apply for farmland alone but also other ecosystems where the function can be interpreted as a service. Forest and woodland ecosystems, for example, are exploited for timber and as a consequence biomass production is an ecosystem service that is strictly monitored. Where woodland ecosystems were some of the first systems where the diversity-productivity relationship was examined in large-scale ecosystems (often plantations), recent insights show the advantages of a high plant species diversity in forests in a changing environment, similar to our findings in grasslands (Paquette & Messier 2011; Aspinwall et al., 2015). As this shows that the diversity-stability paradigm can be applied to both natural as well as agricultural ecosystems, more research has to be done into these mechanism in order to translate the diversity-stability paradigm for management and policy making. Overall, our results suggest an important role of plant species diversity in maintaining ecosystem functions under environmental stress. Loss of biodiversity may result in ecosystems that are more vulnerable to climate extremes with subsequent loss of ecosystem functions and services (Cardinale et al., 2012). While the results presented in this thesis suggest an important role of species diversity

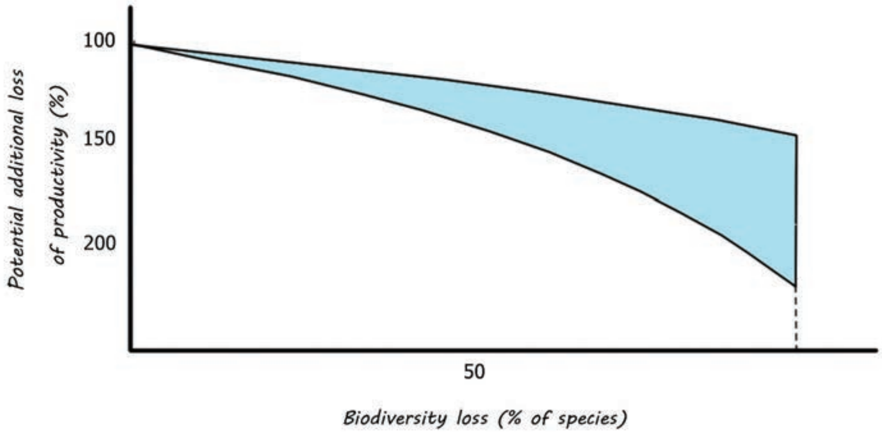


Figure 6.1 Relationship between the additional relative loss of productivity as a result of the loss of resistance during a drought and the loss of biodiversity compared to the maximum number of species according to several linear regression models presented in this thesis. The lines represent the two most extreme models in this thesis and blue shaded area depicts the variation between the models.

in the stability of ecosystem functioning, it remains a challenge to predict the consequences of species loss for ecosystem stability. All models presented in this thesis showed a significant diversity-stability relationship, resulting in a decreased resistance in relatively species-poor communities. In the studies presented here the diversity did not significantly change over time, however many ecosystems suffer species loss due to (anthropogenic) environmental disturbances like climate change, pollution, fragmentation, intensification and management. The loss of species in these systems decreases the chance of compensatory dynamics within an ecosystem during a potential drought. Figure 6.1 visualizes the extrapolation of the outcomes of our models to the additional loss of productivity during a drought period, related to a decreased plant species-richness within a similar plant community.

The model depicted in Figure 6.1 can be illustrated as followed, assuming all species present have an equal role in ecosystem functioning. Under optimal circumstances a grassland has a certain resistance to drought. This means that it will lose some of its productivity, however complementary dynamics between the species present stabilizes the loss of productivity. Now, due to a new management regime, 50% of the species have disappeared from this grasslands. Under the same drought conditions, the grassland loses up to 27 percent of its resistance resulting in an additional 40% decrease of production (thus a 140% decrease of production compared to the initial situation under similar drought conditions).

At extensive species loss, productivity loss due to drought may increase over 200%. Note that species do not have equal roles within ecosystem functioning. With the absence of key species, the loss of stability during drought perturbations will significantly increase.

Among other studies, Tilman et al. (2001) presented a positive relationship between plant species richness and long-term productivity, suggesting a decrease in productivity as species number decrease. Using the models presented in this thesis it can be theorized that the occurrence of a drought further impedes production. Moreover, a decreased productivity due to a lower plant species richness in combination with a decreased resistance related to low plant species richness within a community, causes an even bigger drop

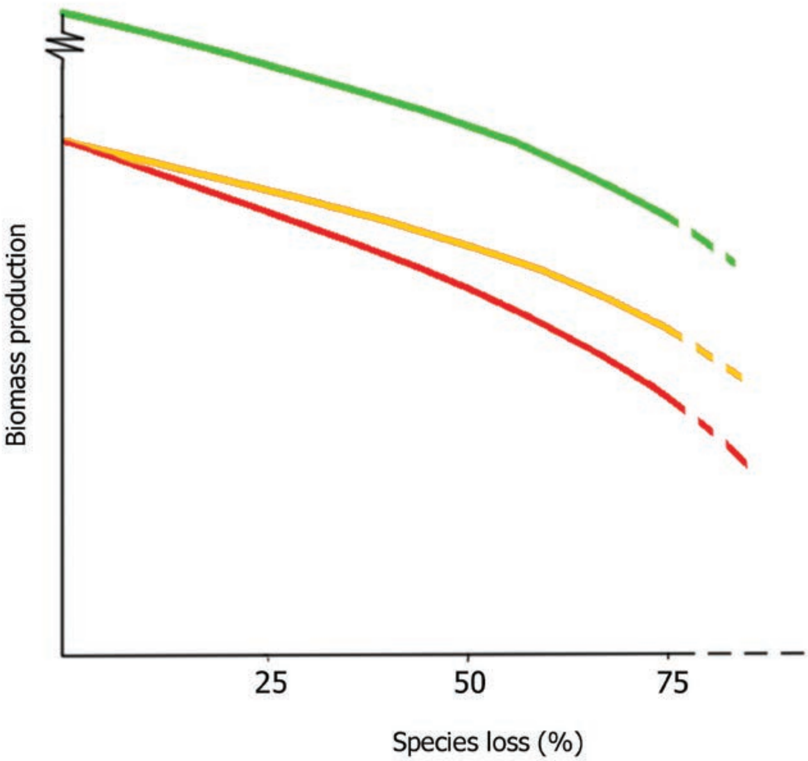


Figure 6.2 Theoretical diversity-productivity relationships when plant species richness in a grassland community decreases relative to a theoretical maximum number of species. In green the diversity-productivity relationship based on Tilman et al. (2001) shows a decrease in productivity when species numbers decline (green). During a drought period productivity drops with a certain amount relative to the productivity maximum (yellow). However, including resistance models, the average of the correlations found in this thesis, to the diversity-productivity relationships adds to the hypothetical loss of productivity. The additional loss increases as species numbers of a certain community further decline (red).

of productivity (Figure 6.2). Given the expected increase in frequency and magnitude of climate extremes and the current biodiversity crisis, we stress the need to conserve and protect global biodiversity on the species level.

