Trade-offs and synergies between forage production, species conservation and carbon stocks in temperate coastal wet grasslands

An ecosystem services and process-based approach

Miguel Ángel Cebrián-Piqueras

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Miguel Ángel Cebrián-Piqueras

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Gutachter: Prof. Dr. Michael Kleyer

Zweitgutachter: Prof. Dr. Boris Schröder-Esselbach

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Contents

Most important definitions

Bundle of ecosystem services: Set of ecosystem services that appear together repeatedly. The association can rise from common underpinning processes or as a response to common pressures (Bennett *et al.* 2009; Mouchet *et al.* 2014).

Community-weighted mean of a trait: The mean of trait attributes in the community, weighted by the relative abundance of the species or populations carrying each value (Garnier *et al.*, 2004; Violle *et al.*, 2007)

Conservation value of habitats and species: Cultural and supporting ecosystem service associated with the social benefits obtained from the conservation of biological diversity and habitats suitable for species (MEA, 2005; Haines-Young & Potschin 2013).

Constructs: Measure concepts that are abstract, complex, and cannot be directly observed by means of (multiple) items. Constructs are represented in path models as circles or ovals and also referred to as *latent variables* (Hair *et al.* 2013).

Direct driver: A driver that unequivocally influences ecosystem processes and can therefore be identified and measured to a different degrees of accuracy (MEA, 2005). See *driver of ecosystem change*.

Driver of ecosystem change: Any natural or human-induced factor that directly or indirectly causes a change in an ecosystem (MEA, 2005).

Ecosystem: A dynamic complex of plant, animal and micro-organism communities and their non-living environment interacting as a functional unit (Convention on Biological Diversity).

Ecosystem function or process: The interactions and mechanisms among biotic and abiotic elements of ecosystems that lead to a definite result (Vandewalle *et al.* 2008).

Ecosystem service (ESS): The ecosystem services are the benefits that the human beings receive from the ecosystems (MEA, 2005).

Ecosystem service' demand: the amount of a service required or desired by society (Villamagna *et al.* 2013).

Final ecosystem service: Ecosystem outputs that receive a societal value (Wong et al. 2015). They are the contributions that ecosystems make to human well-being. These services are final in that they are the outputs of ecosystems (whether natural, semi-natural or artificial) that most directly affect the well-being of people. A fundamental characteristic is that they retain a connection to the underlying ecosystem functions, processes and structures that generate them. (MEA, 2005; Haines-Young & Potschin 2013).

Forage or fodder production: Provisioning ecosystem service associated with the social benefits obtain from forage-based goods provided by pastures (MEA, 2005; Haines-Young & Potschin 2013).

Human well-being: the state of feeling healthy and happy. Human well-being is partly dependent on the aggregated output of ecosystem goods and benefits (Haines-Young & Potschin 2013).

Indicator variable: Directly measured variable, which, in combination with of other indicator variables, explain a latent variable. See *latent variable*.

Latent variable (latent construct): Are the (unobserved) theoretical or conceptual elements in the structural model. A latent variable that only explains other latent variables (only outgoing relationships in the structural equation model) is called exogenous, while latent variables with at least one incoming relationship in the structural equation model are called endogenous (Hair *et al.* 2013). See *Constructs*.

Observed variable: Directly measured variable, e.g. salinity.

Partial least square-structural equation modeling (PLS-SEM): PLS-SEM is a causal modeling approach aimed at maximizing the explained variance of the dependent latent constructs. If the research objective is prediction and theory development instead of theory confirmation, then the appropriate SEM' method is PLS-SEM (Hair *et al.* 2011).

Perception: a belief or opinion, often held by many people and based on how things seem.

Plant functional trait: A feature of a plant, which has demonstrable links to the organism' function (Vandewalle *et al.* 2008). Functional traits underlie the delivery of ecosystem services in different trophic levels (DeBello *et al.* 2008).

Socio-ecological system: A system that includes societal (human) and ecological (biophysical) subsystems in mutual interactions and thus captures interactions between people, biodiversity and ecosystem (Vandewalle *et al.* 2008).

Stakeholder: A person or group of people having an interest in a physical resource, ecosystem service, institution, or social system, or someone who is or may be affected by a public policy (Assessment, 2005).

Synergies between ecosystem services: Situations where the use of one ecosystem service directly increases the benefits supplied by another service (Turkelboom *et al.*, 2015).

Trade-offs between ecosystem services: Situations where the use of one ecosystem service directly decreases the benefits supplied by another. A change of ecosystem service use could be triggered by the demand and/or the supply side. A trade-off could take place in the same place or in a different area (Turkelboom *et al.*, 2015).

List of abbreviations

AGB	Above-ground standing biomass
ANPP	Above-ground net primary productivity
CEC	Cation exchange capacity
CH	CWM Canopy height
Clay	Soil clay content
CWM	Community-weighted mean
Decomposition	Native biomass decomposition rates
Endan. breeding birds	Habitat value to conserve endangered breeding birds
Endan. plants	Habitat value to conserve endangered plants
ESP	Ecosystem properties
ESS	Ecosystem services
GW	Groundwater
Humus	Soil humus content
K	Potassium
LA	CWM Leaf area
LDMC	CWM Leaf dry matter content
LDW	CWM Leaf dry weight
LES	Leaf economic spectrum
LNC	CWM Leaf nitrogen content
N	Nitrogen
NUT/NUTRIENTS	Plant soil nutrient availability
P	Phosphorus
Plants	Plant species richness
PLS-SEM	Partial least square-structural equation model
RDMC	CWM Root dry matter content
RNC	CWM Root nitrogen content
SA	Size axis
Sal	Salinity
Sales/forage sales	Sales of forage-based products
Sand	Soil sand content
SDMC	CWM Stem dry matter content
SDW	CWM Stem dry weight
SEM	Structural equation model
SLA	CWM Specific leaf area
SN	CWM Seed number
SNC	CWM Stem nitrogen content
SOC	Soil organic carbon
SRL	CWM Specific root length
SSL	CWM Specific stem length
WATER	Water gradient (Groundwater and salinity co-variation)

“Dedicated to Alba”

Part I

Chapter 1

Preface

Miguel Ángel Cebrián-Piqueras

Chapter 1: Preface

Since the revelation of the world' environmental crisis in the 20th century, several new scientific disciplines have arisen with the purpose of restoring balance in humanity' consumption of natural resources.

In order to effectively identify, understand and combat the dangers of the crisis many accompanying phenomena, such as loss of biodiversity, air pollution or rising sea levels, new scientific disciplines, incorporating interdisciplinary approaches into their methodologies, were needed. Drawing from a plethora of traditional scientific fields, including Ecology, Geography, Sociology or Economy, multidisciplinary research has thrived, yielding new disciplines such as Landscape Ecology, Sustainability Science and more recently, the Ecosystem Service approach.

Ecosystem Services are the various beneficial services directly or indirectly provided to human beings by their surrounding ecosystems. The ecosystem service approach has since the institution of the Millenium Assessment in 2005 been heralded by two distinct groups of scientists: economists, seeking to attribute purely financial values to an ecosystem (e.g. its provisioning services), and ecologists, focusing on their ecosystem properties and processes.

However, in line with the complex physical nature and all-encompassing scope of the concept of the ecosystem, the spectrum of established scientific fields that the new approach builds on has grown considerably, allowing researchers to study and assess ecosystem services from a more comprehensive perspective. Thus, the Ecosystem Service approach, seeks to equally emphasize economic values as well as the more intangible ones, such as those provided by the ecosystem' cultural services (e.g. landscape aesthetics), but also regulating services (e.g. climate and water dynamics) or supporting services (e.g. soil nutrients availability).

Coastal regions are among the most threatened ecosystems in the world (Barbier *et al.* 2011): Worldwide, 50% of all coastal saltmarshes have been lost or degraded and 69 % of all coastal wetlands are considered in decline. In some areas of Northwestern Europe, the expanse of wet extensive grasslands has within a century been decimated by 80% (Valiela *et al.* 2001; MEA, 2005; Krause *et al.* 2011; Wesche *et al.* 2012).

These developments and the associated losses in coastal ecosystem biodiversity have notably reduced their capacity to provide valuable services, such as water purification, storm mitigation, carbon sequestration, pasture supply or the potential for touristic and recreational activity (Chmura *et al.* 2003; Cochard *et al.* 2008; Koch *et al.* 2009; Turner *et al.* 2009).

A plethora of threats which are expected to significantly affect coastal wetlands in the coming century has been identified: eutrophication, climate change and sea level rise, increasing CO2 concentrations, pollution or marsh reclamation (Barbier *et al.* 2011; Silliman *et al.* 2014).

In the past decades, far-reaching land use modifications have affected the cultural marshes landscape of northwest Europe. Most of the lowlands wet meadows in northwestern Germany have been affected by to high agricultural intensification: It has lowered water levels, caused groundwater eutrophication and reduced biodiversity in favor of agricultural and forage production interests (Krause *et al.* 2011; Wesche *et al.* 2012; Joyce 2014).

Conversely, most of the original human-modified saltmarshes situated seawards of the dyke line have been nature-protected and thus secluded from human intervention (Bakker, 2014). This has led to a radical spatial segregation between natural protection and agricultural production goals. However this apparently balanced situation may produce ecological and social controversies (Yu & Chmura 2009; Deegan *et al.* 2012).

The present thesis is framed in the collaborative project COMTESS: Sustainable Coastal Land Management: Trade-offs in Ecosystem Services. This project gave me the chance to combine and reinforce my previously-acquired experience in vegetation ecology and sustainability science in a trans-disciplinary and socio-ecological approach such as the ecosystem services framework.

Thanks to the structure and functioning of COMTESS, headed and coordinated by Prof. Dr. Michael Kleyer and Dr. Martin Maier respectively, I was able to collaborate with other project members and incorporate valuable information about the perceptions and preferences of stakeholders, the richness of breeding bird species and plant traits from other nearby regions such as Denmark or the Netherlands. These collaborations broadened my horizons as to the approaches of the thesis and the proposed hypotheses. With this work, I hope to offer an authentic, innovative and scientifically-rigorous document to expand available knowledge in sciences such as landscape ecology, functional ecology and sustainability science in order to understand the functioning and interactions of landscape' ecological and sociological processes.

The thesis uses the ecosystem services framework and combines several assessment approaches which are explained in next chapter (chapter 2): (1) A process- and functional based approach (Bennett *et al.* 2009; Lavorel & Grigulis 2012), (2) a socio-ecological approach (MEA, 2005) and (3) a place-based approach (Potschin & Haines-Young 2013) to unravel the nature and origin of trade-offs and synergies between ecosystem services at different levels in a temperate coastal marsh landscape of Northwest Germany.

As a rather novel approach, partial least square-structural equation modeling (PLS-SEM) is used here as statistical method to unravel causal relationships and associations between land use parameters, ecosystem properties, values of final ecosystem services, plant functional traits and stakeholder perceptions.

Chapter 2

Introduction

Miguel Ángel Cebrián-Piqueras

Chapter 2: Introduction

2.1 The ecosystem service approach

2.1.1 Overview

Ecosystem services are the benefits that the human beings receive from ecosystems (MEA, 2005). This concept emerges as an holistic approach in order to understand and to study the complexity of socio-ecological systems. Essentially it is a multidisciplinary approach that works at the interface between disciplines such as economy, ecology and sociology, integrating concepts developed by the sustainability sciences (Daily 1997; Clark 2007). It therefore differs from other disciplines such as conservation biology, which usually contrasts human well-being with nature conservation (Ingram *et al.* 2012).

The ecosystem service approach places the human being as an undisputed or uncontested part of the ecosystem (Liu *et al.* 2010). This approach aims to achieve a comprehensive valuation of ecosystems through the eyes of human beings, in order to promote a sustainable relationship between nature and society (Carpenter *et al.* 2009). If human beings receive direct or indirect benefits from ecosystems, it is expected that they will use them to satisfy their needs. Under the circumstances, human beings have traditionally modified their surroundings, creating a range of landscapes that can vary from multifunctional (Fry 2001) to monocultures (Lamb *et al.* 2005), with the general aim of obtaining raw materials, food or shelter. Therefore most ecosystems have evolved according to contemporary human needs along with the co-occurring biodiversity (Gedan *et al.* 2009). However, during the past decades, ecosystems have drastically reduced their capacity to provide services, and therefore this has claimed increasing attention to ecosystem services research (Mace *et al.* 2012).

The ecosystem service approach aims to answer questions related to how some services are not compatible in space and time, how maximizing some services might lead to the decline of others (Rodríguez *et al.* 2006), how bundles of services are generated, and how trade-offs occur between them (Raudsepp-Hearne *et al.* 2010; Martín-López *et al.* 2012). On the other hand, it is expected that environmental and land-use changes will affect the biodiversity and directly or indirectly alter the ecosystems' capacity to provide services (Lamarque *et al.* 2014a). Thus questions related to disentangling these effects are of primary importance (Bennett *et al.* 2009).

2.1.2 Classification

Since the ecosystem service approach emerged in the research mainstream agenda (MEA, 2005) four main classification categories have been widely accepted and used during the past years (Fisher *et al.* 2009; Haines-Young *et al.* 2012; Haines-Young & Potschin 2013) (1) *Provisioning ecosystem services* are the products that the human beings obtain from the ecosystems such as food, fiber, materials or fuel; (2) *regulating ecosystem services* are services derived from the ecosystems such as climate regulation, water purification, or erosion and pest control; (3) *cultural ecosystem services* are those benefits associated to intangible benefits such as spiritual improvement, cognitive development, recreation or benefits associated to the aesthetic enjoyment; (4) *supporting ecosystem services* are those services which allow that the functioning and provision of the rest is maintained e.g. biomass primary productivity, oxygen production or soil formation.

2.1.3 Valuing ecosystem services

One important issue concerning the ecosystem services valorization is the distinction between final and intermediate services (Wong *et al.* 2015). The intermediate services are analogous to the supporting services, in fact they are ecosystem properties or functions which support and generate other services which are more closely related to direct and more easily measurable benefits. Several intermediate or supporting services can interact to generate a single or several ecosystem final services, which would be the case of soil fertility, vegetation forage quality or biomass productivity. All these properties have a direct effect on a final service such as a farmer' economic benefit.

The ecosystem services values vary according to the beneficiary, therefore this fact increases the complexity of analyzing (Boyd & Banzhaf 2007). Valuing the ecosystem services depends on the social context, because a single service may be understood in different ways depending on the stakeholder group or person (Hein *et al.* 2006). For instance the soil fertility understood as a supporting service can have several meanings depending on whether the target stakeholder group is the farming sector or the nature conservation sector (Lamarque *et al.* 2011). But also a service can act as intermediate or final depending on the beneficiary needs.

Following both the utilitarian and non-utilitarian paradigms about ecosystem services valuation (MEA, 2005), four types of values are attributed to ecosystem services (d'Arge *et al.* 1997; De Groot *et al.* 2002; Hein *et al.* 2006; Haines-Young & Potschin 2013): (1) direct use values are associated to the direct consumption of products e.g. agricultural harvest or clean water. A majority of provisioning services and some cultural services e.g. recreational enjoyment, belong to this category; (2) indirect use values are those indirectly enjoyed by

society, therefore they have been traditionally put aside from most common valuations e.g. some regulating services such as purification of air and water; (3) option values are those attributed to particular potential benefits and (4) non-use values are inherent in the ecosystem itself and they can be anthropocentric, such as natural beauty, or eco-centric, e.g. the species' right to exist (Hein et al. 2006) (Fig. 2.1).

Authors such as Kolstad *et al.* (2000) distinguish between three types of non-use values: the existence value would be based on the utility that something exists, the altruistic (or philanthropic) value refers to the utility that somebody else may benefit and the bequest value is associated with the potential that the future generations may profit from non-used resources of today (Fig. 2.1).

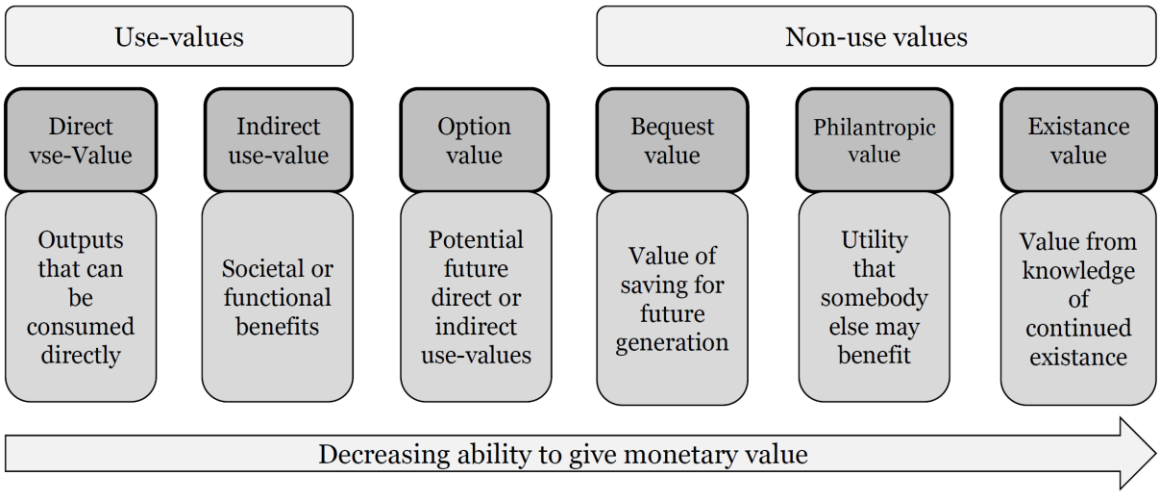

Fig. 2.1: Values' categories commonly assigned to ecosystem services (MEA, 2005). The figure shows how the ability of give monetary value to ecosystem services decrease from use-values to non-use values. Adaptation from Mace *et al.* (2011), Kolstad *et al.* (2000) and Hein *et al.* (2009).

2.1.4 The conceptual framework

The ecosystem services research is clearly situated in the center of socio-ecological systems (Fig. 2.2) (Andersson *et al.* 2007). A comprehensive study of the ecosystem services requires the analysis of both the social and the ecological components and its interactions at different scales (Carpenter *et al.* 2009). In the social component the human beings and their well-being are highlighted, subsequently in the ecological component the ecosystems and biodiversity play a relevant role (MEA, 2005).

Certain ecosystem services, such as some regulating or cultural services, exert a positive effect on human beings without a previously deliberated intervention e.g. pure air in rural areas, clean water in non-polluted areas or aesthetic value of the landscape. Although many of these

services have a strong positive effect on human beings, they are extremely vulnerable and at risk of disappearing due to a lack of active and conscious regulation. It is estimated that up to 60% of the ecosystem services have already disappeared on a global scale (MEA, 2005).

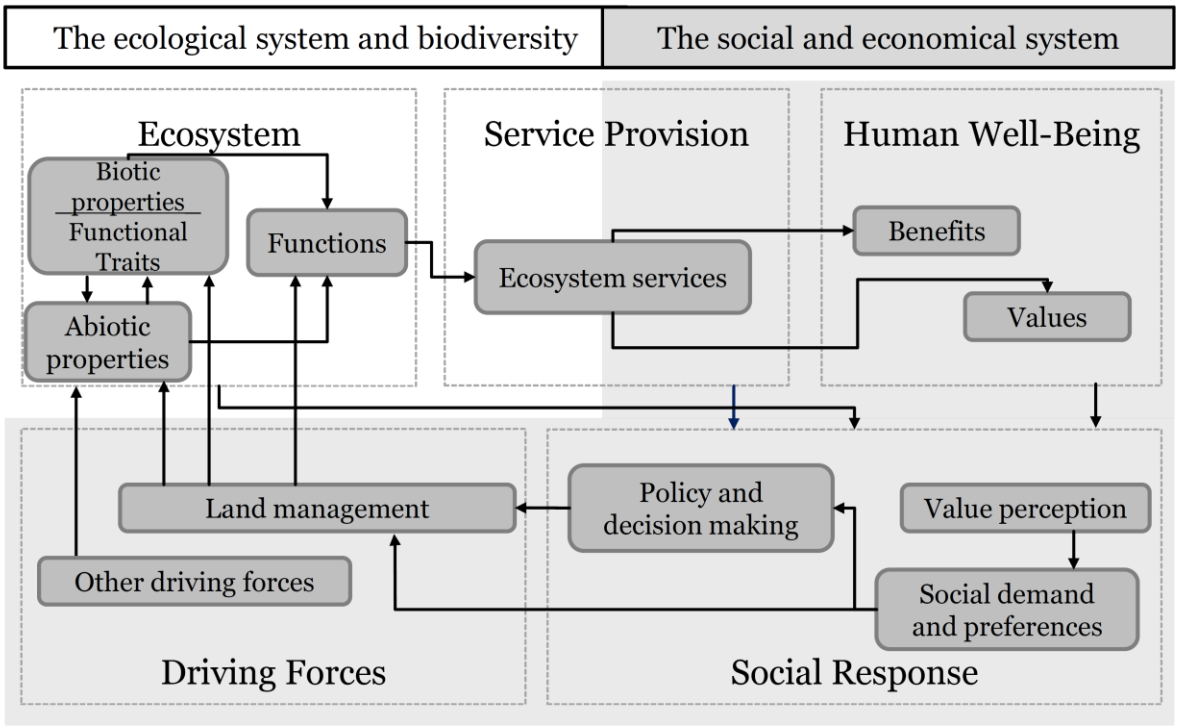

Fig. 2.2: General framework used to assess the present thesis vegetation-mediated ecosystem services. Adaptation from Van Oudenhoven *et al.* (2012) and Haines-Young and Potschin (2013).

On the other hand many of the benefits originating in the ecosystems have been previously regulated; this is the case for most of the provisioning services, but also many of the cultural services and some regulating services. These services are managed through land use strategies and policies which vary from the individual level or group e.g. cropland management, to international agreements e.g. trans-boundary national parks.

Therefore human beings take decisions and act deliberately on environmental parameters which modify ecosystem properties and biodiversity in order to obtain certain ecosystem services (Santos-Martín *et al.* 2013). These drivers of change can exert direct or indirect effects on ecosystem properties and services; for instance population growth exerts pressures which indirectly change the policies about land use on global or regional scales. On the other hand local agricultural management decisions modify directly the local biodiversity and ecosystems (Lamarque *et al.* 2014a; Martín-López *et al.* 2012).

The ecosystems and biodiversity reach natural thresholds which are highly dependent on environmental and biophysical parameters. Therefore the ecosystems potential to supply ecosystem services is limited to certain possible ranges not dependent on human activity

(Bastian *et al.* 2012). However, the environmental changes associated with global change or land use generate substantial pressures on the ecosystems and the associated biodiversity, a fact that compromises the ecosystem resilience (Mumby *et al.* 2007).

2.1.5 Biodiversity and ecosystem services

Biodiversity plays a primary role on all levels of the ecosystem services provision hierarchy (Mace *et al.* 2012). The biodiversity acts as a structural and functional component of the ecosystem affecting directly its properties and functions. Biodiversity-ecosystem functioning relationships (B-EF) have been extensively explained for processes such as biomass decomposition, biomass productivity and carbon stocks (Lienin & Kleyer 2012; Conti & Díaz 2013; Lewandowska *et al.* 2016).

There is increasing evidence of the role of biodiversity on the ecosystem functioning and its relationship with the ecosystem services provision (Diaz *et al.* 2004; Hooper *et al.* 2005; Duncan *et al.* 2015). Expected relationships between species numbers, ecosystem functioning and services provision may follow both positive linear and non-linear curves (Kremen 2005). Empirically-based meta-analysis, as conducted by Isbell *et al.* (2011), has shown how species numbers should be maintained in time and space to achieve higher ecosystem functionality and higher ecosystem services provision. These authors showed that although species may appear functionally redundant when one function is considered under one set of environmental conditions, many species are needed to maintain multiple functions at multiple times. At larger scales, it has been shown how habitats in a favourable conservation status provided more biodiversity and had a higher potential to supply, in particular, regulating and cultural ecosystem services than habitats in an unfavourable conservation status (Maes *et al.* 2012).

Nevertheless understanding of B-EF-ES (Biodiversity-Ecosystem Functioning-Ecosystem Services) relationships represent a rather new field of research that offers great possibilities for novel research (Duncan *et al.* 2015). Several topics that have been recently highlighted and need to be addressed are (1) understanding of provision of single final ecosystem services' outputs in relation to several ecosystem functions; (2) characterization of which ecosystem functions underpin the provision of ecosystem services; (3) addressing trade-offs and synergies between multiple ecosystem functions and ecosystem services (Duncan *et al.* 2015). However, the historically rather common top-down approaches in ecosystem service research have often ignored the understanding of ecological mechanisms (Bennett *et al.* 2009; Nicholson *et al.* 2009).

As a response to these research needs, the present thesis addresses these topics by using a rather novel structural equation model formalism that reveals the ecological mechanisms affecting (1) final ecosystem service variation at the site level; (2) perceived bundles of ecosystem services; (3) responses of plant functional traits to environmental gradients and (4) the subsequent causes of trade-offs and synergies between properties and services.

On the other hand biodiversity may work, in some situations, as a final service *per se* depending on the beneficiary. This would be the case with biodiversity components related to provisioning services, e.g. diversity of wild edible fruit species in a given local community. But also human beings assign certain "non-use" values to biodiversity components such as existence values, altruistic values (or philanthropic) and bequest values, e.g. flagship or umbrella species or one specific protected ecosystem (Haines-Young & Potschin 2010; Bastian 2013). In other contexts human beings assign "optional" values to biodiversity and its components leaving the door open to future potential benefits, e.g. pharmaceutical active ingredients (Hein *et al.* 2006; de Groot *et al.* 2010). The present thesis addresses the mechanistic understanding of how non-use values such as the habitat value to conserve endangered species relates to forage production.

2.1.6 Assessment approaches

a) Scale matters:

Undoubtedly, due to the complexity in which the ecosystem services are generated, demanded and interrelate between themselves it is necessary to set up spatial and temporal limits to study them (Hein *et al.* 2006). Different approaches may be used depending on the scope and research questions. Study units which are commonly used for ecosystem services research are the ecosystem or habitat (de Groot *et al.* 2010). But also the plot level, vegetation units or biotopes are commonly used in studies with a strong ecological component (Lavorel & Grigulis 2012). Studies explicitly based on land use units often deal with the role of the human being in the genesis of ecosystem services, therefore some authors call them socio-ecological services (Huntsinger & Oviedo 2014). Whatever the scale is, ecosystem services research should tend to maximize the spectrum of services types (e.g. provisioning, cultural, supporting and regulating) and the spectrum of units which may explain a certain landscape in which the services interrelate with each other (Raudsepp-Hearne *et al.* 2010).

b) The place- or context-based approach:

Both in the field of sustainability science and the study of ecosystem services there is a growing recognition of the importance of studies based on local or regional contexts for an adequate development of the knowledge of ecosystem services (Potschin & Haines-Young 2013). A feature associated with a place-based approach is that the services under study are generally selected by the local or regional community. This approach can provide an accurate understanding of the context and set priorities and values from the early stages. It can also facilitate the understanding of the patterns of use, demand and provision of services (García-Llorente *et al.* 2015). The use of place-based approaches allows a direct engagement of the users or stakeholders through participatory processes so that potential conflicts can be resolved through feedback and adaptive mechanisms. In contrast the results obtained by place-based approaches cannot be generalized easily, this fact makes necessary to create cooperation networks to launch comparative projects (Carpenter *et al.* 2009).

c) The habitat-based approach:

Since the emergence of the ecosystem millennium assessment reports (MEA, 2005), an extensive number of broad-scale assessments has been conducted. Many of these studies have used land use units or main ecosystem units as providers of several ecosystem services (Potschin & Haines-Young 2013). Advantages of this approach are: (1) it makes clear links between conservation approaches, (2) focuses more on the potential (capacity) to supply services, (3) often makes use of existing biodiversity data, and (4) emphasizes the multi-functionality of the ecosystem (Potschin & Haines-Young 2013).

Conversely several disadvantages have been highlighted: (1) Substantial errors may be produced when it comes to explain biophysical provision of services when non-primary data sets are used (proxies or ecosystem functions from other regions) (Eigenbrod *et al.* 2010; Wong *et al.* 2015), (2) besides it is not yet clear how the habitats should be weighted to perform overall assessments or (3) how the overall output of services is generated by the combinations of several habitats.

However, due to the broad scope of habitat-based approaches, an increasing and valuable knowledge about general patterns and a stimulating debate about the current trends in ecosystem services provision have been generated (Haines-Young *et al.* 2012).

d) The socio-ecological approach:

The ecosystem services research bases part of its principles on the sustainability sciences which is by definition multidisciplinary and integrative (Carpenter *et al.* 2009). Ecology, economy and sociology play all determinant roles (Clark 2007). The sustainability science and ecosystem services research aim to achieve a sustainable landscape where the natural resources are

maintained in space and time whilst the human beings achieve a fair and equitable well-being by the use of them (Haines-Young & Potschin 2013). The study of ecosystem services thus transcends the usual approached used by other traditional sciences such as ecology, biology or economy and it emphasizes the interrelation between the social and biophysical systems (Carpenter *et al.* 2009).

It is therefore essential to understand the social component in relation to the perception and demand of ecosystem services and the biotic ecosystem components that generate the services, but also to undertake research about how the ecosystems are passively or actively modified by society, affecting subsequently the provision of services (Lamarque *et al.* 2014b). Depending on the research scope it will be necessary to integrate several social actors varying all the way up from the individual through community leaders and stakeholders to national or international institutions (Hein *et al.* 2006).

Due to the fact that it is not always possible to achieve a monetary valuation of some ecosystem services, it is gaining acceptance to conduct social valuations by community members where the study takes place about their ecosystem services preferences (Karrasch et al. 2014). In that way it is possible to detect how society members or individuals perceive positive associations of services, which might be called bundles (Raudsepp-Hearne *et al.* 2010), but also trade-offs between other services irrespective of their economic value (Kiker *et al.* 2005). It is evident that the human well-being not only depends on the ecosystem services which are valued economically; this is the case of a multitude of cultural or regulating ecosystem services which are not easy to evaluate economically (Milcu *et al.* 2013).

Some approaches use qualitative analysis about the meaning, perceptions or demand of local ecosystem services. These techniques, that use *in-depth* interviews, provide valuable information about what the ecosystem services community values are (Lamarque *et al.* 2014b).

However, in order to understand socio-ecological processes, place-based studies, which combine both primary social- and ecological-data, are required (Anadón *et al.* 2009; Andersson *et al.* 2015). Moreover, how biophysical parameters explain social responses and perceptions is required in order to understand and predict social attitudes associated with ecosystem service management (Martín-López *et al.* 2012; Quijas *et al.* 2012; Lamarque *et al.* 2014b).

The present thesis addresses these needs by applying a place-based approach that uses structural equation models to explain bundles of ecosystem service perceptions in response to field-measured drivers and indicators of ecosystem services.

e) The process-based approach:

However, it is extremely important to investigate the biophysical processes that affect ecosystems if a proper understanding of the ecological component in ecosystem services research is to be achieved (Gordon & Enfors 2008; Bennett *et al.* 2009). Land use and the subsequent alteration of abiotic gradients cause strong direct or indirect changes in ecosystem properties (Lienin & Kleyer 2012). Ecosystem services are extremely dependent on ecosystem modifications and they are expected to be strongly affected by social demand and climatic alterations in the coming years. Therefore, understanding the processes underpinning ecosystems is of primary importance to appreciate potential future landscape scenarios (Lamarque *et al.* 2014a)

Thus, how abiotic gradients and land use affect the processes and components of the ecosystems need to be studied (Bennett *et al.* 2009; Wong *et al.* 2015). The study of the ecological processes and their drivers of change make it possible to detect where synergies and trade-offs between the ecosystem components are produced. These synergies and trade-offs may be detected at different scales. Trade-offs are synergies between ecosystems services can be detected at the spatial scale by habitat-based approaches (Raudsepp-Hearne *et al.* 2010). However detection of these trades-offs and synergies does not necessarily imply an understanding of the drivers of ecosystem change (Eigenbrod *et al.* 2010; Lavorel *et al.* 2011).

The plant functional traits and the functional approach: Recently, functional approach or trait-based approach has gained research focus in the ecosystem services research agenda (de Bello *et al.* 2010; Lavorel 2013). The trait-based approach is a particular type of process-based approach that focuses on how certain plant traits, or plant strategies indicated by these traits, respond to the environment and subsequently affect and explain ecosystem properties and services, respectively (de Bello *et al.* 2010; Lavorel & Grigulis 2012). Essentially, plant functional traits are those sensitive plant traits that express or capture the variation of environmental parameters or drivers of change, e.g. abiotic and land use parameters (Diaz et al. 2004; Violle et al. 2007).This should represent a straightforward tool, due to the fact that by knowing certain plant functional traits and the composition of a given vegetation community, it would be possible to understand the environmental conditions and make predictions of ecosystem service supply under several climate scenarios (Lamarque et al. 2014a).

The trait-based approach scales up to the community level, and therefore to ecosystem functioning, based on the premise that a certain vegetation community expresses an average value for a certain functional trait and therefore relates to ecosystem properties. This community functional structure can be quantified through different metrics (standards of measurement), such as the community-weighted mean (CWM), which expresses a vegetation

community average trait value based on the relative abundance of the plant species in the community as follows (Grime 1998; Garnier *et al.* 2004):

$$CWM_x = \sum_{i=1}^{Species} \frac{cover_i}{cover_{total}} \times x_i$$

where x = plant trait; x_i=trait value for species i; cover $_i$ =cover value for the species i; cover $_{total}$ = total cover value of all species occurring in the community in question.

For example, variation of the community-weighted mean of canopy height (plant functional trait) might positively indicate variation of soil organic carbon content (ecosystem property) (Conti & Díaz 2013) or variation of leaf traits might indicate litter decomposition and agronomic value (Garnier *et al.* 2004; Lavorel *et al.* 2011). However most of these approaches deal with the system capacity to provide ecosystem services but not with how plant traits predict the supply of final ecosystem service outputs, e.g. agricultural goods supply or endangered species occurrence, (Wong *et al.* 2015). As provision of services depends in both the ecological and social systems, combination of both trait data and social demand and supply of services might represent a straightforward approach (García-Llorente *et al.* 2015).

As response to these research gaps, the present thesis test how fundamental plant traits relate in response to variation of soil-nutrient availability, disturbance and groundwater levels. Leaf, stem and root plant traits were tested for this system following previous expectations as described by the leaf economic spectrum (Wright *et al.* 2004), plant leaf economic spectrum (Freschet *et al.* 2010) and size axis (Diaz *et al.* 2004). Subsequently expectations for trade-offs and synergies between ecosystem properties and services as final outputs in response to the traits variation are explained.

Other community parameters based on trait parameters expressing functional diversity, e.g. functional dispersion (FDis) or functional trait divergence index (FDvar), are being increasingly studied and they represent a promising field of research in functional ecology and ecosystem services research (Mason *et al.* 2003; Díaz *et al.* 2007; Laliberté & Legendre 2010). Nevertheless, generalizations about the significance of these parameters on ecosystem functioning and ecosystem services provision still remain unclear and more research is needed in this field (Díaz *et al.* 2007; Laughlin 2011; García-Llorente *et al.* 2015).

2.2 Thesis outline, aim and major questions

The present thesis is divided into three parts. The first part is an introduction composed of four chapters: **Chapter 1** is a preface to the entire thesis, while **chapter 2** gives an overview of the ecosystem service approach and of the state-of-the-art in this field. **Chapter 3** sketches out general grasslands ecosystem dynamics with a focus on temperate coastal wet grasslands. Lastly, **chapter 4** describes the study area, namely the temperate coastal marsh landscape of East Frisia (Germany), as well as the data used for the study cases. In the second part, three empirical study cases conducted in the study area are documented (**chapter 5**, **chapter 6** and **chapter 7** respectively). These study cases were used to achieve and answer the next aim and major questions.

(i) *Our major aim is to understand the nature and origin of trade-offs and synergies between multiple ecosystem services and properties associated with nature conservation value, forage production and carbon stocks in temperate coastal wet grasslands.*

(ii) *How do abiotic parameters and land use drivers affect ecosystem properties and cause changes in ecosystem services? How these drivers affect the provision and interaction between services?*

As suggested by Bennett *et al.* (2009), ignoring ecosystem dynamics may increase the risk of regime shifts in which sudden, unexpected, and often unwanted changes in ecosystem services are experienced. **Chapter 5** answers questions related to the effects of abiotic and land-use drivers on ecosystem properties and services (Path A, Fig. 2.3). The role of abiotic and land-use gradients, such as biomass removal, soil nutrients availability, fertilization rates, groundwater and salinity levels, and nature protection status was here modeled. Trade-offs and synergies between final ecosystem services, as indicated by nature conservation value and gross economic benefit derived from forage production, were revealed at different levels in a chain of responses and effects by using a structural equation model formalism.

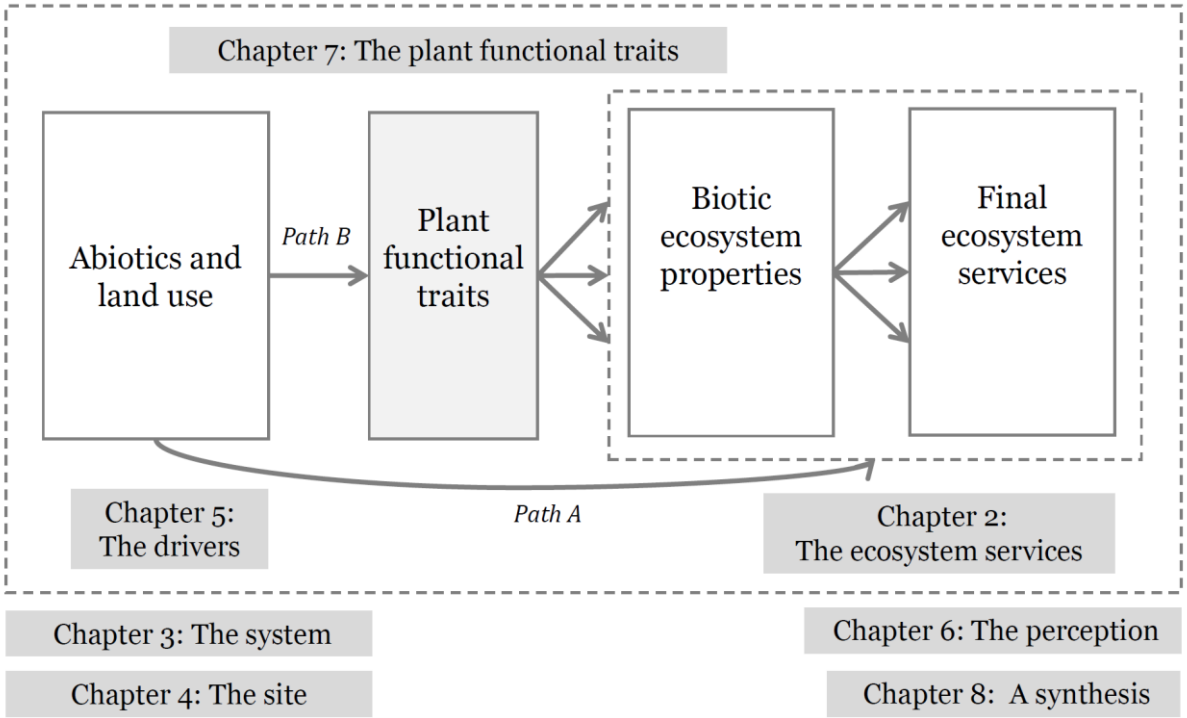

Fig. 2.3: Specific framework used for this thesis' analysis of vegetation-mediated ecosystem services (**chapter 2**) in temperate coastal grasslands (**chapter 3 and 4**). Stakeholder understanding of landscape and its capability to provide ecosystem services (**chapter 6**). Path A indicates the effects of environmental parameters (abiotic ecosystem properties and land use) on ecosystem properties and services (**chapter 5**). Path B indicates how plant strategies and plant functional traits capture and express the variation of environmental parameters and explain ecosystem properties and services (**chapter 7**). Parameters indicated with blank backgrounds were measured at site-level, parameters indicated with light grey background were measured at regional level. **Chapter 8** highlights and synthesizes major results. Adaptation from Lavorel and Grigulis 2012 and Haines-Young and Potschin 2013.

(iii) How do regional stakeholders, which have a strong influence in the landscape management such as nature conservationists and farmers, perceive the landscape capability to provide ecosystem services and to what extent these perceptions respond to ecosystem services indicators measured at a landscape and plot level?

Despite increasing research on the associations between social demand and supply of ecosystem services (Andersson *et al.* 2015), little has yet been done to detect interactions between experts' perceptions or knowledge about the capability of ecosystems to provide services on the one hand and field-measured indicators of ecosystem services on the other (Desbiez *et al.* 2004). As a rather novel socio-ecological, place-based but also process-based approach **chapter 6** explains how regional stakeholder groups perceive the landscape'

capability to provide services associated with forage production, soil fertility, carbon sequestration, nature conservation value and regional belonging. Here, the extent to which these perceptions responded to the field-measured indicators of ecosystem services was explored.

(iv) To what extent do key plant functional traits and plant strategies respond to environmental changes and explain the dynamics of ecosystem properties and services?

An alternative path to explain vegetation-mediated ecosystem services was also tested. **Chapter 7** explores the role of plant functional traits and plant strategies in capturing and expressing variation of abiotic and land use gradients (Path B, Fig. 2.3). Trade-offs and synergies between certain plant functional traits were used to explain trade-offs and synergies between multiple ecosystem properties and services. Community-weighted means were calculated for plant trait values retrieved from a database of plant individuals collected at regional level. These plant trait values were used here in order to explain variation of ecosystem properties and services as an extension of the effect-response framework (Lavorel & Garnier 2002; Lavorel *et al.* 2011; Minden & Kleyer 2011).

The third and final part, i.e. **chapter 8**, summarizes the thesis highlights and discusses the study results as well as further revelations obtained from synergies amongst individual findings.

Chapter 3

Temperate coastal wet grasslands

Miguel Ángel Cebrián-Piqueras

Chapter 3: Temperate coastal wet grasslands

3.1 Introduction

Temperate coastal wet grasslands of the northwest European lowlands comprise vegetation whose soils are permanently or temporarily waterlogged by fresh, brackish or salt water. Over the centuries, these grasslands have been transformed by human activity, to provide agriculture land, peat, and protection against floods (Perillo *et al.* 2009; Barbier *et al.* 2011).

Extensively-used wet grasslands are often the common ecosystem developed by drainage and subsequent traditional grazing and mowing activities in former wetland types, such as fens or marshes on coastal areas, floodplains and around lakes (Toogood & Joyce 2009). Wet grasslands are valuable systems, not only for their nature conservation value but also for their economic functions such as the provision of high-quality food products, for their regulating services such as water- and air-quality improvement, or flood regulation, but also for their cultural services such as recreation and tourism, sense of belonging or aesthetic value (Joyce & Wade 1998; Mountford *et al.* 2006).

European wet grasslands of nature conservation importance are highly threatened by abandonment or intensification. However restoration of these systems after a long period of abandonment has been found to be a complex and difficult issue (Joyce 2014). According to a recent review of wet grasslands restoration, the focus of such efforts should be prioritized on grasslands with less than 20 years of abandonment (Joyce 2014).

Agricultural intensification, which took place in Europe during the second half of the twentieth century, has produced enormous economic benefits for local communities. In contrast, it has also produced a great decline of freshwater coastal marshes and extensive wet grasslands in northwest Europe. Coastal marshes and wetter grasslands have been substituted for croplands, or drier and more productive grasslands. The use of inorganic fertilizers has been increased and the water table has been substantially lowered. These changes may have produced a decrease of multi-functionality of coastal grasslands, as well as a general decrease of plant and animal biodiversity and a loss of aesthetic value, as has been shown for temperate floodplains (Krause *et al.* 2011; Wesche *et al.* 2012).

Coastal saltmarshes are a particular type of wet grassland situated at the interface between land and sea; they are located in the upper part of the coastal intertidal zone that is regularly flooded by salt or brackish water. Saltmarshes occur in temperate and high latitudes in both

the southern and northern hemisphere and they are dominated by salt-tolerant plants such as herbs, grasses or low shrubs and are replaced by mangrove vegetation in tropical and sub-tropical regions (Adam 1993).

3.2 Groundwater, inundation and salinity

Drainage and the subsequent lowering of the groundwater table are the major causes of the loss of wet grasslands (Rosenthal & Hölzel 2009; Prajs & Antkowiak 2010). Coastal wet grasslands have been substantially reduced during last decades. Studies from UK coast showed reductions of up to 90 % by conversion to arable lands (Williams & Hall 1987). On the other hand some studies have shown a high and fast responsiveness of wet grasslands to groundwater table improvement, showing that management practices exerted a limited influence (Toogood & Joyce 2009).

It has been proved that hydrology is a key factor controlling the competitive abilities of wet grasslands plant species (Kennedy *et al.* 2003). Other studies conducted in The Netherlands have shown how dry grasslands species are replaced by wet grasslands species within 5 years (Oomes *et al.* 1996). According to some authors transport of seeds with flood water was once an important dispersal agent, however the constructions of dykes has certainly decreased this ability (Hölzel & Otte 2001).

Environmental parameters such as inundation frequency and salinity are determining the plant species composition, zonation and functionality of saltmarshes (Rozema *et al.* 1985). Following Grime' scheme about plant strategies (Grime 1998), the stress tolerant species are located in the lower saltmarsh areas where inundation and salinity are higher; contrarily competitors are located further away from the shore at higher altitudes where the stress is lower and the availability of nutrients higher (Minden & Kleyer 2011). Some studies have shown how the plant species found on the upper parts of the saltmarsh have negative responses of growth rates when they are exposed to conditions similar to those of low saltmarshes (Bakker *et al.*, 1993).

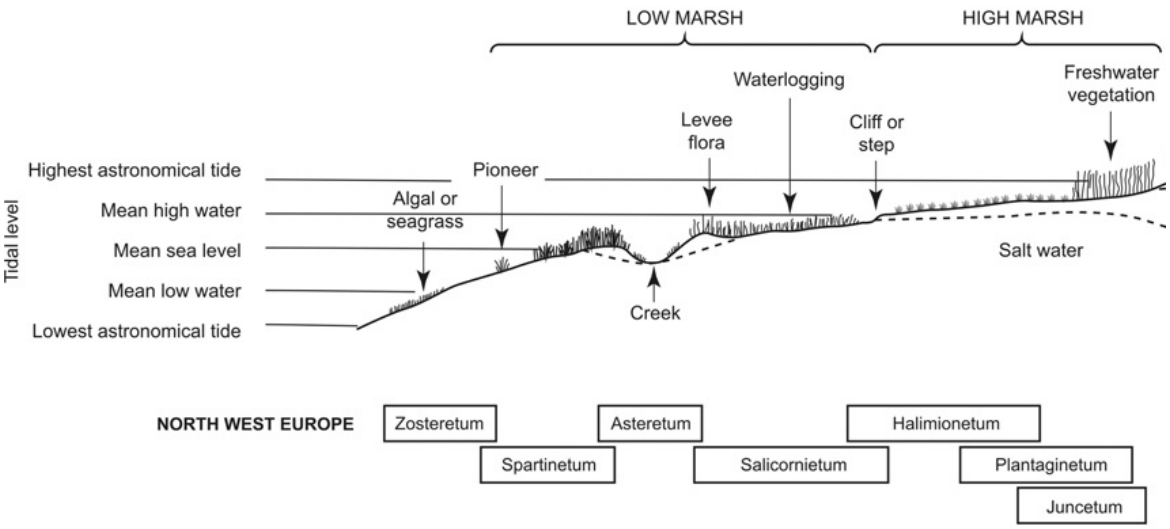

Fig. 3.1: Representation of an ideal vegetation zonation in a Norwest European coastal marsh. From "Temperate coastal wetlands: morphology, sediment processes, and plant communities", (Pratolongo *et al.* 2009), in "Coastal Wetlands" (Perillo *et al.* 2009).

The root: shoot ratio for the species which are more exposed to seawater inundation (lower saltmarsh) is higher than that of the species located at higher areas. Several studies relate this feature to the anchoring function that the saltmarshes plants develop under the pressure of often unstable sediment (Bakker *et al.* 1993).

Often the number of coastal saltmarshes species is relatively low; however most of these species are only able to grow in this environment, therefore most of them are rare (Barbier *et al.* 2011).

3.2 Nutrients

According to the studies of Hillebrand *et al.* (2007), the primary productivity of aquatic and terrestrial ecosystems is limited by both nitrogen and phosphorus. However in the ecosystems of the temperate regions nitrogen limitation plays a major role (Reich & Oleksyn 2004).

The available nitrogen level in saltmarshes is determined by several causes such as the input coming from the inundation, the soil texture (sand and clay contents) and by the organic matter content (Rozema *et al.* 1985).

The soil nitrogen availability in saline habitats may exert an important limitation for the biomass productivity due to the fact that halophytes invest a high fraction of available nitrogen to synthesize compatible osmotic solutes in order to maintain the osmotic equilibrium (Ungar 1991; Bakker *et al.* 1993; Van Wijnen & Bakker 1999). Nutrient limitation can occur in areas

with high levels of sand, subsequently this fact can trigger a competition for soil resources (Berendse & Möller 2009). Phosphorus availability only becomes a limiting factor for plant growth in saltmarshes when nitrogen levels are high enough (Cargill & Jefferies 1984).

However in many coastal ecosystems the average values for soil nitrogen have increased substantially during last decades due to anthropogenic reasons (Barbier *et al.* 2011; Deegan *et al.* 2012). It is estimated that high levels of soil nutrients produce changes in the species composition favoring the proliferation of more competitive species, i.e. *Elymus athericus* in coastal saltmarshes or *Phragmites australis* in brackish conditions (Rozema *et al.* 1985; Kiehl *et al.* 1997; Gedan *et al.* 2009). This would be in line with the Grime' scheme (1998) about the plant strategies (competitors, stress-tolerant and ruderals; CSR). However the growth of these competitor species might also be associated with later successional states of the vegetation community where the nutrient availability would be higher (Rozema *et al.* 2000).

On the other hand, some empirical studies about artificial nutrient enrichment in coastal saltmarshes demonstrate the negative effect of high nutrient availability on the below-ground biomass growth. This fact ultimately causes a loss of sediment because it is not properly retained by a well-developed root system (Turner *et al.* 2009; Deegan *et al.* 2012). Contrarily, the mentioned studies reveal that above-ground biomass increments occur at higher rates of available nutrients (Emery *et al.* 2001).

Grazed or mowed semi-natural species-rich freshwater grasslands are generally poor in nutrients (Joyce & Wade 1998; Bobbink *et al.* 2010). It has been proved that nutrient addition causes positive effects on above-ground biomass productivity on wet grasslands (Ceulemans *et al.* 2013). However it has been shown to that it causes negative effects in the plant species richness and composition (Klimek *et al.* 2007; Wellstein *et al.* 2007; Stevens *et al.* 2010). Studies of temperate European semi-natural grasslands have shown a significant negative relationship between species richness and nitrogen addition (Bobbink *et al.* 2010). Some studies have shown that significant changes occur at low levels of nutrient addition within 5 and 9 years (Clark & Tilman 2008). These studies have also shown that these negative effects are particularly negative on rare plant species.

3.3 Vegetation biomass productivity

Biomass productivity is relatively low on wet grasslands rich in plant species, compare to mesic intensive grasslands or coastal saltmarshes, due to the fact that most of these ecosystems are poor in nutrients and allow the occurrence of non-competitor species (Joyce 2014). Still, eutrophication of these systems due to agricultural intensification of adjacent areas has affected the species composition and biomass productivity of extensive wet grasslands (Stevens

et al. 2010; Ceulemans *et al.* 2013). It has been found that nutrient enrichment causes a higher productivity of competitor species which ultimately affect, through light competition exclusion, the ability of small plant species to survive (Hautier *et al.* 2009).

According to some authors and following recent theories about nutrient limitation in terrestrial systems, it has been shown that limitation of phosphorus also has a high impact on biomass productivity of nutrient poor systems such as some grasslands attaining significant changes in plant species composition and richness (Elser *et al.* 2007; Ceulemans *et al.* 2013).

Although salinity may negatively affect the productivity of plants (Munns 2002; Munns & Tester 2008), saltmarshes are referred to as one of the most productive ecosystems in the world (Whittaker & Marks 1975; Howes *et al.* 1986). Above-ground biomass production has been reported to vary between 300 and 1500 g m^{-2} on the European North Sea coast (Bakker *et al.* 1993). Due to the strong stress exerted by the frequent tidal inundation, salt marsh plants allocate a higher percentage of the total biomass to the below-ground parts in order to reinforce an anchoring function (Groenendijk & Vink-Lievaart 1987; Bakker *et al.* 1993).

Nutrient availability affects primary productivity in saltmarshes (Kiehl *et al.* 1997), however recent studies in saltmarshes have shown that the high eutrophication, common in most coastal areas, may affect the below-ground biomass allocation potential of saltmarshes vegetation leading to a loss of sediment and a regression of saltmarshes (Turner *et al.* 2009; Deegan *et al.* 2012). Contrarily these studies have shown that vegetation allocates an increasing percentage of biomass to the above-ground parts at increasing nutrient enrichment rates.

3.4 Vegetation biomass decomposition

Both primary productivity and biomass decomposition are directly affected by the soil nutrient availability (Bakker *et al.* 1993). On the other hand Fortunel *et al.* (2009) found how disturbance modifies the community composition and structure facilitating the occurrence of species with higher decomposition rates of the above-ground biomass structures.

Disturbed areas have generally shown higher decomposition rates than undisturbed areas in several ecosystems (Bakker *et al.* 2011). Three major factors such as litter quality, decomposer community and physicochemical environment determine the litter decomposition rates (Swift *et al.* 1979). The importance of these three factors varies between ecosystems, with climate conditions playing the major role according to Hobbie (1996). However, litter quality was found to be the most important driver for decomposition rates variation between biomes

(Cornwell *et al.* 2008) and it seems to play a determinant role when climatic conditions are favorable (Swift *et al.* 1979; Lavelle *et al.* 1993).

Plant strategies and plant functional traits have been used to explain litter quality and decomposability in grassland communities (Fortunel *et al.* 2009; Freschet *et al.* 2010). These studies have shown how plant functional traits associated with the leaf and plant economic spectrum such as specific leaf area or leaf nitrogen content work as good markers for litter decomposability variation (Wright *et al.* 2004; Freschet *et al.* 2010).

Bakker *et al.* (1993) found that decomposition rates are relatively high in saltmarshes and this fact leads to a high release of nutrients and carbon which are available for different organisms. Apart from external environmental processes and biotic activity, the decomposition rates are strongly dependent on biochemical plant traits such as tissue composition (nitrogen and lignin content) (Hemminga & Buth 1991).

Some studies conducted on wet grasslands have shown positive effects of grazing on decomposition rates (Rossignol *et al.* 2006). These studies have shown a high heterogeneous N-mineralization pattern which varied following the vegetation composition changes associated to the groundwater gradient.

3.5 Vegetation forage quality

A general trade-off between vegetation forage quality, biomass production and plant diversity has been frequently reported in different types of grasslands (White *et al.* 2004; Pavlů *et al.* 2006). Vegetation height associated with non-used and extensively used grasslands is related to lower forage quality, by contrast lower short swards related to different rates of grazing activity show higher forage quality (Fleurance *et al.* 2001; Loucougaray *et al.* 2004). Both Hofmann *et al.* (2001) and Audic *et al.* (2002) have shown that swards from extensive grasslands have lower nutritional values than those found in intensively used grasslands.

Most of the European temperate costal saltmarshes have been traditionally grazed by cattle due to its relatively high productivity and forage quality (Esselink *et al.* 2000; Bos *et al.* 2004). On the other hand it is not clear if environmental parameters such as salinity may exert a negative effect on the vegetation forage quality, by contrast the opposite effects have been found for some saltmarsh species (Gray 1992).
Disturbance by grazing activity has shown to cause a positive effect on the vegetation forage quality, contrarily abandonment of livestock activity has led to an increase of plant species with relative lower forage quality such as *Elymus athericus* in high saltmarsh, *Atriplex*

portulacoides in low saltmarsh and *Phragmites australis* in brackish water conditions (Prop & Deerenberg 1991; Esselink *et al.* 2000)

3.6 Biomass removal, productivity and plant richness

Several empirical studies have shown that biomass removal by grazing or mowing negatively affect the primary productivity of freshwater and saltmarsh vegetation, causing, on the other hand, positive effects on species richness in temperate coastal grasslands (Bakker 2014; Minden *et al.* 2016).

Some authors have reported positive effects of grazing activity on below-ground productivity of saltmarshes vegetation and soil organic carbon stocks under certain climatic conditions, which is associated to a stimulation of the fine roots growth (Yu & Chmura 2009).

Recent studies conducted in coastal wet grasslands have shown negative effects of biomass removal by grazing or mowing on above-ground biomass productivity (Minden *et al.* 2016) which is related to the removal of strong competitor and productive species (i.e. *Phragmites australis*). These results are in line with those found in North American wetlands (Silliman *et al.* 2014). By contrast these studies have shown positive effects on plant species richness and endangered plant species occurrence. Some other empirical studies conducted on mesic grasslands also showed positive effects on species richness but in contrast to what was found on wet grasslands they showed positive effects on biomass productivity (Minden *et al.* 2016).

According to empirical studies conducted on sub humid mountain grasslands (850 mm year $^{-1}$ of rainfall) the biomass removal by grazing triggered substantially the total below-ground biomass productivity and fine root productivity but affected negatively the above-ground biomass productivity (Pucheta *et al.* 1998; Pucheta *et al.* 2004). Similar results have been found in other systems (Piñeiro *et al.* 2010). By contrast few positive effects or no effects have been reported in other systems such as semiarid grasslands (Milchunas *et al.* 1989), steppe grasslands (van der Maarel & Titlyanova 1989) or savannah systems (McNaughton *et al.* 1998).

3.7 Soil organic carbon stocks

Grasslands may contain around 12% of the total earth' soil organic carbon and the soil organic matter in temperate grasslands may contain 331Mg/ha on average (Schlesinger 1977; Conant *et al.* 2001). Three major pathways have been found to control the soil organic carbon stocks in freshwater grasslands: 1) net primary productivity changes; 2) nitrogen stocks changes; 3) changes in organic matter decomposition rates (Piñeiro *et al.* 2010). A meta-analysis

conducted by Piñeiro *et al.* 2010 showed that below-ground biomass, a primary control for SOC formation, was higher on grazed plots than in their un-grazed counterparts at driest and wettest plots but were lower at intermediate precipitation (~400 mm to 850 mm). This review showed how mean annual precipitation causes different effects of grazing on SOC.

Contrary to freshwater systems, vegetation is not the only source of carbon in saltmarshes, seawater supplies a high amount of organic matter and therefore organic carbon (Long & Mason 1983). Organic carbon stock densities of saltmarsh soil have been reported to reach average values up to 0.039 ± 0.003 g cm^{-3} according to a meta-analysis conducted by Chmura *et al.* (2003). Rates of soil carbon sequestration were similar to what was found in other coastal systems such as mangroves. Saltmarshes might sequester millions of tons of carbon annually (Mitsch & Gosselink 2000; Mitsch *et al.* 2013). Variation in temperature has been shown to reduce the soil organic carbon stocks in saltmarshes and other coastal systems (Chmura *et al.* 2003).

Recent studies in saltmarshes have shown a positive effect of grazing activity on total soil organic carbon accumulation under certain climatic conditions, due to a root growth stimulation and subsequent accumulation of organic matter (Yu & Chmura 2009), however at bigger scales above-ground standing biomass, which is strongly associated with climatic conditions, has been highlighted as a major driver of soil organic carbon accumulation (Doblas Miranda *et al.* 2013). On the other hand, studies in coastal areas have demonstrated the primary role of soil organic carbon associated with root growth in saltmarsh accretion (Nyman *et al.* 2006).

3.8 Forage production

Forage production and associated goods have been the main benefits traditionally derived from the management of wetlands (Hopkins & Holz 2006). Huge land use transformations after the Second World War exerted strong modifications in the European rural landscape, being particularly strong on the European north-west lowlands (Krause *et al.* 2011; Wesche *et al.* 2012). On the one hand non-profitable extensive pastures, usually located in nutrient-poor soils or inaccessible areas were abandoned. On the other hand high productive areas were highly intensified or transformed on crops (Hopkins & Holz 2006).

In temperate regions wet extensive grasslands bring about relatively high values for provisioning services (e.g. meat and milk), supporting services (e.g. flood attenuation, water quality, groundwater recharge, carbon sequestration, biodiversity, pollination) and cultural

services (e.g. traditional practices and recreation) (Macleod & Ferrier 2011). Studies conducted in wet grasslands of South-West England have recently estimated losses of 9.7 million pounds for regulating services such as carbon stocks and water regulation since 1900.
Most of the temperate saltmarshes of Europe have been artificially modified and altered during centuries by local communities to obtain benefits and goods such as raw material, food and coastal protection (Gedan *et al.* 2009). Harvesting and grazing have played a major role due to the high biomass productivity and fodder quality of the saltmarsh vegetation. Although abandonment of saltmarshes is a common trend throughout Europe due to nature conservation regulations and decreasing economic profit (Esselink *et al.* 2009) grazing activity still produces relatively high monetary income in some coastal saltmarshes around the globe (King & Lester 1995; Gedan *et al.* 2009).

The debate about the effects of the abandonment of saltmarsh grazing or mowing activities on ecosystem functioning has a long tradition in coastal ecology empirical research (Bakker *et al.* 1993; Kiehl *et al.* 2007; Bakker 2014; Nolte *et al.* 2015). Many studies conducted in temperate European saltmarshes have reported an increase of competitor species such as *Elymus athericus* and *Atriplex portulacoides* after several years of abandonment (Schröder *et al.* 2002; Kiehl *et al.* 2007). Similar effects have also been found for brackish marshes where cessation of grazing activity has driven to an increase of *Phragmites australis* (Esselink *et al.* 2000). However these patterns have not been found on saltmarshes within the first five years after abandonment (Kiehl *et al.* 1997). On the other hand recommendations for low stocking grazing rates are given by authors for mainland saltmarshes in order to maintain vegetation diversity (Andresen *et al.* 1990; Bouchard *et al.* 2003).

3.9 The nature conservation value

Extensively used wet grasslands have a relatively high level of groundwater tables during part of or throughout the year, this fact allows them to maintain a singular and diverse vegetation of grasses and sedges which is not found on intensively managed and drainage grasslands (Joyce 2014). However it has been estimated that 80% of the different types of wet grasslands have already been lost worldwide during 20th century due to agricultural intensification and drainage. In regions or countries such as Eastern England or Finland only 1% of the former wet extensive grassland area remains (Clark & Wilson 2001; Luoto *et al.* 2003; Joyce 2014).

The traditional agricultural use of wet grasslands during centuries has produced high-valued and cultural landscapes with high biodiversity. A part of the maintenance of groundwater levels, the biodiversity of wet grasslands is kept and promoted by associated management

practices. Extensive grazing and cutting decrease the tall competitor vegetation species e.g. *Phalaris arundinacea*, *Calamagrostis canescens* or *Phragmites australis*, allowing a diverse assembly of plant species. On the other hand open landscapes associated with extensively managed wet grasslands benefit the occurrence of wildfowl and wading birds (Joyce 2014). According to some estimations half of the European wading birds breed on wet extensive grasslands (Hötker *et al.* 1991).

In the western countries there has been a long tradition of saltmarshes conservation. Countries such as Germany, The Netherlands or Denmark have developed ambitious trilateral agreements creating the transboundary Wadden Sea nature protected area, which later became a UNESCO world heritage site. Saltmarshes located in the Wadden Sea regions of North-West Europe comprise an area of up to 400 km^2 which represents 20% of all European saltmarshes (Esselink *et al.* 2009). These saltmarshes include back barrier, foreland marshes, green beaches and Hallig saltmarshes. In countries such as England saltmarshes nature conservation has been conducted since the mid-twentieth century. North Norfolk saltmarshes have been preserved for reasons such as habitats for rare species, research or education goals. Still 50 % of the original saltmarshes have already lost or degraded globally and in some areas of North America the loss comprises 90 % of the former saltmarshes area (Barbier *et al.* 2011).

Saltmarshes provide particular habitat conditions determining the occurrence and proliferation of salt tolerant plants (Ungar 1991). As it is pointed out by Adam (1993) species rarity depends on spatial and temporal scales, therefore several saltmarshes species are not catalogued as endangered in temperate regions where coastal ecosystems constitute a relative high percentage of the whole area of the country (e.g. Denmark).

Plant species such as *Plantago maritima* and *Triglochin maritima,* which occur in European temperate coastal saltmarshes, are included in the German national or regional red lists (Ludwig *et al.* 1996). As moderate grazing has been shown to positively affect species richness and diversity at different scales (Lefeuvre *et al.* 2003), abandonment of this activity in many coastal regions of Europe has led to an impoverishment of the plant community assemblies and the nature conservation value in saltmarsh vegetation (Bakker 2014). As the saltmarsh ecosystems struggle to survive under climate change threats, eutrophication, abandonment and direct human pressure (Barbier *et al.* 2011), maintenance of biodiversity and rich species pools should be tackled in an effective way by ecologists, conservationists and managers (Esselink *et al.* 2000)

Chapter 4

Study site

Miguel Ángel Cebrián-Piqueras

Chapter 4: The site

4.1 Study site

The communities of Krummhörn and Emden are embedded in the wide coastal lowlands of the European continent. Here, thousands of hectares are located at or below sea level in countries such as Germany, The Netherlands or the western part of Denmark (Wolff *et al.* 2010). High levels of salty, brackish or fresh groundwater characterize these coastal marshes. The former natural landscape has been intensively modified by human beings for centuries, resulting in today' coastal cultural landscape (Knottnerus 2005).

Regional inhabitants have constructed water-discharging networks to make land use possible and protect the land from floods and storm-surge events by building a coastal sea wall. The increasing population and associated needs for costal protection and ecosystem services, such as livestock production, crops, peat extraction and construction material, have strongly shaped the landscape (Knottnerus 2005), which can be regarded as its own social-ecological system (Huntsinger & Oviedo 2014).

The regional population, especially farmers, have played an important role in this landscape modification and some of them may see this agro-ecosystem as a valuable cultural landscape which they feel proud of (Saugeres 2002; Karrasch *et al.* 2014). During past centuries, or even millennia, large areas of the landscape have been used by farmers as extensive wet grasslands, both on the seaward and landward side of the sea wall (Lotze *et al.* 2005). Despite profound changes that have eliminated habitats and species during past centuries, the remaining extensive areas have created and maintained suitable habitat conditions for some rare plant and bird species (Plieninger *et al.* 2006). For decades now, these have been internationally acknowledged by nature conservation legislation and regulation.

However, during recent decades, several important changes took place in these landscapes. In saltmarshes, on the one hand, extensive land use has gradually been abandoned, due to a constant decline of economic benefits - despite their high agronomic value - and due to increasing nature conservation awareness and protection (Esselink *et al.* 2000). Nevertheless, some authors have shown some negative effects on plant and bird richness due to high nature protection and the abandonment of extensive usage of saltmarshes (Bakker 2014) . On the landward side of the sea wall, on the other hand, wet extensive grasslands have to a great extent been reduced by land-use intensification, which caused a decline of species diversity and the occurrence of endangered species (Schrautzer *et al.* 1996).

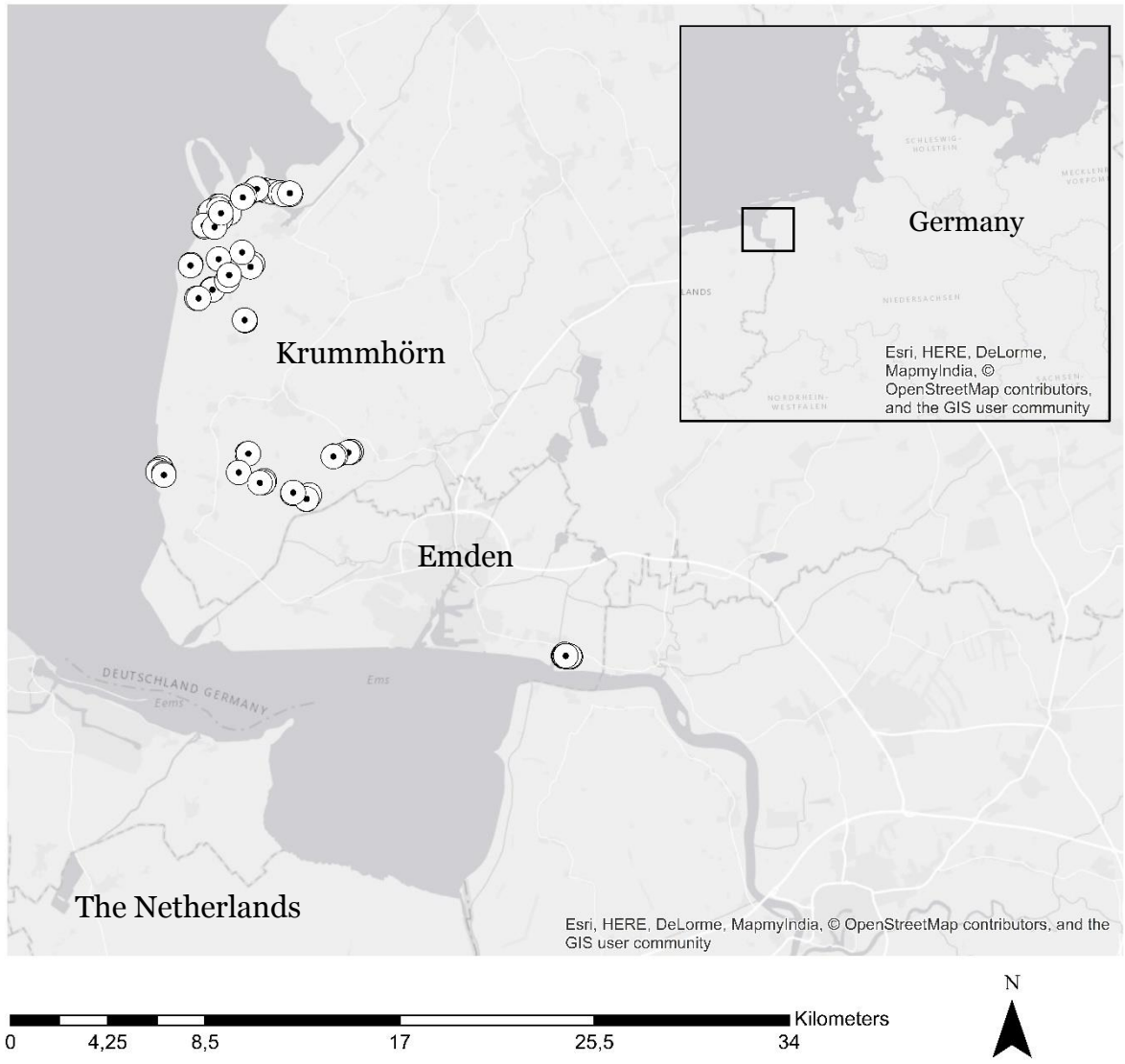

Fig. 4.1: The study area was located on East Frisia which is a region from the North-West coast of Germany. The plots were distributed within the communities of Krummhörn and Emden. White-colored points indicate the plots where the biophysical data was collected (N: 49).

The field work for the present thesis was conducted on the coastal region of East-Frisia of North-West Germany (Fig. 4.1), within the communities of Krummhörn and Emden (E 07°02', N 53°27', NW-Germany). The study area has a mean annual precipitation of 823 mm and annual temperature of 9.4° C (Deutscher Wetterdienst 2011/2012). The sea wall protects the agricultural landscape landwards, which is mainly dedicated to pastures and crops. Seawards the sea wall saltmarshes are nowadays highly protected and rarely used as pastures. 49 plots were randomly stratified through the main four coastal grassland ecosystems: (1) saltmarshes (2) reeds and sedges (3) wet extensive grasslands and (4) intensive grasslands. A major

gradient of groundwater and salinity characterized the study site which decreased landwards. The groundwater gradient showed a general positive association with the nature protection status and a negative association to agricultural intensification.

4.2 Distribution of parameter values between vegetation units

All the saltmarshes plots were located on the seaward side of the sea wall and were composed by the vegetation communities found in temperate coastal lower saltmarshes (i.e. *Atriplex portulacoides* and *Puccinellia maritima*) and upper saltmarshes (i.e. *Elymus athericus* and *Festuca rubra*). Reed and sedges plots (namely "reeds"; *Phragmites australis* and *Scirpus maritimus* communities respectively) were located both seaward and landward the sea wall. Wet extensive grasslands were grazed, mowed or both at relative low rates and they were not inorganically fertilized. By contrast, intensive grasslands were fertilized with inorganic fertilizers and showed relatively higher rates of intensity (grazing, mowing or both). Groundwater levels were on average relatively higher on wet extensive grasslands (mean value: -0.50 m) compared to intensive grasslands (mean value: -0.70 m). Table 4.1 shows the mean values and standard deviation for all parameters on every vegetation unit.

4.2.1 Data collection and analysis

Details about the methodology used in this thesis to collect and measure abiotic ecosystem properties, land use, biotic ecosystem properties and ecosystem services' values are thoroughly explained in chapter 5 (Section 5.2), except for sand and clay contents and mowing and grazing intensities. *Sand and clay content:* Soil samples were air dried, sieved through a 2 mm sieve and analyzed for sand and clay content following (Ad-Hoc-AG 2005). *Mowing and grazing* intensities were obtained from interviews with the regional farmers during the year 2012.

4.2.2 Abiotic parameters

Cation exchange capacity (CEC), commonly used as indicator for soil fertility, is the amount of exchangeable cations per dry weight that a soil is capable of holding, at a given pH value, and available for exchange with the soil water solution (Robertson *et al.* 1999). CEC was significantly high on plots located on the landward side of the sea wall, such as intensive grasslands and wet extensive grasslands where clayed soils occurred. By contrast saltmarshes and reeds showed a relatively lower value for cation exchange capacity compared to wet extensive grasslands and intensive grasslands. Reeds plots showed relatively higher sand content compared to other vegetation units, however the differences were not significant.

Both intensive grasslands and wet extensive grasslands showed significantly higher values for soil clay content than saltmarshes and reeds. Plant-available soil nitrogen (N) and plant-available soil potassium (K) showed the highest levels on saltmarshes; by contrast N showed the lowest values in both intensive and extensive wet grasslands and potassium showed the lowest values in wet extensive grasslands. By contrast we found a relative homogenous distribution for plant available phosphorus (P) values at the landscape level. The results did not show a significant difference between vegetation units for this soil parameter (Fig. 4.2). Soil carbonate decreased landwards and therefore showed the highest values on saltmarshes and the lowest values on intensive grasslands.

The average value for the groundwater table was situated relatively high in the whole study area (mean value: -35.40 cm; max: -6.3; min<-100.0; N: 49). Saltmarshes showed the highest values for this parameter and intensively used grasslands the lowest. Salinity showed a moderate association with groundwater level ($CC_{Spearman}$: 0.55; $p<0.01$) and decreased landwards.

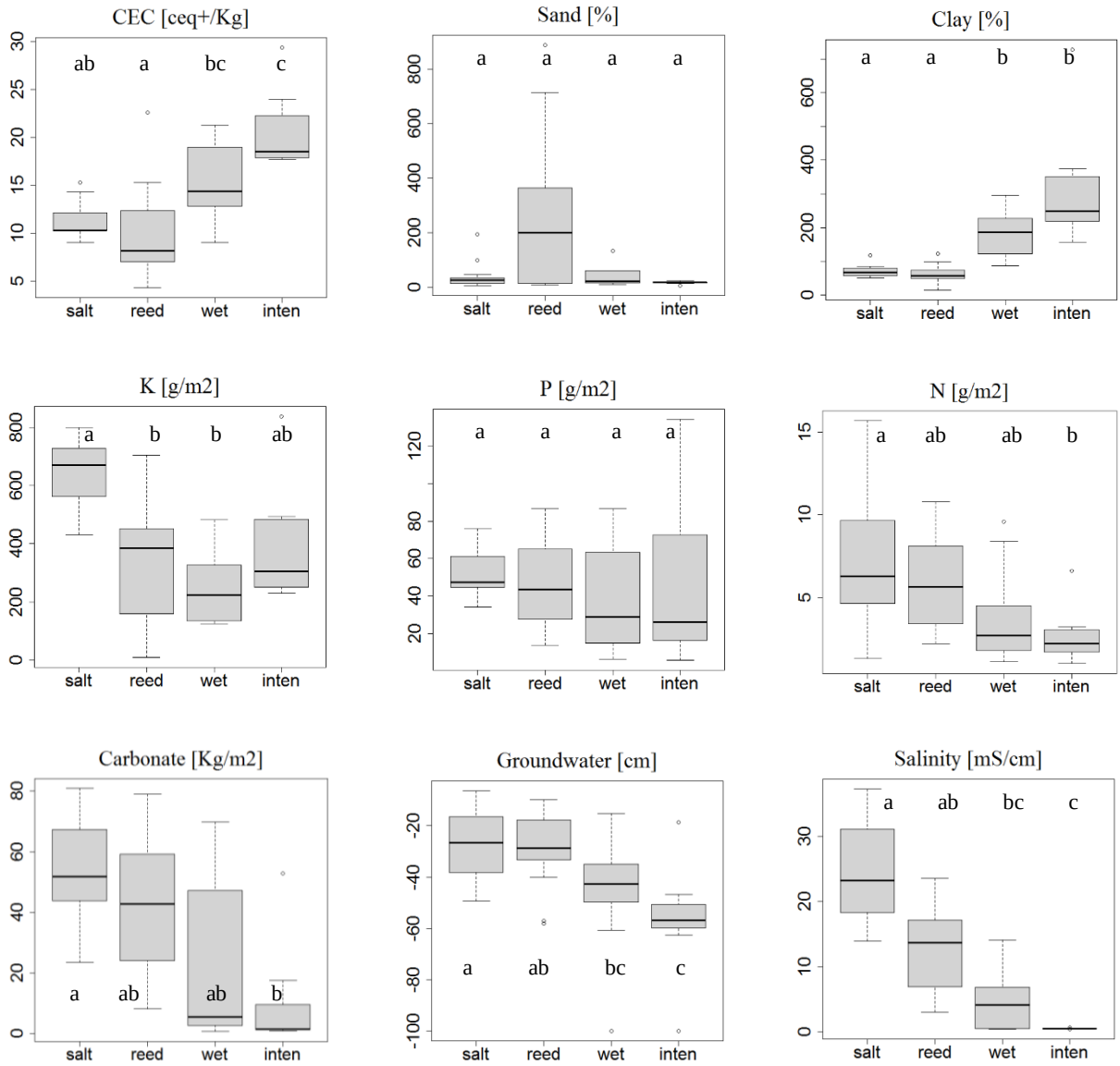

Fig. 4.2: The figure shows abiotic parameter variation between main vegetation units. Abbreviations; salt: saltmarshes; reed: reed and sedges vegetation, wet: wet extensive grasslands and inten: intensive grasslands; CEC: cation exchange capacity; sand: soil sand content; clay: soil clay content; K: plant available potassium (80 cm depth); P: plant available phosphorus (80 cm depth); N: plant available nitrogen (First horizon). Homogenous subgroups as results of post hoc Kruskal-Wallis test after Nemenyi are shown by the use of the same letters (p-value > 0.05).

4.2.3 Land use

The study area showed, on average, relative high values for biomass removal in intensive grasslands, where 80% of the biomass was removed by grazing and/or mowing activity. Wet extensive grassland showed an average value of 65% of biomass removed by cutting or grazing (See Table 4.1). Some saltmarsh patches were grazed at relative low stocking rates. The total average value for biomass removal on saltmarshes was 16.9 %, however most of the plots were not managed (11:16).