6.6 Recommendations for future research

Although our understanding of the diversity-stability paradigm is growing, we are still in the beginning of explaining the processes at work. Therefore, many challenges and opportunities remain in up-scaling the diversity-stability paradigm to the scales relevant for natural ecosystems. Therefore, we recommend the following.

A broader view on the diversity-stability paradigm

The methods and approaches described in this thesis may be applied in a broader spectrum of research on diversity-stability relationships. Varying between different ecosystem functions, environmental disturbances, and indices on plant-species diversity, trait diversity and phylogenetic diversity may produce more valuable insights in stability mechanisms and ecosystem functioning.

a. Ecosystem functions

In this study, above-ground primary production was used as an indicator for ecosystem functioning. Therefore, all results should be interpreted in the context of biomass production. Although biomass production does reflect many functions of plant performance, which may also be reflected in other ecosystem functions, extrapolation to other ecosystems functions should be done with caution. Other ecosystem functions and services, such as, for example, gas and nutrient fluxes like methane emissions (Sanderson et al., 2004; Niklaus et al., 2016), carbon sequestration (Lange et al., 2015) and nitrogen fluxes (Bloor & Bardgett 2012), need to be examined more closely in the context of the diversity-stability paradigm (Mace et al., 2012; Balvanera et al., 2014).

b. Environmental disturbances

The same caution in extrapolating our findings should be taken when interpreting different stressors or environmental disturbances in the context of the diversity-stability paradigm. As the disturbance studied is drought variability, inferences regarding other disturbances like flooding, pests or pollution need to be subject of additional research. As an example, Wright et al., (2015) observed a reversed effect of flooding on diversity-stability relationships in grassland field experiments as compared to drought.

c. Ecosystem types

The results presented here were obtained for grassland habitats. Forests, tundra's, marshes or even aquatic environments are subject to a different ecology, harbouring different dynamics and species interactions (Wang & Loreau 2014). As described earlier, there are examples of diversity-stability studies in woodland settings (Scherer-Lorenzen et al., 2007; Aerts & Honnay 2011; Paquette & Messier 2011) showing results similar to ours. In order to make real generalisations, a larger variety of ecosystems should be studied including peat lands, arid, alpine, aquatic and marine ecosystem.

d. Functional and phylogenetic diversity

As there are multiple interpretations of diversity, the diversity-stability relations found should not be generalized as being applicable to all diversity indices. Especially non-taxonomic indices of diversity, such as functional diversity (Cadotte et al., 2011; Mouillot et al., 2013) and phylogenetic diversity (Flynn et al., 2011; Venail et al., 2015), need more attention. This thesis attempted to include functional diversity into the analyses and found no significant effect on the stability of grassland ecosystem functioning. However, no definitive conclusions could be drawn, due to data limitations and a lack of experimental or field based validations. Therefore, more research using a functional approach to study the diversity-stability relationship is explicitly recommended. This stresses the need for additional data and research using different functional diversity indices over a broader spectrum of ecosystems. Although theoretical and experimental evidence of the importance and the ecological role of functional diversity is growing and supporting the diversity-stability paradigm (Mason & de Bello 2013; Wright et al., 2016), up-scaling that research to natural environments is still in its infancy.

This is also applicable for genetic and phylogenetic diversity. The response of plants, populations and species to drought is largely determined by their genetic adaptations suggesting an important role of genetic and phylogenetic diversity. Recent studies show different outcomes showing a stabilizing effect of genetic diversity on biomass production (Cadotte et al., 2012; Pu et al., 2014), but also an inferior role of genetic diversity in maintaining ecosystem stability opposed to species diversity (Venail et al., 2015) dependent on the studied ecosystem. The main challenge in upscaling research into genetic and phylogenetic diversity on natural scales is the amount available data. In order to determine these phylogenetic diversity indices more information has to become available on the evolutionary history of species and a more unified approach in order to quantify (phylo-) genetic diversity needs to be developed (Winter et al., 2013).

Moreover, using these approaches, more understanding can be gained about the role of individual species in stabilizing ecosystem functioning. This is vital in order to make predictions on the consequences of species loss for the stability of functioning of specific systems. For all species have a different role and a different share in the functioning of ecosystems under certain circumstances, as well as a different vulnerability towards environmental disturbances, it is hard to predict the consequences of species loss for the stability of ecosystem functioning.

e. Integral community approach

Diversity-stability can also be examined in a broader perspective, including a broader spectrum of taxonomic groups. Not only do vascular plant species interact with others within their communities. Non-vascular plants and animal and microbial species also interact with the entire community and may have a role in stabilizing an ecosystems' output. This notably includes below-ground communities as well (Pellkofer et al., 2016), where mycorrhizal fungi's and macro- and micro invertebrates are intrinsically linked to the above-ground performance of an ecosystem (Eisenhauer et al., 2011; Bardgett & van der Putten 2014).

Technical improvements

Next to a wider focus, the possibilities of applying Remote Sensing techniques, data bases and analysis techniques continues to improve. Therefore, it is recommended to keep pace with modern research possibilities.

f. High spatial resolution Remote Sensing

As techniques in Remote Sensing are continuously developing, the details and precision of observation is improving rapidly (Keersmaecker et al., 2014; Jetz et al., 2016). Repeating the studies presented in this thesis at higher temporal and spatial resolutions may improve the accuracy and precision of the results found in the studies presented here. Recent studies have explored the opportunities of hyperspectral Remote Sensing techniques to assess on-ground biodiversity (Rocchini et al., 2015), distinguishing the floristic composition (Feilhauer et al., 2013) and even predict environmental co-variables (Möckel et al., 2016). Further up-scaling research to larger areas (continentally or even globally) may greatly attribute to our understanding of diversity-stability mechanisms.

g. Environmental measurements

The availability of measurements of abiotic and environmental conditions, which can be correlated with site-specific vegetation, are still very limited. The need for this data to verify the used proxies and to extend the existing models should be emphasized and implemented in monitoring programs. Especially for permanent plot observations, adding this information to future observations may lead to new insights.

h. Time-series

Whereas a declining trend is visible in the Netherlands where it comes to monitoring permanent quadrats, this study among others, proves the high added value of these observations in up-scaling ecological research and unveiling long-term processes in ecosystems. In many other research fields, like meteorology and geography, the need for long-term time-series is acknowledged. In ecosystem ecology, however, the use of time-series seems to decline (Smits et al., 2002) and deserves much more attention in regards to the great scientific value of its data produced.

In ecological research, field observations and experimental research are intrinsically linked. Trends unveiled in correlational studies should always be examined in experimental studies in search for ecological mechanisms. *Vice versa*, an extrapolation of experimental research to field situations should always be validated with field observations (Wardle 2016). Large amounts of large-scale and long-term field observations are therefore indispensable in unravelling ecological principles.

Jacobea vulgaris

Appendices

Appendix A

Appendix to chapter 2

# Pixels	Vclass	Dominant vegetation class	% of pixels
3	12	Plantaginetea majoris[1]	6.25
40	14	Koelerio-Corynephoretea[2]	83.33
1	17	Trifolio-Geranietea sanguinei[3]	2.08
3	19	Nardetea[4]	6.25
1	20	Calluno – Ulicetea[5]	2.08

[1] Plantaginetea majoris: a very common vegetation class in the Netherlands, consisting of common plant species. This class is often associated with minor disturbance systems due to trampling by large grazers.