Wet extensive grasslands showed average values of 248.5 Livestock units*days*ha^{-1}*$year^{-1}$ and 1.4 cuts per year for grazing and mowing respectively. Intensive grasslands showed average values of 1024.80 livestock units*days*ha^{-1}*$year^{-1}$ and 2.57 cuts per year, however due to the low sample sizes (N: 10 and N: 7 respectively) the differences were not significant. Only intensively used patches were fertilized and the average value for this parameter was 190 kg ha^{-1}. The study area showed a decreasing nature protection status varying all the way from saltmarshes to reeds, wet extensive grasslands and intensified grasslands, which was slightly correlated to groundwater levels and strongly correlated to the salinity level ($CC_{Spearman}$: 0.30; $p<0.05$ and $CC_{Spearman}$: 0.84; $p<0.01$; N:49).

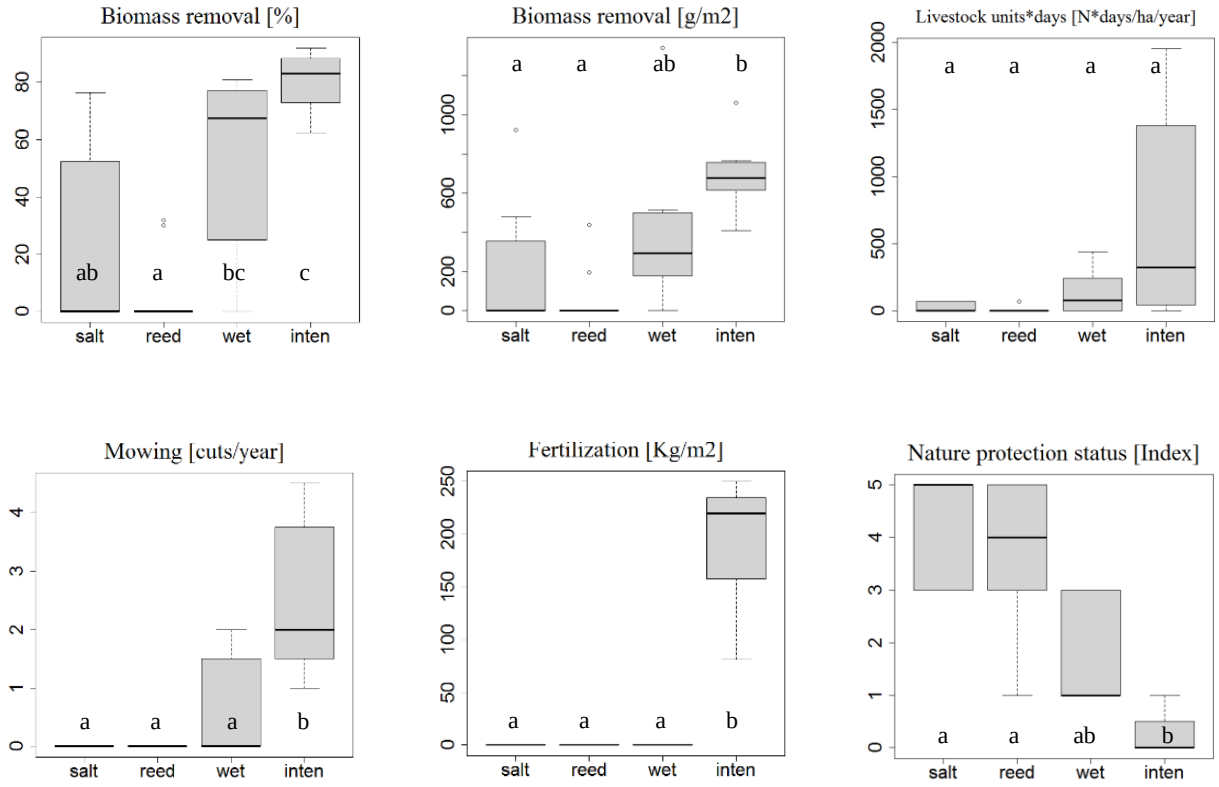

Fig. 4.3: The figure shows the variation of land use parameters between main vegetation units. Abbreviations: salt: saltmarshes; reed: Reed and sedges vegetation, wet: Wet extensive grasslands and inten: intensive grasslands. Homogeneous subgroups as results of post hoc Kruskal-Wallis test after Nemenyi are shown by the use of the same letters (p-value > 0.05).

4.2.4 Biotic ecosystem properties

We found a strong correlation between the landscape variation of above-ground biomass net primary productivity (ANPP) and above-ground standing biomass (AGB) ($CC_{Spearman}$: 0.93; $p<0.01$; N: 49). Significant higher values for ANPP and AGB were found in reeds vegetation patches (1582.4 g $m^{-2}year^{-1}$ and 2099.7 g m^{-2} $year^{-1}$ respectively), followed by the saltmarsh vegetation (866.9 g m^{-2} $year^{-1}$ n and 1186.3 g m^{-2} $year^{-1}$respectively). However saltmarshes showed similar values to wet extensive and intensive grasslands and none of these three vegetation units showed a significant difference between AGB and ANNP values.

Native biomass decomposition rates were negatively correlated to both above-ground standing biomass and net primary productivity ($CC_{Spearman}$:-0.52; $p<0.01$; $CC_{Spearman}$:-0.51; $p<0.01$ respectively; N: 49). Higher values were found on intensive grasslands (0.4 % day^{-1}) and lower values on reed vegetation (0.2 % day^{-1}), both wet extensive grasslands and saltmarsh vegetation showed the same average values (0.3 % day^{-1}), however non-significant differences were found between vegetation units due to the small sample size.

Soil organic carbon (SOC) showed relatively homogeneous values between vegetation units. We did not find any significant differences between vegetation units at both 30 and 80 cm depth (See Fig. 4.4 Post hoc Kruskal-Wallis test after Nemenyi). However, wet extensive grasslands showed slightly higher values. Soil humus content ("Humus") followed the same pattern. Average mean values of 10.7 kg m^{-2} and 44.5 kg m^{-2} for SOC and humus were found in the study area respectively. The grassland utilization indicator value showed the highest levels on intensive grasslands (mean=7.0; median=7); however saltmarshes showed a relative high value for this parameter (mean=6.4; median=6) which was not significantly lower than the values found on intensive grasslands. By contrast, wet extensive grasslands (mean=4.8; median=5) and reeds (mean=3.5; median=3) showed significant lower values.

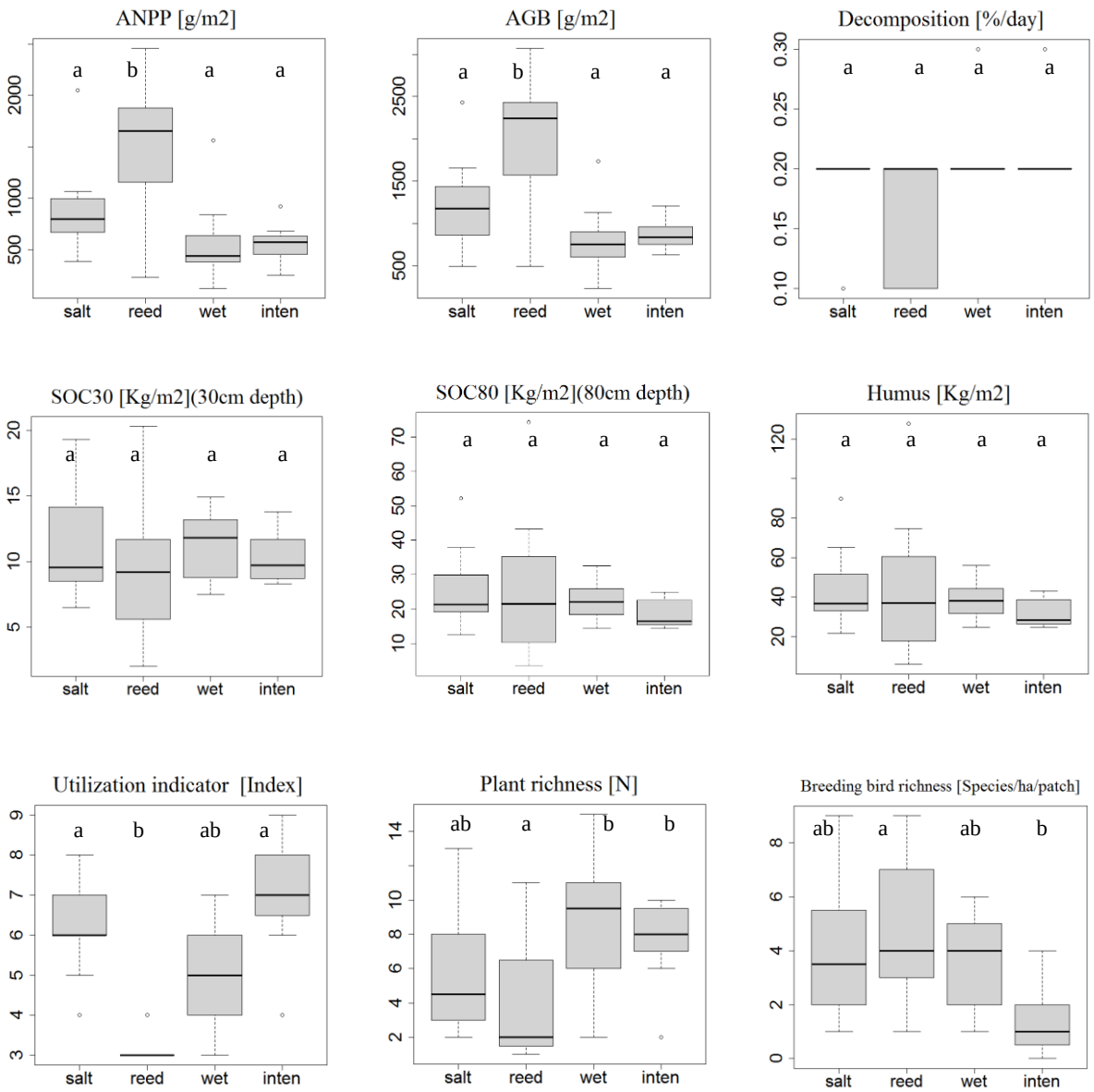

Fig. 4.4: The figure shows the variation of biotic ecosystem properties parameters between main vegetation units. Abbreviations: salt: saltmarshes; reed: reed and sedges vegetation, wet: wet extensive grasslands and inten: intensive grasslands. Homogeneous subgroups as results of post hoc Kruskal-Wallis test after Nemenyi are shown by the use of the same letters (p-value > 0.05).

Both wet extensive grasslands and intensive grasslands showed the highest values for plant species richness which were significantly higher than the values found on reed vegetation. Saltmarshes showed values between reed vegetation and wet extensive and intensive grasslands. Intensive grasslands showed the lowest values for breeding bird richness, which were significantly lower than the values found on reeds but not significantly different from values found on saltmarshes and wet extensive grasslands.

4.2.5 Values of final ecosystem services

Forage production: Intensive grasslands showed, on average, a higher value for gross economic benefit (sales of forage-based products) than both wet extensive grasslands and saltmarshes: 3457.1 € ha^{-1} $year^{-1}$; 1529.0 € ha^{-1} $year^{-1}$; 156.3 € ha^{-1} $year^{-1}$ respectively. However, the values between intensive grasslands and wet extensive grasslands were not significantly different.

Nature conservation value: The endangered breeding bird index showed the highest values on wet extensive grasslands (10.0 mean value; median=13) and both saltmarshes and intensive grassland showed similar and significantly lower values (3.6 and 3.4 mean values respectively; median= 0 and 2 respectively). By contrast no endangered breeding bird species was found on reed vegetation. Endangered plants occurred at relative higher levels on saltmarshes compared to the other vegetation units (2.6 mean value; median=2), however non-significant differences were found between vegetation units, probably due to the low number of samples. Both reeds and wet extensive grasslands showed relatively low values for the endangered plant species occurrence index (0.4 and 0.6 mean values respectively; 0 and 0 median values respectively) and no endangered plant species were found on intensively used grassland.

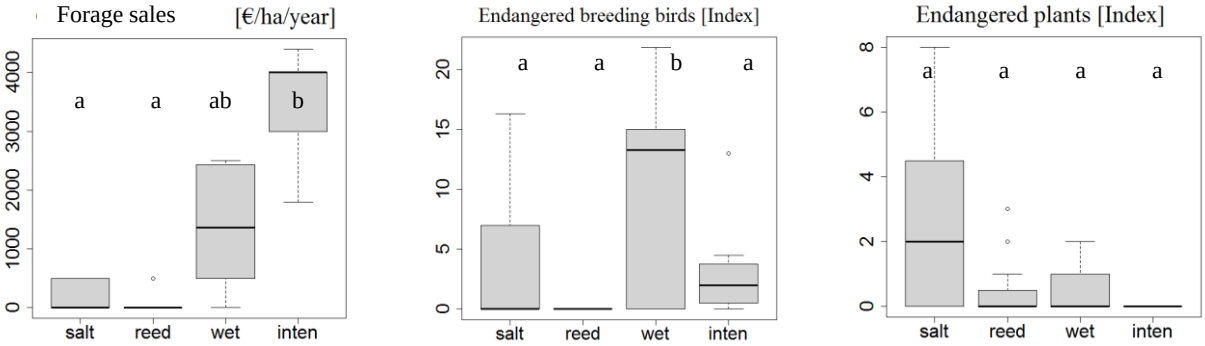

Fig. 4.5: The figure shows the variation of values of final ecosystem services between main vegetation units. Abbreviations: salt: saltmarshes; reed: reed and sedges vegetation, wet: wet extensive grasslands and inten: intensive grasslands. Homogeneous subgroups as results of post hoc Kruskal-Wallis test after Nemenyi are shown by the use of the same letters (p-value > 0.05).

Table 4.1: The table shows the average mean values and medians (ordinal variables) for abiotic, land use, biotic and values for final ecosystem services. N: 49; Saltmarshes (N: 16); Reeds (N: 16); Wet extensive grasslands (N: 10) and Intensive grasslands (N: 7); *N: 46; Saltmarshes (N: 16); Reeds (N: 13); Wet extensive grasslands (N: 10) and Intensive grasslands (N: 7). Med.: Median.

Table 4.1 a			Saltmarshes		Reeds		Wet extensive grasslands		Intensive grassland	
	Abbre.	Unit	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Abiotic parameters										
Cation exchange capacity	CEC	cmol+ kg^{-1}	27.79	5.71	20.40	8.40	37.75	15.46	44.01	7.91
Sand content	Sand	%	38.41	46.93	326.14	284.96	56.14	48.86	17.21	5.67
Clay content	Clay	%	71.66	20.88	57.33	28.11	170.39	79.17	325.25	192.19
Plant soil nutrients availability	NUT									
Potassium	K	g m^{-2} (80 cm. depth)	638.1	109.3	300.2	192.9	226.5	133.8	406.0	219.3
Phosphorus	P	g m^{-2} (80 cm. depth)	52.1	11.7	48.9	23.4	35.8	28.7	49.3	49.9
Nitrogen	N	g m^{-2} (30 cm. depth)	7.1	4.0	6.3	2.7	3.0	2.2	2.7	1.8
Carbonate		Kg m^{-2} (80 cm. depth)	52.67	17.28	43.02	22.34	22.15	28.46	10.94	19.41
Water gradient (GW and salinity)	WATER									
Groundwater	GW	cm	-29.3	13.0	-39.0	21.6	-50.4	8.7	-70.6	25.9
Salinity	Sal	mS cm^{-1}	24.6	7.6	12.4	7.0	5.1	4.6	0.2	0.3

Table 4.1: Extended

Table 4.1 b			Saltmarshes		Reeds		Wet extensive grasslands		Intensive grasslands	
	Abbre.	Unit	Mean/Med.	SD	Mean/Med.	SD	Mean/Med.	SD	Mean/Med.	SD
Land use parameters										
Biomass removal index		%	19.6	30.6	0.0	0.0	65.2	21.8	80.0	11.7
Biomass removal		g m^{-2}	162.0	277.3	39.7	117.0	379.3	390.5	699.3	198.4
Grazing		Livestock units days hectare $^{-1}$ year $^{-1}$	71.1	0.00	0.00	0.00	248.5	11.52	1024.8	883.6
Mowing		Times year $^{-1}$	0.0/0	0.00	0.00/0	0.0	1.4	0.42	2.57/2	1.4
Fertilization rates	Fertilization	Kg ha^{-1}	0.0	0.0	0.0	0.0	0.0	0.0	190.9	63.2
Nature protection status		Index	4.4/5	0.7	3.3/4	1.0	1.6	0.8	0.6/0	0.5

Table 4.1: Extended

Table 4.1 c			Saltmarshes		Reeds		Wet extensive grasslands		Intensive grasslands	
	Abbre.	Unit	Mean/Med.	SD	Mean/Med.	SD	Mean/Med.	SD	Mean/Med.	SD
Biotic ecosystem properties	**ESP**									
Above-ground net primary productivity	ANPP	g m^{-2} $year^{-1}$	866.9	373.2	1582.4	612.1	586.0	409.7	559.3	217.1
Above-ground standing biomass	AGB	g m^{-2}	1186.3	466.6	2099.7	687.2	824.5	408.9	869.9	191.9
Soil organic carbon at 30 cm depth	SOC30	Kg m^{-2}	11.2	3.9	9.5	5.9	11.5	2.7	10.4	2.2
Soil organic carbon at 80 cm depth	SOC80	Kg m^{-2}	25.5	9.9	24.37	18.31	22.35	5.46	18.8	4.5
Soil humus content	Humus	Kg m^{-2}	43.8	17.1	42.7	35.1	56.3	53.7	32.4	7.7
Breeding bird richness*		Number of species ha^{-1} $Patch^{-1}$	4.3/3.5	2.6	4.9/4	2.6	3.7/4	1.8	1.4/1	1.4
Plant richness	Plants	N	6.4/4.5	3.4	4.2/2	3.4/3	8.9/9.5	3.1	7.7/8	2.6
Native biomass decomposition rates	Decompo-sition	% day-1	0.3	0.1	0.2	0.1	0.3	0.1	0.4	0.1
CWM Grassland utilization indicator value		Index	6.4/6	1.1	3.5/3	1.0	4.8/5	1.0	7.0/7	1.6

Table 4.1: Extended

Table 4.1 d			Saltmarshes		Reeds		Wet extensive grasslands		Intensive grasslands	
	Abbre.	Unit	Mean/Med.	SD	Mean/Med.	SD	Mean/Med.	SD	Mean/Med.	SD
Values of final ecosystem services										
Forage sales	Sales	Gross € ha^{-1} $year^{-1}$	156.3	239.4	0.0	0.0	1529.0	874.6	3457.1	951.9
Endangered plant species	Endan. plants	Index	2.6/2	2.8	0.4/0	0.8	0.6	0.8/0	0.0/0	0.0
Endangered breeding birds*	Endan. birds	Index	3.6/0	5.8	0.0/0	0.0	10.0/13	8.4	3.4/2	4.6

Part II

Chapter 5

Interactions between ecosystem properties and land use resolve trade-offs between forage production and species conservation in coastal lowlands

Miguel A. Cebrián-Piqueras, Juliane Trinogga, Celia Grande, Vanessa Minden, Martin Maier and Michael Kleyer

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Chapter 5: Interactions between ecosystem properties and land use resolve trade-offs between forage production and species conservation in coastal lowlands

Abstract

We modeled forage production and conservation value in a coastal landscape as dependents in a chain of responses and effects, starting with abiotic environmental conditions affecting the spatial distribution of land uses and biotic ecosystem properties, which in turn affect services. We asked which relationships in this causal chain determine trade-offs or synergies, specifically between sales of forage-based agricultural products and the habitat value to conserve endangered plant and breeding bird species.

Forty-six plots were established in salt marshes, reeds, extensively, and intensively-used grasslands in a coastal marsh landscape of East Frisia, Northwest Germany. On each plot, we recorded plants and breeding birds, mean groundwater level and salinity, available soil nutrients, soil texture, biomass removal by grazing and mowing, ANPP, and soil organic carbon. For each site with plots, plant and bird conservation values were calculated using Red Lists, and sales of forage-based agricultural products were assessed by interviewing farmers. We used a partial least square structural equation model to model effects between abiotic and biotic ecosystem properties, land use intensity, sales and conservation values.

Co-varying groundwater depth and salinity represent the most relevant ultimate cause for the landscape-wide variation in sales and conservation value. The water gradient then translated into more proximate causes, such as land-use intensity affecting ANPP, forage quality, and species richness, which then determined the services. A potential trade-off between provisioning and bequest services was resolved because (i) plant species conservation and forage production were segregated according to the water gradient, and (ii) both bird conservation and forage production depended on grassland management and its effects on ecosystem properties, albeit at different fertilization levels.

Identifying ultimate and proximate, direct and indirect causes of ecosystem service variation in landscapes allows targeting the most relevant determinants of provisioning and bequest services for better planning and management schemes. Our study points to segregation and integration as two alternative spatial strategies resolving trade-offs between services on the landscape scale.

5.1 Introduction

Land-use modifications have been recognized as major drivers affecting ecosystem properties (Sala *et al.* 2000; Poschlod *et al.* 2005; Quétier *et al.* 2007; Walther 2010). The resulting shifts in ecosystem properties may directly or indirectly affect the provision of ecosystem services (Schröter *et al.* 2005; Metzger *et al.* 2006; Montoya & Raffaelli 2010) and therefore human well-being (Santos-Martín *et al.* 2013).

Due to the intensification of food production and the abandonment of historic land usage, such as semi-natural grasslands, many authors report an increasing trade-off between provision of agricultural goods and species conservation, as agricultural landscapes now host fewer species than in earlier centuries (Vitousek *et al.* 1997; Chapin *et al.* 2000). However, given the huge variety of agricultural landscapes and different habitat requirements of species, whether land modification leads to a decline or increase in species' numbers is not easily predicted (Tscharntke *et al.* 2005; Gerstner *et al.* 2014). Therefore, recent studies have called for a theoretical understanding of the multiple relationships between drivers and ecosystem services (Bennett *et al.* 2009). This requires a systems-based approach, addressing structural and functional relationships between environment, ecosystem parameters and service outputs (Potschin & Haines-Young 2013).

Such an approach should quantify how ecosystem functions and properties respond to changes in the environment and how their resulting marginal changes affect ecosystem services (Wong *et al.* 2015), i.e. the provision of forage and related sales on the one hand and species conservation on the other. However the extent of changes in particular ecosystem services may differ between landscapes (Eigenbrod *et al.* 2010). For instance, limited soil water supply constrains forage production intensity in dry grasslands, whereas excess water in wetlands can be drained and forage production be intensified. Therefore, the relationships between the provisioning services and species conservation need to be linked to measured ecosystem properties variation and land uses in a given landscape.

Because trade-offs and synergies may occurr at different scales (Lavorel & Grigulis 2012), research on the biophyiscal processes that drive ecosystem services is essential for implementation of successful management schemes (Wong *et al.* 2015). However, in a recent review, Seppelt *et al.* (2011) found that few ecosystem service studies base their results on measured or observed data, and few identify interactions among ecosystem functions generating ecosystem services, indicate the uncertainty in their results, or capture relationships between ecosystem services.

Globally, coastal lowlands are some of the most strongly threatened and modified landscapes (Huston 2014). These modifications comprise dykes to exclude storm surges, artificial

drainage, agricultural intensification, settlements and technical infrastructure construction, which altogether compromise a wide range of ecosystems (Temmerman *et al.* 2013). Forage production for cattle and sheep is the predominant agricultural land use in temperate coastal lowlands (Huyghe *et al.* 2014). Recent intensification of forage production by high levels of fertilizer application, drainage and earlier onset of grazing and mowing may have led to an increased threat to plants and animals, as in floodplains (Krause *et al.* 2011; Wesche *et al.* 2012).

Here, we aim at identifying the relevant predictors which determine the value of ecosystems to provide forage-based agricultural products and their value to conserve endangered plants and breeding birds in coastal lowlands. In ecosystem service classifications e.g. Haines-Young & Potschin (2013), the generation of sales from forage-based products (forage sales) falls into the category of provisioning services, translated into an economic value (de Groot *et al.* 2010). The habitat value to conserve endangered plant species and breeding birds represent non-use existence, bequest or philanthropic cultural values. We conceive ecosystem services as depending on a causal chain of abiotic conditions determining land use intensity, which affect ecosystem properties. We seek to understand at which stage in this chain trade-offs or synergies between the services arise (Lavorel & Grigulis 2012; Wong *et al.* 2015). Forage production and species conservation were both highly ranked by regional stakeholders in the study area (Karrasch *et al.* 2014). They both depend on ecological functions provided by the ecosystem, such as species diversity, biomass production, soil organic carbon stocks, biomass decomposition rates and forage quality. In turn, these ecosystem properties depend on biotic properties such as groundwater and nutrient availability, soil aeration, and on the land uses that modify these conditions (De Bello *et al.* 2010; Lavorel *et al.* 2011; Lavorel & Grigulis 2012).

To specify our hypotheses, we constructed a conceptual model based on a priori knowledge (see below, Fig. 5.1), which was tested against a dependence model using structural equation modelling (Grace & Pugesek 1997; Minden & Kleyer 2015; Peppler-Lisbach *et al.* 2015). The model allowed us to identify direct and indirect interactions between ecosystem properties, land use and and services, and to quantify the explained variation of the final services as a measure of uncertainty.

5.2 Methods

The study area was situated in the lowlands of the northwest German coast of East Frisia (E 07°02', N 53°27', NW-Germany). It has a mean annual temperature of about 9.4 °C and receives a mean annual rainfall of 823 mm. A single large sea wall of up to 9 m height protects the mainland from flooding by storm surges. The mean tidal range is approx. 2.7 m and the agricultural hinterland has elevations between -2.0 and +2.50 m a.s.l. Salt marshes are found seawards of the dyke, and crop fields in a narrow elevated strip of a few kilometers width behind the sea wall. Further inland, at lower elevations, wet and mesic grasslands predominate. The whole area is artificially drained by a dense system of ditches. Before construction of the dikes, the natural vegetation consisted of extensive brackish reed stands and this vegetation is now prevalent where land use was abandoned. Forty-six plots located in unfertilized extensive wet meadows, grazed and non-grazed salt marshes, fertilized grasslands and reed vegetation were chosen by random stratified sampling based on elevation and land use.

5.2.1. Abiotic ecosystem properties

For each soil horizon on each plot down to a depth of 80cm, soil samples were collected in March 2012 with a soil sample ring of 100 cm^3, air dried and sieved. Bulk density was evaluated from 200 cm^3 of soil (Schlichting *et al.* 1995). From each plot, plant-available potassium (K) and phosphorus (P) were extracted with ammonium lactate-acetic acid at pH 3 (Egnér *et al.* 1960) and analyzed using atomic absorption spectroscopy and continuous flow analysis (Murphy & Riley 1962), respectively. Available nitrogen was calculated from the combined nitrate and ammonium values (CFA analysis) for the uppermost soil layer.

Potential cation exchange capacity (CEC) was calculated from soil texture according to (Ad-Hoc-AG 2005). In each plot, a drainage pipe (10 cm diameter) was installed 80 cm vertically in the ground. In these pipes, groundwater levels were recorded fortnightly during the vegetation period between March and October of 2012. Additionally, for plots in which variation in water levels was common (i.e. reeds , salt marshes and some wet meadows), groundwater was data-logged every half an hour with Sensus Ultra Divers (Reefnet Inc.) between May and October 2012. Along with the biweekly groundwater recordings, as a proxy for salinity, groundwater electrical conductivity was measured with WTW ph/Cond340i/SET using a Tetracon 325 electrode (See Table 5.1 for variable descriptors).

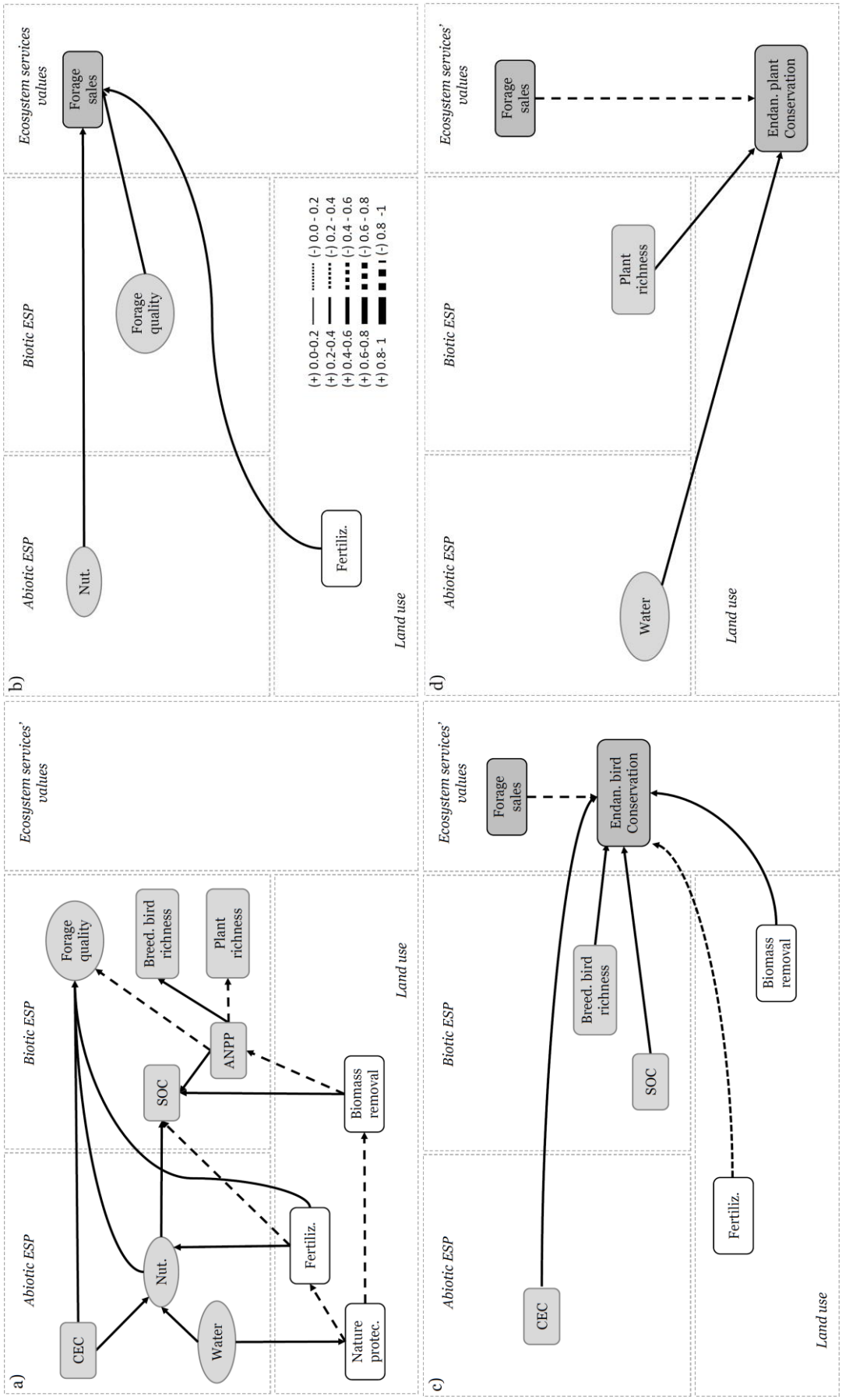
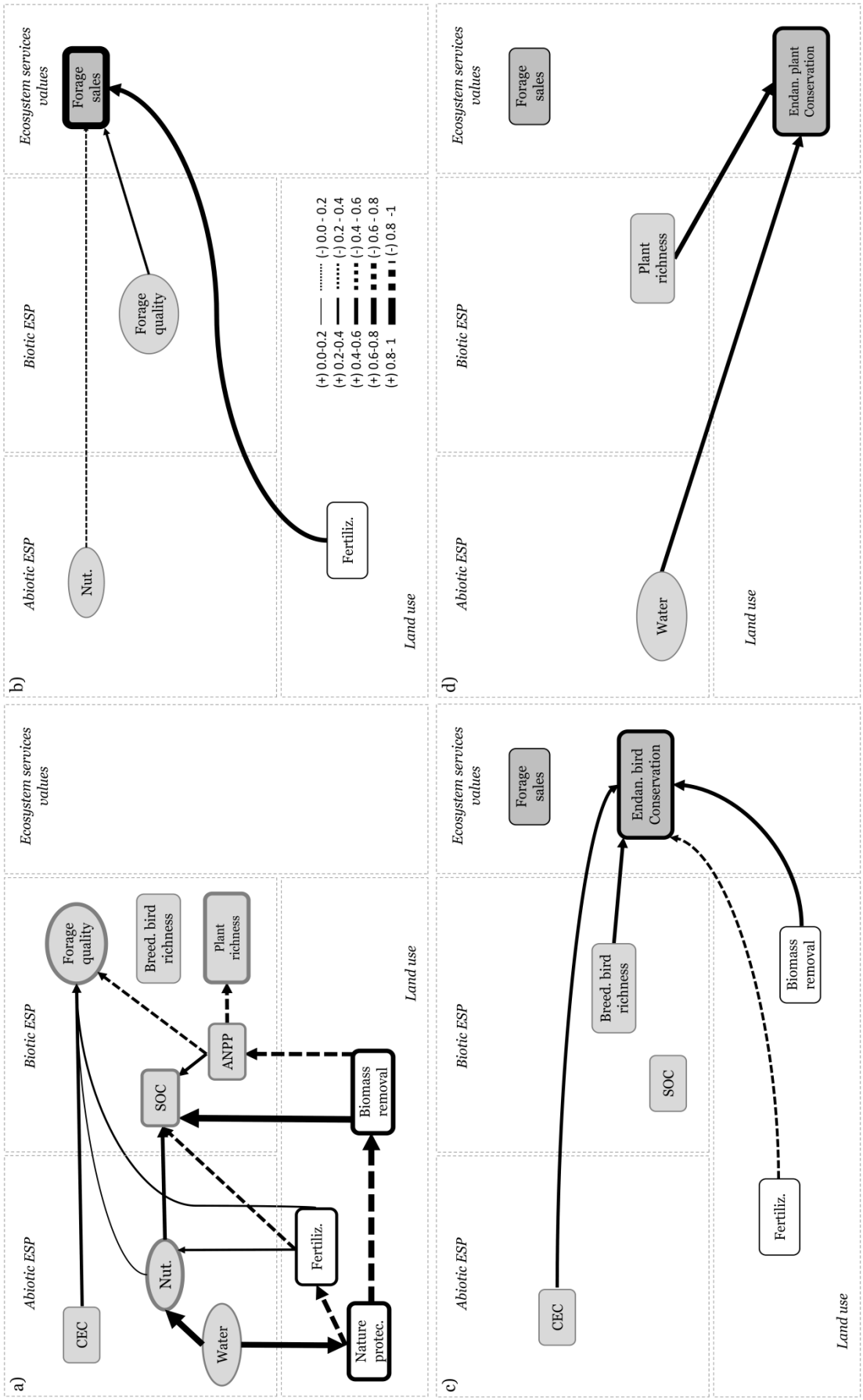

a)
Abiotic ESP
Biotic ESP
Ecosystem services' values
Land use
CEC
Nut.
Water
Fertiliz.
Nature protec.
SOC
ANPP
Biomass removal
Forage quality
Breed. bird richness
Plant richness
b)
Abiotic ESP
Biotic ESP
Ecosystem services values
Land use
Nut.
Forage quality
Forage sales
Fertiliz.
(+) 0.0-0.2
(+) 0.2-0.4
(+) 0.4-0.6
(+) 0.6-0.8
(+) 0.8- 1
(-) 0.0 - 0.2
(-) 0.2 - 0.4
(-) 0.4 - 0.6
(-) 0.6 - 0.8
(-) 0.8 -1
c)
Abiotic ESP
Biotic ESP
Ecosystem services' values
Land use
CEC
Breed. bird richness
SOC
Fertiliz.
Biomass removal
Forage sales
Endan. bird Conservation
d)
Abiotic ESP
Biotic ESP
Ecosystem services' values
Land use
Water
Plant richness
Forage sales
Endan. plant Conservation

Fig. 5.1: Initial model showing expected responses and effects between ecosystem properties, land use and final ecosystem services. Latent variables: Nut. ("NUTRIENTS"): Expected positive co-variation of availability of soil phosphorus, potassium and nitrogen; WATER: Positive correlation of mean groundwater level and salinity; FORAGE QUALITY: Expected positive correlation of native biomass decomposition and species based forage value (See Table 5.2). A) Expected relationships between land use and ecosystem properties. B) C) and D) Expected direct effects of land use and ecosystem properties on forage sales, habitat value to conserve endangered breeding birds and endangered plants respectively. Expected positive effects are shown with solid black arrows and negative effects with dashed black arrows. Variables in light grey background represent ecosystem properties (supporting ecosystem services); land use parameters: white ovals; variables in dark grey background and solid black frame represent values of final ecosystem services (See Table 5.1 and 5.2). Abbreviations: CEC: soil cation exchange capacity [cmol+/Kg]; SOC: soil organic carbon in 30 cm. depth [g/m^2]; breed. bird richness: Breeding bird richness [species/ha/patch]; ESP: Ecosystem properties.


a)
Abiotic ESP
Biotic ESP
Ecosystem services values
Land use
CEC
Water
Nut.
Forage quality
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Fertiliz.
Nature protec.
Biomass removal
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Breed. bird richness
Plant richness
b)
Abiotic ESP
Biotic ESP
Ecosystem services values
Land use
Nut.
Forage quality
Forage sales
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(+) 0.0-0.2
(+) 0.2-0.4
(+) 0.4-0.6
(+) 0.6-0.8
(+) 0.8- 1
(-) 0.0 - 0.2
(-) 0.2 - 0.4
(-) 0.4 - 0.6
(-) 0.6 - 0.8
(-) 0.8 -1
c)
Abiotic ESP
Biotic ESP
Ecosystem services values
Land use
CEC
Breed. bird richness
SOC
Forage sales
Endan. bird Conservation
Biomass removal
Fertiliz.
d)
Abiotic ESP
Biotic ESP
Ecosystem services values
Land use
Water
Plant richness
Forage sales
Endan. plant Conservation

Fig. 5.2: Results of the PLS-SEM analysis for a) biotic and abiotic ecosystem properties and three final ecosystem services, b) forage production sales, c) habitat value to conserve endangered breeding birds and d) habitat value to conserve endangered plants. Values of final ecosystem services: dark grey ovals; intermediate or supporting services (biotic and abiotic ecosystem properties): light grey ovals; land use drivers: white ovals. Responses and effects are shown in black arrows, the arrow thickness represent standardized regression coefficients value for both positive and negative values (See legend); solid arrows for positive effects and dashed arrows for negative effects. The explained R^2 is shown through the frame thickness (See legend). Abbreviations: Nut: nutrient availability ("NUTRIENTS") (N (+), P (+) and K (+); CEC: potential cation exchange capacity; Water ("WATER"): Groundwater level (+) and salinity (+); Fertiliz.: fertilization; ESP: Ecosystem properties; Endan.:Endangered.

5.2.2 Land use

We assessed land-use regulation according to German legal nature-protection categories and converted them in an ordinal nature-protection index for each plot, with 0 (no protection, 5 plots), 1 (bird conservation area, 9 plots), 2 (protected landscape or biosphere reserve, 0 plots) 3 (nature conservation areas, 13 plots), 4 (nature monument, nature feature or nature park, 0 plots) or 5 (national park, 19 plots).

Land-use intensity was described by two parameters: biomass removal and fertilization. Biomass removal was quantified using fenced exclosures of 4 m^2, where grazing or mowing was not possible. We collected biomass samples using a subplot size of 0.5 m^2 inside and outside each exclosure during peak vegetation (de Leeuw *et al.* 1990). Samples were sorted according to live and dead biomass, oven dried at 70°C for 72 hours, and then weighed. Percentage of biomass removal was calculated from the difference between both samples. Biomass values were normalized to 1m^2. The amount of applied inorganic fertilizer (Kg of applied nitrogen per hectare and year) was obtained by interviewing farmers and land owners managing the different plots during 2012. Most plots were fertilized with Calcium Ammonium Nitrate (27% N and 10% Ca).

Table 5.1: Variables' descriptors and abbreviations (N: 46). *Variables which are used as indicator variables (observed) for nutrient availability-latent variable (non-observed variable). **Indicator variables used for water gradient (WATER) latent variable. ***Variables used as indicator variables for FORAGE QUALITY latent variable. CWM: Community weighted mean. Sales: Sales of forage-based agricultural products. Endan. breeding birds: Habitat value to conserve endangered breeding birds. Endan. plants: Habitat value to conserve endangered plant species.

Variable	Abbreviation	Units.	Min.	Max.	Mean	Median
(a) Abiotic ESP						
Plant available soil potassium content*	K	g/m² (80 cm. depth)	9.57	837.79	417.81	
Plant available soil phosphorous content*	P	g/m² (80 cm. depth)	5.66	134.55	47.21	
Plant available soil nitrogen*	N	g/m² (30 cm. depth)	9.80	157.10	53.30	
Mean groundwater level**	GW	cm.	-100	-7.6	-42.9	
Mean groundwater conductivity**	Salinity	mS/cm	0.00	37.32	13.20	
Cation exchange capacity	CEC	cmol+/kg	8.83	72.70	30.33	
(b) Land Use						
Inorganic fertilization	Fertilization	Kg of N /ha/year	0.00	250.00	29.04	
Nature protection status index	Nature Protection	Index	0	5		2.5
Biomass removal	Biomass removal	%	0.00	91.94	32.89	
(c) Biotic ESP						
*** Utilization indicator value (CWM)	Utilization value	Index	3.00	9.00		5
***Native biomass decomposition rate	Decomposition	%/day	0.01	0.45	0.26	
Plant species richness	Plant richness	Number of Species/Plot	1.00	15.00		7
Soil organic carbon stock	SOC	kg/m2 (30 cm depth)	3.46	119.97	25.88	
Above-ground net primary productivity	ANPP	g/day/m2	0.79	13.66	5.68	
Breeding species richness	Breeding birds richness	Number of Species/ha/Patch	0.00	9		4
(d) Ecosystem services						
Forage sales	Sales	Gross €/ha/year	0.00	4400.00	912.83	
Endangered breeding birds habitat conservation value	Endan. breeding birds	Index	0.00	21.80	3.94	
Endangered plant species habitat conservation value	Endan. plants	Index	0.00	8.00		0

5.2.3 Biotic Ecosystem Properties

Plant species composition and abundance was recorded by frequency analysis at each plot in the summer of 2012, using a 1x1m grid of 100 cells (each 10x10cm). Breeding bird species were surveyed according to (Südbeck *et al.* 2007) on nine visits during each breeding season over 3 years (2011-2013), recording territorial or breeding behavior in homogenous patches that included the target plot. Patch size ranged from 0.3 to 10.9 ha, with an average of 2 ha.

Plot species-based forage values were obtained by community weighted means of the grassland utilization indicator values of all vascular plant species of a plot (Briemle *et al.* 2002). These values indicate the forage value of plant species on an ordinal scale from 1 to 9, based on grazer preference and the species' tolerance to mowing, grazing and trampling. Grassland utilization indicator values were retrieved from the BIOLFLOR database (http://www2.ufz.de/biolflor/index.jsp).

Litter mass loss (or decomposition rate) was determined using a litterbag experiment. Fresh plant material was collected in autumn 2011 and left to decompose for 12 months in the field on the soil surface in 1 mm mesh litterbags (5 g per litterbag and six replicates per plot). The recovered material was oven dried and weighed. The rate of litter mass loss was calculated relative to its initial mass as the rate of biomass decomposition per day (%/day, (Garnier *et al.* 2007).

In addition, total soil carbon was measured in all horizons for the upper 80 cm of soil. Soil organic carbon was measured for the first 30 cm as the difference between $CaCO_3$ and Total Carbon values.

Calcium carbonate ($CaCO_3$) was determined by adding 10 ml hydrochloric acid (dilution 1:3) to a 10 g soil sample and by measuring the carbon dioxide produced (gasometric technique (Schlichting *et al.* 1995). Total carbon was measured using a CHNS-Analyser Flash EA (Thermo Electron Corporation) after oven-drying the sample at 105° C for 17 hours.

From the above-mentioned biomass samples we obtained above-ground biomass productivity. One sample was collected at the beginning of the vegetation growing season (March) and a second at peak vegetation (August). The samples were oven dried for 72 hours at 70° C. ANPP was expressed as the difference between the two values, divided by the number of days between the first and second collection (g/m^2/day, (Scurlock *et al.* 2002; Garnier *et al.* 2007).

5.2.5 Values of final ecosystem services

If sites with plots were mown or grazed, we asked the farmer to provide us with the sales obtained from all forage-based products produced on the respective site per hectare and year in € during 2012.

The habitat value to conserve endangered plant species was calculated as an index. Every plant species was assigned a value following an ordinal scale according to the German Red List (www.floraweb.de) translated into IUCN endangerment categories: Not evaluated (NE) and Lesser concern (LC): 0; Near threatened (NT): 1; Vulnerable (VU): 2; Endangered (EN): 3; Critically endangered (CR): 4. Subsequently, the final plot value for endangered plant species' variable was the sum of all species values from the species occurring in a plot.

The habitat value to conserve endangered breeding birds was calculated according to (Behm & Krüger 2013). According to the German red list status of a species (Südbeck *et al.* 2007), points were given per breeding pair per plot. The sums for all red list species occurring on one plot were calculated and corrected for plot size. Only breeding bird species with red list status corresponding to IUCN category Vulnerable (VU), Endangered (EN) and Critically Endangered (CR) were included in the index.

5.2.6 Statistical analysis

We used a structural equation model based on partial least square analysis (PLS-SEM) (Hair *et al.* 2013) to test our hypothesized model (Fig. 5.1). PLS-SEM has been extensively used in the social sciences and recently introduced into ecological studies (Peppler-Lisbach *et al.* 2015). PLS-SEM aims at maximizing the explained variance of the dependent variables (R^2), but does not offer a general goodness-of-fit as in covariance-based methods. It allows using latent variables, which are non-observed variables composed of several observed variables or indicators. PLS-SEM accepts a relatively low number of samples (here: 46) as compared to covariance-based methods, and does not require normality for the variables (Hair *et al.* 2011). We used the software SmartPLS v2 (Ringle *et al.* 2005). A bootstrap analysis of 5000 runs was used to test path significance. All paths showing bootstrapped path values lower than 1.95 (Significance level: 5 %) were removed from the model (Appendix 5.3 and Fig. 5.2), because they were not significant (Hair *et al.* 2011). Previously, we performed a non-parametric Spearman' test to check for pairwise correlations between the predicted indicator variables for the latent variables in the model. The following latent variables were used to aggregate correlated observed variables: NUTRIENTS (increasing with available P, K and N), WATER (increasing with groundwater level and salinity) (Minden & Kleyer 2011), and FORAGE QUALITY (aggregation of decomposition rates and the abundance-weighted mean grassland

utilization indicator values) (White *et al.* 2004; Fortunel *et al.* 2009; Gillman *et al.* 2015) (See Table 5.1 and Fig. 5.1).

5.2.7 Initial model

For better visualization, the initial model was divided into four graphs, one for biophysical processes (Fig. 5.1 a) and one for each final ecosystem services values (Fig. 5.1b-d). The model assumed that abiotic ecosystem properties conditions influence land-use intensity and both determine biotic ecosystem properties, which together affect sales and habitat value. These final ecosystem services are expected to be negatively correlated. To represent a potential trade-off, we assumed a negative correlation between the latter (Fig. 5.1 c, d) (Kleijn *et al.* 2006; Zhang *et al.* 2007).

Abiotic ecosystem properties and land use relationships (Fig. 5.1 a): Soil texture and water conditions often determine the allocation of land uses (Desbiez *et al.* 2004). We assumed the gradient ranging from fresh to saline and from low to high levels of groundwater to be a major constraint (latent variable "WATER") driving nature protection status and land-use intensity (fertilization and biomass removal) (Minden *et al.* 2012). Soil nutrients (latent variable "NUTRIENTS") should increase with the water gradient ("WATER") due to inputs into salt marshes from sea water inundations, indirectly reinforced by the runoff of nutrients to the sea from adjacent agricultural land (Deegan *et al.* 2012).

A gradient from sandy to clayey soils expressed as potential cation exchange capacity (CEC) should constitute a second constraint driving nutrient availability and land use, as farmers are expected to more intensively cultivate soils with higher CEC. WATER and CEC were considered exogenous with no response to any other variables. All other variables were considered endogenous and with measurement error.

Relationships among ecosystem properties (Fig. 5.1 a): Vegetation forage quality (latent variable "FORAGE QUALITY") should increase with nutrient availability, cation exchange capacity (CEC) and fertilization (Lavorel & Grigulis 2012). Soil organic carbon (SOC) should increase with nutrient availability and ANPP (Bateman *et al.* 2013; Conti & Díaz 2013; Doblas Miranda *et al.* 2013). Increasing biomass removal should decrease ANPP (Lienin & Kleyer 2012), but may increase or conserve SOC due to compensatory growth of roots and rhizomes (Yu & Chmura 2009; Piñeiro *et al.* 2010; Paula & Pausas 2011). Conversely, we expect a reduction in SOC where land use intensification is accompanied by high levels of fertilization (Van Wesemael *et al.* 2010). We expected that reed vegetation would show the highest ANPP (Windham 2001) and the lowest FORAGE QUALITY (Briemle *et al.* 2002), whereas pasture productivity should be lower but of higher quality. Therefore the relationship between ANPP and FORAGE QUALITY should be negative, with unknown associations for salt marshes (Ngai

& Jefferies 2004; De Deyn *et al.* 2008). Plant species richness should decrease with increasing ANPP (Grime 1973), whereas moderate biomass removal by grazing and mowing may increase plant species richness by breaking the dominance of tall species (Esselink *et al.* 2000; Huston 2014). Breeding bird richness should increase with productivity, due to a positive effect of plant productivity on insect abundance as a food resource for birds (Haddad *et al.* 2001; Bonn *et al.* 2004).

Land use and ecosystem properties effects on final ecosystem services (Fig. 5.1 b; c and d): Forage sales should increase with forage quality, NUTRIENTS, CEC and fertilization, whereas biomass productivity (ANPP) is unlikely to affect forage sales, as unmanaged reeds produce high amounts of biomass. The probability of finding both endangered plant and bird species should increase with species richness.

We expected that the majority of endangered breeding birds would be meadow bird species, being one of the species groups threatened by strong population decline all over Europe (Gregory *et al.* 2005). Abundance for meadow bird species should depend on sufficient prey for precocial chicks and and adults (Beintema *et al.* 1991). We were not able to collect data on prey abundance and energy quality. Therefore, we used SOC and CEC as proxies for soil fertility, which we expected to have a positive effect on the plant and animal biomass in soils, as it may form an important base of the food chain exploited by birds (Vickery *et al.* 2001; Wissuwa *et al.* 2013). Fertilization, however, which is commonly associated with the early onset of grazing and increased number of mowing events and should lead to a more uniform sward, can negatively affect grassland invertebrates and should therefore decrease the habitat value to conserve endangered breeding birds (Vickery *et al.* 2001; Newton 2004).

5.3 Results

The structural equation model (separated into several sections in Fig.5.2) was consistent with the initial model; only 5 out of 29 paths were not significant and were removed from the final model. The most relevant deviation from the initial model was that there was no direct trade-off between forage sales and endangered breeding bird or plants (Fig. 5.2 and Table 5.2).

Furthermore, the following paths were removed because they were not significant: CEC→NUTRIENTS, SOC→endangered birds, ANPP→ breeding bird richness. As a consequence, breeding bird richness was unrelated to any ecosystem property or land use (Fig. 5.2 and Table 5.2). Since it still explained the endangered bird index, it became the third exogenous variable (together with WATER and CEC).

All latent variables were significant and goodness-of-fit measures, such as average variance extracted (AVE; Indicator for converge validity) and composite reliability (indicator for

internal consistency reliability), were equal to or higher than 0.5 and 0.7 respectively (Hair *et al.* 2011) (Appendix 5.1).

According to the standardized regression coefficients of the direct, indirect and total effects (Fig. 5.2 and Appendix 5.2), the following relationships were most relevant: NUTRIENTS increased from landward to seaward following WATER (groundwater and salinity). The latter also determined nature protection, as most salt marshes belonged to the area of the Wadden Sea National Park. In many protected areas, land use had been abandoned, so correlations with disturbance and fertilization were negative. Soil organic carbon strongly increased with biomass removal.

The following paths were weaker, yet also significant: Fertilization of landward grasslands increased nutrient availability. Biomass removal increased with potential cation exchange capacity, but with decreased ANPP. Fertilization decreased and NUTRIENTS increased SOC. FORAGE QUALITY responded positively to biomass removal, CEC, fertilization, WATER, and nutrient availability and negatively to ANPP (See Fig. 5.2 and Appendix 5.2). Plant species richness decreased with increasing ANPP.

5.3.1 Responses of final services' values to ecosystem properties and land use

Forage sales were largely well explained by the model (Fig. 5.2 and Table 5.2). In accordance with our initial model (Fig. 5.1), forage sales were associated with FORAGE QUALITY, though not strongly. Both intensive grasslands landward of the sea wall and salt marshes seaward of the sea wall featured relatively high FORAGE QUALITY (Fig. 4.1). However, the salt marshes did provide relative low sales from forage due to conservation regulations that led to the abandonment of mowing and grazing in most of the region (Villbrandt *et al.* 1999). Forage sales increased with fertilization and decreased with WATER, which points to the intensively managed, clayey and well-drained grasslands landwards of the sea wall, where most forage was produced. In contrast, both ANPP, which was higher in reeds (Fig. 4.1), and NUTRIENTS, which was highest in the salt marshes (Fig. 4.1) were negatively associated with forage sales.

Endangered breeding birds were moderately well explained (Fig.5.2 and Table 5.2) and responded positively to biomass removal and potential cation exchange capacity, but negatively to fertilization and also indirectly and negatively to the water gradient (Table 5.2). Contrary to our expectations, soil organic carbon did not affect the occurrence of endangered breeding birds.

Endangered plants were also moderately well explained by WATER and plant species richness (Fig.5.2 and Table 5.2). We also found indirect positive effects of biomass removal, as well as indirect negative effects of nature protection and ANPP. This fact points to seaward grazed salt marshes and to landward wet meadows, which all host relatively high numbers of endangered plants.

Table 5.2: Total, indirect and direct effects (TE; IE and DE respectively) between ecosystem properties, land use parameters and values of final ecosystem services: forage sales and habitat conservation value for endangered breeding birds and endangered plant species. The values represent standardized regression beta path coefficients from the PLS-SEM. ESP: Ecosystem property. ESS: Ecosystem service. All relationships are significant at $p<0.05$, NS: non-significant. Total effects are the sum of direct and indirect effects, indirect effects are the product of direct and direct effects.

		Values of final ecosystem services								
		Forage sales (R^2:0.76)			Endangered breeding bird conservation value (R^2: 0.49)			Endangered plant conservation value (R^2: 0.49)		
Variable type	Variable	TE	IE	DE	TE	IE	DE	TE	IE	DE
Abiotic ESP	NUTRIENTS	-0.30		-0.30						
Abiotic ESP	CEC		NS		0.41		0.41			
Abiotic ESP	WATER	-0.50	-0.50		-0.23	-0.23		0.42	-0.12	0.54
Land use	Fertilization	0.74	0.08	0.66	-0.35		-0.35			
Land use	Nature protection	-0.50	-0.50		-0.17	-0.17		-0.17	-0.17	
Land use	Biomass removal	0.08	0.08		0.70	0.20	0.50	0.23	0.23	
Biotic ESP	FORAGE QUALITY	0.22		0.22						
Biotic ESP	ANNP	-0.09	-0.09					-0.42	-0.42	
Biotic ESP	Breeding birds richness				0.42		0.42			
Biotic ESP	Plant species richness							0.6		0.6
Biotic ESP	Soil organic carbon				NS	NS	NS			
Final ESS	Forage sales				NS		NS	NS		NS

5.4 Discussion

Our approach demonstrates a chain of responses and effects leading from basic abiotic conditions to provision and bequest ecosystem services. These effects were either direct or indirect, via changes in ecosystem properties. The PLS-SEM model allowed us to discern ultimate and proximate causes of variations in these services.

Most relationships modeled were consistent with our initial model. Based on the strength of standardized regression coefficients, we identified the water gradient, a latent variable aggregating groundwater level and salinity, as the main constraint for nutrient availability and land-use intensity. The latter, described by its nature protection status and by biomass removal and fertilization, affected biotic ecosystem properties such as ANPP, soil organic carbon, plant diversity and forage quality. Finally, sales from forage and endangered species were dependent on the water gradient, potential cation exchange capacity, land use intensity, and species richness.

We found only a few deviations from the initial model:

1. Potential cation exchange capacity (CEC) did not have a significant effect on nutrient availability, because the import of nutrients to salt marshes from sea water (Rozema *et al.* 2000) outweighed the effect of CEC, which was lower in salt marshes than in the more clayey inland soils.

2. Contrarily to initially expectations (Bonn *et al.* 2004), breeding bird richness did not depend on ANPP. We attributed this non-significant effect to the fact that this initially hypothesized relationship would be expected in nitrogen limited systems (Haddad *et al.* 2001), which, however was not the case here. Breeding bird richness was similar in reeds with high ANPP, salt marshes with intermediate ANPP and inland grasslands with relatively low ANPP. It should be noted that our peak biomass measurement in August may have underestimated the ANPP of managed inland grasslands, which reached peak biomass earlier than August. Endangered breeding birds were unrelated to soil organic carbon (SOC). Adult birds and precocial chicks require prey, such as terrestrial invertebrates, to ensure growth and survival (Beintema *et al.* 1991). Prey identity and quality can vary strongly across coastal habitats (Schrama *et al.* 2013) and total invertebrate density was a poor predictor of prey availability (Schekkerman & Boele 2009). Even more so, our assumption of SOC being informative on prey supply was probably too simplistic to capture the relationship between birds and their habitat requirement resources.

3. Most importantly, we did not find a direct trade-off between forage sales and endangered species occurrence, although this trade-off has been reported in many other studies (Zhang *et al.* 2007; Gabriel *et al.* 2013).

The model revealed responses and effects showing how the potential trade-off between provisioning and bequest ecosystem services was resolved. The water gradient, ranging from rain-fed, well-drained to saline sites with high groundwater tables, was an ultimate factor. Agricultural land use is allocated to the more benign end of the water gradient, i.e. the landward marshes, and species protection to the stressful end, i.e. the seaward salt marshes. This is particularly evident for the vegetation component of the ecosystem, i.e. forage production versus plant species protection. The more proximate causes for the generation of economic benefits from forage production were fertilization and forage quality, the latter being negatively related to ANPP and positively to NUTRIENTS (Lienin & Kleyer 2012). On the other hand, NUTRIENTS was negatively related to sales from forage. This apparent contradiction had its ultimate cause in the protection of salt marshes and subsequent abandonment of grazing, although salt marshes are acknowledged for their high forage value because of high soil and leaf nutrient contents (Groenendijk 1984; Knottnerus 2005; Minden & Kleyer 2014; Minden & Kleyer 2015a). Salt marsh forage quality was similar to the inland pastures, but nature protection precluded the generation of farming economic benefits from the resource. This is reflected in the opposed paths from NUTRIENTS to FORAGE QUALITY and forage sales.

On the landward, rain-fed marshes, the trade-off between plant species protection and forage production was decided in favor of the latter, by converting former species-rich wet grasslands to well-drained, fertilized grasslands. This eliminated the species pool of wet grasslands (Schrautzer *et al.* 1996), except for a few common species such as *Alopecurus geniculatus*. Thus, this trade-off could not be documented with current data and did not come out in our model. Conversely, the seaward salt marshes were abandoned and designated as a conservation site, although FORAGE QUALITY and ANPP were both as high as on the landward pastures.

Habitat value to conserve breeding birds depended on the same direct and indirect predictors as sales from forage production, except for a negative relationship with fertilization. This indicates that the most endangered breeding birds were meadow birds (Vickery *et al.* 2001; Atkinson *et al.* 2005) found on less fertilized pastures, whereas forage sales increased with fertilization. Lower fertilisation accompanies less drainage and lower stocking rates, facilitating successful reproduction of meadow birds (Newton 2004; Kentie *et al.* 2013).

In summary, trade-offs between species conservation value and sales from forage on inland marshes were uncovered despite not being visible in the model. They resulted in the almost complete elimination of the wet grassland species pool. Already deprived of endangered plants, the less intensively used grasslands were still habitats for endangered meadow birds, until, with further fertilization, drainage and increasing stocking rates, sales from forage was optimised at the expense of species protection. Decisions to increase forage production from less intensively used grasslands might thus put their protection service at risk (Kremen & Miles 2012).

Recently, studies focused on spatial aspects of multiple ecosystem service provisioning (Chan *et al.* 2006). Our study points to two spatial strategies to resolve potential trade-offs among ecosystem services. The first is spatial segregation of agriculture and nature conservation, which is still the most relevant spatial land management policy in Northwest-Europe (van Lier 1998; Scherr & McNeely 2008). In our study area, most grasslands landward of the sea wall are optimized to provide a single service, i.e. forage production and associated economic benefits. Seaward of the dyke, all land use was abandoned and strict nature protection applied. This resulted in two adjacent monofunctional landscapes expressed on the water gradient. The segregation approach appears promising for nature conservation, as farming is prohibited on protected sites and endangered populations can be effectively managed. In practice, however, most segregation schemes allocate nature protection to marginally productive land, such as salt marshes, mountains, fens and bogs, or dry grasslands, which are relatively rare in space. The more widespread fertile, mesic landscapes are reserved for maximizing provisioning services, which leads to strong impoverishment of their species pools (Walker *et al.* 2004).

In contrast to the segregation of forage production and endangered plant protection, endangered breeding bird protection and the restoration of wetland plant species requires an integrated approach, i.e. landward landscapes should be a mosaic composed of moderately-managed and drained grasslands to allow breeding of meadow birds, and restored wetlands and other grasslands optimized for forage production and associated economic benefits. The integrated approach has a long history in spatial planning (e.g Haber (1973) and requires sensitive management both at the catchment and the local scale, so as to conserve endangered species and yield forage production in the same landscape (de Groot *et al.* 2010; Maes *et al.* 2012; Gonthier *et al.* 2014). Sales loss due to reduced management intensity is now often compensated by subsidies (payments for ecosystem services, (van Noordwijk *et al.* 2012). The spatial arrangement of land-use intensities may, however, not necessarily be static in time. In fact, historical land usage was often characterized by shifting mosaics (Kleyer *et al.* 2007). However, it is still an open question whether to arrange the mosaic in space and time so as to optimize the provisioning of service bundles on the landscape scale (Chan *et al.* 2006;

Willemen *et al.* 2010) and optimization models are increasingly used to tackle this question (Seppelt & Voinov 2003; Polasky *et al.* 2008; Schröter & Remme 2015).

5.5 Conclusion

Recent reviews called for a better understanding of the direct and indirect causes for variations in ecosystem services in order to improve landscape management (Bennett *et al.* 2009). Here, we modelled multiple ecosystem services in a coastal landscape as dependents of a chain of responses and effects, starting with abiotic properties affecting land uses and biotic ecosystem properties, which in turn affect services indicated. We identified a water gradient of groundwater depth and salinity as the most relevant ultimate cause for landscape-wide variation in service provisioning. The water gradient then translated into more proximate causes such as land-use intensity affecting ANPP, FORAGE QUALITY and species richness, which then determined the final services. Direct negative interactions between final services could not be confirmed, which was due to a segregation of plant species conservation and forage production on the water gradient and to a minor synergy between meadow bird conservation and forage production, both depending on grassland management, albeit at different fertilization levels. Identifying the chain of causes and effects on final services allows targeting the most relevant determinants of services in planning and management schemes. For instance, biomass removal, ANPP and fertilization need to be well balanced on the landscape scale in order to both conserve endangered birds and yield sales from forage production. Incorporating this chain of responses and effects into new spatial optimization models should allow us to identify the best spatial planning strategy that resolves the trade-off between sales of forage-based products and species conservation in multifunctional landscapes.

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Chapter 6

Coupling stakeholder assessments of ecosystem services with biophysical ecosystem properties reveals importance of social contexts

Miguel A. Cebrián-Piqueras, Leena Karrasch and Michael Kleyer

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Chapter 6: Coupling stakeholder assessments of ecosystem services with biophysical ecosystem properties reveals importance of social contexts

Abstract

It has been argued that ecosystem service assessments should be carried out by stakeholders because they benefit from the services provided by ecosystems. The question then arises whether different stakeholder groups perceive a given ecosystem service in similar ways and how stakeholder assessments relate to measured ecosystem properties.

We asked farmers and conservationists from the East-Frisian coast, northwest Germany, to state (1) their preference for provisioning, regulating and cultural ecosystem services and (2) their perception about the value of four relevant grassland vegetation units in providing each service. These units were: fertilized intensive grasslands, wet extensive grasslands, reeds and salt marshes. Additionally, biophysical parameters and land use data typically associated with these services were collected on 46 plots distributed across these vegetation units. Partial least square structural equation models were applied to test the degree to which stakeholder perceptions corresponded to the field-measured data.

We found significant differences between conservationists' and farmers' perceptions of given ecosystem services. For conservationists, the services regional belonging and soil fertility were strongly correlated to nature conservation value, whereas farmers associated them with forage production. Conservationists' perception of forage production was related to the biophysical properties forage quality, biomass removal and groundwater level and to the sales from forage production, whereas farmers employed a more ecosystem-based view that focused on the potential of ecosystem to produce forage, rather than the actual land use. The nature conservation perception of farmers was related to a suite of biophysical parameters indicating richness in species and low land use intensity, whereas the conservationists associated nature conservation with endangered meadow birds. Conservationists associated carbon sequestration with below-ground peat formation, whereas farmers associated it with above-ground plant productivity.

Perceived notions and values of ecosystem services are strongly influenced by different social contexts, involving current livelihoods, professional interests and traditions. Use of stakeholder assessments of ecosystem services to establish or improve sustainable land management needs to take into account the fact that stakeholder groups interpret ecosystem services in different ways and with different meanings.

6.1 Introduction

Ecosystem Services have recently emerged as a powerful inter- and trans-disciplinary approach to assess the benefits people obtain from ecosystems (MEA, 2005; Fisher *et al.* 2009; Hutchison *et al.* 2013). A participatory approach involving stakeholders is seen as crucial to evaluate the services from the point of view of their beneficiaries, and so to include local knowledge and societal demands in service assessments and land management decision making (Cowling *et al.* 2008; Koschke *et al.* 2012). Common perceptions of ecosystem services of stakeholders from different societal sectors may increase landscape level partnership and identity (Fürst *et al.* 2014). Therefore, an increasing number of assessments was based on stakeholder perceptions, either for the identification of relevant ecosystem services or the evaluation of suitable management options (Seppelt *et al.* 2011). However, ecosystem services may have different meanings for different stakeholder groups, depending on their knowledge, professional experience, and socio-economic situations (Lamarque *et al.* 2011; Martín-López *et al.* 2012; Orenstein & Groner 2014). Often, a given ecosystem service is perceived as representation of different ecosystem properties (Buijs *et al.* 2008; Quétier *et al.* 2010; Lamarque *et al.* 2011), which points towards multidimensional cognitive constructs (Law & Wong 1999; Edwards 2001; Fischer & Young 2007).

Stakeholders may be very familiar with services closely linked to their profession. For instance, farmers successfully produce agricultural goods if they are capable of evaluating the ecosystem properties and processes determining agricultural yield. Likewise, conservationists usually have good knowledge of the value of habitats for species protection (Barrera-Bassols & Zinck 2003; Desbiez *et al.* 2004; Anadón *et al.* 2009). On the other hand, regulating services such as water retention or carbon sequestration are hard to assess even by experts (Fang *et al.* 2007; Eigenbrod *et al.* 2010). Here we aim at answering the following questions: How are provisioning, regulating and cultural services assessed by local stakeholders? To what extent is there a mutual understanding of services between stakeholders of different societal sectors? (Herzon & Mikk 2007; Lamarque *et al.* 2011) How do stakeholder assessments relate to measured ecosystem properties?

Although most studies address ecosystem assessments either from the biophysical or from the social aspect, some studies showed how stakeholder perceptions of individual ecosystem functions conform to data measured in the field. For instance, Anadón *et al.*(2009) showed that shepherds in southeastern Spain could well assess the abundance of terrestrial tortoises. Desbiez *et al.* (2004) compared soil fertility assessments by Nepalese farmers with measured indicators of soil fertility. There is also a growing number of assessments involving biophysical measurements and questionnaire surveys, each for different services (Andersson *et al.* 2015; García-Llorente *et al.* 2015). It has, however, rarely been studied how stakeholder perceptions

of services link to the biophysical properties and functions of ecosystems on which service outputs are based (Quétier *et al.* 2010; Martín-López *et al.* 2012). In this study, we address this question in a collaborative approach, together with local farmers and conservationists (see also Karrasch *et al.* (2014)) by assessing conservation values (cultural and supporting services), forage production (provisioning service), soil fertility (supporting service), carbon sequestration (regulating service) and regional belonging (cultural service). The assessments were made in the coastal agricultural landscape of northwest Germany.

In agricultural landscapes, farmers and conservationists often hold opposing views on the value of vegetation units for the provision of ecosystem services, particularly agricultural values and species conservation on grasslands and wetlands (Bignal & McCracken 1996; Kremen & Miles 2012). This is due to a trade-off between highly productive meadows and pastures, where a few common species are favoured, and semi-natural grasslands, which are less productive and rich in endangered species (Vitousek *et al.* 1997; Chapin *et al.* 2000). Farmers have been regarded as a key stakeholder group for the local implementation of conservation management schemes in agricultural landscapes (Siebert *et al.* 2006; Bugalho *et al.* 2011). A successful adoption of such schemes depends to a great extent on their knowledge, perception and attitudes about biodiversity and nature conservation (Morris & Potter 1995; Herzon & Mikk 2007; Burton *et al.* 2008).

We used partial least squares structural equation modelling (PLS-SEM) to explore the relationships between the stakeholders' perceptions and ecosystem properties measured in the field. PLS-SEM has been recently introduced into ecological studies (Peppler-Lisbach *et al.* 2015), though it has been extensively used in social sciences (Serrano-Cinca *et al.* 2009; Hair *et al.* 2011; Henseler *et al.* 2012; Ayeh *et al.* 2013). It allowed us to use both ordinal assessment data and continuous ecological data without the need of normalizing the variables (Hair *et al.* 2013).

We expect that conservationists and farmers have different preferences for the ecosystem services, reflecting their professional and social interests. We assume that they have a common understanding of the services, as they have been living and working in the same landscape for a long time. As an alternative, farmers' and conservationists' perceptions of certain services may be significantly different, indicated by diverging correlations with measured ecosystem properties. This would point to diverse social contexts strongly affecting stakeholder-based service assessments (Quétier *et al.* 2010).

6.2 Methods

6.2.1 Study site

The study area is located in the municipality of Krummhörn (E 07°02', N 53°27', NW-Germany). It has a mean annual temperature of about 9.4 °C, an elevation ranging from -2.5 m to 1.5 m above sea level, and a mean of 823 mm annual rainfall (Wetterdienst 2012). Most of the landscape is covered by different types of grassland vegetation ranging from salt marshes and reed vegetation to managed grasslands such as wet and fertilized mesic grasslands. Sea walls, so-called dikes, protect the land against storm surges. The salt marshes in front of the dike are exposed to regular inundations with sea water, whereas the land use in the low-lying hinterland is secured by extensive drainage systems (Wolff *et al.* 2010).

The earlier natural landscape has been intensively modified and drained by human beings for centuries, resulting in today' coastal cultural landscape (Knottnerus 2005). For centuries, or even millennia, large areas of the landscape were used rather extensively by farmers as wet grasslands, both, seaward and landward of the dike (Lotze *et al.* 2005). Although recent land use intensification has eliminated many habitats during the last few decades (Schrautzer *et al.* 1996), the remaining wetlands have maintained habitat conditions for rare plant and bird species (Plieninger *et al.* 2006). Use of most salt marshes was abandoned as a consequence of the establishment of the Wadden Sea National Park of Lower Saxony in 1986.

6.2.2 Stakeholder survey

Groups of farmers (n=4, Appendix 6.3) and local conservationists (n=7, Appendix 6.3) were asked to state their preferences for four vegetation units and their ecosystem services (see Appendix 6.1). The units were (i) extensively-used wet grasslands, (ii) fertilized and frequently grazed or mown mesic grasslands, (iii) reed vegetation and (iv) saltmarshes. Stakeholders were asked to rank each of these units in terms of the following ecosystem services (scale 0-5): forage production, soil fertility, carbon sequestration, conservation value and regional belonging (Milcu *et al.* 2013). Subsequently, the stakeholders were asked to rank the vegetation units and ecosystem services in terms of preference (scale 0-100). This ranking shows which landscape unit and which ecosystem service were most relevant to the stakeholders (Table 6.1). Prior to the ranking, stakeholders were introduced to the concepts of both ecosystem services and vegetation units and had the opportunity to extensively discuss these concepts with regard to their rankings.

6.2.3 Biophysical indicators of ecosystem services

Independent of the stakeholder survey, during 2011-2013 we collected biophysical indicators of ecosystem services on plots in the study regions (Table 4.1). These plots (4 m^2, n=46) were randomly placed in the same vegetation units as assessed by the stakeholders: fertilized intensive grasslands (n: 7), wet extensive grasslands (n: 10), salt marshes (n: 16) and reeds (reed and sedges vegetation; n: 13) (Appendix 6.1). Assignment of plots to vegetation units was verified based on interviews with the owners of the site and on vegetation classification.

At each plot, soil samples from each soil horizon down to a depth of 80cm were collected in March 2012, air dried and sieved. Plant-available potassium (K) and phosphorus (P) were determined by extraction with ammonium lactate-acetic acid at pH 3 (Egnér *et al.* 1960), atomic absorption spectroscopy and continuous flow analysis (CFA, (Murphy & Riley 1962), respectively. Available nitrogen was calculated from the combined nitrate and ammonium values (CFA analysis) for the uppermost soil layer.
In each plot, we recorded groundwater levels fortnightly between March and October of 2012, using a drainage pipe installed vertically in the ground. On plots with strong groundwater variation (reeds, salt marshes and wet meadows), groundwater level was data-logged half-hourly with Sensus Ultra Divers (Reefnet Inc.) between May and October 2012. As a proxy for salinity, groundwater electrical conductivity was measured fortnightly with WTW ph/Cond340i/SET using a Tetracon 325 electrode (Soil organic carbon was measured for the uppermost 30 cm of the soil profile as the difference between $CaCO_3$ and Total Carbon values.

Plant species frequencies were recorded in a 1x1m grid of 100 cells (each 10x10cm). Over 3 years (2011-2013), breeding bird species were surveyed according to Südbeck et al., (2007) on nine visits during each breeding season, recording territorial or breeding behavior in homogenous patches that included the target plot. Patch size ranged from 0.3 to 10.9 ha, with an average of 2 ha.

Forage values for each plant species were obtained by community weighted means of the grassland utilization indicator values of all vascular plant species of a plot (Briemle *et al.* 2002). Grassland utilization indicator values were retrieved from the BIOLFLOR database (Klotz *et al.* 2002).

Decomposition rate was determined with litter bags. Fresh plant material was collected in autumn 2011 and left on the soil surface in the field to decompose for 12 months in 1 mm mesh litter bags (5 g per litter bag, 6 replicates per plot). The recovered material was oven dried and weighed. The decomposition rate over 12 months was calculated relative to the initial mass as percentage loss per day (Garnier *et al.* 2007). Above-ground standing biomass was determined

from the samples in the exclosures at peak vegetation (August). The samples were oven dried for 72 hours at 70° C and weighed.

6.2.4 Values of final ecosystem services

In order to assess the habitat value to conserve endangered plant species, every plant species received a rank according to the German Red List (www.floraweb.de) translated into the following IUCN categories: Not evaluated (NE) and Lesser concern (LC): 0; Near threatened (NT): 1; Vulnerable (VU): 2; Endangered (EN): 3; Critically endangered (CR): 4. The habitat value to conserve endangered plant species was calculated as the sum of all values of the species co-occurring in a plot. Endangered breeding birds' value per plot was calculated according to (Behm & Krüger 2013), based on the German red list of birds (Südbeck *et al.* 2007). Only breeding bird species with red list status corresponding to IUCN category Vulnerable (VU), Endangered (EN) and Critically Endangered (CR) were included in the index. The sum of all red list species occurring in a patch was calculated and corrected for patch size.

Table 6.1: Average values and standard deviations for stakeholder groups' perceptions about how relevant a given landscape unit is to provide or support one ecosystem service (0: no relevance; 5: maximal relevance). Two groups of stakeholders are included, farmers (n: 4) and conservationists (n: 7). Preference (0-100) for vegetation units and ecosystem services are indicated in brackets.

Conservationists (n:7)	Forage production (37)	SD	Nature conservation value (100)	SD	Soil fertility (75)	SD	Carbon sequestration (78)	SD	Regional belonging (63)	SD
Wet extensive grasslands (92)	3.4	1.27	4.7	0.49	4.4	0.79	3.9	1.21	3.3	0.95
Reeds (85)	0.4	0.53	4	1.00	3.4	1.81	4.3	0.76	3.1	0.69
Intensive grassland (28)	4.7	0.49	2.3	1.25	2.1	1.86	2.3	0.76	2.9	0.90
Saltmarsh (92)	0.9	0.69	4.9	0.38	4.1	1.86	3.7	0.76	4.1	0.69

Farmers (n:4)	Forage production (92)	SD	Nature conservation value (80)	SD	Soil fertility (92)	SD	Carbon sequestration (33)	SD	Regional belonging (63)	SD
Wet extensive grasslands (25)	2.25	0.5	4.5	1.00	2.5	1.29	2.25	0.96	2.25	1.26
Reeds (62)	1.00	0.82	4	0.82	2.5	0.58	4	0.82	2.75	0.50
Intensive grassland (87)	5.00	0.00	2.75	1.26	3.75	0.50	3.5	1.00	3.5	0.58
Saltmarsh (95)	3.25	1.93	3.38	0.82	3.75	0.50	2.5	1.00	3.75	0.96

6.2.5 Land use parameters

We reviewed the nature-protection status of each site with plots and converted the information to an ordinal nature-protection index, with 0 (no protection, 5 plots), 1 (bird conservation area, 9 plots), 2 (protected landscape or biosphere reserve, 0 plots) 3 (nature conservation areas, 13 plots), 4 (nature monument, nature feature or nature park, 0 plots) or 5 (national park, 19 plots).

Biomass removal by land use was quantified using fenced exclosures of 4 m^2, where grazing or mowing was not possible. We collected biomass samples using a subplot size of 0.5 m^2 inside and outside each exclosure during peak vegetation (de Leeuw *et al.* 1990). Samples were sorted according to live and dead biomass, oven dried at 70°C for 72 hours, and then weighed. Percentage of biomass removal was calculated from the difference between both samples and normalized to a size of 1 m^2. Farmers cultivating the sites with plots were asked to disclose the amount of applied inorganic fertilizer (Kg N per hectare and year). They also provided information on the gross profit per hectare for the year 2012.

6.2.5 Statistical analyses

We used Spearman non-parametric statistics to test for correlations between ecosystem service perceptions, separately for each stakeholder group. Positively correlated perceptions were used as indicators for dependent latent variables in the PLS-SEM model. Likewise, strongly correlated predictor variables were aggregated to latent variables.

PLS-SEM was used to relate dependent variables to independent variables. PLS-SEM maximizes the explained variance of the independent variables, does not require normal distributions and does not offer a general goodness-of-fit as covariance-based methods do (Hair *et al.*, 2013). We used the software "SmartPLS v2" (Ringle *et al.* 2005). A bootstrap analysis of 5000 runs was used to test path significance. All paths showing bootstrapped path values lower than 1.95 (Significance level: 5 %) were removed from the model, because they were not significant (Hair *et al.*, 2011). The model was used in an exploratory, rather than a confirmatory way, which means that multiple paths were tested and those retained that were significant.