[2] Koelerio-Corynephoretea is the dominating vegetation class in the observed dune systems. The vegetation can be found on relatively nutrient poor to moderately nutrient rich sandy soils and is dominated by grass species and small herbs.

[3] Trifolio-Geranietea sanguinei is vegetation class mostly found on moderately nutrient rich sandy soils and is associated with calcareous conditions. Grass species are dominating this class.

[4] Nardetea is a grass dominated vegetation class on relatively poor soils and is often associated with the presence of cattle.

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

According to (Schaminée et al., 1996)

Appendix B

Appendix to chapter 3

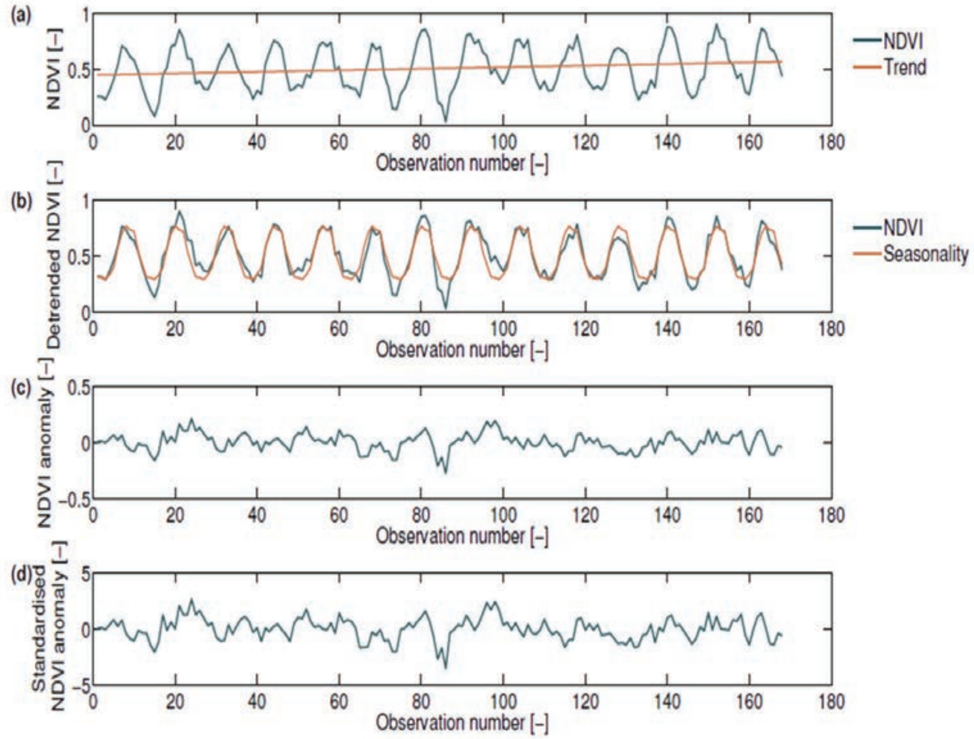


Figure B-I: Illustration of standardised NDVI anomaly extraction from NDVI time-series: an example NDVI time-series with linear trend (a), the detrended time-series (i.e. NDVI anomaly - linear trend), together with its seasonality (b), the NDVI anomaly (i.e. detrended NDVI - seasonality) (c) and the standardised anomaly (d).

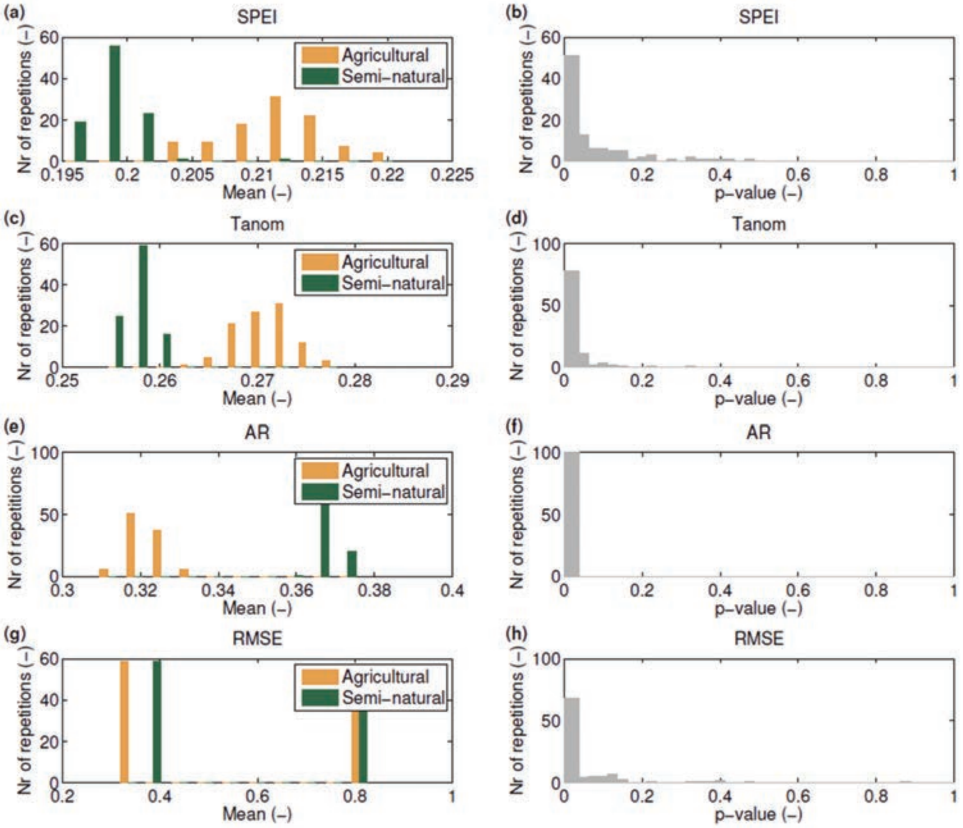


Figure B-II: The histogram of the mean and p-value for each of the stability metrics (i.e. resistance against droughts (a and b), resistance against droughts (c and d) and resilience (e and f)) and RMSE (g and h) of intensively managed agricultural and semi-natural grasslands.