6.3 Results

6.3.1 Ecosystem properties and land use

The four vegetation units differed strongly in terms of observed abiotic properties, biotic properties and land use parameters (Table 4.1). Salt marshes were nutrient-rich and had high groundwater levels and salinity, whereas wet, extensively-used grasslands were nutrient-poor. Sales from forage production, biomass removal and fertilization was highest on intensively-used grasslands, whereas groundwater level was lowest. Salt marshes and intensively-used grasslands were similar with respect to grassland utilization indicator value, decomposition rate, soil organic carbon and plant species richness. Salt marshes exhibited the highest plant conservation value, whereas wet, extensively-used grasslands had the highest bird conservation value. Reeds had the highest productivity and standing biomass and a relatively high protection status, together with salt marshes.

6.3.2 Stakeholders' perceptions and preferences for vegetation units and ecosystem services

Conservationists preferred wet, extensively-used grasslands, salt marshes and reeds over intensively-used grasslands and conservation value, carbon sequestration, soil fertility of forage production (Table 6.1). Conversely, farmers preferred intensively-used grasslands, salt marshes and reeds over wet, extensively-used grasslands and forage production, soil fertility and conservation value over carbon sequestration (Table 6.1).

Several latent variables were combined into aggregate correlated variables: (i) WATER from groundwater level and salinity ($R_{Spearman}$ = 0.55); NUTRIENTS from soil phosphorus, potassium and nitrogen ($R_{Spearman}$ = 0.54, 0.37, and 0.25); FORAGE QUALITY from litter decomposition rate and species-based forage value ($R_{Spearman}$ = 0.54). Several stakeholder perceptions were also correlated and therefore aggregated to latent variables. Conservationists assessed vegetation units similarly in terms of conservation value, soil fertility and regional belonging ($R_{Spearman}$ = 0.72, 1.00, 0.72). The resulting latent variable was called PRESERVATION. Farmers on the other hand ranked vegetation units similarly in terms of forage production, soil fertility and regional belonging ($R_{Spearman}$ = 0.90, 0.63, 0.88) with AGRICULTURE as the latent variable.

6.3.3 Partial Least Squares-Structural Equation Model results

Figures 6.1 and 6.2 show the results from the PLS-SEM analysis. Paths represent standardized beta path coefficients of ordinary least squares regressions. Path values and r-square values are shown in Table 6.2. Only significant path coefficients were kept in the model. All latent variables showed values equal to or higher than 0.5 and 0.7 for consistency for average variance

extracted (AVE; indicator for convergence validity) and composite reliability (indicator for internal consistency (Hair *et al.* 2011), Appendix 6.2: Quality criteria).

6.3.3.1 Relationships between perceptions and measured components of forage production

The conservationists' perceptions on forage production were well explained by the measured parameters (R^2:0.86, Fig. 6.1a; Table 6.2). They are linked to sales from forage production, high forage quality and biomass removal by grazing and mowing. Sites with high protection status, high groundwater levels and salinity (WATER) were seen as unsuitable for forage production. NUTRIENTS and fertilization were not significant.

Farmers associated the services soil fertility and regional belonging as closely related to forage production. The latent variable AGRICULTURE was substantially explained by (R^2:0.80, Fig. 6.1c; Table 6.2) and positively related to FORAGE QUALITY, NUTRIENTS and fertilization. Nature protection, WATER, biomass removal, and soil organic carbon were not significant and removed from the model. Surprisingly, sales generated from forage production was also not significant and therefore removed.

6.3.3.2 Relationships between perceptions and measured components of conservation value

In contrast to farmers, conservationists associated soil fertility and regional belonging to conservation value. The corresponding latent variable PRESERVATION was moderately well explained by the model (R^2: 0.56; Fig. 6.1b; Table 6.2). This bundle of perceived services was positively linked to the endangered breeding bird index of the plots, but not to endangered plants, indicating that the conservationists´ perceptions were biased to the protection of birds. PRESERVATION also increased with higher ground-water table, salinity and biomass removal and decreased with fertilization. Nature protection, endangered plants, plant richness, breeding bird richness and humus were not significant.

The farmers' perceptions of conservation value were substantially explained by the model (R^2: 0.75; Fig. 6.1d; Table 6.2). Farmers associated a high conservation value with vegetation units displaying high plant species richness. Surprisingly, the nature protection and endangered plant species status of the plots was negatively correlated to the perception of conservation value. Endangered breeding birds played no role. Paths to FORAGE QUALITY and fertilization were negative. Paths to WATER and biomass removal were not significant.

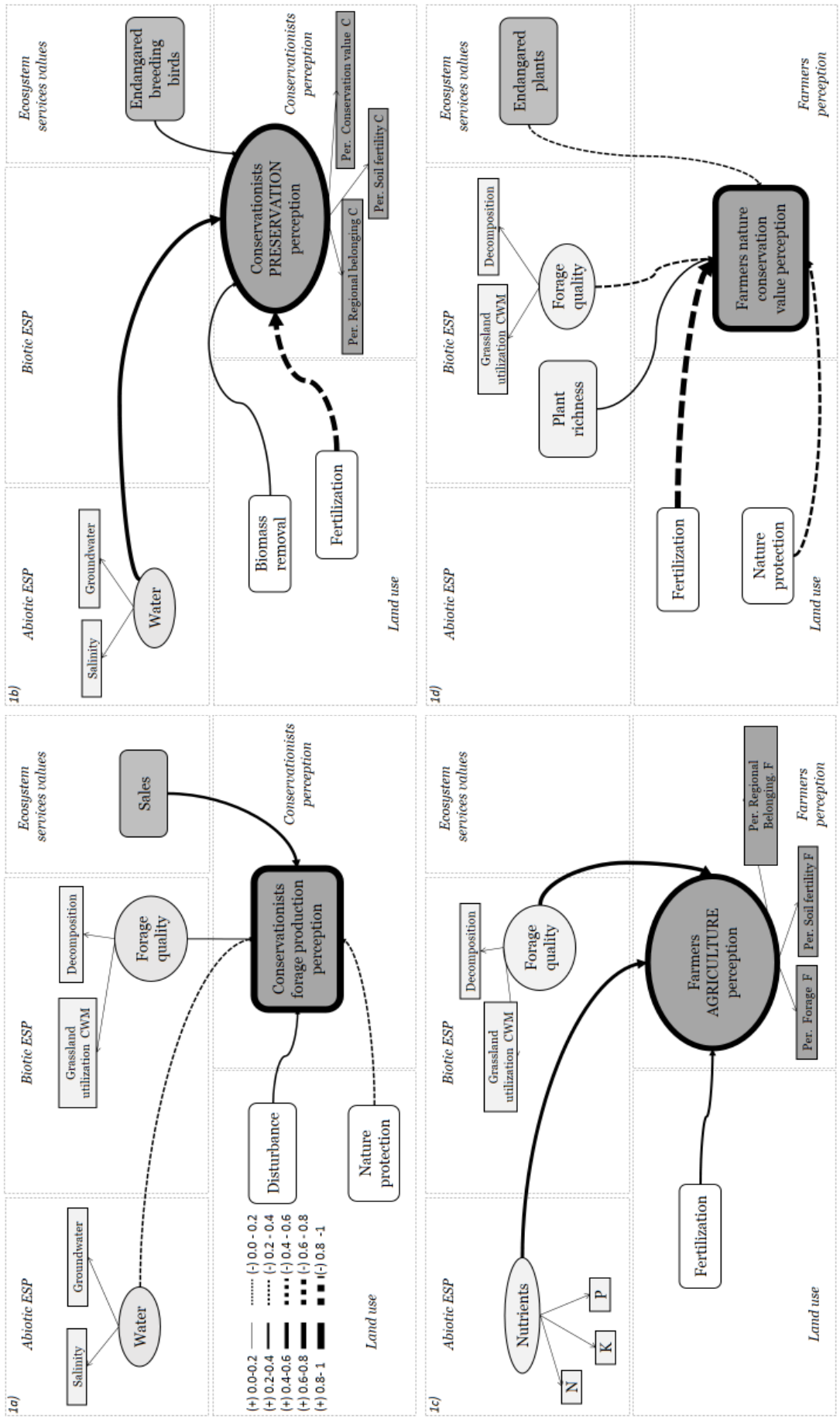
1a)
Abiotic ESP
Biotic ESP
Ecosystem services values
Salinity
Groundwater
Water
Grassland utilization CWM
Decomposition
Forage quality
Sales
Conservationists forage production perception
Conservationists perception
Disturbance
Nature protection
Land use
(+) 0.0-0.2
(+) 0.2-0.4
(+) 0.4-0.6
(+) 0.6-0.8
(+) 0.8-1
(-) 0.0 - 0.2
(-) 0.2 - 0.4
(-) 0.4 - 0.6
(-) 0.6 - 0.8
(-) 0.8 -1
1b)
Abiotic ESP
Biotic ESP
Ecosystem services values
Salinity
Groundwater
Water
Endangared breeding birds
Conservationists PRESERVATION perception
Per. Regional belonging C
Per. Soil fertility C
Per. Conservation value C
Conservationists perception
Biomass removal
Fertilization
Land use
1c)
Abiotic ESP
Biotic ESP
Ecosystem services values
Nutrients
N
K
P
Grassland utilization CWM
Decomposition
Forage quality
Farmers AGRICULTURE perception
Per. Forage F
Per. Soil fertility F
Per. Regional Belonging F
Farmers perception
Fertilization
Land use
1d)
Abiotic ESP
Biotic ESP
Ecosystem services values
Grassland utilization CWM
Decomposition
Forage quality
Plant richness
Endangared plants
Farmers nature conservation value perception
Farmers perception
Fertilization
Nature protection
Land use

Fig. 6.1a) 6.1b) 6.1 c) and 6.1 d): Conservationists' and farmers' perceptions about ecosystem services provision in a temperate coastal marsh landscape of North Sea Germany (Krummhörn community). Path model using PLS-SEM statistics. The strength of the path effect' coefficients between parameters and the perception latent variables is shown by the arrows' thickness (see legend; 0.0-1.0). These values represent standardized beta coefficients of ordinary least squares regressions. The R square value (R^2) for the endogenous variables (perceptions) is shown with the variable frame thickness (0.0-1.0). Latent variables (non-measured) are indicated by ovals, observed variables are indicated by rectangles.

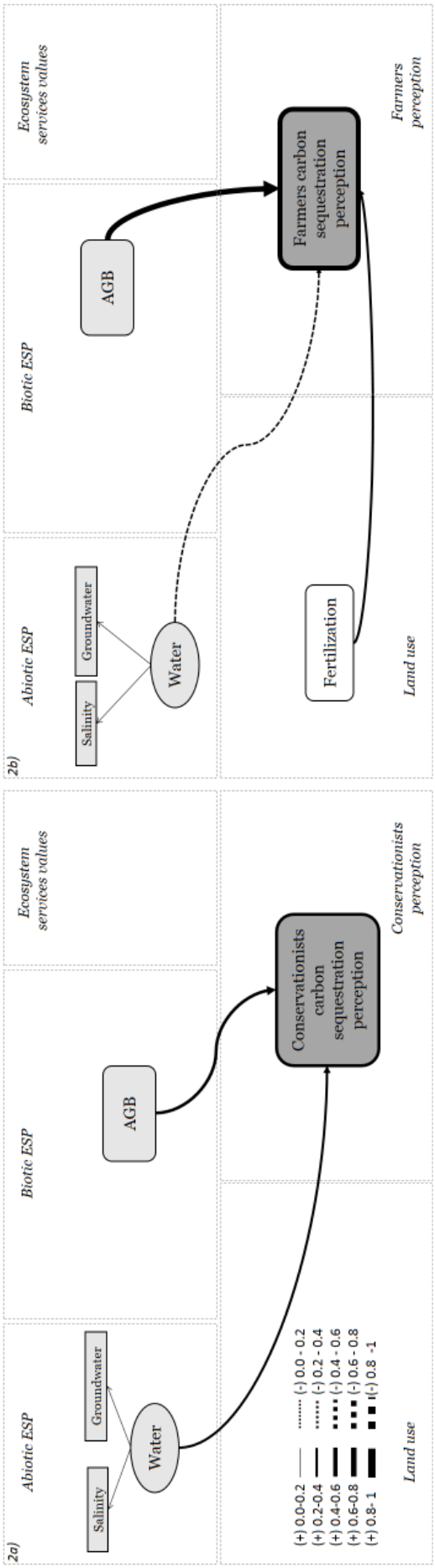

Fig. 6.2a) and 6.2b): The figures show conservationists' and farmers' perceptions for carbon sequestration in a temperate coastal marsh landscape of North Sea Germany (Krummhörn community). Path models using PLS-SEM statistics. The strength of the path effect' coefficients between parameters and the perception latent variables is shown by the arrows' thickness (see legend). These values represent standardized beta coefficients of ordinary least squares regressions. The R square value for the endogenous variables (perceptions) is shown through the variable frame thickness (See legend). Latent variables (non-measured) are indicated by ovals, observed variables are indicated by rectangles.

	Conservationists' forage production perception R^2: 0.86	Conservationists' PRESERVATION Perception R^2: 0.80	Farmers' AGRICULTURE perception R^2: 0.76	Farmers' nature conservation perception R^2: 0.80	Conservationists' carbon sequestration perception R^2: 0.37	Farmers' carbon sequestration perception R^2: 0.59
WATER		0.52			0.37	-0.41
NUTRIENTS			0.44			
Nature protection	-0.21			-0.44		0.44
Biomass removal	0.25	0.26				
Fertilization		-0.64	0.28	-0.89		0.49
AGB					0.37	0.61
FORAGE QUALITY	0.13		0.51	-0.36		
Plants				0.26		
Endangered plants				-0.31		
Endangered breeding birds		0.17				
Forage sales	0.46					

Table 6.2: The table shows responses of stakeholders' perception to biophysical data. The response values represent regression beta path coefficients from the structural equation models. R squared values (R^2) are indicated for every perception.

6.3.3.3 Relationships between perceptions and measured components of carbon sequestration

The perception of carbon sequestration by conservationists was related to high groundwater level (WATER) and above-ground standing biomass (R^2: 0.45; Fig. 6.2a; Table 6.2), indicating that this stakeholder group associated carbon sequestration with peat formation on water-logged soils. Fertilization and SOC were not significant. Farmers associated carbon sequestration with vegetation units having lower groundwater tables, higher AGB and receiving fertilizer (R^2: 0.58; Fig. 6.2b; Table 6.2). This combination of paths indicates that farmers related carbon sequestration to high above-ground plant standing biomass, rather than to peat formation. SOC was not significant.

6.4 Discussion

Stakeholder assessments of ecosystem service provision by different habitats were increasingly applied in recent years (Hutchison *et al.* 2013; Smith & Sullivan 2014). They represent an important resource for participatory processes and a valuable tool, due to their potential for policy making and societal acceptance (Brown *et al.* 2001). We found that stakeholders from different societal sectors not only preferred different ecosystem services, but their views on a certain service also corresponded to different biophysical properties of the ecosystems assessed. These relationships indicate specific contexts of stakeholder perceptions, reflecting different professional interests and cultural traditions.

6.4.1 Preferences and bundles

Not surprisingly, farmers preferred provisioning services and associated vegetation units (Quétier *et al.* 2010; Lamarque *et al.* 2011), whereas conservationists preferred cultural services, particularly the conservation value. It was, however, interesting that farmers associated soil fertility and regional belonging with forage production, whereas conservationists associated these services with conservation value. These service bundles (Raudsepp-Hearne *et al.* 2010; Martín-López *et al.* 2012) were highly linked to the stakeholders' main activities, i.e. farming or conservation management.

Regional belonging describes the attachment of the people to the land, i.e. its heritage value (Paasi 2003). For the farmers, heritage derived from the legacy of their Frisian ancestors who converted a landscape once covered with vast brackish reeds and salt marshes (Behre 2008) into a cultural landscape protected by dikes and designed to provide agricultural land and protection against floods (Meier 2004; Knottnerus 2005) They saw themselves responsible for and proud of establishing extensive drainage systems and the reclamation of land from the sea to yield direct benefit for the people (Van den Berg *et al.* 1998). As one of the interviewed

farmers stated: [F2] *"We do not need to discuss that East Frisia is not a natural landscape; it is a man-made landscape, evolved over hundreds of years"*.

On the other hand, conservationists viewed the heritage landscape as a mosaic of extensively-used wetlands, reeds and salt marshes that provide multiple habitats for the unique biodiversity of the northwest European coastal lowlands. Their reference was the historic, semi-natural landscape. This heritage landscape has come under pressure through agricultural intensification, as in other landscapes worldwide: [C5] *"There are salt marshes that have been strongly influenced by humans in the past, in particular by drainage measures and the narrow system of ditches and trenches. If there is no possibility to renaturalize the salt marshes, i.e. due to coastal protection reasons, the areas can be extensively used in accordance with specific species- and habitat protection measures, i.e. extensive grazing to support meadow birds and geese"*.

The apparent disagreement about what constitutes a heritage landscape was underpinned by strong differences in relationships between the ecosystem services assessments by the stakeholders and the biophysical properties of the ecosystems.

6.4.2 Forage production

Regarding forage production, the conservationists' perceptions were positively related to the sales from forage production as well as the forage quality of the vegetation and negatively related to the nature protection status. This shows that conservationists could appraise the economic value of mesic grasslands for forage production well and that they restrict the provision of this service to the unprotected sites currently managed for dairy farming.

In contrast, farmers employed a more ecosystem-based view on forage production, linked to the soil nutrients and the forage quality of the vegetation that ultimately supports the bundle of provisioning and cultural services described above (Lamarque *et al.*, 2011). Sufficient soil nutrients and plant nutrient content to provide forage in high quantity and quality occur landward and seaward of the dyke, i.e. on both intensively-used grasslands fertilized by farmers and on salt marshes nourished by sea-water inundations and sediment deposition. Salt marsh plants synthesize nitrogen-rich osmoprotectants to cope with salinity and therefore display high forage quality (Minden & Kleyer 2014). Salt marshes, used by farmers for centuries, are, however, now strongly protected in the study area and therefore no longer provide economic benefits to farmers, which has driven community conflicts in other regions (Buller & Morris 2004; Dobbs & Pretty 2008; Matzdorf & Lorenz 2010). The more ecosystem-based view of the farmers seeing the potential, yet unrealised, forage yield of the salt marshes, is the reason why there was no positive link between the perception of AGRICULTURE and forage sales.

6.4.3 Conservation value

The conservation value perception of conservationists was linked to groundwater table, salinity, biomass removal, low fertilisation and the breeding bird rarity index, but not to endangered plants. This indicates that conservationists prioritize the conservation of a single guild, the breeding meadow birds (Vickery *et al.* 2001; Atkinson *et al.* 2005). Meadow birds require grasslands of low mowing and grazing intensity, and low fertilization, facilitating their reproductive success (Newton 2004; Kentie *et al.* 2013). These conditions are characteristics of the wet, extensively-managed grasslands in the coastal regions of northwest Europe. Our result indicates that conservationists see the greatest land management conflicts in the preservation of inland wet grasslands as habitats for meadow birds (Krause *et al.* 2011). Wet grasslands are often not protected and are easily converted to intensively-used grasslands by further drainage, fertilization and frequent biomass removal. Endangered plants are most prevalent in salt marshes, which are protected, and therefore currently not at risk.

Endangered plant communities were not in the focus of the conservationists, although wetlands have experienced a drastic decline in plant species during the last few decades (Wesche *et al.* 2012).

Farmers' perception of conservation value on the other hand focused on ecosystems rather than endangered species. All ecosystems not intensively managed, i.e. reeds, wet meadows and salt marshes, were highly valued for conservation although their preference was low. The farmers´ view was utilitarian in a provisioning context, but also involved a heritage vision of a mosaic landscape composed of semi-natural and managed vegetation units (see also, (Frouws 1998; Quétier *et al.* 2010): [F2] *"Concerning nature protection areas: it is always difficult when highly productive soils are taken out of use. We as farmers are willing to support nature protection, but nature protection with an integrative and multifunctional landscape character. We should combine agricultural protection and nature protection. This is underlined by the fact that land is a finite resource"*.

6.4.4 Carbon sequestration

The conservationists' perception of carbon sequestration could be linked to peat formation under water-logged conditions, whereas the farmer's perception was mainly related to above-ground carbon stocks in productive grasslands. Although both views are not obviously incorrect, greenhouse gas measurements in the study area show a more complex picture (Witte & Giani 2015). First, carbon sequestration by peat formation is not very great and organic soils are rare because the whole landscape was drained and partly reclaimed from the Wadden Sea during the last few centuries. Second, carbon sequestration on freshwater-inundated wetlands is outweighed by methane emissions having a much higher global warming potential, whereas

salt marshes do not emit significant amounts of methane (Witte and Giani, 2015). Third, although carbon is fixed from the atmosphere while plants are growing, it is released again by decomposition processes on well-aerated soils (Piñeiro *et al.* 2010). Greenhouse gas emission and fixation are complex processes depending on the interplay of various environmental conditions, and are still being investigated scientifically (Lal 2004; Koch *et al.* 2014). Carbon sequestration may therefore be hard to assess by stakeholders, as also noted for other regulating ecosystem services (Carpenter *et al.* 2006; Primmer & Furman 2012; Kandziora *et al.* 2013). Nevertheless, links between the perception of carbon sequestration and measured biophysical properties revealed a contrasting appropriation of this service: whereas conservationists claimed the service for the protected wetlands, farmers associated it to farming activities yielding highly productive vegetation.

In summary, our results reveal that service assessments by stakeholders are strongly linked to the tasks, activities and functions those stakeholders fulfill in landscapes and the heritage and traditions influencing them (Quétier *et al.* 2010; Lamarque *et al.* 2011). Farmers see themselves in the tradition of the coastal people who for centuries strived to reclaim, drain and maintain the coastal land (Behre 2008). Therefore, they viewed all services the landscape provides as connected to their use of the land. This also involves potential benefits that cannot be realized, such as forage production on protected and abandoned salt marshes. Our study also revealed that farmers and conservationists see a trade-off between forage production and conservation (Siebert *et al.* 2006) but both groups acknowledge the need to integrate conservation and agricultural management, as exemplified by the following quotations from two farmers participating in the study: [F3] *"Agriculture is nature protection, as long as it is sustainable. Different use interests have to be balanced and linked. Everyone needs to make compromises"* and [F1] *"Nature conservation and agriculture – these are not two independent management approaches, these two land uses have to be combined. Nature protection needs to be integrated in farming activities. What we need are flexible and intelligent nature protection measures"*.

6.5 Conclusions

Do stakeholders understand a given service in similar ways? Are their perceptions linked to the same biophysical properties of the environment? Our study shows that this is not the case. Even elementary provisioning services such as forage production were linked to different values, ecosystem properties and land uses. Our results indicate that notions and values of services are strongly influenced by different social contexts, involving current livelihoods, professional interests and traditions. Formal stakeholder assessments of ecosystem services to establish or improve sustainable land management thus need to take into account that stakeholder groups interpret ecosystem services in different ways and give them different meanings. We therefore argue that ecosystem service assessments by stakeholders should be complemented by determining indicators of biophysical ecosystem properties, allowing the evaluation of the correspondence between stakeholder perceptions. Ultimately, analyses of the complex social-ecological contexts forming stakeholder attitudes towards ecosystems should be encouraged.

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Chapter 7

Plant functional traits respond to environmental gradients and explain trade-offs and synergies between bundles of ecosystem properties and services

M.A. Cebrián-Piqueras

Chapter 7: Plant functional traits respond to environmental gradients and explain trade-offs and synergies between bundles of ecosystem properties and services

Abstract

Recent empirical and theoretical approaches have called for an understanding of the processes underpinning ecosystem service provision. Environmental gradients have shown effects on key plant functional traits that subsequently explain ecosystem properties of several systems. However, little is known concerning how trade-offs and synergies between plant functional traits predict variation of ecosystem properties and services. Furthermore, few studies have used independently-measured final ecosystem services, which represent endpoints in the ecosystem services provision cascade.

Our goals were (1) to understand responses of plant functional traits to environmental gradients and (2) to detect how trade-offs and synergies between plant functional traits explain trade-offs and synergies between multiple ecosystem properties and services.

Forty-four plots were studied in a coastal marsh landscape of the German the North Sea Coast. We used a structural equation model approach to test the initially-hypothesized model.

We found that (1) a trade-off exists between plant traits pertaining to a size axis variation and variation of traits explaining both plant growth (roots and stems) and the leaf economic spectrum; (2) variation of the plant traits' trade-off responded significantly to the land use gradient and nutrient availability, which were both strongly driven by the groundwater gradient; (3) the plant traits' trade-off explained an initial major trade-off between ecosystem properties and final services, indicating ecosystem carbon stocks at one extreme of the axis and both the plant's nature conservation value and forage production at the other extreme. However a secondary trade-off was also found between nature conservation value and forage production indicated by a trade-off between leaf economic spectrum and plant growth in response to the intensity gradient.

Trade-offs and synergies between bundles of ecosystem services such as forage production, plants' nature conservation value and ecosystem carbon stocks were explained by plant strategies that were indicated by plant functional traits in response to the environment.

7.1 Introduction

Ecosystem services are the benefits that humans obtain from ecosystems (MEA, 2005). Human beings deliberately exert strong modifications on the landscape in order to achieve the expected benefits (MEA, 2005). Nevertheless, maximizing the procurement of provisioning services has frequently weakened the ecosystems' capacity to provide other supporting, regulating and cultural services (Bennett & Balvanera 2007; Raudsepp-Hearne *et al.* 2010). These services are, however, frequently not valued, despite their positive effect on human well-being (Santos-Martín *et al.* 2013).

Mechanistic and process-based approaches are emerging as promising tools to understand and predict changes in the provision of multiple services (Bennett *et al.* 2009). Habitat-based approaches based on land cover, however, despite showing trends in global patterns at the spatial level, may fail to accurately predict the provision of services (Eigenbrod *et al.* 2010). Understanding of vertical process-based relationships (i.e. trophic levels relationships) appears to be a prerequisite for a proper understanding of horizontal spatial relationships of ecosystem services (Lavorel *et al.* 2011; Lamarque *et al.* 2014a).

There is growing evidence that certain plant traits, so-called plant functional traits, vary in response to environmental gradients (Lavorel & Garnier 2002; Paula & Pausas 2011). Variation of key leaf functional traits (e.g. specific leaf area (SLA), leaf nitrogen content (LNC) and leaf dry matter content (LDMC)), have been found to indicate a trade-off between a resource acquisition strategy (i.e. high values of SLA, LNC and low values of LDMC) and a resource conservation strategy (i.e. high values of LDMC and low values of SLA and LNC). This trade-off has been called the leaf economic spectrum (Wright *et al.* 2004). Variation of these functional traits was found to respond strongly to biomass removal (Lienin & Kleyer 2011), soil nutrient availability or the altitude of grassland communities (Lavorel & Grigulis 2012). Recently evidence of a coordinated whole plant economic spectrum as an extension of the leaf economic spectrum was described (Freschet *et al.* 2010), showing that variation of root, stem and leaf traits operate in a coordinated fashion in response to environmental changes.

Studies on a global scale have shown an alternative group of plant functional traits that may operate independently from the leaf economic spectrum (Diaz *et al.* 2004). Plant height or biomass dry weights are key plant traits associated with the so-called size axis (Westoby *et al.* 2002). Variation of plant traits explaining the size axis are good candidates to predict plants' abilities to capture light resources (Westoby et al. 2002), plant life history (Moles & Westoby 2006) or reproductive abilities (Grime 1977; Westoby & Wright 2006).

A co-variation between size axis and leaf economic spectrum in response to biomass removal was found in agriculture systems from North West Europe (Lienin & Kleyer 2011). However, when several systems were included, e.g. both managed grasslands and heaths, this relationship was not obvious.

Recently, the responses of several plant functional traits to environmental parameters such as saline groundwater have been studied in temperate saltmarshes (Minden and Kleyer 2011 and 2015) and in freshwater grasslands (Lienin & Kleyer 2011). However studies showing response effects on broader scales in such temperate coastal grasslands, including both freshwater and saltwater systems, have not yet been addressed.
The "biomass ratio" hypothesis (Grime 1998) states that dominant species from a community control the main ecosystem properties; conversely, less abundant species do not exert significant effects on these properties. Following this hypothesis, recent empirical studies have shown evidence of how plant functional traits measured at the community-level respond to environmental gradients. Trade-offs and synergies between these plant functional traits drive, subsequently, trade-offs and synergies between ecosystem properties (Minden & Kleyer 2015). These coordinated and structured relationships between functional traits and ecosystem properties are expected to explain single- (Conti & Díaz 2013) or multiple-services interactions (Lavorel & Grigulis 2012).

Here we asked how variations in plant functional traits explain trade-offs and synergies between ecosystem carbon stocks (regulating service), plants' nature conservation value (cultural service) and forage production (provisioning service) in temperate coastal grasslands. Associations between above-ground biomass and soil organic carbon stocks are being increasingly studied (Conti & Díaz 2013; Doblas Miranda *et al.* 2013). However, the relationship between ecosystem carbon stocks and final services such as cultural and provisioning services, e.g. endangered species and agricultural-associated economic benefits, respectively, has rarely been comprehensively studied (Lamarque *et al.* 2014a). We propose a process-based approach that uses a structural-equation model formalism as an extension of the effect-response framework (Lavorel & Garnier 2002; Minden & Kleyer 2011) introduced by Lavorel & Grigulis (2012) to test our hypothesized initial model (see next section). However, here we incorporated both supporting services (ecosystem properties that support the provision of final services) and values of final services following Wong *et al.* (2015).

Our goals were: (1) to understand trade-offs and synergies between plant functional traits, (2) to understand responses of plant functional traits to abiotic parameters and land use (environmental parameters). Which environmental parameters, i.e. biomass removal, groundwater gradient, soil nutrient availability, explain the trade-offs and associations between groups of functional traits? (3) To detect how associations and trade-offs between plant functional traits explain ecosystem properties and services trade-offs and synergies. How are these trade-offs and synergies generated?

INITIAL MODEL

Fig. 7.2 summarizes the initial model, with the expected response effects and latent variables. We hypothesized several latent variables, which are "non-observed" variables inferred from several indicator variables, and "observed" variables (Grace & Keeley 2006). A positive association of plant-available soil nutrients, such as phosphorus, potassium and nitrogen, was expected (Minden & Kleyer 2011). This latent variable was called soil nutrient availability (hereafter NUTRIENTS). We also hypothesized a positive co-variation of groundwater level and salinity. This latent variable was called water gradient, hereafter WATER (Minden & Kleyer 2011). A positive association between community above-ground native biomass decomposition and the community species-based grassland utilization indicator was expected (White *et al.* 2004; Fortunel *et al.* 2009; Bakker *et al.* 2011). This latent variable was called FORAGE QUALITY (See Fig. 7.2).

(i) PLANT FUNCTIONAL TRAITS ASSOCIATIONS AND TRADE-OFFS

We used plant traits' measurements based on community-weighted means of the species occurring at the plot level (community level). Only plots from which trait plant species explained the majority of the plants' community composition were retained for analysis.

We expected a positive correlation of plant traits' indicators of a soil resources acquisition strategy such as fine root growth, i.e. root nitrogen content (RNC), specific root length (SRL), and a negative correlation with root dry matter content (RDMC). We called this latent variable root growth stimulation (ROOT GROWTH) (Paula & Pausas 2011; Prieto *et al.* 2015).

A positive association between leaf traits such as leaf nitrogen content (LNC) and specific leaf area (SLA), with a negative association to leaf dry matter content (LDMC) was also expected. We called this latent variable leaf economic spectrum (LES) following Wright *et al.* (2004).

A positive co-variation of above-ground biomass dry weight such as stem and leaf with canopy height (CH) and leaf area (LA) was expected following (Lavorel and Grigulis 2012, Diaz *et al.* 2004). We also expected an association of reproductive abilities, indicated by seed number, and the size axis, following a competitors vs. ruderals trade-off in a highly productive environment (Grime 1977). This latent value was called size axis (hereafter SIZE AXIS).

(ii) TRAITS' RESPONSES TO THE ENVIRONMENT

We expected that the variation of environmental parameters such as WATER, NUTRIENTS and biomass removal may have significant effects on community plant strategies indicated by the plant traits' associations and trade-offs (ROOT GROWTH, LES and SIZE AXIS) operating as stressors or plants soil resources (e.g. nutrient availability) (Grime 1998). ROOT GROWTH has been related to the acquisition of soil resources such as nutrients or water, therefore variation of this parameter is expected to affect root growth (Prieto *et al.* 2015). We expect that

high nutrient availability might limit root growth, as has been shown in similar systems under certain humidity conditions (Deegan *et al.* 2012). In addition, plant functional traits indicating root growth might respond positively under disturbance events such as biomass removal (Piñeiro *et al.* 2010; Prieto *et al.* 2015). Alternatively, root growth stimulation might be expected under the influence of stressors such as seawater inundation, in order to improve their anchoring function in environments such as coastal saltmarshes (Nyman *et al.* 2006).

The water gradient was expected to be an exogenous variable, therefore no responses were expected from WATER to the other model variables.

We expected that higher values of plant traits pertaining to the SIZE AXIS (i.e. high community above-ground dry biomass weight and canopy height) may show a negative effect on several plant traits of the leaf economic spectrum (high SLA and LNC values, low LDMC values) and plant traits indicating ROOT GROWTH (High RSL, RNC and low RDMC). This could be for two reasons: (1) the strong indirect effect of biomass removal, and (2) the fact that a highly competitive species, e.g *Phragmites australis,* did show lower values for SLA. In contrast, the opposite effects are expected on temperate salt marshes or alpine grasslands where the variation of abiotic parameters such as salinity/nutrients and altitude may determine a positive association between above-ground biomass and SLA values respectively (Minden and Kleyer 2015, Lavorel and Grigulis 2012). Therefore we expected that reduction of the community above-ground biomass and canopy height (SIZE AXIS), driven by biomass removal and by the water gradient, might stimulate a resource acquisition strategy indicated by ROOT GROWTH (Piñeiro et al. 2010 and Bakker et al. 1993) and higher values of LNC and SLA (LES) (Lienin & Kleyer 2011).

(iii) ESP AND ESS TRADE-OFFS IN RESPONSE TO PLANT FUNCTIONAL TRAITS

A positive effect of above-ground biomass on below-ground carbon stocks (hereafter carbon stocks bundle) is expected (Doblas Miranda *et al.* 2013). It is expected that forage quality may well indicate the economic benefit perceived by farmers (forage sales). Both parameters are associated with forage production, therefore we call this group of parameters forage production bundle. It is also expected that higher plant species' richness positively affects endangered plant species' occurrence (Joyce 2014), therefore we call this group of variables plant nature conservation bundle.

Biotic ecosystem properties associated with the carbon stock bundle (above-ground biomass and soil organic carbon) are expected to respond positively to plant traits explaining the size axis, i.e. higher above-ground dry weight, taller plants, higher leaf area and seed number (Conti and Diaz 2013). Here, plant communities with these traits' values are expected to be associated with plant mono-specific, undisturbed and nutrient-rich plots, i.e. *Phragmites australis* or

Elymus athericus (Esselink *et al.* 2000; Joyce 2014). However, here, contrary to what may be expected in other grassland systems (Lavorel & Grigulis 2012), we expected that higher levels of carbon stocks would be in trade-off with forage quality and forage sales (forage production bundle) due to the commonly-reported removal of ecosystem carbon stocks by agriculture activity (Zhang *et al.* 2007). Also contrary to what may be expected in other systems (Tilman & Downing 1996; Kumar 2011), here we also hypothesized that higher carbon stock values would be in trade-off with the plants' nature conservation value bundle (plant species richness and endangered plants occurrence), due to the expected association of higher above-ground biomass production with mono-specific species vegetation (Esselink *et al.* 2000). We expected therefore that this trade-off (hereafter trade-off 1 (non-disturbed vs. disturbed vegetation)) would be explained by the variation of the size axis (i.e. canopy height, above-ground dry weight).

We expected that components of both the forage production bundle and the plant nature conservation value bundle would respond positively to biomass removal and therefore the variation of the size axis might show an initial association of these two bundles (association 1). However, by contrast, both plant nature conservation and forage production bundles may respond to traits' variation on LES. It is expected that plant traits' variation on the LES may be effective as a marker to differentiate between endangered plant species and forage sales (trade-off 2). We hypothesized that traits' variation on the LES might explain forage sales due to its relationship to foraging intensity (Lavorel & Grigulis 2012; Lamarque *et al.* 2014a); thus negative effects on endangered plant species are expected. High values of SLA and LNC (and low values of LDMC) may be good predictors of highly-intensified fields (Lavorel and Grigulis 2012; Lamarque et al. 2014a) and therefore higher sales associated with forage production.

Both LES and ROOT GROWTH were expected to be associated with higher plant species' richness; conversely SIZE AXIS is expected to be associated with low plant species' richness.

7.2 Methods

The study site was located in a temperate coastal marsh landscape of East Frisia (E 07°02', N 53°27', NW-Germany). It has a mean annual temperature of 9.4 °C, an elevation ranging from -2.5 m to 1.5 m above sea level, and a mean of 823 mm annual rainfall (German meteorogical service, 2010). Forty-four plots were randomly selected from four major grassland ecosystems, such as salt marshes, reeds, wet extensive grasslands and intensively-fertilized mesic grasslands. We collected data on environmental parameters, ecosystem properties and ecosystem services parameters.

Individual plants from which we took plant traits' measurements were collected from: (1) the above mentioned locations (44 plots) and (2) several other regions located in temperate coastal marshes of Germany, the Netherlands and Denmark, which comprised a total of 304 locations (Fig. 7.1) (See below, plant traits' measurements).

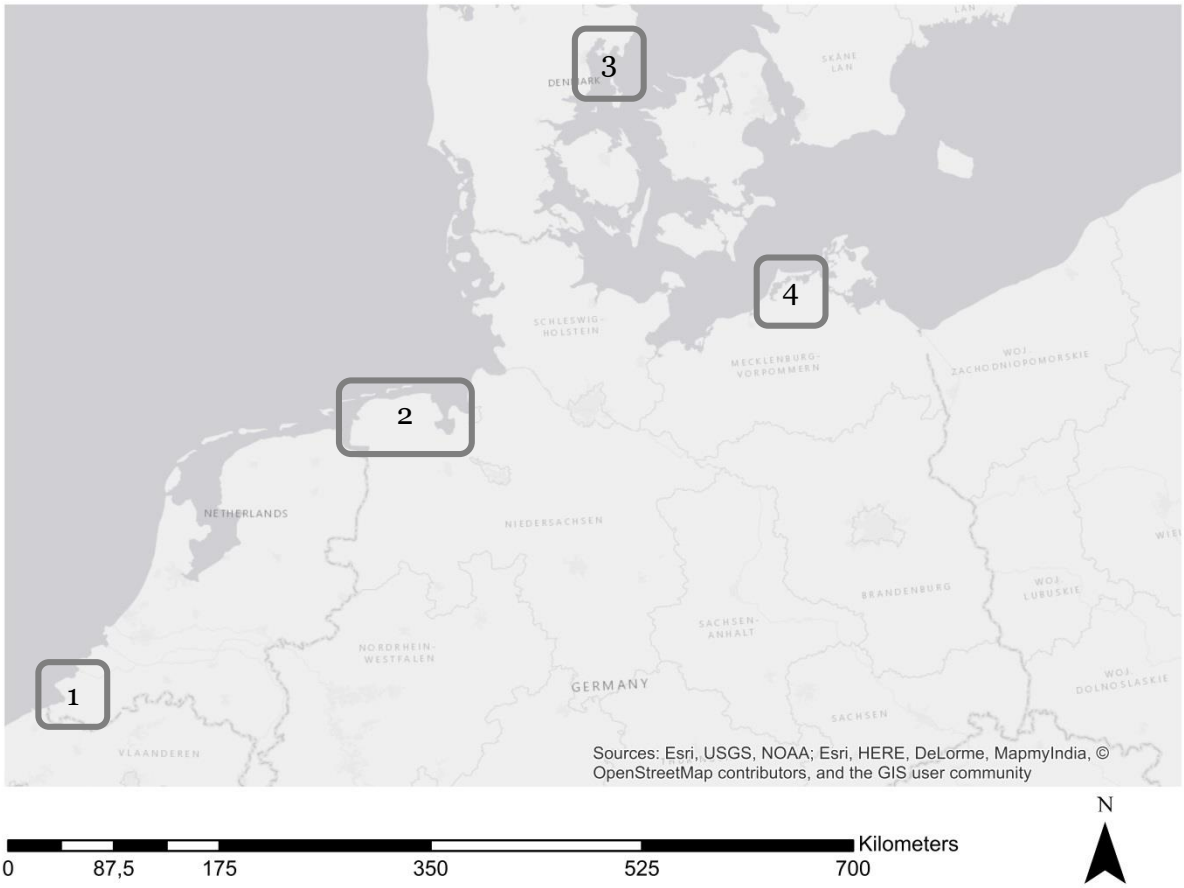


Fig. 7.1: Locations where the trait-plants where collected: 1) Zeeland region in The Netherlands; 2) Coastal lowlands of Norwest Germany including the "National Park Wadden Sea" and several coastal barrier islands of the North Sea coast; 3) "Nationalpark Mols Bjerge" located in Danish Baltic Sea Coast; 4) National Park "Vorpommersche Boddenlandschaft" in the German Baltic Sea coast. Trait-plants where collected from four main vegetation units occurring in all four regions (i.e. saltmarshes, extensively managed wet grasslands, intensively managed grasslands and reeds).

For each soil horizon of each plot down to a depth of 80cm, soil samples were collected in March 2012 with a soil-sample ring of 100 cm^3, and were then air dried and sieved. Bulk density was evaluated from 200 cm^3 of soil (Schlichting *et al.* 1995). From each plot, plant-available potassium (K) and phosphorus (P) were extracted with ammonium lactate-acetic acid at pH 3 (Egnér *et al.* 1960) and analyzed using AAS (atomic absorption spectroscopy) and CFA (continuous flow analyses (Murphy & Riley 1962), respectively. Calcium carbonate ($CaCO_3$) was extracted following Scheibler, in Schlichting et al. 1995.

Biomass removal was quantified using fenced exclosures of 4 m^2, where grazing or mowing was not possible. We collected biomass samples using a subplot size of 0.5 m^2 inside and outside each exclosure at peak vegetation (de Leeuw *et al.* 1990). Samples were sorted according to live and dead biomass, oven dried at 70°C for 72 hours, and then weighed. The percentage of biomass removal was calculated from the difference between both samples. Biomass values given refer to 1m^2.

At each plot, a drainage pipe (10 cm diameter) was vertically installed to a depth of 80 cm in the ground. In these pipes, mean groundwater levels were recorded biweekly during the vegetation period between March and October 2012 (Minden and Kleyer 2011). Additionally, for plots in which variation in water levels was common, i.e. reeds, salt marshes and wet meadows, groundwater was data-logged every half an hour with Sensus Ultra Divers (Reefnet Inc.) between May and October 2012. Along with the fortnightly groundwater recordings, groundwater electrical conductivity was measured with WTW ph/Cond340i/SET, using a Tetracon 325 electrode as a proxy for salinity (See Table 4.1 and Table 5.2 for variable descriptors).

A total number of 2104 plant individuals (92 plant species) were collected during 2006-2014. The trait plants were collected in the above-mentioned 4 regions (Fig.7.1). Morphological traits such as canopy height were directly measured in the field. Other morphological traits (i.e. specific leaf area), chemical traits (i.e. leaf nitrogen content) and biomass traits (i.e. leaf dry weight) were analyzed and calculated in the lab (see methods below). From 1318 individual plants, soil blocks (20x20x40 cm), including roots, were collected in the field to measure root traits. Due to logistic restrictions, only aerial parts were collected from the rest of the individuals (N: 988). Roots and rhizomes were cleaned and separated with tweezers. Plant organs were separated in the lab, oven dried at 70 °C for 72 h and weighed. We scaled-up from species plant traits to the community level following Grime (1998). Mean trait values of every species were weighted by individual species' frequency per plot and subsequently averaged by the total frequency of all the species occurring on each plot. Thus the community weighted mean (CWM) traits values for each plot were obtained (Violle *et al.* 2007). Seed number per plant individuals were measured by direct counting and extrapolation method (Kleyer 2008).

Specific lengths of stems and roots were calculated as the ratio between the length of the organ section and its dry weight. SLA (specific leaf area) was calculated as the ratio of leaf area to leaf dry mass ($mm^2\ mg^{-1}$) following Kleyer (2008). Dry matter content of stems, roots and leaves were measured as the dry mass of the organ section divided by its water-saturated fresh mass ($mg^{-1}g^{-1}$), following Kleyer (2008).

Organ nitrogen and carbon content (stem, root and leaf) was analyzed using CHNS- Analyzer Flash AE (Thermo Electron Corp., DE) following (Grimshaw *et al.* 1989). Nitrogen content was measured after grinding the plant material in a planetary mill for 2 to 10min at 300 to 400 revolutions (pulverisette 7, Fritsch). Each sample was then dried at 105 °C for 4 to 5hr. Two to three milligrams of material were placed in tin tubes (0.1 mg precision balance CP 225 D, Sartorius; tin capsules for solids, Säntis Analytical).

Plant species composition and abundance were recorded by frequency analysis at each plot in the summer of 2012, using a 1x1m grid of 100 cells (each 10x10cm).

Total soil carbon was measured in all horizons for the upper 80 cm of soil. Soil organic carbon was determined for the first 80 cm as the difference between $CaCO_3$ and Total Carbon values. For this study, we used soil organic carbon (hereafter SOC) down to a depth of 30 cm, because of the expected greater influence from current vegetation and land use.

The above-ground standing biomass was collected in August 2012. Biomass samples were oven dried at 70°C for 72 hours. Biomass values correspond to 1 m^2.

Plot species'-based forage values were obtained by community-weighed means of the grassland utilization indicator values of all vascular plant species of a plot (Briemle *et al.* 2002). These values indicate the forage value of plant species on an ordinal scale from 1 to 9, based on grazer preference and the species´ tolerance to mowing, grazing and trampling. The grassland utilization indicator values were retrieved from the BIOLFLOR database (Klotz *et al.* 2002).

Litter mass loss (or decomposition rate) was determined using a litterbag experiment. Fresh plant material was collected in the autumn of 2011 and left to decompose for 12 months in the field on the soil surface in 1 mm mesh litterbags (5 g per litterbag and six replicates per plot). The recovered material was oven dried and weighed. The rate of litter mass loss was calculated relative to its initial mass as the rate of biomass decomposition per day (%/day) (Garnier *et al.* 2007).

The endangered plant species' value was calculated as an index based on the endangerment category of the plant species occurring at plot level. Plant species were assigned an ordinal value based on the German Red List (für Naturschutz 2011) translated into IUCN endangerment categories. Not evaluated (NE) and lesser concern (LC): 0; near threatened (NT): 1; vulnerable (VU): 2; endangered (EN): 3; critically endangered (CR): 4. Subsequently, the final plot value for the endangered plants species' variable was the sum of all species' values from the species that occurred in a plot.

Sales of forage-based products was obtained from interviews with farmers providing information about the gross economic benefit obtained from the land management per hectare and year in € during 2012.

Statistical analysis

The initial model (Fig. 7.2) was tested using a partial least squares structural equation model (PLS-SEM). We used the software Smart-PLS V2.0 (Ringle *et al.* 2005). PLS-SEMs have been extensively used in social science research (Hair *et al.* 2011; Lowry & Gaskin 2014) and recently introduced into ecological studies (Peppler-Lisbach *et al.* 2015). Several variables, i.e. endangered plants and forage sales, showed a high heterogeneity and many zero values (i.e. non-normal distribution). Therefore we decided to use a partial-least squares SEM, instead of a covariance-based SEM, due to the difficulties in normalizing the parameters (Hair *et al.* 2011). A bootstrap analysis of 5000 runs was used to test path significance. All paths showing bootstrapped path values lower than 1.95 (significance level: 5 %) were removed from the model (Fig. 7.2 and Fig. 7.3), because they were not significant (Hair *et al.*, 2011). Following Hair et al. (2011), we used several measures to check model quality: (1) Model internal consistency reliability: Composite reliability should be higher than 0.70 (in exploratory research, 0.60 to 0.70 is considered acceptable); (2) Indicator reliability: Indicator loadings should be higher than 0.70; (3) Convergent validity: The average variance extracted (AVE) should be higher than 0.50.

7.3 Results

Two of the 6 initially-hypothesized latent variables were not significant. Several indicators (observed variables) from ROOT GROWTH and LES latent variables were not significant. After modification of these two latent variables (see modifications below), all the resultant latent variables of the final model (Fig. 7.2) were significant for quality measures (Composite reliability coefficients (>0.7) and average variances extracted (AVE) (>0.5) (see appendix 7.1)). Five paths were excluded because they were not significant ($p>0.05$) (compare figures 7.2 and 7.3). The model showed a moderate explanatory power to predict two final services: forage sales, R^2: 0.57; and endangered plant species, R^2: 0.52.

PLANT FUNCTIONAL TRAITS' ASSOCIATIONS AND TRADE-OFFS

Both RNC and RDMC were not significant and therefore were removed from the initially hypothesized ROOT GROWTH. By contrast, specific root length (SRL) was kept in the model. Additionally, stem specific length (SSL) and stem nitrogen content (SNC) were tested together with SRL, following empirical results of a coordinated plant economic spectrum found in

certain systems (Freschet *et al.* 2010; Reich 2014). However only SRL and SSL were retained in the model. The resulting significant latent variable was named PLANT GROWTH (SRL and SSL co-variation; see latent variables' consistency in Appendix 7.1). The leaf economic spectrum latent variable (LES) was modified, because both LNC and LDMC were not significant; only SLA was kept in the model due to its higher explanatory power. The SIZE AXIS latent variable was significant (Appendix 7.1).

TRAITS' RESPONSES TO ENVIRONMENTAL GRADIENTS

Several expected direct paths from NUTRIENTS to plant traits were removed and only the direct negative effect from NUTRIENTS to PLANT GROWTH was retained. The expected direct effect from WATER to PLANT GROWTH was removed, since on the contrary, a total negative effect was found (-0.31) due to the negative effect of WATER on biomass removal. The direct positive path from biomass removal to LES was not significant; however this effect was confirmed by the total positive effect (0.41). The rest of the expected direct paths were correctly predicted (See Fig. 7.2 and Fig. 7.3). Table 7.2 shows total, indirect and direct effects between variables (regressions' beta path coefficients).

TRADE-OFFS BETWEEN ESP AND ESS IN RESPOND TO PLANT FUNCTIONAL TRAITS' VARIATION

Endangered plants' occurrence and plant species' richness (plant nature conservation value bundle) were moderately well explained by the model (R^2: 0.52 and R^2: 0.55 respectively, add this info in Table 7.2), as were forage quality and forage sales (Forage production bundle), (R^2: 0.36 and R^2: 0.57 respectively, Table 7.2). SOC and AGB were slightly and substantially explained by the model (R^2:0.22 and R^2:0.62, respectively, Table 7.2).

The hypothesized trade-offs and associations between properties and services were confirmed by the indirect and direct effects from plant functional traits' variation. Trade-off 1, trade-off 2 and association 1 were confirmed by the results. However, some slight deviations were found.

The results revealed a third trade-off between plant functional traits. High values of SLA and PLANT GROWTH explained negatively- and positively-endangered plant species, respectively (Fig. 7.3 and Table 7.2). This was called trade-off 3.

A relatively small effect from SIZE AXIS variation on SOC was found (0.12). However, variation of SIZE AXIS showed two significant, indirect opposite paths on SOC (See Fig. 7.3 and Table 7.2). Increments on the SIZE AXIS showed a positive effect on SOC via increasing AGB. In contrast, increments of SIZE AXIS showed an alternative, negative effect on SOC via decreasing values of PLANT GROWTH. Subsequently biomass removal showed opposite, indirect effects on SOC.

PLANT GROWTH showed an indirect, positive effect on endangered plant species (See Table 7.2).

Correlations between species' richness and associations of plant trait

Accordingly to the variables' correlations, PLANT GROWTH and SLA were associated with species-rich plant communities (Correlation coefficient ($CC_{Spearman}$): 0.68, $p<0.001$ and 0.5, $p<0.001$ respectively). SLA was also associated with forage sales ($CC_{Spearman}$: 0.70 $p<0.001$). SIZE AXIS was negatively correlated to plant species richness ($CC_{Spearman}$:-0.58$p<0.001$).

Table 7.1: The table shows the values for community-weighted means of plant traits used in the structural equation model. The values represent mean values for several vegetation units. CWM: Community-weighted. N: 44. See section list of abbreviations.

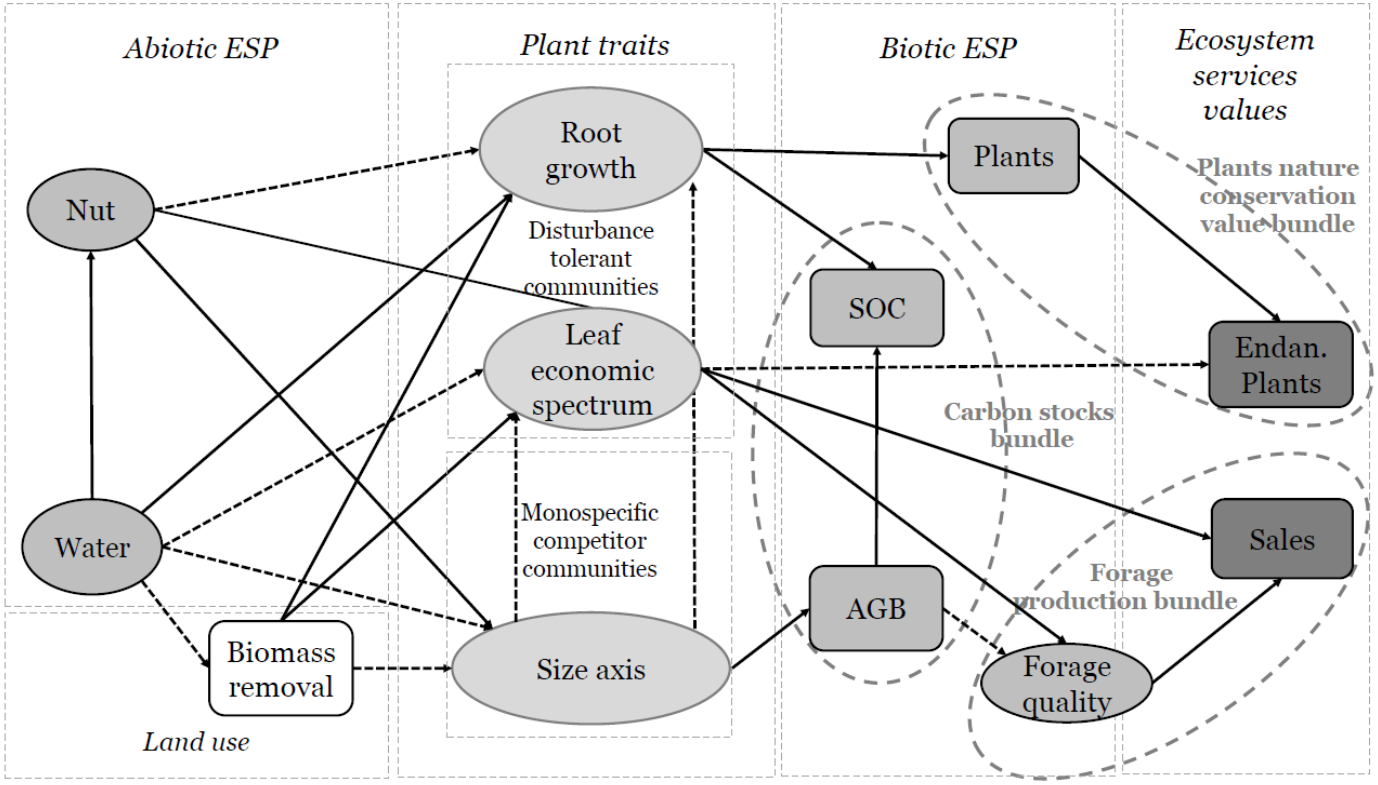
			Saltmarshes (N:16)		Reeds (N:13)		Wet grasslands (N:8)		Intensive grasslands (N:7)	
	Abbre.	Unit	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Plant traits										
Root and stem growth										
CWM Specific root length (SRL)	SRL	mm mg^{-1}	26.67	10.89	17.73	14.36	50.30	12.31	50.34	12.84
CWM Root nitrogen content (RNC)	RNC	%	1.07	0.11	1.19	0.08	1.09	0.10	1.07	0.08
CWM Specific stem length (SSL)	SSL	mm mg^{-1}	3.09	2.17	0.93	0.89	5.10	1.46	2.95	0.60
CWM Stem nitrogen content (SNC)	SNC	%	0.83	0.13	0.62	0.10	0.79	0.11	0.66	0.05
CWM Root dry matter content (RDMC)	RDMC	mg g^{-1}	254.20	55.76	225.42	27.27	202.68	31.61	205.53	22.92
CWM Stem dry matter content (SDMC)	SDMC	mg g^{-1}	345.16	80.79	293.23	30.68	235.49	37.01	239.73	16.10
Leaf economic spectrum	LES									
CWM Specific leaf area (SLA)	SLA	mm^2 mg^{-1}	18.30	4.01	16.72	5.08	26.82	2.36	27.56	1.08
CWM Leaf nitrogen content (LNC)	LNC	%	1.56	0.39	2.08	0.32	1.91	0.27	1.69	0.13
CWM Leaf dry matter content (LDMC)	LDMC	mg g^{-1}	318.83	55.31	396.13	65.12	273.64	33.82	261.27	17.52
Size axis	SA									
CWM Canopy height (CH)	CH	g	34.70	9.46	129.60	26.71	31.69	9.87	42.53	8.67
CWM Stem dry weight (SDW)	SDW	g	1963.27	1318.83	6740.31	2422.59	539.81	421.99	992.68	957.25
CWM Leaf dry weight (LDW)	LDW	g	501.63	252.02	2164.50	753.10	318.09	235.22	499.98	801.17
CWM Leaf area (LA)	LA	mm^2	584.28	356.52	3405.76	1359.60	879.54	222.24	850.61	570.35
CWM Seed number	SN	n	348.13	251.47	4429.56	2213.09	329.20	164.06	253.63	130.81

Table 7.2: Total (TE), indirect (IE) and direct effects (DE) between abiotic ESP, biotic ESP, land uses and values of final ecosystem services. N: 44. The values show significance ($p<0.05$). The effect values represent regression beta path coefficients β from the partial least squares structural equation model results. R^2: R-square values obtained by the predicted variable in the PLS-SEM. See section list of abbreviations

		Abiotic ESP			Land use			Plant traits								
		NUTRIENTS R^2: 0.39			Biomass removal R^2: 0.32			PLANT GROWTH R^2: 0.74			SLA R^2: 0.67			SIZE AXIS R^2: 0.43		
		TE	IE	DE	TE	IE	DE	TE	IE	DE	TE	IE	DE	TE	IE	DE
Abiotic ESP	WATER	0.62		0.62	-0.57		-0.57	-0.31	-0.31		-0.64	-0.01	-0.63	-0.01	0.44	-0.45
Abiotic ESP	NUTRIENTS							-0.19		-0.19						
Land use	Biomass removal							0.82	0.47	0.35	0.41	0.41		-0.80		-0.80
Plant traits	SIZE AXIS							-0.58		-0.58	-0.51		-0.51			

		Biotic ESP												Final ecosystem services					
		SOC R^2:0.22			AGB R^2: 0.57			FORAGE QUALITY R^2: 0.36			Plants R^2:0. 55			Endan. Plants R^2: 0.52			Sales R^2: 0.57		
		TE	IE	DE	TE	IE	DE	TE	IE	DE	TE	IE	DE	TE	IE	DE	TE	IE	DE
Abiotic ESP	WATER	-0.29	-0.29		0.00	0.00		0.00	0.00		-0.23	-0.23		0.23	0.23		-0.37	-0.37	
Abiotic ESP	NUTRIENTS	-0.17	-0.17								-0.14	-0.14		-0.12	-0.12				
Land use	Biomass removal	0.23	0.23		-0.63	-0.63		0.38	0.38		0.61	0.61		0.23	0.23		0.35	0.35	
Plant traits	PLANT GROWTH	0.90		0.90							0.74		0.74	0.62		0.62			
Plant traits	SLA													-0.66		-0.66	0.59		0.59
Plant traits	SIZE AXIS	0.12	0.12		0.79		0.79	-0.47		-0.47	-0.43		-0.43	-0.06		-0.06	-0.44	-0.44	
Biotic ESP	AGB	0.80		0.80				-0.6	-0.6								-0.17	-0.17	
Biotic ESP	FORAGE QUALITY																0.29		0.29
Biotic ESP	Plants													0.83		0.83			

Fig. 7.2: Initial model with hypothesized pathways. Abbreviations: SOC: Soil organic carbon; AGB: Above-ground standing biomass; sales: sales from forage-based products; Nut: Soil plant available nutrients; Endan.; endangered; plants: plant richness. Dashed arrows represent expected negative effects. Solid arrows represent expected positive effects. Latent variables: WATER (positive association of groundwater level and salinity); FORAGE QUALITY (positive association of community-weighted mean species-based grassland utilization indicator and vegetation decomposition rates): SIZE AXIS: positive association of 5 indicator variables (CWM of canopy height, leaf dry weight, stem dry weight, leaf area and seed number); ROOT GROWTH: Positive association of 3 indicator variables (CWM of Specific root length, root nitrogen content and root dry matter content) with negative association to another indicator variable (CWM of root nitrogen content).



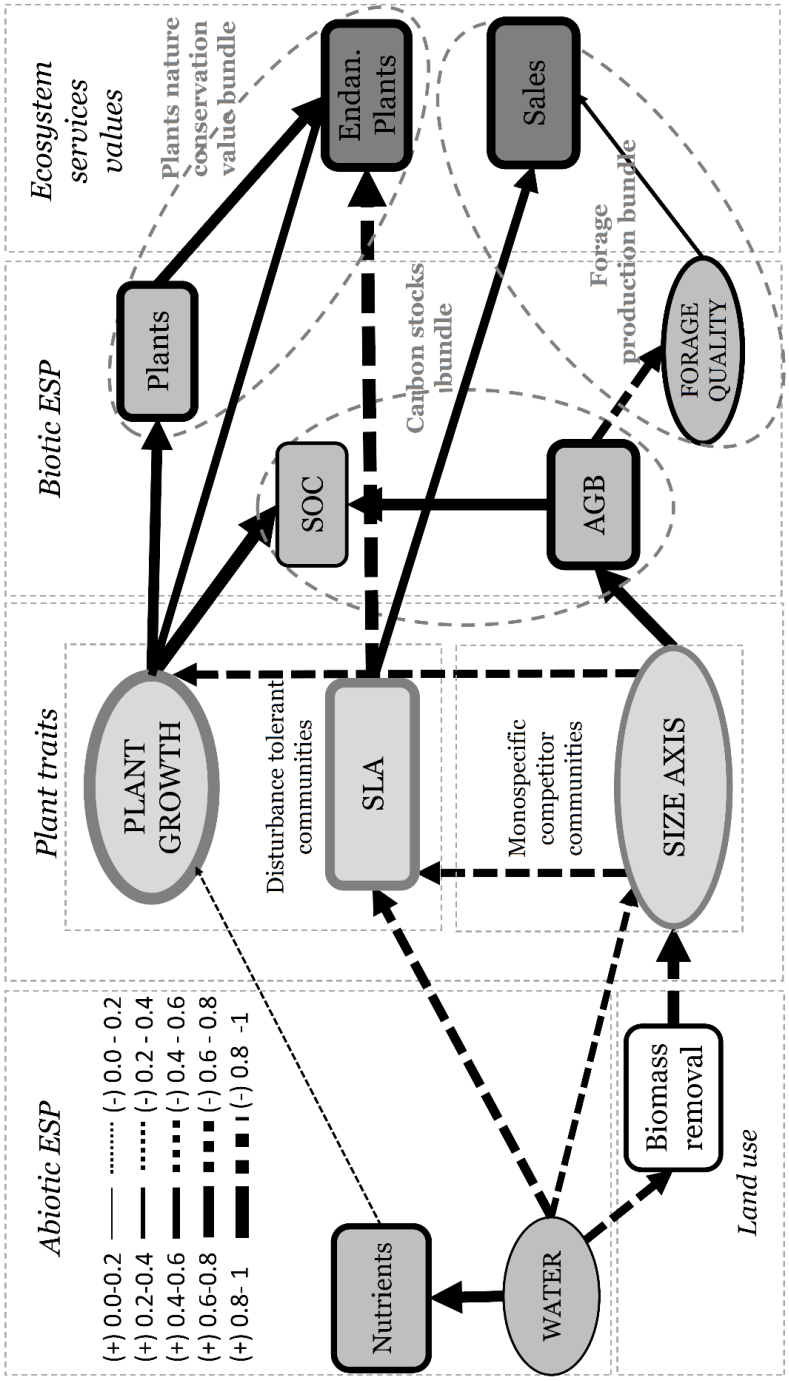


Fig. 7.3: Results for the structural equation model of temperate coastal grasslands (44 plots, East Frisia on the North-Sea coast, Germany). Abbreviations: SOC: Soil organic carbon; AGB: Above-ground standing biomass; sales: sales of forage-based products. Paths arrows represent PLS-SEM regression beta path coefficient values. Dashed arrows represent negative effects. Solid arrows represent positive effects. The explained R^2 for endogenous variables is indicated by the frame thickness (See legend inset). Latent variables: WATER (positive association of groundwater level and salinity); FORAGE QUALITY (positive association of the community-weighted mean (CWM) of species-based forage value and vegetation decomposition rates): SIZE AXIS: positive association of 5 indicator variables (CWM of canopy height, leaf dry weight, stem dry weight, leaf area and seed number); PLANT GROWTH: Positive association of 3 indicator variables (CWM of Specific root length and specific stem length)

7.4 Discussion

COORDINATION OF PLANT FUNCTIONAL TRAITS

(i) Coordination of plant growth, LES and SIZE AXIS

In line with what has been shown in other North-West European grasslands (Lienin & Kleyer 2011), variation of plant traits' values associated to a size axis (canopy height, above-ground dry weight and leaf area) co-varied negatively with traits expressing the LES, such as SLA. Here, we also found a strong association between the size axis and the vegetation reproductive abilities (seed number). In addition, we also found a negative association with high values of plant functional traits associated with a plant-growth and a soil-resources acquisition strategy (i.e. SRL and SSL). Thus taller vegetation showed higher biomass values (size axis), but, in contrast, lower values for several traits explaining an extreme of a plant economic spectrum or leaf economic spectrum, i.e. SRL, SSL and SLA. Empirical results from Díaz *et al.* (2004) suggested the existence of at least these two axes in plant functional traits' variation. However, a general co-variation between these two axes has not been proven, at least on a global scale. On the contrary, an orthogonal relationship between these two axes might be expected (Diaz *et al.* 2004).

Contrary to our results, a positive association between high values of traits belonging to the size axis and high values of traits belonging to a resource-acquisition plant strategy was reported in other systems, such as European alpine grasslands (Lavorel & Grigulis 2012) or Mediterranean woody vegetation (Riva *et al.* 2016). A positive association between high values for traits such as canopy height (size axis) and high values of LNC was also reported in the alpine system. This was explained by the fact that altitude may gradually act as a strong negative filter for plant height and a resource-acquisition strategy (higher LNC values), because of resource limitations, such as water- or nutrient availability. These empirical results showed how vegetation is situated in a co-variation of a strong acquisition vs. conservation gradient and a size axis gradient. However, in our system, as is explained in detail below, neither nutrients nor groundwater gradient played an important direct role as environmental filters when compared to disturbance, due to the fact that both nutrients and water were not scarce. Therefore here, the variation in the plant functional traits was mainly related to a major axis associated with a disturbance gradient.

Our results showed an initial major co-variation between leaf, root and stem traits, suggesting a potential plant economic-spectrum coordination as shown for sub-arctic or semi-arid environments in which a limitation of resources occurred along an environmental gradient (Freschet *et al.* 2010; Riva *et al.* 2016).

(ii) Fine roots and fine stems growth (plant growth)

High values of RDMC or SDMC are often situated at one extreme of the trade-off between resource acquisition and resource conservation vegetation strategies (Riva *et al.* 2016). Higher values of these traits indicate a vegetation with higher lignin content for roots and stems, and a development of a resource conservation strategy in response to plant resources limitation (Lopez-Iglesias *et al.* 2014). At the other extreme of the gradient, higher values of SRL, SSL, RNC and SNC might indicate the development of a resource-acquisition strategy under certain environmental conditions (Paula & Pausas 2011). However, here, neither RDMC, SDMC nor RNC and SNC were in significant trade-off with SRL or SSL. This result might indicate that plants here did not need to reinforce a resource conservation strategy, probably due to the fact that groundwater and soil nutrients were not scarce enough (Lavorel & Grigulis 2012).

(iii) Leaf economics

Contrary to expectations, several variables explaining the leaf economic spectrum, i.e. leaf nitrogen content (LNC) and leaf dry matter content (LDMC) (Wright *et al.* 2004; Gardarin *et al.* 2014), were not significant and therefore did not explain the expected latent variable LES (Leaf economic spectrum). This might be related to the fact that the system was not nutrient limited (See Table 7.2), contrary to what has been shown in European alpine grasslands (Lavorel & Grigulis 2012) or Mediterranean forests (Riva *et al.* 2016). Therefore these plant traits did not express a significant variation, because there was no need for a resource conservation strategy according to C-S-R Grime´s scheme (1998) for major plant strategies. However SLA was kept in the model as a single variable, because it showed a relative high explanatory power, probably due to the fact that: (1) plants from salt marshes showed a low SLA due to the occurrence of plants with succulent leaves and (2) plants from intensive grassland showed high values for the same parameter (Table 7.1). In other studies, SLA has been shown to have a higher explanatory power than LDMC (Hodgson *et al.* 2011).

ENVIRONMENT-TRAITS' EFFECTS

We did not find a significant positive effect of soil nutrient availability on plant traits, probably due to the strong effect of biomass removal in the plant traits' responses (Lienin and Kleyer 2011) and probably also due to the fact that nutrient availability was relatively high in the system. Despite the expectation of positive effects of soil nutrient availability on the traits such as SLA and above-ground dry weights (Garnier *et al.* 2007), here, this effect was masked by the effect of environmental parameters such as the water gradient (positive co-variation of salinity and groundwater) and disturbances such as biomass removal. In contrast, here increasing values of soil nutrients showed a negative effect on plant growth, i.e., both specific

root length and specific stem length. Contrary to expectations from a plant economic spectrum perspective (Freschet *et al.* 2010), high nutrient availability may limit a resource-acquisition strategy in highly productive systems. This effect has been found in empirical studies in North American temperate coastal grasslands, where increasing values of soil eutrophication have been shown to significantly modify the root: shoot ratio, with subsequent negative effect on sediment retention (Turner *et al.* 2009; Deegan *et al.* 2012).

Contrarily to expectations (Nyman *et al.* 2006), the water gradient showed neither a significant direct positive effect nor a total positive effect on the plant growth strategy. A total insignificant effect of the water gradient on the plant growth strategy was probably due to two confirmed but opposite mechanisms of plant growth stimulation (Fig. 2): (1) positive effect by the water gradient following Nyman *et al.* (2006) and Bakker *et al.* (1993); and (2) indirectly negative effect by water gradient via segregation of biomass removal landwards. The strong effect of biomass removal on plant traits' variation probably masked the effects of the water gradient.

TRADE-OFFS BETWEEN ESP AND ESS IN RESPONSE TO PLANT FUNCTIONAL TRAITS' VARIATION

(i) Decoupling plant growth and leaf economic spectrum (Trade-offs 2 and 3)

Higher values of plant traits indicating plant growth, such as SRL and SSL, might be associated with a resource acquisition strategy (Paula & Pausas 2011) or a vegetative strategy initiated by competition for survival (Moles & Westoby 2006). Contrary to expectations on a whole-plant economic spectrum (Freschet *et al.* 2010), here a plant-growth strategy was decoupled from components of the LES (SLA). On the one hand, SLA negatively explained endangered plant species' occurrence and positively explained forage sales (Trade-off 2); on the other hand, high values of plant growth positively explained endangered plant species' occurrence (Trade-off 3). These findings indicated two different plant strategies whose operation depended on land use variation. (1) Plant growth strategy (fine roots and fine stems growth) was triggered by biomass removal under extensive management on grasslands, generating a higher plant richness and a subsequent competition for resources and survival (i.e. light and soil nutrient uptake) (Freschet *et al.* 2010; Prieto *et al.* 2015). By contrast, (2) higher SLA values, despite being also triggered by biomass removal, were here associated with a higher intensification, which might indicate a lower competition for soil resources (Lavorel & Grigulis 2012; Kleyer & Minden 2015). This may imply that plants do not allocate resources to roots and stems and they are therefore available to be allocated to leaves (Minden & Kleyer 2014).

(ii) Traits explaining SOC in respond to land-use variation (Trade-off 4).

A total negative effect of size axis reduction on soil organic carbon due to biomass removal was not obvious in this system. Two opposite mechanisms explained indirect effects of biomass removal on SOC. On the one hand, an overall negative effect was found due to the fact that removal of above-ground biomass might reduce both litter accumulation and an overall below-ground productivity (Conti & Díaz 2013; Doblas Miranda *et al.* 2013). Our results showed that higher values of above-ground biomass had a positive effect on soil organic carbon. However there was a secondary and opposite path on soil organic carbon accumulation associated with fine root growth. We found a positive effect of plant growth (RSL and SSL) on soil organic carbon, due to the fact that biomass removal may trigger below-ground productivity of fine roots and subsequent soil organic carbon accumulation (Yu & Chmura 2009; Piñeiro *et al.* 2010). We suggest that a potential trade-off between these two opposite paths masks the total indirect effect of biomass removal on soil organic carbon, so that this is not visible in the resulting model (trade-off 4).

(iii) Forage sales responses to SLA and forage quality

Contrarily to SLA, community-based forage quality did show a slightly positive effect on forage sales. This fact highlighted the strong explanatory power of a single trait, such as SLA, which was in line with that found by Gardarin *et al.* (2014). SLA was a better predictor of forage sales than forage quality, due to the fact that salt marsh vegetation does show relatively high values of forage quality, but relatively low values of SLA.

7.5 Conclusions

The model showed significant interactions between environmental gradients, plant traits, ecosystem properties and services that were explained by a structural equation model**.** An initial first trade-off between non-disturbed and disturbed vegetation was shown to be responsible for a major trade-off between above-ground carbon stocks and both plant nature conservation value and forage production (endangered plants and plant richness; and forage quality and forage sales respectively). This trade-off was explained by plant traits associated with a variation of the size axis in co-variation with traits pertaining to the plant economic spectrum. However, a secondary trade-off related to detailed variation between extensive vs. intensive management, explained a trade-off between nature conservation value and forage production (endangered plant species and forage sales, respectively). This ecosystem services trade-off was explained by a trade-off between a plant strategy associated with plant growth (both roots and stems) and a plant strategy associated with leaf resources acquisition (higher SLA values). This result suggests the existence of vegetation allometric patterns that operate independently between several plant parts in response to environmental gradients, as has been

suggested in other systems (Fortunel *et al.* 2012). These results are contrary to the generalization of a co-variation of leaf, stem and root traits indicated on a plant economic spectrum, which is expected to function under other environmental conditions (Freschet *et al.* 2010).

Contrary to the initial expectations, variation of land use intensity did not significantly affect the soil organic carbon stocks due to two opposite, alternative mechanisms explained by variation of the size axis and plant growth.

Land use intensity, quantified here as biomass removal, was found to be the main direct environmental driver of plant trait responsiveness on these temperate coastal grasslands, which, on the other hand, was strongly affected by the co-variation of groundwater and salinity levels. Contrary to the plant- or leaf economics, our results suggest the trade-offs and synergies between plant functional traits found here are not explained by a resource acquisition vs. resource conservation trade-off. Here the variation of plant functional traits in respond to disturbance, may express a trade-off on a gradient of well-established competitors' species (persistence) vs. competition for establishment (growth) (Grime 1998; Minden & Kleyer 2014). This gradient seems not to respond to soil-nutrient availability, in contrast to biomass removal. Abundance of soil-available nutrients might, however, explain how later stages of vegetation succession may be associated with competitor mono-specific vegetation, such as *Phragmites australis* in fresh and brackish water and *Elymus athericus* in high-salt marsh vegetation.

These results indicate that plant community assemblies and associated specific key plant traits can well explain the variation of determinant environmental parameters and their effects on ecosystem properties and services. Empirical approaches, as used here, may help to optimize management strategies under the threats of environmental change and strong land-use pressure.

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Part III

Chapter 8

A synthesis

Miguel Ángel Cebrián-Piqueras

Chapter 8: A synthesis

8.1 Ecosystem services provision in relation to stakeholders' perceptions, environmental drivers and plant functional traits

8.1.1 Forage production, provisioning service

a) Soil fertility, supporting service

Soil fertility corresponds to the ability of soils to support vegetation growth by the provision of nutrients, water, cycling of organic matter and physical properties of soil (Turbé *et al.* 2010; Lamarque *et al.* 2011). Soil fertility represents a valuable supporting service for agriculture, therefore deep and fertile soils have been traditionally appropriated by farming activity (Desbiez *et al.* 2004). Distinctive properties of fertile soils comprise a good balance of: (i) available soil nutrients (ii) soil organic matter (soil organic carbon or humus), (iii) cation-exchange capacity (iv), soil texture and (v) soil biota. However soil fertility it is usually ameliorated in agro-ecosystems by several management techniques (Laidlaw & Frame 2013). Productivity of grassland systems is highly related to soil fertility (Humphreys 2007).

The two stakeholder groups that participated in this thesis work showed a high preference for this ecosystem service (**chapter 6**). However, both groups showed a different perception of it, which was associated with different properties of the ecosystem in each case. In general, both groups associated soil fertility with different management practices. On the one hand the farmers associated this property with factors related to the physical properties of soil, nutrient addition of anthropogenic origin or to the supply of nutrients in salt marshes due to sea water inundation. Instead conservationists associated this service with the ecosystem conservation value, i.e. lesser degree of intensity and higher groundwater table, and they did not associate this service with the addition of inorganic fertilizers or forage production. For farmers, soil fertility, forage production and regional belonging was part of the same thing. Farmers showed an ecosystem-based view of the landscape associated with its agricultural capacity.

The results of **chapter 4** did not show a significant variation of soil humus content between vegetation units, therefore this property appears to be, a priori, relatively homogeneous throughout this system. Despite the general high soil nutrient availability in the system, a relatively high variation of soil nutrients availability was observed between vegetation units. Nutrients availability in soil was relatively high in the salt marshes, although the cation exchange capacity was relatively low.

A subsequent evaluation of the ecosystem processes in **chapters 5 and 7** allowed us to observe which mechanisms were operating behind the variation of parameters associated with

soil fertility, such as soil organic carbon and availability of soil nutrients. Results of **chapter 5** show how several alternative paths produce a positive effect on the soil organic carbon levels. According to these results, it is observed how both an increase in soil nutrients and an increase in aboveground biomass are associated with an increase of soil organic carbon stocks.

On the other hand, it is interesting to observe how the removal of biomass, through grazing and mowing activities, produces an alternative positive effect on the content of soil organic carbon as it is pointed out in other empirical studies (Yu and Chmura, 2009, Piñeiro *et al.*, 2010). It is very likely that due to the action of these two opposite paths a variation in the content of soil organic carbon between the main vegetation units is not observed. As discussed later in the section on carbon stocks, above-ground biomass removal might be responsible for the stimulation of fine roots' growth (**chapter 7**; Path B) (Piñeiro *et al.*, 2010).