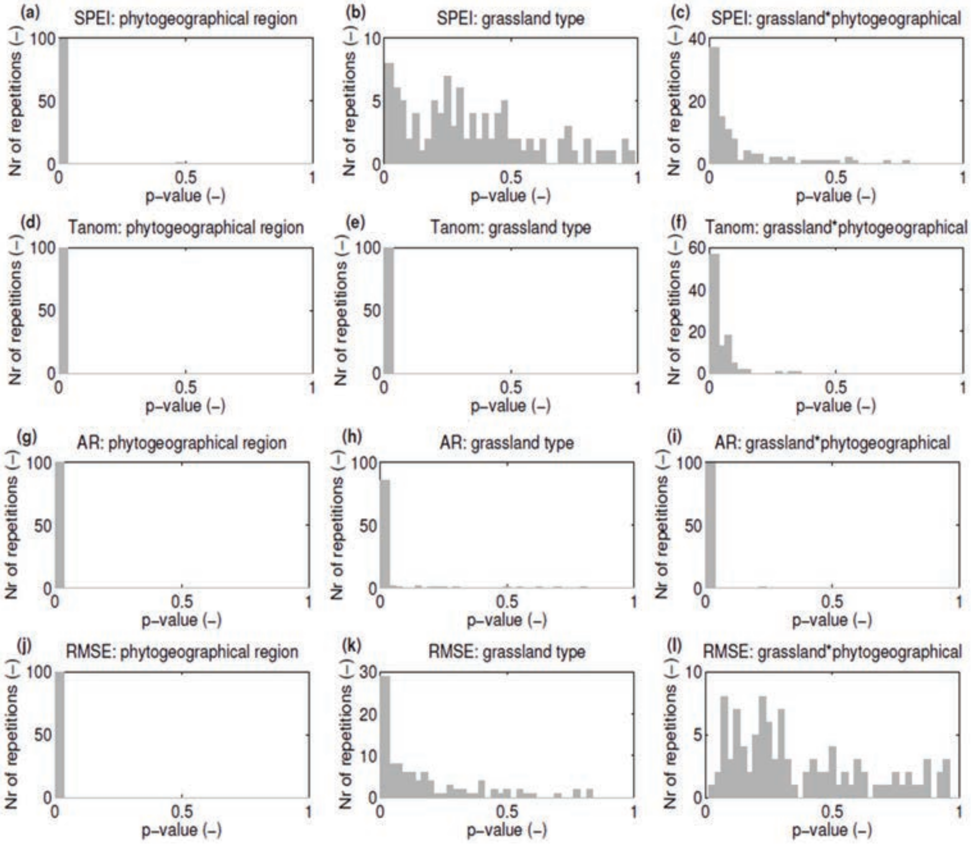


Figure B-III: The histogram of the p-value for each of the coefficients of the interaction model (Eq. 3.2).

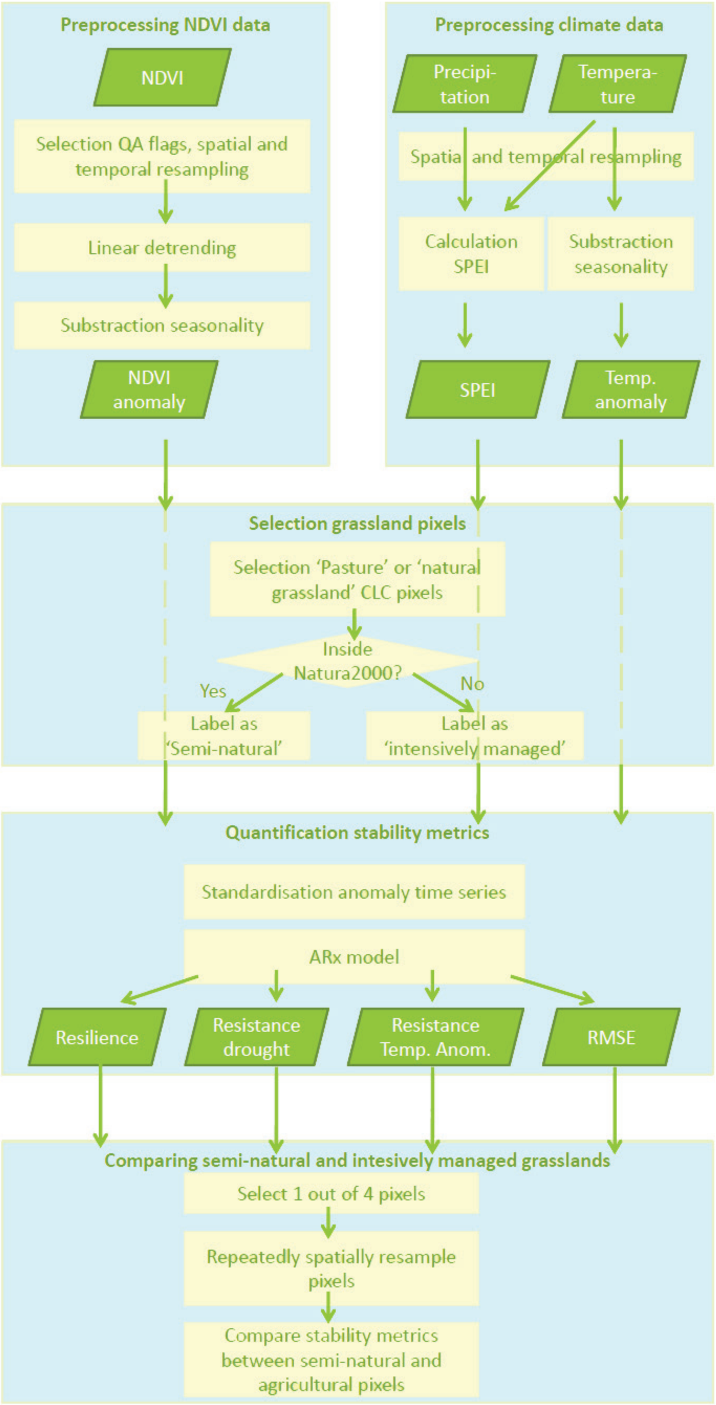


Figure B-IV: General flow chart of the methodology.

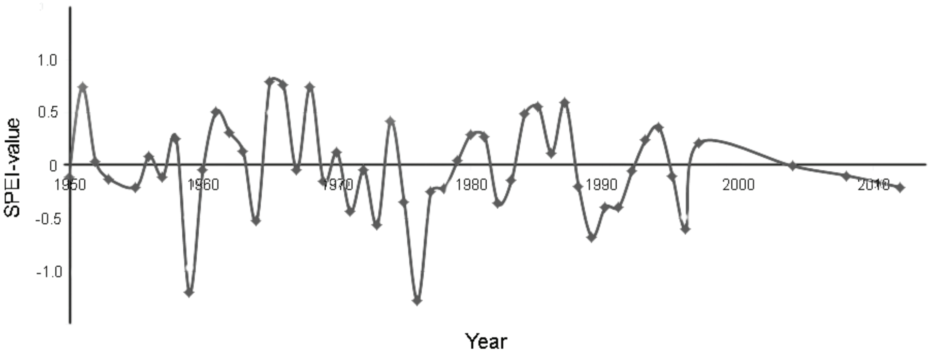


Fig C-I This time-series of average yearly SPEI-values between 1950 and 2012 for grid cell area UL 50.75-3.25/ LR 53.75-7.25) derived from SPEIbase, gives an indication of the variation of SPEI-values through time.

Table C-I: Results and significances of a linear mixed-effect model with repeated measures, evaluating the effects of the environmental co-variables and plant species richness on the production of above-ground biomass.