On the other hand, results from **chapter 7** suggest that increasing plant-available soil nutrients might exert a negative effect on the growth of fine roots, with subsequent negative effects on soil organic carbon stocks. The apparent contradiction between the effects of drivers such as soil nutrients, biomass production, and biomass removal on the soil carbon stocks might indicate different origins of soil organic carbon accumulation. This highlights the need to study which properties and quality of the soil organic carbon stocks are associated with which origins.

The results of **chapter 5** ("Path A") showed how the natural location of the salt marshes along the coastline allows an external supply of nutrients, which remarkably increases soil fertility as other studies highlight for other regions (Turner *et al.* 2009; Deegan *et al.* 2012). By contrast, it can be seen that the cation exchange capacity has no significant effect on the overall fertility of the system.

This understanding of the system does not seem unnoticed by the group of farmers (**chapter 6**) who positively evaluated the physical capacity of the ecosystem and its location to provide and maintain soil nutrients availability, as it is pointed out by other studies on ethno-pedology (Desbiez *et al.* 2004). On the other hand, it is interesting to see how farmers have an accurate knowledge to detect which areas are less capable to provide nutrients. According to **chapter 5**, it is seen how extensive grassland areas have a relatively lower cation exchange capacity and a relatively lower level of plant available potassium in soil.

According to the study cases carried out, it can be seen which inherent factors of the system and which external factors lead to increased soil fertility. Thanks to structural equation modelling, processes that provide increased availability of nutrients are revealed. On the other hand it can be seen how management practices conducted in extensive pastures maintain relatively high levels of soil organic carbon (equivalent to soil humus content).

b) Forage quality, supporting service

Several ecosystem properties are associated with vegetation forage quality: plant nutrient content, protein content (crude protein content), palatability, digestibility, levels of cellulose and lignin (neutral detergent fiber (NDF) and lack of anti-quality components (toxic alkaloids, tannins.) (Laidlaw & Frame 2013). On the other hand, in line with the results of Cornwell *et al.* (2008) and Fortunel *et al.* (2009) and according to the results obtained in the three case studies of this thesis (**chapter 5, 6 and 7**), a strong association between forage quality and biomass decomposition rates is shown. Thus the role of the ratios of decomposition of biomass as a good indicator of forage quality is revealed (Pavlů *et al.* 2006; Fortunel *et al.* 2009).

According to the results of **chapter 6**, the group of farmers showed a high degree of association between their perception of the landscape capability of forage production and the measured vegetation forage quality. This result, together with the positive association between this perception and the measured soil nutrient availability, show how farmers have a comprehensive knowledge of the ecosystem in relation to its forage production potential. Other studies have demonstrated the high capacity of farmers to properly detect the agronomic value of agricultural fields at landscape level (Desbiez *et al.* 2004).

In **chapter 4** it is shown how intensively grazed grasslands have the highest forage quality values. Although salt marshes show relatively lower values than intensively-grazed fields landwards of the sea wall, these are not significantly lower. This result is in line with the perception of regional farmers of the ability of the landscape to provide vegetation with good forage quality (**chapter 6**).

In line with farmers' expectations (**chapter 6**), we observed how the forage quality value was positively affected by environmental parameters such as soil nutrients availability levels, inorganic fertilization or cation exchange capacity (**chapter 5**). It is also shown how disturbance events such as biomass removal positively affect forage quality (**chapter 5**). These results highlight the importance of properties inherent in the soil and nutrient availability for improved forage quality as well as the importance of management for improved quality. In contrast, the results show how increments of biomass production have a negative effect on forage quality. **Chapter 7** shows how agricultural activities such as grazing and mowing, which remove above-ground biomass, decrease the occurrence of competitive dominant species which have lower forage quality. Contrarily this process increases the occurrence of better adapted species to disturbance processes, which have better forage quality. The results obtained here (**chapter 5 and 7**) show how this process occurs regardless of the chemical properties of the groundwater, i.e. salt, brackish or fresh water.

c) The economic value of forage production, a direct-use value

At present there is a clear segregation of land uses in the landscape studied here (**chapters 4 and 5**). Most of the areas located at the seaward side of the dyke are dedicated to nature conservation and there are no significant economic benefits derived from agricultural activity. Activities such as grazing in saltmarshes are rare due to the strong regulations for nature protection (Esselink *et al.* 2009). However, farmers interviewed in our study show a high preference for both intensively grazed pastures located landwards and saltmarshes located seawards and both areas are highly associated to forage production (**chapter 6**). According to their perception, both areas have a high agronomic value, which should not be at odds with nature protection. The results of **chapter 4** clearly show how properties such as availability of soil nutrients or forage quality reach relative high levels in saltmarshes. Therefore, when farmers were asked about the forage production service, their perception was related more to the ecosystem capacity to provide forage than to the actual provision of economic benefit associated with forage production.

On the other hand, according to our empirical results shown in **chapter 4**, extensive wet pastures show a relatively lower level of forage sales compared to intensively used pastures. However, probably due to the small number of samples of both vegetation units, the results were not significant. Nevertheless, due to the higher energetic demand and associated production costs of intensive grasslands, here wet extensive grasslands might perform indeed a relatively high net benefit. However, farmers showed low preference for those areas that are directly associated with nature conservation goals. Despite this fact, farmers highly valued the ecosystem service nature conservation value. This apparent initial contradiction might indicate a prior, positive attitude to nature conservation. However they might not perceive that there is enough reward in adopting agri-environmental measures in agricultural fields, as has been commonly reported (Morris & Potter 1995; Herzon & Mikk 2007; Dobbs & Pretty 2008).

Chapter 4 shows how the areas that have better physical soil properties such as cation exchange capacity of the soil or adequate levels of clay, and therefore more suitable for agriculture have lower groundwater levels.

The results from the structural equation models of **chapter 5** reveal how a reduction in groundwater levels here is associated with higher intensity levels, i.e. characterized by high levels of inorganic fertilization, as well as high levels of livestock units per hectare, and therefore greater economic benefits. In contrast, **chapter 5** shows how abiotic properties, such as availability of soil nutrients and forage quality, are not the major drivers positively affecting the sales of forage-based products. This contradiction was identified in the farmers' perception about the landscape' capability to provide forage production.

On the other hand, the results on **chapter 4** show how some of the areas located on the landward side of the dike showing less optimal physical soil properties for agriculture are not intensively managed. This indicates a secondary segregation pattern occurring landwards the dyke that locates initially less suitable areas for other uses such as extensive production (wet extensive grasslands) or nature conservation (reeds). This pattern has been found in most European landscapes following the high land use intensification of the 2nd half of the twenty century (Prishchepov *et al.* 2013). However the results of **chapter 4** do not show significant differences for above-ground biomass productivity between extensive and intensive fields.

The results of **chapter 7** show a positive association between the variation of sales of forage-based products and specific leaf area (vegetation community-weighted-mean, see **chapter 7**). On the other hand, despite the existence of a positive association be-tween forage quality and forage sales (**chapter 7**), specific leaf area is found as a better predictor of forage sales than the general vegetation forage quality value. Here this is explained by the fact that areas with relatively high vegetation forage quality such as saltmarshes do not show high values for specific leaf area. Conversely, the results of **chapter 7** show how the vegetation with taller plants and more biomass is negatively associated with the sales of forage-based production.

A first spatial segregation in the landscape determines which areas are intended for agricultural production and which for high nature protection. This is explained by the segregation of the salt water system and freshwater system via seawall. A second segregation caused by the physical soil properties determines where greater intensity occurs on the landward side of the seawall (freshwater system). Therefore this secondary segregation determines where other secondary uses such as extensively used pastures or nature protection take place. Additionally, agricultural intensity of the freshwater system is subsequently associated with the reduction of groundwater levels, increased fertilization and lower vegetation height, but also with high values of community measured specific leaf area. All these abiotic and biotic properties and land uses determine where the highest gross economic benefits are currently obtained. According to the results of **chapter 6**, the group of conservationists relates grassland forage production with the above mentioned ecosystem properties and land uses. In contrast, farmers associate agricultural production with the ecosystem capacity rather than with the current production status quo.

8.1.2 The nature conservation value, a cultural service

As explained in **chapter 2,** species richness and occurrence of endangered species not only work as structural components of the ecosystems and their functions but also as cultural ecosystem services (Haines-Young & Potschin 2010; Mace *et al.* 2012). The cultural value of

biodiversity is associated with various types of the so-called "non-use values" such as the biodiversity existence value, the bequest value or the philanthropic value (altruistic value) (Hein *et al.* 2006; Potschin & Haines-Young 2013). This way to assess the biodiversity value has traditionally been the basis of the nature conservation perspective (Ingram *et al.* 2012).

Our study shows how the group of farmers associates a higher nature conservation value with a lower agronomic value of the ecosystem and with the extensive use of the landscape (Fig. 6.1 d; **chapter 6**). The group of farmers shows a high preference for nature conservation value as an ecosystem service. However, this group perceives both a negative impact associated with a high nature protection on biodiversity conservation goals, and the negative effects that high intensification produces on nature conservation values (Fig. 6.1 d; **chapter 6**).

Due to logistical reasons, just the richness of the plants and breeding birds' species, as well as the occurrence of endangered species of these groups have been considered in present thesis. The results based on the comparison of the main vegetation units of **chapter 4** suggest that the vegetation units where biomass removal is applied, due to activities such as grazing or mowing, show higher plant species richness, as it is shown by empirical results in similar systems (Esselink *et al.* 2000; Joyce 2014). However, the effects of management on endangered plant species are not visible in **chapter 4,** although they are shown afterwards in the analysis of **chapters 5 and 7** by the use of structural equation modeling.

In contrast, results of **chapter 4** suggest that fields where agricultural management takes place may have lower breeding birds' richness, although the occurrence of endangered species of breeding birds, frequently associated with extensive wet grasslands, seems to benefit. These previous results initially suggest that increased biomass can determine a greater breeding bird' species richness, as studies conducted by Haddad *et al.* (2001) and Bonn *et al.* (2004) suggest. The results based on the understanding of ecosystem processes at plot and patch level of **chapter 5** confirm some of our expectations. These results show how biomass removal has a positive effect on the plant species richness and the occurrence of threatened species of plants and breeding birds, as empirical results show on both freshwater and saltwater pastures (Joyce & Wade 1998; Bakker 2014). On the other hand, it can be seen that a high degree of nature protection has a negative effect on the services indicated by these values (**chapter 5**) because this high protection is often associated with a lack of disturbance of the ecosystem, e.g. due to nature protection regulations of the Wadden Sea National Park (Esselink *et al.* 2009; Bakker 2014).

Factors such as the groundwater gradient show a positive effect on the occurrence of endangered plant species, since at one extreme of this gradient tolerant species towards salinity and towards high levels of groundwater are found. Some of these plants are included in the regional and country red lists. However, the study of **chapter 5** shows how this effect is reinforced if extensive management with associated biomass removal is included. Conversely, increasing values of the groundwater gradient showed a negative overall effect on endangered breeding birds' species. This may be the case because in general the groundwater level is accompanied by a high degree of nature protection and a lack of management. This causes a vegetation growth and an excessively increased groundwater level being both not optimal conditions for endangered breeding birds' species frequently found on extensive wet pastures (Gregory *et al.* 2005).

On the other hand, as it should be expected (Vickery *et al.* 2001; Newton 2004), it can be shown here how a high intensification, i.e. inorganic fertilization and soil drainage, generates negative effects on the occurrence of endangered breeding birds. However, due to the strong spatial segregation of land uses, the structural equation model of **chapter 5** does not show a negative effect of a high intensification in the occurrence of endangered plant species. This might be because extensive freshwater pastures have been strongly altered in the study area as found in similar nearby systems (Krause *et al.* 2011), and therefore a high occurrence of endangered plant species at intermediate intensities and groundwater levels cannot be found.

Correspondingly, no negative effect of the biomass removal on species richness of breeding birds can be observed. Neither variables such the groundwater gradient nor the degree of nature protection show a significant effect on the breeding birds' species richness. As it is shown in **chapter 5**, this result might be due to the high availability of soil nutrients in the system (Haddad *et al.* 2001).

Higher values of above-ground biomass are here associated with plant communities of lower plant species richness but with relatively high average plant height and large plant leaves. These species-poor communities, which contain no endangered species, are composed of competitor species and are related to a lack of agricultural management, abandonment of agricultural activity or a high degree of nature protection as shown in **chapters 5 and 7.** These results are in line with previous empirical studies (Esselink *et al.* 2000; Joyce 2014). On the other hand the species-rich communities show here a positive association with increased stimulation of fine root growth. The results of **chapters 5 and 7** show how these plant communities have a positive response to the biomass removal.

According to the joint assessment of the results of **chapter 4** and **chapter 7,** it is possible that a certain lack of nutrients of extensive areas can have a positive effect on the stimulation of fine roots growth. As some empirical studies show for freshwater and salty extensive grasslands, this stimulation is intended to a more efficient absorption of nutrients (Yu & Chmura 2009; Deegan *et al.* 2012). Furthermore, it is likely that soil nutrients increments have a negative effect on this stimulation, as the results of Degaan *et al.* (2012) show. However an increase of extensive disturbance, could improve this property, which has been shown, on the other hand, to improve the ability of vegetation to retain the sediment in coastal salt marshes (Turner *et al.*, 2009). Moreover, it is very likely that here a greater interspecific competition can occur in situations where lower levels of soil nutrients occur, as the results of empirical studies in extensive pastures suggest (Joyce, 2014). This process, associated here with higher plant species richness, may determine a higher ecosystem functionality (Díaz *et al.* 2007; Ceulemans *et al.* 2013).

Farmers positively associate extensive wet grasslands with nature conservation value (**chapter 6**). Yet they are also aware that these areas are usually located on places with environmental conditions suboptimal for farming such as more nutrient-poor soils that less suitable for intensive agriculture. However, although the group of farmers has a high opinion of the ecosystem nature conservation value as ecosystem service, extensive wet grasslands were assessed as lower despite being considered very suitable for the provision of this service. On the other hand, this perception responds positively to greater species richness. However, farmers show a certain degree of disagreement as to the way in which saltmarshes are managed because, according to their perception (see the farmers' comments below), a lack of management produces a decrease in biodiversity.

[F3: *"Nature protected grassland areas also needs cutting and maintenance"*]

[F2: *"Nature conservation and agriculture – these are not two independent management approaches, these two land uses have to be combined. Nature protection needs to be integrated in farming activities. What we need are flexible and intelligent nature protection measures"*

[F3: *"Agriculture is nature protection, as long as it is sustainable. Different land use interests have to be balanced and linked. Everyone needs to make compromises"*]

[F3*"It is always the question how you define "nature areas". Precisely, all areas are nature. If they are not in use, there would be monocultures. And is that what the nature conservation sector wants?*]

The empirical results of **chapter 5 and 7** show some degree of compliance with this perception. According to these empirical results, it is shown here how extensive management

can benefit the occurrence of plant species richness, endangered plant species and endangered breeding birds. In addition, according to the results of **chapter 5,** it cannot be shown here that biomass removal has a significant negative or positive effect on overall breeding bird richness.

Chapter 6 shows how the perception of conservationists about the nature conservation value seems to be related to factors that explain the occurrence of endangered breeding birds such as the maintainance of relatively high groundwater levels accompanied by some degree of disturbance. Endangered breeding birds have been successfully used as flagship for many nature conservation projects worldwide (Clucas *et al.* 2008). However, here (**chapter 5 and 6**) most of the areas that are related to the occurrence of endangered breeding bird species, which need a landscape land use aggregation pattern (both extensive production and nature conservation goals), are still not enough nature-protected. Conversion from extensive to intensive management has been a common trend during last decades in areas with high agronomic value such as the middle Europe plain. This trend has occurred due to the general low attention paid to agro-ecosystems from a nature protection perspective (Krause *et al.* 2011). Due to this fact most of the extensive pastures have been led into a vulnerable situation under the intensification threat (Rook *et al.* 2004).
On the other hand, despite certain degree of disturbance may benefit endangered plant species occurrence (**chapters 5 and 7**), associated agro-environmental measures are rarely explicitly included as nature management tools in coastal grasslands (Nolte *et al.* 2015).

8.1.3 Ecosystem carbon stocks, a regulating service

Carbon sequestration by the ecosystems is a complex process in which a multitude of mechanisms that act at spatial and temporal scale are involved (Jobbágy & Jackson 2000; Mitsch *et al.* 2013). Changes in land use, with the consequent reduction of biomass, as well as variations in environmental parameters, produce large variations in the ecosystems' organic carbon stocks at regional and global level (Van Wesemael *et al.* 2010).

The group of conservationists who participated in this study showed a comprehensive knowledge of carbon sequestration ecosystem service (**chapter 6**). Their collective knowledge appeared to be associated with the maintenance of natural processes in the landscape, i.e. conservation of higher levels of biomass, but also with the production of peat (higher values of soil organic carbon), often associated with maintaining waterlogged soils. According to the results obtained in the three study cases (**chapters 5, 6 and 7**), the knowledge of regional conservationists was in agreement with the values obtained for overall ecosystem carbon stocks, but did not especially conform to the variation of below-ground carbon stocks.

Correspondingly, farmers showed an understanding of this process which was related to the biomass productivity and inorganic fertilization (Khan *et al.* 2007). However, this perception was not shown to be associated with the peat accumulation processes, i.e. soil organic carbon accumulation, which is caused by a relatively high level of groundwater and accumulation of dead biomass (Bridgham *et al.* 2006).

As expected, the results of **chapter 4** suggest that above-ground carbon stocks are higher in plots where agricultural management does not occur, i.e. reeds or non-used saltmarshes (Jobbágy & Jackson 2000). According to **chapters 5 and 7**, foraging and mowing produce a noticeable decrease of above-ground biomass and thus the above-ground carbon stocks. On the other hand, according to the results of **chapter 4**, there is no variation at landscape level between the four main vegetation units for soil organic carbon stocks.

However, the results of **chapters 5 and 7** show a main pathway in the production of soil organic carbon stock. According to **chapters 5 and 7**, increased soil organic carbon is positively related to increases in above-ground biomass, which would be in line with is expected on a large scale (Jobbágy & Jackson 2000; Doblas Miranda *et al.* 2013).

On the other hand, the results of the structural model in **chapter 5** (Path A. See Chapter 1) suggest an alternative pathway in the production of soil organic carbon. According to our study and in line with empirical results found in other regions (Piñeiro *et al.* 2010), here a significant total decrease of soil organic carbon, related to activities such as grazing or mowing, is not detected. In contrast, the removal of above-ground biomass seems to positively affect the accumulation of soil organic carbon stocks. Later on, thanks to a more detailed study in **chapter 7,** it is shown that it may be due to the fact that removal of biomass from such activities produces an increase in the production of fine roots (Prieto *et al.* 2015). The growth of fine roots would have a positive effect, to some extent, on the soil organic carbon stocks (Yu & Chmura 2009; Piñeiro *et al.* 2010). On the other hand, according to the results of **chapter 7**, the stimulation of root growth would not be as evident when the intensity is higher, e.g. higher level of inorganic fertilization, although, in this case, there is a strong removal of above-ground biomass. This result might be related to the fact that plants from most intensified areas which therefore receive inorganic fertilization, decrease the investment in the growth of structures for nutrient capture, as noted by the empirical results of (Deegan *et al.* 2012), which were found in other pastures.

In contrast, plots with extensive activity, and therefore with fewer nutrients available to plants, may harbor vegetation with a more developed root system to search for and capture of nutrients (Turner *et al.* 2009) as long as the environmental conditions are suitable (Piñeiro *et*

al. 2010). The results obtained in the case studies of this thesis (**chapter 5 and 7**), based on structural equation models, confirm these expectations. On the other hand, the results of **chapter 7** show that the stimulation of fine roots growth operates in conjunction with a general stimulation of the plant growth, e.g. the growth of longer and less dense stems.

Maintaining high levels of the groundwater table and above-ground biomass are shown here to be positively associated with higher total organic carbon stocks in the ecosystem. This result is in line with the conservationist' perception and in line with many studies on carbon stocks (Conti & Díaz 2013; Doblas Miranda *et al.* 2013). However, recent studies conducted in these wetlands show that it is particularly in some of the areas with high groundwater tables that higher emissions of greenhouse gases are produced, e.g. methane, although the above-ground biomass is higher (Witte & Giani 2015). This indicates that further studies are needed to better understand the carbon cycle and to understand the processes that lead to an overall accumulation or loss of carbon stocks in coastal wetlands (Mitsch *et al.* 2013).

8.2 Biodiversity, multi-functionality and ecosystem services, the supporting value of biodiversity

There is a long tradition on the study of biodiversity and the functioning of ecosystems (Duffy 2008). The relationship between biodiversity and the functioning of ecosystems is being extensively studied in grassland ecosystems (Scherber *et al.* 2010; Minden *et al.* 2016). In contrast to expectations in other grassland communities (Tilman *et al.* 1996), the ecosystem studied here shows a negative relationship between plant species richness and above-ground biomass productivity (**chapter 5 and 7)** which would be in line with what is expected in humid temperate pastures (Esselink *et al.* 2000; Joyce 2014).

The results of this study for this system show an initial positive relationship between removal of biomass and plant species richness (**chapter 5 and 7**). This relationship seems to be stronger when the agricultural management is extensive (**chapter 4**). In contrast, both total abandonment of agricultural activity and a high intensification produce a decrease in plant species richness. The results of **chapter 7** show how this mechanism could be explained because of disturbance events remove highly competitive species which have relative high biomass such as *Phragmites australis* or *Elymus athericus*. These disturbance events would trigger a process of competition for resource which is explained in **chapter 7**. This mechanism is indicated by plant functional traits associated with plant growth of fine roots and fine stems in extensively managed grasslands.

Increments in values of ecosystem properties and services such as the decomposition of biomass, forage quality, the occurrence of endangered plants and occurrence of endangered breeding birds appear to be associated with a relatively high species richness of plants and extensively managed pastures in both fresh and salty groundwater conditions. However, high levels of plant species richness show lower values of above-ground biomass productivity (**chapter 5 and 7**). In contrast, the plots with species-poor vegetation are normally represented by more competitive species with higher above-ground biomass productivity but with lower quality forage e.g. *Phragmites australis* or *Elymus athericus*.

This lower plant diversity is linked therefore to larger above-ground carbon stocks. However the level of soil organic carbon does not seem to vary globally possibly due to the two opposite mechanisms mentioned above (**chapter 5 and 7**). It seems that a possible global decline in above-ground carbon stocks due to biomass removal does not impair the overall carbon stocks balance in soil in this system. This possible and initial mechanism of loss of carbon stocks seems to be compensated due to an increase in species richness with the subsequent underground competition for resources (root growth) and a probable increase in diversity of decomposers microorganisms of soil (Eisenhauer *et al.* 2010; Doblas Miranda *et al.* 2013).

On the other hand, this study does not show a clear variation in species richness of breeding birds. According to the results presented here, no cause for variation of total richness of breeding birds can be found. Contrarily to the previously expected (Bonn *et al.* 2004), the results of this thesis show no association between this property, plant species richness or production of above-ground biomass. Despite this fact, the results show that increases in the richness of breeding birds positively affects the occurrence of endangered breeding birds. The gross benefits derived from forage production are associated with a relatively high level of species richness. As shown in our study cases more intensively grazed pastures have higher plant species richness than abandoned or unmanaged grasslands. However, species richness appears to be highest in extensive fields.

The results of this thesis show how high species richness of plants and relatively lower levels of plant available soil nutrients, related to extensively used grasslands, can produce an extra specific competition for exploitation of resources such as nutrients and light (Toogood & Joyce 2009; Ceulemans *et al.* 2013; Joyce 2014). Under the circumstances, the growth of fine roots seems to be responsible for maintenance of organic matter in soil. However, increasing levels of soil nutrients may slow down the below-ground biomass production associated with fine roots as it is shown in **chapter 7**. Further intensification of pastures usually involves higher

levels of fertilization and a selection of species of better forage quality (Lamarque *et al.* 2011; Lavorel *et al.* 2011). Both events can influence plant species that derive fewer resources for growth of roots or stems, due to the fact that under the circumstances less competition for soil resources or light may occur (Ceulemans *et al.* 2013). Consequently, these plants can derive more resources for the growth of leaves, as indicated by the results of this study (higher levels of specific leaf area). On the other hand, the results of **chapter 5** show how organic carbon levels seem to decrease with intensification, which could be linked to a reduced growth of fine roots and probably to a decline in the diversity of decomposers microorganisms as shown in other empirical studies (Eisenhauer *et al.* 2010).

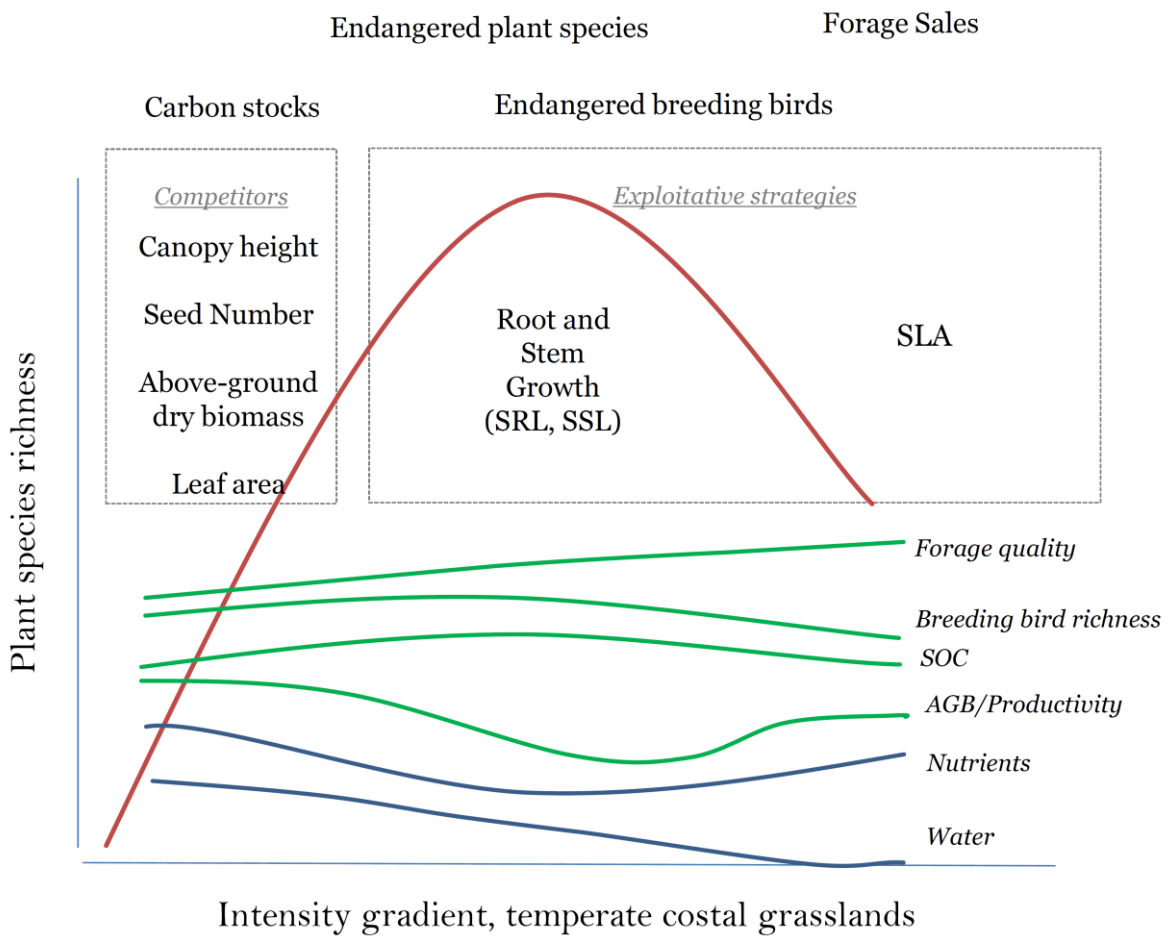

Fig. 8.1: The figure shows the hypothetical potential variation of plant species richness in response to the intensity gradient in temperate coastal grasslands according to the results obtained in the present thesis (red line). Maximal values for carbon stocks and final services such as habitat value to conserve endangered plant species, endangered breeding birds and forage sales situate in different positions of the intensity gradient (upper part of the graph). Variation of biotic and abiotic ecosystem properties (green and blue lines respectively) are indicated in the lower part of the graph. In the middle part of the graph community-weighted means of plant traits are situated where maximal values should be expected. Abbreviations: SLA: Specific leaf area; SRL: specific root length, SSL: specific stem length; SOC: Soil Organic Carbon; AGB: Above-ground standing biomass.

8.3 Trade-offs and synergies between ecosystem services in response to environmental drivers and plant functional traits, management implications

The results of the structural equation models of **chapters 5 and 7** revealed how variation of the land use and abiotic gradients cause positive or negative effects in/on ecosystem properties and services (See summary in Table 8.1).

The results of this thesis show that an increasing degree of nature protection on coastal grasslands of the study area is generally accompanied by higher groundwater levels and increased production of above-ground vegetation biomass and subsequent higher above-ground carbon stocks. Major goals of highly nature protected areas on this landscape include the maintenance of the natural processes without human intervention (Villbrandt *et al.* 1999; Wolff *et al.* 2010). This might lead, however, to a decline of plant species richness and to the spread of high competitor plant species with higher reproduction abilities and higher productivity, a fact that might be reinforced when the availability of soil nutrients is high. Increasing nature protection with an associated lack of biomass removal might also exert negative effects on (1) the occurrence of endangered plants and endangered breeding birds and (2) in one fraction of the below-ground organic carbon stocks i.e. soil organic carbon (Fig. 8.1).

However, biomass removal, here showed a positive effect on the overall nature conservation value, at least for plant species richness, endangered plant species and endangered species of breeding birds. Despite these circumstances, extensive areas used for nature conservation goals, which usually include agri-environmental measures, are rarely included on highly protected areas of temperate coastal marshes (Joyce 2014; Nolte *et al.* 2015). On the other hand, on the landward side of the seawall extensive areas show relatively low levels of nature protection which may lead to a fragile situation as to land use transformations (Krause *et al.* 2011).

Increasing intensification might, however, negatively affect endangered breeding birds. In contrast, the total value of species richness of breeding birds does not appear to be significantly affected with the gradient of intensity, which does not mean that certain groups of birds cannot be affected or damaged by certain land uses (Vickery *et al.* 2001; Atkinson *et al.* 2005). Direct negative effects of intensification on endangered plant species were not directly found probably due to the absence of highly intensified fields in saltmarshes. However, in areas where most of the endangered plants occurred the strong spatial segregation indicates a potential strong negative effect.

On the other hand, our study shows that extensive activity generates lower, but not significantly lower sales of forage-based products than intensive agricultural activity. However, it would be necessary to expand the sample size to analyze and compare the outputs of ecosystem services in conventional and extensive production with respect to the costs associated with both types of forage production (Kremen & Miles 2012; Gabriel *et al.* 2013).

In this study extensive activity is in general related to grasslands of lower agricultural potential, since the results show a lower cation exchange capacity, lower levels of certain nutrients in soil and subsequently lower forage quality. The suggested segregation of extensive activity due to the biophysical properties of the soil prevents a proper comparison between intensive and extensive activity under the same environmental conditions.

According to the analysis of the results of the study cases in this thesis and a comprehensive review of previous empirical studies (Joyce & Wade 1998), it appears that the extensive removal of biomass on these coastal pastures, which is accompanied by intermediate groundwater levels (**chapter 4**), can positively affect various cultural services whilst economic benefits might remain relatively high due to the production capacity of this system (see Fig. 8.1).

The above-ground carbon stock is reduced by grazing or mowing activities, however the below-ground carbon stock does not seem to vary. Contrary alternative mechanisms, shown in **chapters 5 and 7**, explain how the soil organic carbon stock is kept by biomass cutting and the subsequent growth of fine roots.

According to the assessment of regional stakeholders who participated in this study (**chapter 6**), both the group of farmers and of conservationists showed a high association between the nature conservation value and an extensive management. However, farmers were more sceptical about the total value of areas where extensive activity is carried out. This scepticism appears to be due to the perception that maintenance of biodiversity, and therefore lower levels of agricultural intensity, can produce lower agricultural benefits (Burton *et al.* 2008). However, farmers are aware of their role in maintaining the landscape and biodiversity, a fact that should be made use of to establish collaborative management strategies (Herzon & Mikk 2007; Lamarque *et al.* 2014b).

Nevertheless, the results of the present thesis show that the current strong spatial segregation of land uses might strongly affect the future of the nature conservation value e.g. occurrence of target species of nature protection programs. The socio-ecological results shown here suggest that an active and joint collaboration between the agricultural sector, the conservation sector and scientists is necessary to implement optimal management strategies to maintain acceptable levels of forage production and nature conservation values if an integrative

approach is considered (Bugalho *et al.* 2011). Alternatively, a conservative scenario associated here with higher above-ground biomass production and higher overall carbon stocks should be, however, cautiously recommended due to uncertain positive effects in regulating services such as carbon sequestration (Witte & Giani 2015), and probable negative effects on several cultural and provisioning services.

Table 8.1: Effects exerted by land use and abiotic ecosystem parameters on (1) plant functional traits and (2) biotic ecosystem properties and (3) values of final services according to models of chapter 5 (Fig. 5.2 and Table 5.2; "Path A") and chapter 7 (Fig. 7.3 and Table 7.2; "Path B"). (+) Positive effect; (-) Negative effect. Abbreviations: WATER: Positive co-variation of groundwater and salinity levels; SLA: Community-weighted mean of specific leaf area; SOC: Soil organic carbon; Rich: Richness; Endan.: Endangered; ESP: Ecosystem properties. NS: Non-significant. ANPP: Above-ground biomass net primary productivity; AGB: Above-ground standing biomass. ** Ecosystem properties which are often target of forage production goals.

		Plant functional traits			Carbon stocks		Forage production			Nature conservation value			
Land use and abiotic ESP		SLA	Size axis	Plant growth	SOC**	Above-ground Biomass**	Nutrients	Forage quality	Forage Sales	Breeding bird rich.	Plants rich.	Enda. plants	Enda. breeding birds
Water →	Path A				+	+(ANPP)	+	-	-	NS	-	+	-
Water →	Path B	-	NS (+/-)	-	-	NS	+	NS	-		-	+	
Nutrients →	Path A				+			+	-		-	-	
Nutrients →	Path B	NS	NS	-	-						-	-	
Nature protection →	Path A				-	+(ANPP)	-	-	-	NS	-	-	-
Nature protection→	Path B												
Biomass removal →	Path A				+	-(ANPP)		+	+	NS	+	+	+
Biomass removal →	Path B	+	-	+	+	-(AGB)		+	+		+	+	
Fertilization →	Path A				-	X	+	+	+	NS	+	x	-
Fertilization →	Path B												

8.4 Thesis highlights

Chapter 5: The drivers

1. Values of final ecosystem services were modelled as a structural equation model of environmental conditions determining land use intensity, which affected ecosystem properties and finally ecosystem services.
2. This model allowed identifying ultimate and proximate causes for sales of forage-based products and plant and bird species conservation value in coastal marshes, with a water gradient as "master" factor.
3. The results reveal the existence of a mismatch between the ecosystem' ability to produce forage and the demand, or how both extremes on land use i.e. abandonment and intensification, may produce negative effects on the habitat value to conserve breeding birds and endangered plants.
4. A negative effect of biomass removal on the soil organic carbon stocks accumulation was not detected.
5. Our results point to segregation and integration as two relevant spatial strategies to resolve potential trade-offs between provisioning and bequest services.

Chapter 6: The perception

1. Ecosystem service perceptions of farmers and conservationists differ significantly, due to different social contexts.
2. Conservationists associate regional belonging and soil fertility with conservation value, farmers with agricultural production.
3. Conservationists' perceptions of forage production was related to forage quality, biomass removal, groundwater level and the actual income from forage production, whereas farmers focused on the potential of ecosystem to produce forage, rather than the actual land use.
4. The farmers' conservation perception was related to species richness in general, whereas conservationists associated conservation value with endangered meadow birds.
5. Conservationists associated carbon sequestration value with below-ground peat formation, whereas farmers associated it with above-ground plant productivity

Chapter 7: The plant functional traits

1. Variation on an axis of competitors vs. exploitative plant strategies in response to environmental gradients explained trade-offs and synergies between forage production, species conservation and carbon stocks.
2. Biomass removal was the main direct driver affecting the trade-off between competitor and exploitative strategies indicated by community weighted means of plant trait values measured at the regional level, i.e., high values of vegetation canopy height-above-ground dry biomass, leaf area, seed number vs. high values of SLA, SRL and SSL.
3. The competitor strategy was associated with higher overall carbon stocks, but not specifically with higher below-ground carbon stocks.
4. The exploitative strategies were associated with a reduction of the overall carbon stocks, with higher plant richness and with an initial synergy between forage production and habitat value to conserve endangered plants.
5. A secondary trade-offs between forage production and habitat value to conserve endangered plant species was explained by the trade-off between SLA and plant growth (SRL and SSL), respectively, in response to increasing intensification and soil-nutrient availability. These results revealed the existence of allometric patterns that operate independently between several plant parts in response to environmental gradients
6. We found a positive effect of the plant growth strategy on soil organic carbon stocks associated with the growth of fine roots which may be caused by biomass removal and low soil-nutrient availability.
7. The plant growth strategy, associated with certain levels of biomass removal and decreasing levels of soil nutrient availability, was a good predictor for endangered plant species. By contrast, SLA was revealed as a good predictor of sales of forage-based products.

8.5 Concluding remarks

1) *Structural equation modelling*. Structural equation models were used in this study to understand and disentangle interactions between biophysical parameters, land use, provision of multiple ecosystem services and landscape managers' perceptions.

Due to (1) the relatively low sample size of the three study cases (N: 44-46), (2) the fact that several variables were difficult to be normalized and (3) the explorative nature of this study, rather than theory confirmation, partial least square structural equation modelling (PLS-SEM) was selected as the preferred multivariate method instead of alternative parametric covariance-based methods (Hair *et al.* 2011; Hair *et al.* 2013).

Besides, PLS-SEM was selected as the preferred tool due to the fact of the additional flexibility that the statistics provide to generate and explore non-directly measured variables (latent variables) such as abstract concepts, e.g. associations of multiple perceptions which are constructs commonly studied in other science fields such as psychology or marketing science (Lowry & Gaskin 2014).

The expectations based on previous knowledge were explored in several models on this thesis (**chapters 5, 6 and 7**). The resulting models were significant for measures of model quality (see appendix 5.2; appendix 6.2 and Table 7.3). The stakeholder perceptions were relatively well explained by several models on **chapter 6** (Fig. 6.2 and Fig.6.3) and the ecosystem properties and values of final services were relatively well explained by both environmental drivers ("Path A", Fig. 2.3 and Fig. 5.2 and Table 5.2) and plant traits ("Path B", Fig.1.1, Fig. 7.3 and Table 7.2). The selected multivariate statistics were valid to explain plant functional traits responses to land use parameters such as biomass removal, groundwater table and soil nutrients availability (**chapter 7**).

According to the results here shown, PLS-SEM appear as a valid tool to explore multivariate relationships between non-normally distributed parameters and to understand the potential sign of the relationships between variables. However, one needs to exercise caution when higher accuracy is required in order to understand when thresholds are reached in non-linear relationships (Koch *et al.* 2009).

2) *Ecosystem services framework*. Following recommendations by recent theoretical approaches (Wong *et al.* 2015), the ecosystem services framework allowed us to differentiate between purer biophysical parameters, which represent ecosystem properties and may operate as supporting services, e.g. nutrient availability, forage quality, soil organic carbon, and indicators of final services outputs, e.g. sales of forage-based products (provisioning service) and habitat value to conserve endangered species (cultural service). The results of the models revealed strong direct and indirect effects between parameters. Trade-offs and synergies

between abiotic parameters, land use drivers and plant functional traits explained trade-offs and synergies between ecosystem properties and final services (Fig. 5.2 and Fig. 7.3). Coupling both perceived ecosystem services by managers and measured indicators of ecosystem services (biophysical parameters) added knowledge about the different meanings of ecosystem services depending on the social context. Both measured and perceived ecosystem services should be considered in landscape planning in order to optimize management practices (Lamarque *et al.* 2014b; Andersson *et al.* 2015; García-Llorente *et al.* 2015).