		Single effect			Multi-effect		
	N=	χ^2	df	Sign.	χ^2	df	Sign.
Species-richness	1966	110.6	1	***	30.42	1	***
SPEI	1888	21.59	1	***	8.47	1	**
Region	1966	244.11	5	***	153.27	5	***
Year of survey	1966	31.40	1	***	1.31	1	n.s
Soil Moisture	1761	0.37	1	n.s	1.43	1	n.s
Soil pH	1761	6.18	1	*	0.92	1	n.s
Soil Type	1966	8.28	2	*	10.41	2	**
Soil N-content	1761	6.04	1	*	8.91	1	**
Soil P-content	1761	6.54	1	*	9.08	1	**

Significances: *<0.05, **0.01,***<0.001, n.s.: non-significant

Table C-II: Results of linear multiple effects models relating the resistance of biomass production to drought to plant species-richness, including the environmental co-variables and interactions separately.

		F-value	P-value	Sign.
Single effect model				
Species-richness	F(1,148)=	19.33	<0.001	***
Multi-effect models				
Species-richness	F(1,138)=	19.137	<0.001	***
Region	F(5,138)=	0.99	0.43	n.s.
Species-richness × Region	F(5,138)=	0.725	0.61	n.s.
Species-richness	F(1,122)=	11.831	<0.001	***
Moisture	F(1,122)=	2.394	0.12	n.s.
Species-richness × Moisture	F(1,122)=	0.387	0.54	n.s.
Species-richness	F(1,122)=	11.038	0.001	**
pH	F(1,122)=	0.16	0.69	n.s.
Species-richness × pH	F(1,122)=	0.05	0.82	n.s.
Species-richness	F(1,2177)=	23.708	<0.001	***
Soil type	F(1,144)=	0.95	0.39	n.s.
Species-richness × Soil type	F(1,144)=	0.7	0.5	n.s.
Species-richness	F(1,122)=	8.739	0.004	**
N-content	F(1,122)=	2.314	0.13	n.s.
Species-richness × N-content	F(1,122)=	0.379	0.54	n.s.
Species-richness	F(1,122)=	8.628	0.004	**
P-content	F(1,122)=	2.242	0.14	n.s.
Species-richness × P-content	F(1,122)=	0.175	0.68	n.s.

*Significances: *<0.05, **0.01, ***<0.001, n.s.: non-significant*

Geranium molle

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English summary

Global climate change will increase the frequency and magnitude of climate extremes, putting ecosystems and their functioning under pressure and possibly jeopardizing ecosystem services in the near future. In recent decades it was theorized that biodiversity may have a stabilizing effect on ecosystem functioning under environmental stress, through the diversity-stability paradigm. These theories are based on the asynchrony and complementarity of responses of species within an ecosystem to an external perturbation. Experimental studies have resulted in a piling amount of evidence that there is indeed a positive diversity-stability relationship in grassland ecosystem under drought stress. However, the majority of these studies, where artificial grassland ecosystem are monitored over time, are relatively small-scaled and are *ex situ*, hampering the extrapolation of the results to real-world ecosystems. The availability of large datasets on vegetation composition and modern non-invasive monitoring techniques, such as remote sensing, provide new opportunities to investigate diversity-stability relationships in nature on large spatial and temporal scales. This study aims investigate and to quantify to what extend the diversity-stability paradigm hold in natural self-assembled unmanipulated grassland habitats, across relatively large spatial and temporal scales. Large datasets on vegetation, climate, functional traits were combined with remote sensing data to create time-series over relevant time-scales in order to study the relationships between biodiversity, ecosystem functioning and stability.

In chapter 2, historical data on vegetation composition was combined with Normalized Difference Vegetation Index data acquired via remote sensing (MODIS satellite imaging) in order to investigate to what extent the stability of dry dune grassland in the Netherlands is mediated by plant species richness, Shannon-Wiener, Evenness and Functional diversity (Rao's quadratic entropy) under drought stress indicated by locally assessed Standardized Precipitation and Evapotranspiration Index values. The anomaly of the NDVI compared to the long-term average corresponded with changes in SPEI-values, a large anomaly indicted a lower resistance. A significant positive relationship was found between plant species richness and the stability of the observed pixels as well as between the Shannon-Wiener diversity. Our results did not show a mediating effect of functional diversity in stabilizing ecosystem functioning.

Chapter 3 aimed to evaluate to what extent species-poor intensively managed agricultural grasslands are able to maintain primary productivity under climate anomalies as compared to relatively rich species-rich, extensively managed (semi-)natural grasslands. Grasslands were distributed over the Netherlands across various habitats represented by the physical geography. The stability of biomass production in response to drought was assessed by monitoring NDVI, temperature and drought for fourteen years. Resistance and resilience were derived using an autoregressive model and compared between the two types of grasslands. Results showed that semi-natural grasslands exhibited a higher resistance of biomass production compared to agricultural grasslands, however agricultural grasslands showed a higher resilience. The differences in resistance and resilience between the two grassland types varied across the habitats and were most pronounced in the coastal dune area.

Where current remote sensing techniques do not provide enough detail to distinguish species within the vegetation observed permanent vegetation plots do provide the necessary detail to make time-series of biodiversity. Chapter 4 returns to the Dutch calcareous dune grassland ecosystems in order to assess long-term relationship between species diversity and the resistance of biomass production to drought variability using 57 permanent plots monitored between 1952 and 2012. While historical data on biomass production was not available, a reliable proxy for primary productivity was calculated using the Leaf Area Index (LAI) and Specific Leaf Area (SLA) to account for interspecific differences in biomass allocation. A significant positive relationship was found between plant species richness and the stability of primary productivity over a period of sixty years.

Earlier studies of diversity-stability relationships in field situations were often criticized for not incorporating environmental co-variables. In chapter 5 we used time-series of permanent to assess the long-term relationship between plant species richness and the stability of biomass production under variating drought, across different extensively managed grassland habitats in the Netherlands. Drought was assessed by exploiting the georeferenced data in the SPEIbase database. The grassland habitats differed in environmental co-variables (soil pH, soil moisture, soil type and soil nitrogen and phosphorus availability) which were assessed using Wamelink Ecological Indicator

Values. Due to the lack of historical data on ecosystem functioning, biomass production was again estimated by using a proxy based on the LAI and SLA. Again, an overall significant positive relation was found between plant species richness and resistance of biomass production. Although the productivity was affected by the environmental co-variables, the diversity-stability relationship remained consistent in all grassland habitats with the environmental co-variables included in the analysis.

Overall, our studies add to the evidence that biodiversity has a mediating role in maintaining the stability of grassland ecosystems. A consistent positive diversity-stability relationship suggests that plant species play a vital role in ecosystem functioning, also on large spatial and temporal scales relevant for management and policy. Moreover, this thesis substantiates the relatively small-scaled *ex situ* experimental studies on diversity-stability relationships and presents an approach, based on the combination of large datasets with remote sensing, to up-scale research on and the interpretation of the diversity-stability paradigm in real-world ecosystems. Therewith, this thesis stresses the importance of biodiversity in maintaining ecosystem functioning in a changing world.

Nederlandse samenvatting

Klimaatverandering zal al in de nabije toekomst zorgen voor een toename van klimaatextremen. Deze klimaatextremen, zoals extreme droogte, zullen niet alleen in frequentie toenemen maar ook in sterkte. Hierbij zullen ecosystemen en de ecosysteemdiensten die ze leveren onder druk komen te staan. De theorie dat biodiversiteit een stabiliserende werking heeft op het functioneren van ecosystemen ten tijde van verstoringen is de afgelopen decennia een speerpunt geweest in het ecologisch onderzoek. Deze theorie is gebaseerd op de asynchrone en complementaire reacties van individuele soorten binnen een vegetatie, gemeenschap of ecosysteem op een externe verstoring zoals een droogte. Door de verschillen tussen soorten kan de ene soort een andere soort ,als het ware, ondersteunen of compenseren tijdens een stressvolle periode. Er komt steeds meer bewijs voor deze positieve diversiteit-stabiliteit relatie, met name uit experimenten die zijn uitgevoerd in graslanden onder droogtestress. Echter, het merendeel van deze experimenten, waarin de biomassaproductie van kunstmatig aangelegde graslanden wordt gevolgd door de tijd, is relatief kleinschalig en tevens *ex situ*. Dit maakt het moeilijk om de resultaten te extrapoleren naar natuurlijke ecosystemen op een grote schaal. De beschikbaarheid informatie over de samenstelling van vegetatie in grote databestanden, evenals moderne niet-invasieve methoden om het functioneren van ecosystemen te meten, bijvoorbeeld door middel van satellieten, maakt het nu mogelijk diversiteit-stabiliteit relaties te onderzoeken op een grotere schaal zowel in de ruimte in de tijd. De studie beschreven in dit proefschrift heeft als doel om te onderzoeken en te kwantificeren in hoeverre dit diversiteit-stabiliteitsparadigma stand houdt in natuurlijke graslandsystemen. Grote databestanden met gegevens over vegetatie, klimaat en functionele eigenschappen werden gecombineerd met satellietgegevens om zo tot tijdreeksen te komen die diversiteit, ecosysteemfuncties en de stabiliteit volgen over de tijd. In hoofdstuk 2 werd onderzocht in tot hoeverre de stabiliteit van droge (grijze) duingraslanden langs de Nederlandse westkust wordt beïnvloed door biodiversiteit ten tijde van droogte. Hiervoor werd historische vegetatie data gecombineerd met *Normalized Difference Vegetation Index* (NDVI; een maat om biomassaproductie te schatten), afkomstig van MODIS-satellieten. Biodiversiteit werd uitgedrukt in soortenrijkdom (aantal soorten), Shannon-Wiener index, Evenness en functionele diversiteit (Rao's kwadratische entropie). Als maat voor droogte werd de Standardized Precipitation and Evapotranspiration Index gebruikt, die werd afgeleid van de lokale weerstations. Een afwijking van de NDVI ten opzichte van het langjarige gemiddelde bleek over alle pixels samen te vallen met veranderingen in de SPEI-waarden. Droogte leidt dus tot verandering in de biomassaproductie. Sommige pixel veranderden echter sterker dan anderen waarbij een sterke verandering in de NDVI, dus de biomassaproductie, duidde op een verminderde stabiliteit. Vice versa, waar pixels slechts weinig veranderden was er sprake van een hoge stabiliteit. Een significante positieve relatie werd er gevonden tussen de stabiliteit van de pixel en de soortenrijkdom. Echter, werd er geen relatie gevonden tussen de functionele rijkdom en de stabiliteit van bovengrondse biomassa productie ten tijde van droogte.

In hoofdstuk 3 werd onderzocht in hoeverre intensief beheerde agrarische graslanden, met een relatief lage soortenrijkdom, in staat waren om de bovengrondse biomassa productie te stabiliseren ten tijde van klimaat extremen. Dit werd vergeleken met de prestatie van de relatief soortenrijkere extensief beheerde (semi-) natuurlijke graslanden. De onderzochte graslanden waren verspreid over verscheidene gebieden in Nederland met eigen omgevingsfactoren welke in dit onderzoek werden gerepresenteerd door fysisch geografische regio's. Hierbij werd de bovengrondse productiviteit, temperatuur en droogte gevolgd over een periode van veertien jaar. Weerstand (resistentie) en veerkracht (resilience) werden berekend door middel van een autoregressie model en vergeleken tussen de twee graslandtypen (agrarische en (semi-) natuurlijk). Hieruit bleek dat semi-natuurlijke graslanden een grotere weerstand hadden ten tijde van droogte dan agrarische graslanden, echter bezitten agrarische graslanden een grotere veerkracht. De verschillen tussen de twee typen grasland varieerden tussen de fysisch geografische regio's en kwamen het duidelijkst naar voren in de graslanden van de duinen.

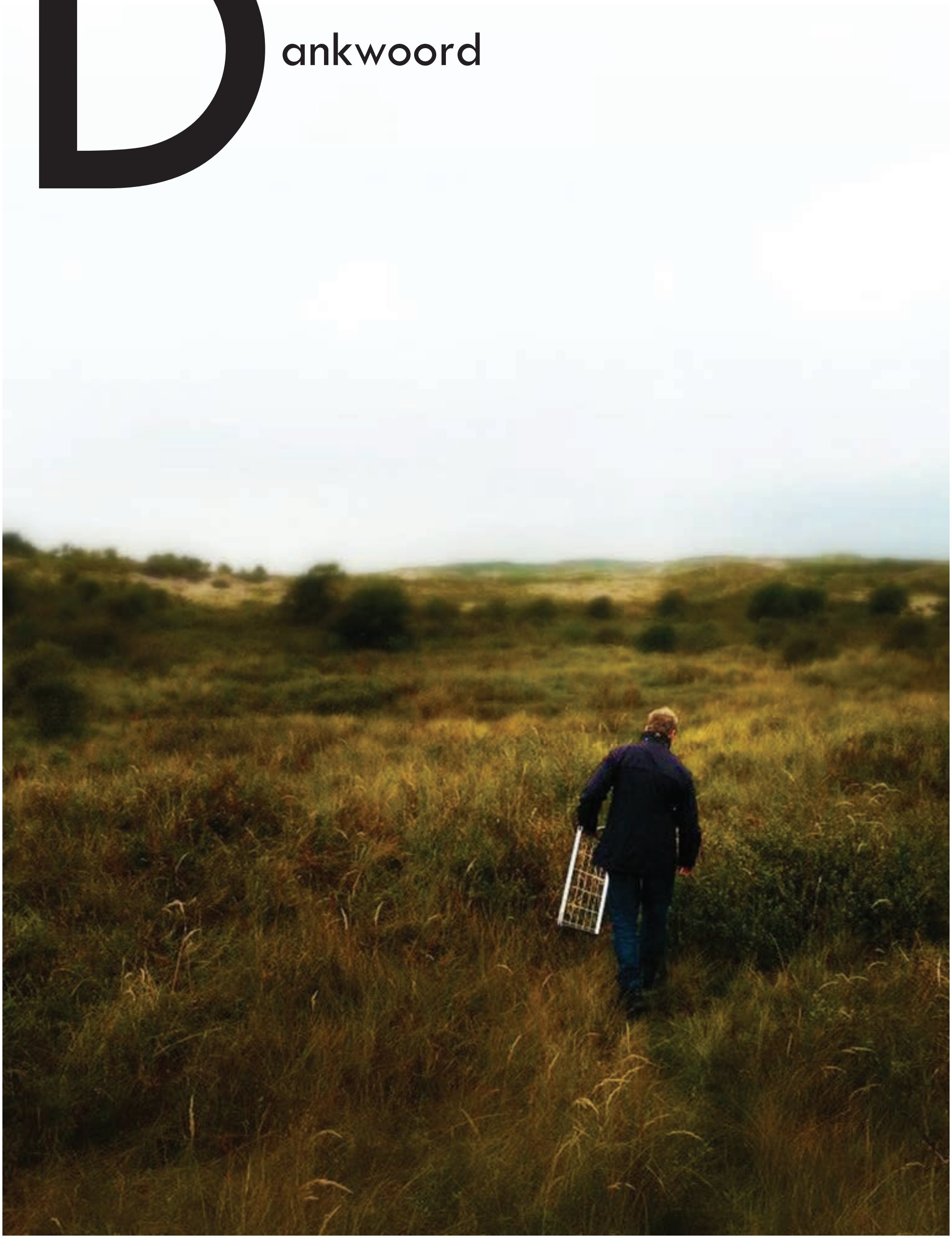
Waar satellietgegevens vaak te weinig gedetailleerd zijn om op het niveau van individuele soorten te kijken, kunnen permanente kwadraten dat wel. Hoofdstuk 4 keert terug naar de Hollandse duingraslanden om de lange termijn relatie tussen soortendiversiteit en de weerstand van bovengrondse biomassaproductie ten tijde van droogte te kwantificeren. Hierbij werden 56 permanente kwadraten gevolgd tussen 1952 en 2012. Omdat er geen historische data over de biomassa productie beschikbaar was werd er een betrouwbare indicatie berekend met behulp van de Leaf Area Index (LAI; oppervlakte bladbedekking per oppervlakte) en de Specific Leaf Area (SLA; oppervlakte per eenheid biomassa) waardoor er rekening gehouden kon worden voor interspecifieke verschillen. Ook over deze periode van zestig jaar werd er een significante positieve relatie gevonden tussen soortenrijkdom en de stabiliteit van primaire productie ten tijde van droogte.

Eerdere studies die de relatie tussen diversiteit en stabiliteit onderzochten werden vaak bekritiseerd omdat ze de effecten van omgevingsfactoren niet voldoende meenamen in de analyse. In hoofdstuk 5 werden er tijdseries gemaakt van permanente kwadraten in verschillende Nederlandse graslandsystemen, om zo de diversiteit-stabiliteit relatie onder invloed van droogte te onderzoeken over lange termijn. Alle plots varieerde in omgevingsvariabelen zoals bodem pH, bodem vochtgehalte, bodemtype en de beschikbaarheid van stikstof en fosfaten. Door de afwezigheid van historische metingen werden de co-variabelen berekend aan de hand van Wamelink Indicatoren. De klimatologische database SPEIbase leverde gelokaliseerde droogte indicaties (wederom in SPEI). Bovengrondse biomassa werd benaderd met behulp van de LAI en SLA. Nogmaals werd er een significant verband gevonden tussen soortenrijkdom en de weerstand van biomassa productie onder invloed van droogte. De resultaten tonen tevens aan dat biomassa productie wordt beïnvloed door de omgevingsvariabelen, echter blijkt de diversiteit-stabiliteit relatie consistent te zijn in alle habitats en ook de verschillende omgevingsfactoren hebben hier geen significant effect.

De studies in dit proefschrift dragen bij aan de toenemende hoeveelheid bewijs voor de stabiliserende rol van biodiversiteit in graslandsystemen ten tijde van klimaatextremen. Deze positieve relatie suggereert een belangrijke rol van soorten in het behoud van het functioneren van ecosystemen, ook over grote ruimtelijke en temporele schalen. Schalen die ook relevant zijn ten behoeve van beheer en beleid. De studies in dit proefschrift onderschrijven de bevindingen van de relatief kleinschalige *ex situ* experimenten en doen suggesties voor methoden om deze experimenten te extrapoleren naar natuurlijke ecosystemen en de bevindingen te interpreteren. Centraal staat hierbij het belang van s in het in stand houden van het functioneren van ecosystemen in een veranderende wereld.

Polygala vulgaris

Dankwoord



Tijdens een van onze velddagen in de duinen van Meijendel zei Joop tegen me: ‘Ik heb nóg nooit in m’n ééntje een vegetatieopname gemaakt. Dat lijkt me helemaal niks.’ Eigenlijk geldt dat voor al het werk. Je kunt in zulke mooie gebieden komen of zulke mooie resultaten hebben, uiteindelijk zijn het de mensen om je heen die je wereld vormen. Voor een doctoraat als dit geldt hetzelfde en ik heb het geluk gehad altijd omringd te worden door ontzettend veel ontzettend geweldige mensen. Als afsluiter van dít hoofdstukje in mijn leven wil ik dan ook mijn dankbaarheid uiten! En dat moet altijd in veel te weinig woorden.

Allereerst natuurlijk mijn promotor Olivier. Jij gaf mij, zo’n koppige Hollander, de kans om mijn doctoraat te doen aan de KULeuven. Dank voor je vertrouwen en je gastvrijheid op het labo in de afgelopen jaren en dat je me de vrijheid gaf om zelfstandig ons project te verkennen en uit te bouwen. Als het aankomt op snelle én scherpe commentaren, kan niemand je overtreffen. Dank voor alles wat ik van je geleerd heb.

Joop, jij bent niet alleen mijn promotor aan de Nederlandse kant geweest, voor mij ben je een echte mentor. Ik heb ontzettend veel van je geleerd. In het veld, tijdens het schrijven en tijdens vergaderingen liet je me jouw wereld zien. Een wereld waar positiviteit, originaliteit, vasthoudendheid en de liefde voor wereld om ons heen altijd overheerst. De vele kansen die me bood om naast mijn PhD ook mijn wereld uit te breiden hebben me immens geïnspireerd. Ik hoop in de toekomst nog veel met jou samen te kunnen werken en door te gaan met bruggen slaan tussen wetenschap, kunst en maatschappij. En natuurlijk planten kijken, fotograferen, Belgische biertjes drinken en zo nu en dan naar de film. Én rare plannen smeden in de auto.

Wim, ook jij bent er de afgelopen jaren altijd bij geweest en met jou praten is altijd een plezier! Met de rust en vriendelijkheid die je uitstraalt breng je rust in elke verhitte discussie en verdwijnen beren op de weg als sneeuw voor de zon. Daarbij komt ook nog dat je zo ontzettend veel weet! Ook je verhalen over je thuis, je geliefde honden en schapen zijn me erg bijgebleven en heel graag kom ik ze snel zelf eens bewonderen.

Mijn paranimfen, Eva en Thomas wil ik in het bijzonder bedanken.

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Thomas, zoals jij al zei in jouw proefschrift, enige tijd geleden, begon onze reis samen in Zuid-Afrika. Een reis waar voor ons beiden ook onze wetenschappelijke reis is begonnen en dat wij daarin samen konden optrekken is mij ontzettend dierbaar! Met jou kan ik altijd sparren over de meest uitvoerige onderwerpen: wetenschap, natuur, films (en het publiek dat daar naar toe gaat), muziek, filosofie en alle andere grote en kleine dingen in het leven. Maar net zo goed kunnen we samen naar feestjes en festivals! Ik hoop dat onze koers nog lange tijd hetzelfde zal zijn! *Engage!*

Wanda heel erg bedankt voor de fijne samenwerking met jou. Jouw magische *remote sensing* krachten hebben immers de basis gelegd van dit proefschrift. Ik heb veel van je geleerd op dat vlak en ik hoop dat je ook nog wat hebt opgepikt tijdens onze mooie velddaagjes in de duinen. Assessoren, Hans en Martin erg bedankt voor jullie scherpe en opbouwende feedback de afgelopen jaren. Ben, Stef, Laurent en Pol veel dank voor jullie hulp en enthousiasme! Tijdens mijn PhD heb ik veel hulp en gezelschap gehad van tal van studenten die ik heb mogelijk begeleiden. Gert, jij was mijn eerst MSc-student dank voor je enthousiasme en liefde voor de natuur. Pieter, dankjewel voor je harde werk en vooral je gezelligheid in Nijmegen en op de terrasjes in Ljubljana! 'Ik ben dropje' Marlijn, mijn meest trouwe student, ook met jou was het altijd fijn om samen te werken en natuurlijk te keuvelen over al die andere dingen. Én dankjewel dat ik élke dag koffie kan drinken! Ook Luisa dankjewel voor je fantastische harde werk en doorzettingsvermogen! Dank voor mijn BSc-studenten Thomas, Juan en Wies voor het werk en de fijne tijd in het veld (en de kou). Constant, ook jij bedankt voor het samenwerken en je enthousiasme voor de natuur. Natuurlijk moet ik ons Nijmeegse vegetatieclubje ook even bedanken: VEGFACC!

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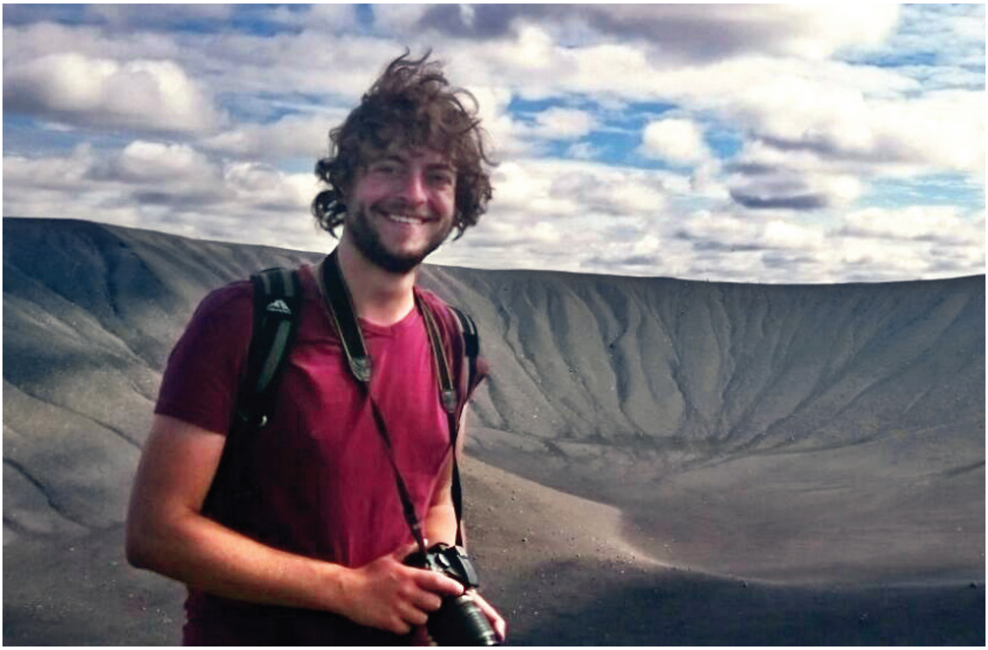

Curriculum Vitae

I, Nils van Rooijen, was born on the 27th of February 1986 in Rhenen, The Netherlands. After growing up surrounded by nature and many animals, first in Malden and later in Ottersum, it was no surprise that I wanted to study the environment. After graduating Atheneum at the Merlet college in Cuijk I decided to study environmental sciences. During my first year of the Bachelor however the miraculously diverse world of biology captivated me and I continued as a Biology student at the Radboud University in Nijmegen. The dunes of Terschelling and the green machairs of Ireland fuelled my fascination in ecosystem dynamics and plant community processes which led to a Masters' internship in South Africa, studying the ecology of the unique Fynbos biome in the Cape Floral Kingdom. Back in the Netherlands, I continued my research on vegetation with a phytosociological study of *Anacamptis morio* (Green Winged Orchid or Harlekijn) in Dutch grassland ecosystems, which resulted in obtaining a Master's degree in Biology (cum laude) in 2011.

Shortly after, I had the opportunity to start my PhD at the universities of Leuven (BE) and Nijmegen of which the results are presented in this thesis. During his

PhD I presented my work on several national and international conferences and participated in a number of BSc-and MSc-courses and excursions at both universities. In addition, I supervised BSc- and MSc-students in writing their theses and doing their internships. In the summer of 2017, I organized a summer school for the Radboud University on biodiversity and nature management in the Netherlands. After obtaining my PhD, I will continue to work on vegetation ecology, this time on dike grasslands, as a post-doctoral researcher at the Experimental Plant Ecology department at the Radboud University in Nijmegen.

Besides my research I have been participating in organisations connecting nature and society. As member of the board of the Royal Botanical Society of the Netherlands (KNBV) and Stichting Nationale Plantencollecties (SNP) and as fellow organizer of the annual Victor Westhofflezing at the Radboud University and LunBo meetings of the IWWR institute, my colleagues and me aim to strengthen the knowledge, interest and integration of plants, ecology, science and nature conservation in society. I participate in several initiatives such as the new scientific Flora of the Netherlands, Nova Flora Neerlandica, the website *Flora van Nederland* (www.floravannederland.nl) and the Levend Archief/National Seed Repository and added to publications such as *Botanische Meesterwerken*, *Wegwijs in de Natuur* and *Botanische tuinen in Nederland*. For the Waddenverening I am a (world heritage) guide in our Wadden area and fellow-organiser of the annual WaddenWerkWeekend beach clean-up festival on Terschelling. When I have some time to spare I enjoy watching and discussing films, playing the guitar and drawing. I spend considerable time on photography which enables me to go outdoors and, as always, be wondered by nature.

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