The present thesis focused on a limited fraction of the ecosystem services cascade framework (Fig. 2.2) due to the fact that this work was mostly based on primary biophysical parameters, land use measurements and social perceptions of regional managers, representing a strong context- and process-based approach. Nevertheless, the understanding of the processes underpinning the ecosystems is strongly recommended for regional landscape planning actions, in order to avoid wrong expectations (Eigenbrod *et al.* 2010).

3) *Plant functional traits approach*. Following empirical approaches on functional ecology (Lavorel & Grigulis 2012; Minden & Kleyer 2015), community-weighted mean values (CWM) of several plant traits were used here to explain trade-offs and synergies between ecosystem properties and services in response to environmental gradients. The model based on plant functional traits (effect-response framework, **chapter 7**, Fig. 7.3 and Table 7.2, path B) showed equivalent explanatory power as the model used on **chapter 5** (Fig. 5.2 and Table 5.2, path A), which was based on direct effects of environmental gradients on ecosystem properties and services. This result shows a promising applicability of functional traits to predict environmental changes and effects on ecosystem properties and services.

Although not all the plant traits previously expected responded to the environmental gradients, this does not imply that they might not be functional in other gradients as it has been shown in other systems (Lavorel & Grigulis 2012). Considerations should be taken in order to generalize the results here obtained for other regions due to the strong place-based nature of this work. More study cases are needed to explore the applicability of the effect-response framework in relation to the prediction of ecosystem services variation under several environmental gradients and ranges.

However, our study confirmed the potential applicability of plant trait values retrieved from regional level data sets in a specific site context. Nevertheless further studies should be conducted to compare the efficacy of both site- and regional-based data sets (Cordlandwehr *et al.* 2013).

4) *Parameters' remarks*. Above-ground biomass primary productivity (ANPP) and above-ground standing biomass (AGB) were strongly correlated in the system studied here (N: 46;

CC $_{Spearman}$: 0.96; $p<0.01$). This fact, together with the results obtained in **chapter 5 and 7**, revealed how vegetation with higher above-ground productivity and standing biomass is associated with species-poor competitor vegetation (e.g. *Phragmites australis* and *Elymus athericus* plots). Nevertheless, ANPP was used for **chapter 5** and AGB was used for **chapter 7**.

The direct-use value associated with forage production represents an economic value that indicates how society values the products derived from a provisioning service such as forage production (Fig. 2.1). However, as shown here, forage production strongly depends on ecological interaction of other supporting services or properties and plant traits, e.g., soil fertility, forage quality and leave traits, and is strongly affected by land use.

The indices used here to assess endangered species are considered non-use values that represent the habitat value to conserve endangered species. Habitat- and species conservation are cultural, non-use values (Fig. 2.1). Nevertheless, due to logistic limitations, here only breeding birds and plants were used. Extending the research to other taxonomic groups would, however, be recommended for future research.

5) *Bundles of ecosystem properties and services*. The results of Spearman pairwise correlations (see Appendix 8.1: correlation matrix) showed how not all previously-expected positive or negative associations between ecosystem properties and services are confirmed. For example, the expected positive association of AGB and SOC, the positive association of forage quality (species-based) and sales of forage-based products, or the negative association of forage production and nature conservation value (both habitat values to conserve endangered plants or breeding birds).

However, although a positive association between AGB and SOC was not found (See Appendix 8.1), the results of the thesis revealed an initial positive effect of increasing values of AGB on SOC (**chapter 5 and 7**).

In addition, the results based on the understanding of the ecosystem mechanisms underpinning ecosystem functioning also showed alternative paths affecting ecosystem properties and service' associations, e.g., below-ground carbon stocks, sales of forage-based products, or habitat value to conserve species.

The results of this thesis revealed, for instance, how biomass removal exerted an alternative, positive effect on the below-ground organic carbon stocks. Due to these two opposite mechanisms, it was not possible to find a correlation between AGB and SOC.

On the other hand, as also pointed out by farmers who participated in this study, we found a certain mismatch between the ecosystem capacity to provide forage (forage quality and soil

nutrient availability) and the current demand and provision of this service as indicated by sales of forage-based products. On the contrary, the community weighted-mean of specific leaf area was found to be a good predictor of high intensity and sales of forage-based products on coastal grasslands.

Contrary to expectations from other systems, a certain degree of disturbance showed a positive effect on plant species' richness, which subsequently triggered the occurrence of endangered plant species (see Table 8.1 and Fig. 8.1). Therefore the correlation results did not show a negative association between forage production and endangered plant species occurrence (see Appendix 8.1).

In addition, the results revealed an initial positive association between sales of forage-based products and endangered breeding birds (Appendix 8.1). However, these initial results may lead to a misinterpretation of the system. The results of **chapter 5,** based on ecosystem processes, showed how, although a certain degree of disturbance may exert a positive effect on breeding-bird occurrence, a higher intensity may exert negative effects on the endangered breeding-bird community.

According to the results found here, and following theoretical recommendations of (Mouchet *et al.* 2014; Wong *et al.* 2015), the understanding of ecosystem mechanisms and therefore of specific causal relationships may offer more robust insights than results that are based only on pairwise correlations.

The results here shown in **chapters 7 and 5** reveal how synergies and trade-offs between ecosystem properties and services are not as static as may be expected. Initially broadly-expected associations may vary following responses to environmental gradients, e.g., a land-use gradient, soil-nutrient availability or groundwater gradient. Thus, due to the dynamic nature of these associations, a highly-sensitive approach is required.

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Summary
Zusammenfassung

Summary

From sciences such as conservation biology, or from more practical approaches such as landscape planning, warnings have been expressed about the increasing loss of biodiversity associated with the intensification of European agricultural landscapes. At present, the area devoted to agriculture represents approximately 40% of the surface of Europe. Although the total agricultural area has declined in recent years, both abandonment and intensification of extensive traditional structures have eliminated habitats and species that is without parallel. Large areas of extensive agriculture, where soil characteristics, groundwater or orography have meant additional difficulties for agriculture, have been abandoned in favor of agricultural intensification in more benign areas. These land-use changes have dismantled valuable socio-ecological structures, depreciated biodiversity associated with agricultural landscapes of high natural value and have produced a decline of ecosystem properties and services.

Drivers of ecosystem change

During the development of the initial phases of this project, I assumed the responsibility to determine which environmental variables (drivers of ecosystem change) would be responsible for the variation of multiple vegetation-mediated properties and services associated with the production of forage and with the habitat' value to conserve species. The study was conducted in a landscape of coastal temperate grasslands (**Chapter 3**) in northern Germany, i.e. the Krummhörn and Emden communities (East Frisia) (**Chapter 4**). Which properties are associated with final services? What are the trade-offs between single or groups of properties and services? Is there always a negative association between forage production and conservation of species and habitats? What is the relationship between soil carbon stocks and other ecosystem properties and services? Or what are the effects of high nature protection, abandonment, or intensification of extensive farming activities on the properties and services? As shown in **Chapter 4**, such questions could not be solved by an approach based merely on the study of vegetation units. Thus these questions were later addressed in a Partial Least Square-Structural Equation Model (PLS-SEM) in **Chapter 5**. Sample size would notably increase due to the study of plots instead of vegetation units. I collected, with the help of students, vegetation and soil biophysical parameters in 49 plots during 2011-2013. My colleague Celia Grande performed bird observations during 2011-2013.

The results of **Chapter 5** identified the latest and proximate causes of variation in the sales of forage-based products and the conservation value of plant and bird species in coastal grasslands. The groundwater gradient was revealed as a "master" factor and removal of biomass as the most proximate factor. The results reveal the existence of a mismatch between the ecosystem' ability to produce forage and the demands upon it, or how both extremes of

land use, i.e. abandonment and intensification, may produce negative effects on the habitat value for conserving breeding birds and endangered plants. Nonetheless our results point to segregation and integration as two relevant spatial strategies to resolve possible conflicts between provisioning and bequest services, i.e. habitat value to conserve species and forage production.

Social perceptions

The vast majority of the area of temperate grasses coasts are destined either to be used for forage production or, to a lesser extent, for nature conservation. Thus it was early apparent that it was necessary to address how both sectors responsible for these objectives, i.e. conservationists and farmers, understand, perceive and value the properties and services associated with these major objectives. Is there an agreement on how both sectors understand the provision of properties and services related to agricultural production, nature conservation and carbon stocks? What does soil fertility for each sector mean? Which other services and properties are associated with this function? How does each sector view the causes that lead to an increase in the biodiversity value? What biophysical variables explain the different perceptions? Which intensity levels are associated with the various properties and final services?

To address these questions, I collaborated with my colleague Leena Karrasch, who conducted interviews and workshops with key members of both sectors responsible for the management of the regional landscape. Perceptions and preferences were obtained in an elaborate process of social participation. My approach which was based on the understanding of the underlying ecosystem processes (plot level) and the approach of Leena which was based on the study of the perceptions and preferences of local actors (habitat level) were combined to disentangle the factors that may determine the knowledge of both sectors i.e. conservationists and farmers. The results obtained in the PLS-SEMs of **Chapter 6** revealed that: (1) ecosystem service perceptions of farmers and conservationists differ significantly, due to different social contexts; (2) conservationists associate regional belonging and soil fertility with conservation value, farmers with agricultural production; (3) conservationists' perceptions of forage production was related to forage quality, biomass removal, groundwater level and the actual income from forage production, whereas farmers focused on the potential of ecosystem to produce forage, rather than the actual land use; (4) the farmers' conservation perception was related to species richness in general, whereas conservationists associated conservation value with endangered meadow birds; (5) conservationists associated carbon sequestration value with below-ground peat formation, whereas farmers associated it with above-ground plant productivity.

Plant functional traits

The results of **Chapter 5** showed the importance of certain drivers of change as determinants of the provision of vegetation-based properties and services. Later questions arose about how certain plant traits can explain the conflicts and synergies between the same ecosystem services and properties. How do the plant traits determine variation in the content of soil organic carbon, biomass productivity and forage quality or even in final services such as the economic value of agricultural pastures? Which plant traits explain this variation? How are these plant traits associated? Do the associations of certain traits explain later associations of properties and services?

These questions were addressed by combining various approaches of functional ecology, such as the effect-response approach and the biomass-ratio hypothesis (**Chapter 7**). The key question arose when I considered whether mean values of traits belonging to plant species collected from individuals in a large coastal area between Baltic Sea and North Sea (Fig.7.1) could be used to explain responses of vegetation to environmental changes and explain trade-offs and synergies between properties and services in a specific site. To answer these questions, several traits were collected in plant individuals within four areas from coastal temperate pastures of this large area (Fig. 7.1). With the help of my colleagues of work package 3 within the collaborative project COMTESS, Silke Eilers, Camilla Fløjgaard, Anastasia Trenkamp and Juliane Trinogga, plant traits from stems, roots, leaves and seeds were collected. This initial database was expanded using a data sub-set collected by my college Dr. Vanessa Minden for an earlier project (TREIBSEL) from salty coastal area pastures bordering the German North Sea. The results of **Chapter 7** of this thesis is based on 2104 plant individuals of a total of 92 species collected from 304 plots. The hypotheses raised in the initial model of this chapter were based on previous empirical work conducted in other grassland systems. Hypotheses such as leaf economic spectrum, plant economic spectrum and size axis were tested using a model of structural equations.

The results shown in **Chapter 7** provided further insights: (1) variation on an axis of competitors vs. exploitative plant strategies in response to environmental gradients explained trade-offs and synergies between forage production, species conservation and carbon stocks; (2) biomass removal was the main direct driver affecting the trade-off between competitor and exploitative strategies indicated by community weighted means of plant trait values measured at the regional level, i.e., high values of vegetation canopy height, above-ground dry biomass, leaf area, seed number vs. high values of SLA, SRL and SSL. (3) The competitor strategy was associated with higher overall carbon stocks, but not specifically with higher below-ground carbon stocks; (4) the exploitative strategies were associated with a reduction of the overall carbon stocks, with higher plant richness and with an initial synergy between forage

production and habitat value to conserve endangered plants; (5) a secondary trade-offs between forage production and habitat value to conserve endangered plant species was explained by the trade-off between SLA and plant growth (SRL and SSL), respectively, in response to increasing intensification and soil-nutrient availability; (6) we found a positive effect of the plant growth strategy on soil organic carbon stocks associated with the growth of fine roots which may be caused by biomass removal and low soil-nutrient availability; (7) the plant growth strategy, associated with certain levels of biomass removal and decreasing levels of soil nutrient availability, was a good predictor for endangered plant species. By contrast, SLA was revealed as a good predictor of sales of forage-based products.

Conclusions

Three case-studies were used to understand the conflicts and synergies between forage production, the nature conservation value, carbon stocks and their relations to several ecosystem properties. The first case study highlights the importance of abiotic gradients and land use parameters in the genesis of conflicts and synergies between services and properties. Identifying the chain of causes and effects on final services allows targeting the most relevant determinants of services in planning and management schemes. For instance, biomass removal, ANPP and fertilization need to be well balanced on the landscape scale in order to both conserve endangered birds and yield sales from forage production. Incorporating this chain of responses and effects into new spatial optimization models should allow us to identify the best spatial planning strategy that resolves the trade-off between sales of forage-based products and species conservation in multifunctional landscapes.

The second case allows us to understand the perceptions of stakeholders, who have a strong concept about how the landscape provides services and ecosystem properties. The different perceptions are revealed through multi-dimensional constructs based on biophysical variables, reflecting the importance of social contexts. Even elementary provisioning services such as forage production were linked to different values, ecosystem properties and land uses. Our results indicate that notions and values of services are strongly influenced by different social contexts, involving current livelihoods, professional interests and traditions. Formal stakeholder assessments of ecosystem services to establish or improve sustainable land management thus need to take into account that stakeholder groups interpret ecosystem services in different ways and give them different meanings. We therefore argue that ecosystem service assessments by stakeholders should be complemented by determining indicators of biophysical ecosystem properties, allowing the evaluation of the correspondence between stakeholder perceptions. Ultimately, analyses of the complex social-ecological contexts forming stakeholder attitudes towards ecosystems should be encouraged.

The third case provides revealing results on the functionality of the vegetation in response to key environmental variables, i.e. biomass removal, soil nutrients and water gradient, and how associations of traits determine trade-offs and synergies between ecosystem properties and services. Contrary to the plant- or leaf economics, our results suggest the trade-offs and synergies between plant functional traits found here are not explained by a resource acquisition vs. resource conservation trade-off. Here the variation of plant functional traits in respond to disturbance, may express a trade-off on a gradient of well-established competitors' species (persistence) vs. competition for establishment. These results indicate that plant community assemblies and associated specific key plant traits can well explain the variation of determinant environmental parameters and their effects on ecosystem properties and services. Empirical approaches, as used here, may help to optimize management strategies under the threats of environmental change and strong land-use pressure.

This thesis is an example of scientific work based on the understanding of a complex socio-ecological system through the study of (1) ecosystem processes and (2) the conceptual system of the main actors responsible for its future. The ecosystem service framework (**Chapter 2**) served as basis to analyze and structure parameters and relationships by applying structural equation models. The use of these results may offer insights to regional managers, policy makers and landscape planners in order to implement successful management solutions.

Zusammenfassung

Die Naturschutzbiologie und angewandte Forschungsbereiche wie der Landschaftsplanung haben immer wieder vor dem fortschreitenden Verlust an Biodiversität durch die landwirtschaftliche Intensivierung in Europa gewarnt. Aktuell beträgt der Anteil landwirtschaftlich genutzter Fläche in Europa etwa 40%. Obwohl die gesamte landwirtschaftliche Nutzfläche in den letzten Jahren zurückgegangen ist, haben sowohl die Nutzungsaufgabe als auch Diendie Intensivierung traditioneller extensiver Strukturen auf beispiellose Weise Habitate und Arten vernichtet. Große extensiv genutzte Flächen, deren Bodenbeschaffenheit oder Lage eine Bewirtschaftung erschwerte, wurden zu Gunsten von landwirtschaftlicher Intensivierung von geeigneteren Flächen aus der Nutzung genommen. Diese Änderung der Landnutzung hat sozial-ökologische Strukturen zerstört, die Biodiversität landwirtschaftlicher Flächen von hohem ökologischen Wert verringert und zu einem Rückgang von Ökosystem-Eigenschaften und –stleistungen geführt.

Triebkräfte der Veränderungen in einem Ökosystem

Während der Anfangsphase dieses Projektes übernahm ich die Aufgabe herauszufinden, welche Umweltvariablen (Triebkräfte der Veränderungen in einem Ökosystem) einen Einfluss auf verschiedene vegetationsbasierte Eigenschaften und Dienstleistungen haben, die im Zusammenhang mit Nahrungsmittelproduktion und dem Naturschutzwert eines Lebensraumes stehen. Die Studie wurde in einer von küstennahem gemäßigtem Grünland geprägten Landschaft (**Kapitel 3**) in Norddeutschland, in den ostfriesischen Gemeinden Krummhörn und Emden (**Kapitel 4**), durchgeführt. Welche Eigenschaften können endgültigen Dienstleistungen zugeordnet werden? Welche Konflikte gibt es zwischen einzelnen oder Gruppen von Eigenschaften und Dienstleistungen? Besteht immer ein negativer Zusammenhang zwischen Lebensmittelproduktion und Schutz von Arten und Lebensräumen? Wie sieht die Beziehung zwischen dem Kohlenstoffbestand im Boden und anderen Ökosystemeigenschaften und –dienstleistungen aus? Und welche Auswirkungen hat der Naturschutz und die Nutzungsaufgabe oder Intensivierung von extensiver Bewirtschaftung auf die Eigenschaften und Dienstleistungen? Wie in **Kapitel 4** gezeigt wird, können diese Fragen nicht allein durch eine auf Vegetationseinheiten basierende Studie beantwortet werden. Daraufhin wurden diese Forschungsthemen mit Hilfe eines Partial Least Squares-Strukturgleichungsmodell (PLS-SEM) untersucht (**Kapitel 5**). Die Stichprobengröße wurde durch die Verwendung von Untersuchungsflächen anstatt von Vegetationseinheiten erheblich erhöht. In den Jahren 2011 bis 2013 erhob ich mit der Hilfe von Studenten Vegetations- und biophysikalische Bodenparameter auf 49 Untersuchungsflächen. Meine Kollegin Celia Grande führte Vogelerfassungen während der Jahre 2011 bis 2013 durch. Die Ergebnisse des **Kapitels 5** zeigen die grundlegenden und unmittelbaren Ursachen der Schwankungen im Verkauf von

Produkten auf Futter-Basis und dem Naturschutzwert der Pflanzen- und Vogelarten in den Küstenwiesen. Der Grundwasser Gradient wurde als "Master" Faktor und der Abbau von Biomasse als am proximaler Faktor enthüllt. Die Ergebnisse zeigen die Existenz einer fehlenden Übereinstimmung zwischen der Fähigkeit des Ökosystems Futter zu produzieren und der Nachfrage davon, oder wie beide Extreme der Landnutzung, d.h. sowohl die Nichtnutzung als auch die Intensivierung negative Auswirkungen auf den Naturschutzwert des Lebensraums von Brutvögeln und gefährdeten Pflanzen haben können. Dennoch weisen unsere Ergebnisse auf Segregation und Integration als zwei relevante räumliche Strategien hin, die mögliche Konflikte zwischen Bereitstellungs- und Vermächtnis-Ökosystemdienstleistungen lösen, das heißt den Naturschutzwert eines Lebensraums zur Erhaltung von Arten und Futterproduktion.

Wahrnehmung der Stakeholders (Interessengruppen)

Große Bereiche der Grünlandgebiete in den gemäßigten Küstenbereichen dienen entweder der Futtermittelproduktion oder, in einem geringeren Umfang, als Naturschutzflächen. Aus diesem Grund ist es wichtig, frühzeitig herauszufinden, wie Landwirte und Naturschützer als Vertreter der zwei wichtigsten Sektoren die Ökosystem-Eigenschaften und -Dienstleistungen, die mit diesen Zielsetzungen verbunden sind, verstehen, wahrnehmen und bewerten. Gibt es eine Übereinstimmung darüber, wie beide Sektoren die Bereitstellung von Ökosystem-Eigenschaften und -Dienstleistungen in Bezug zu der landwirtschaftlichen Produktion, dem Naturschutz und der Kohlenstoffspeicherung verstehen? Welche Bedeutung hat die Bodenfruchtbarkeit für den jeweiligen Sektor? Welche anderen Ökosystem-Eigenschaften und -Dienstleistungen sind mit diesen Eigenschaften verbunden? Was sind für den jeweiligen Sektor die Gründe, die zu einer Erhöhung des Wertes der biologischen Vielfalt führen? Welche biophysikalischen Variablen erklären die unterschiedlichen Wahrnehmungen? oder Welche Intensitätsstufen sind mit den verschiedenen Ökosystem-Eigenschaften und End-Dienstleistungen verbunden?

Um diese Fragestellungen zu beantworten habe ich mit meiner Kollegin Leena Karrasch zusammengearbeitet. Sie hat Interviews und Workshops mit Schlüsselakteuren beider Sektoren durchgeführt, die auch verantwortlich für das Regionalmanagement der Landschaft sind, Ihre Wahrnehmungen und Präferenzen wurden in einem aufwendigen partizipativen Prozess erhoben. Mein Ansatz, basierend auf dem Verständnis der zugrundeliegenden Prozesse im Ökosystem (Plot-Ebene), und der Ansatz von Leena, basierend auf der Untersuchung der Wahrnehmung und Präferenzen der lokalen Akteure (Habitat-Ebene) wurden kombiniert, um die Faktoren zu analysieren, die das Wissen beider Sektoren (Naturschützer und Landwirte) bestimmen. Die erzielten Ergebnisse in den PLS-SEMs von **Kapitel 6** ergaben, dass: (1) die Wahrnehmungen von Ökosystemdienstleistungen auf Grund

der unterschiedlichen sozialen Kontexte der Landwirte und Naturschützer erheblich voneinander abweichen; (2) die Naturschützer das Gefühl der regionalen Zugehörigkeit und die Bodenfruchtbarkeit mit dem Naturschutzwert verbinden, die Landwirte dagegen mit der landwirtschaftlichen Produktion; (3) die Wahrnehmung der Naturschützer in Bezug auf Futterproduktion in Zusammenhang mit der Futterqualität, Entfernung von Biomasse, dem Grundwasserspiegel und der tatsächlichen Erträge aus der Futterproduktion stand, hingegen die Wahrnehmung der Landwirte sich eher auf das Potential der Ökosysteme Futtermittel zu produzieren fokussierte, als auf die tatsächliche Landnutzung; (4) die Wahrnehmung der Landwirte in Bezug auf den Naturschutzwert im allgemeinen Zusammenhang mit Artenreichtum gestellt wurde, während die Naturschützer Naturschutzwert mit gefährdeten Wiesenvögel in Verbindung gebracht haben; und (5) die Naturschützer den Wert der Kohlenstoffsequestrierung mit unterirdische Torfbildung assoziierten, während die Landwirte sie mit oberirdischen Pflanzenproduktivität verbanden.

Funktionseigenschaften der Pflanzen

Die Ergebnisse aus **Kapitel 5** zeigten die Wichtigkeit einiger Einflussgrößen vegetationsabhängiger Ökosystem-Eigenschaften und –dienstleistungen. In diesem Zusammenhang kam die Frage auf, inwieweit funktionelle Pflanzeneigenschaften (FPE) die positiven und negativen Wechselwirkungen zwischen eben diesen Eigenschaften und Dienstleistungen erklären können. Wie beeinflussen FPE die Unterschiede im Bodenkohlenstoffgehalt, der Biomasseproduktion, der Futtermittelqualität, oder selbst die von abgeleiteten Dienstleistungen wie dem Marktwert von Weideflächen? Welche FPE sind dabei von Bedeutung? Welche Zusammenhänge zwischen FPE gibt es? Und lassen Zusammenhänge zwischen FPE auf solche zwischen Ökosystem-Eigenschaften und –dienstleistungen schließen? Diesen Fragen wurde durch die Kombination verschiedener Forschungsansätze der funktionellen Ökologie nachgegangen, wie dem effect-response framework und der biomass-ratio-Hypothese (**Kapitel 7**). Die Schlüsselfrage kam auf, als ich mich damit befasste, ob Durchschnittswerte der Eigenschaften von Pflanzenspezies, die von Pflanzenindividuen in einem großen Küstenbereich zwischen der Ostsee und der Nordsee gesammelt wurden (regionale Kontext; Abb. 7.1)., verwendet werden könnten, um Reaktionen der Vegetation auf Umweltveränderungen zu erklären und auch Konflikte und Synergien zu erklären zwischen Eigenschaften und Dienstleistungen an einem bestimmten Ort (Spezifischen Kontext; Abb. 4.1).Um diese Fragen zu beantworten, habe ich in Zusammenarbeit mit anderen Forschern der COMTESS-Forschergruppe verschiedene FPE von Pflanzen gesammelt, die in einem großen Untersuchungsgebiet, das von den Küsten der Nord- bis zur Ostsee reichte, wachsen (Abb. 7.1). Die in **Kapitel 7** präsentierten Ergebnisse meiner Arbeit stammen von 304 Untersuchungsflächen, auf denen 2104 Pflanzenindividuen

aus 92 Arten beprobt wurden. Die im Anfangsmodell dieses Kapitels gestellten Hypothesen entstanden auf der Grundlage von anderen in Grasländern durchgeführten Untersuchungen. Hypothesen wie das leaf economics spectrum, das plant economics spectrum, und die size axis wurden mithilfe von Strukturgleichungsmodellen geprüft.

Die in diesem Kapitel gewonnenen Erkenntnisse waren insbesondere: (1) die Variation auf einer Achse von kompetitiven vs. ressourcenzentrierten (i.e. schnelle Aufnahme von Ressourcen) Pflanzenstrategien erklärten Konflikte und Synergien zwischen Futterproduktion, Arterhaltung und Kohlenstoffbestand. (2) Der Abbau von Biomasse war der direkte Hauptverursacher, der den Konflikt zwischen kompetitiven und ressourcenzentrierten Strategien berührte, wie sie angezeigt wurden durch das gewichteter Mittelwert für die Gemeinschaft von Werten der Pflanzenmerkmale, die auf regionaler Ebene gemessen wurden, d.h. hohe Werte bei der Vegetations(kronen)höhe, oberirdische trockene Biomasse, Blätterbereich, Zahl der Samen vs. hohen Werten von SLA, SRL und SSL. (3) Die kompetitive Strategie war verbunden mit höheren Gesamtbeständen von Kohlenstoff, aber nicht besonders mit höheren Kohlenstoffbeständen unter dem Boden. (4) Die ressourcenzentrierten Strategien waren verbunden mit einer Reduktion der Gesamtkohlenstoffbestände, mit höherem Pflanzenreichtum und mit einer ursprünglichen Synergie zwischen Futterproduktion (Futterbau) und Habitat-Wert, um gefährdete Pflanzen zu erhalten. (5) Ein sekundärer Konflikt zwischen Futterproduktion (Futterbau) und Habitat-Wert, um gefährdete Pflanzenarten zu erhalten, wurde erklärt durch den Konflikt zwischen SLA und, entsprechend, dem Pflanzenwachstum (SRL und SSL), in Reaktion auf die wachsende Intensivierung und Verfügbarkeit von Bodennährstoffen. (6) Wir fanden einen positiven Effekt der Pflanzenwachstumsstrategie auf organische Kohlenstoffbestände im Boden, verbunden mit dem Wachstum dünner Wurzeln, was vielleicht verursacht wird durch Beseitigung von Biomasse und niedriger Verfügbarkeit von Bodennährstoffen. (7) Die Pflanzenwachstumsstrategie, verbunden mit gewissen Niveaus des Abbaus von Biomasse und abnehmenden Niveaus der Verfügbarkeit von Bodennährstoffen, war ein guter Indikator für gefährdete Pflanzenarten. Im Gegensatz dazu wurde SLA als ein guter Indikator für den Verkauf von futtergestützten Produkten erkannt.

Schlussfolgerungen

Drei Fallstudien wurden verwendet, um die Konflikte und Synergien zwischen Futterproduktion, dem Wert von Naturschutz, den Kohlenstoffbeständen und ihre Beziehungen zu mehreren Ökosystem-Eigenschaften zu verstehen. Die erste Fallstudie befasst sich mit der Bedeutung von abiotischen Gradienten und Landnutzungsparametern in der Genese von Konflikten und Synergien zwischen Ökosystem-Dienstleistungen und -eigenschaften. Das Identifizieren der Kausalkette und der Effekte auf letztendliche Leistungen

erlaubt es, die wichtigsten Determinanten von Leistungen bei den Planungs- und Management-Verfahren ins Auge zu fassen. So müssen z.B. der Biomasse-Abbau, ANPP und die Fruchtbarmachung auf der Landschaftsskala gut ausgeglichen sein, um sowohl gefährdete Vögel zu erhalten als auch Verkäufe aus der Futterproduktion zu gewährleisten. Wenn diese Kette von Reaktionen und Effekten in neue räumliche Optimierungsmodelle eingefügt werden, sollten diese uns erlauben, die beste räumliche Planungsstrategie zu erkennen, die den Konflikt zwischen Verkäufen von futtergestützten Produkten und Artenerhaltung in multifunktionalen Landschaften löst. Die zweite Fallstudie erlaubt uns, die Sichtweisen von Interessenvertretern zu verstehen, die eine feste Vorstellung davon haben, wie die Landschaft Leistungen und Ökosystem-Eigenschaften gewährleistet. Die unterschiedlichen Sichtweisen werden deutlich durch multidimensionale Konstrukte, die auf biophysikalischen Variablen basieren, welche die Bedeutung sozialer Kontexte widerspiegeln. Selbst elementare Versorgungsleistungen wie z.B. Futterproduktion waren mit verschiedenen Werten verbunden, Ökosystem-Eigenschaften und Landnutzung. Unsere Ergebnisse zeigen an, dass Vorstellungen und Werte von Leistungen stark beeinflusst werden von unterschiedlichen sozialen Kontexten, die gegenwärtige Lebensunterhalte, berufliche Interessen und Traditionen umfassen. Bei formalen Interessenvertreter-Bewertungen von Ökosystem-Leistungen, um nachhaltige Landbewirtschaftung einzurichten oder zu verbessern, ist somit zu berücksichtigen, dass die Gruppen von Interessenvertretern Ökosystemleistungen auf verschiedene Weise interpretieren und ihnen verschiedene Bedeutungen zuweisen. Wir argumentieren daher, dass Bewertungen von Ökosystemleistungen durch Interessenvertreter ergänzt werden sollten durch entscheidende Indikatoren biophysikalischer Ökosystem-Eigenschaften, die es erlauben, die Korrespondenz zwischen den Wahrnehmungen von Interessenvertretern zu bewerten. Schließlich sollte zu Analysen der komplexen sozio-ökologischen Kontexte ermutigt werden, die die Haltungen von Interessenvertretern gegenüber Ökosystemen formen. Die dritte Fallstudie liefert aufschlussreiche Resultate zur Funktionsweise der Vegetation in Reaktion auf Schlüsselvariablen der Umwelt, z.B. Abbau der Biomasse, Bodennährstoffe und Wassergefälle, und wie Verbindungen von Merkmalen Konflikte und Synergien zwischen Ökosystem-Eigenschaften und –Leistungen bestimmen. Im Gegensatz zu den so genannten „plant economic spectrum“ oder „leaf economic spectrum“ lassen unsere Ergebnisse darauf schließen, dass die Konflikte und Synergien zwischen funktionalen Pflanzenmerkmalen, die hier gefunden wurden, nicht erklärt werden durch einen Konflikt von Ressourcenbeschaffung vs. Ressourcenerhaltung. Hier mag die Variation von funktionalen Pflanzenmerkmalen als Reaktion auf Störungen einen Konflikt zum Ausdruck bringen auf einem Gradienten von gut etablierten konkurrierenden Arten (kompetitiven) gegenüber einem Wettbewerb um Etablierung. Diese Ergebnisse zeigen an, dass Ansammlungen von Pflanzengemeinschaften und damit verbundene spezifische

Schlüsselmerkmale von Pflanzen sehr wohl die Variation von bestimmenden Umweltparametern und ihrer Effekte auf Ökosystemen-eigenschaften und –dienstleistungen erklären können. Empirische Annäherungen, wie sie hier gebraucht wurden, können helfen, unter den Drohungen des Umweltwandels und dem starken Druck der Landnutzung Managementstrategien zu optimieren. Diese Dissertation soll das Beispiel einer wissenschaftlichen Arbeit sein, die basiert auf dem Verständnis eines komplexen sozio-ökologischen Systems durch das Studium (1) von Ökosystemprozessen und (2) und eines konzeptuellen Systems der Hauptakteure, die für seine Zukunft verantwortlich sind. Der Rahmen der Ökosystemleistungen (**Kapitel 2)** diente als Basis, um Parameter und Beziehungen zu analysieren und strukturieren indem Strukturgleichungsmodelle angewandt wurden. Die Verwendung dieser Resultate mag führenden Personen von Regionen, politischen Entscheidungsträgern und Landschaftsplanern Einsichten bieten, um erfolgreiche Management-Lösungen zur Anwendung zu bringen.

Appendices

Appendices

Appendices Chapter 5

Appendix 5.1: PLS-SEM results quality criteria. All latent variables were significant and goodness of fit measures such as average variance extracted (AVE; Indicator for converge validity) and composite reliability (indicator for internal consistency reliability) were equal or higher than 0.5 and 0.7 respectively (Hair *et al.*, 2011).

	AVE	Composite Reliability	R Square
ANPP	1.0	1.00	0.30
Breeding birds richness	1.0	1.00	
CEC	1.0	1.00	
Biomass removal	1.0	1.00	0.56
Endangered breeding birds	1.0	1.00	0.49
Endangered plants	1.0	1.00	0.48
Fertilization	1.0	1.00	0.37
Forage quality	0.76	0.86	0.52
Forage sales	1.00	1.00	0.76
Nature protection	1.0	1.00	0.52
NUTRIENTS	0.55	0.78	0.43
Plant richness	1.00	1.00	0.49
SOC	1.0	1.00	0.39
WATER	0.75	0.86	

Appendix 5.2: Total effects between abiotic ecosystem properties, land use parameters and biotic ecosystem properties. The values represent the standardized regression coefficients extracted from the PLS-SEM analysis. See Table 4.1 for Abbreviations.

	ANPP	FORAGE QUALITY	Nutrients	Plant richness	SOC
CEC →		0.28			
Nutrients →		0.16			0.44
WATER	0.31	-0.14	0.68	-0.23	0.10
Fertilization →		0.29	0.27		-0.24
Biomass removal →	-0.58	0.25		0.42	0.65
Nature protection →	0.43	-0.37	-0.17	-0.32	-0.34
ANPP →		-0.44		-0.73	0.43

Appendix 5.3: Bootstrapping analysis. N: 46. 5000 runs. T values higher than 1.96 are significant at 5% (Hair *et al.* 2014). Only significant pathways were retained in the final model. See Table 4.1 and Table 5.2 for abbreviations.

	Original Sample (O)	Sample Mean (M)	Standard Deviation (STDEV)	Standard Error (STERR)	T Statistics (|O/STERR|)
ANPP Biomass productivity -> FORAGE QUALITY	-0.41	-0.41	0.12	0.12	3.44
ANPP Biomass productivity -> Plant diversity	-0.70	-0.70	0.06	0.06	11.84
ANPP Biomass productivity -> SOC	0.40	0.39	0.17	0.17	2.36
Breeding birds diversity -> Endangered breeding birds	0.41	0.42	0.13	0.13	3.28
CEC -> Endangered breeding birds	0.41	0.37	0.20	0.20	2.05
CEC -> FORAGE QUALITY	0.30	0.29	0.12	0.12	2.60
Biomass removal -> ANPP Biomass productivity	-0.55	-0.55	0.08	0.08	6.52
Biomass removal -> Endangered breeding birds	0.50	0.53	0.16	0.16	3.11
Biomass removal -> SOC	0.87	0.87	0.13	0.13	6.76
Fertilization -> Endangered breeding birds	-0.35	-0.33	0.14	0.14	2.57
Fertilization -> FORAGE QUALITY	0.36	0.36	0.12	0.12	2.97
Fertilization -> Forage sales	0.65	0.62	0.10	0.10	6.84
Fertilization -> SOC	-0.33	-0.32	0.11	0.11	2.95
FORAGE QUALITY -> Forage sales	0.21	0.22	0.07	0.07	3.09
Nature protection -> Biomass removal	-0.74	-0.75	0.06	0.06	11.84
Nature protection -> Fertilization	-0.60	-0.60	0.09	0.09	6.84
NUTRIENTS-> Forage sales	-0.29	-0.30	0.08	0.08	3.87
NUTRIENTS -> SOC	0.44	0.43	0.11	0.11	4.13
Plant diversity -> Endangered plants	0.59	0.61	0.08	0.08	7.84
WATER -> Endangered plants	0.54	0.55	0.07	0.07	8.13
WATER -> FORAGE QUALITY	0.27	0.27	0.14	0.14	2.00
WATER -> Nature protection	0.72	0.72	0.06	0.06	12.98
WATER -> NUTRIENTS	0.65	0.68	0.07	0.07	9.11

Appendices Chapter 6

Appendix 6.1: Definitions for vegetation units and ecosystem services developed by the stakeholders.

Vegetation units	
Intensive grassland	Agricultural used areas, mowing and grazing. Intensively-used areas with up to 5 mowings, high nutrient input. High stocking rates.
Extensive wet grasslands	Protected areas or areas which are in use under protected standards. Maintenance of soils, no artificial nutrients, cut once per year. Low stocking rates.
Reed stands and sedges	Natural or human made. Vegetation associated with high groundwater levels where the vegetation is mainly dominated by reed or sedges. Typical wetland vegetation.
Salt marshes	Dike foreland. Area between main dike and water line, flooded area. Natural coastal protection, wave attenuation.
Ecosystem services	
Forage production	Forage production.
Carbon sequestration	Reed promotes peat-formation and therefore reduction of CO_2
Regional belonging	Regional belonging, the willingness to live there, traditional relations and land use in terms of ecosystems (“natural” landscape features).
Nature conservation value	Presence of species and habitats with high conservation status.
Soil fertility	Soils are habitats for plants, animals and humans. They act as a groundwater filter, store nutrients and accumulate organic matter.

Appendix 6.2: Quality criteria measures for the latent variables. AVE: average variance extracted and composite reliability (indicator for internal consistency reliability), should be higher than 0.5 and 0.7 according to Hair et al. (2011).

Model 1a) Conservationists' forage production perception model			
	AVE	Composite Reliability	R Square
Forage quality	0.76	0.86	
Conservationists' forage production perception			0.86
Model 1b) Conservationists' PRESERVATION perception model			
	AVE	Composite Reliability	R Square
Conservationists' CONSERVATION or PRESERVATION perception	0.85	0.98	0.80
Water	0.77	0.87	
Model 1c) Farmers' AGRICULTURE perception model			
	AVE	Composite Reliability	R Square
Farmers' AGRICULTURE perception	0.86	0.95	0.76
Forage quality	0.76	0.86	
Nutrients	0.52	0.75	
Model 1d) Farmers' nature conservation perception model			
	AVE	Composite Reliability	R Square
Farmers' nature conservation perception			0.80
Forage quality	0.76	0.86	
Model 2a) Conservationists' carbon sequestration perception model			
	AVE	Composite Reliability	R Square
Conservationists' carbon sequestration perception			0.37
Water gradient	0.77	0.87	
Model 2b) Farmers' carbon sequestration perception model			
	AVE	Composite Reliability	R Square
Farmers' carbon sequestration perception			0.59
Nature protection			
Water gradient	0.76	0.86	

Appendix 6.3: Positions and affiliations of the stakeholders that joined the participatory process.

	Stakeholder position	Affiliation	Abbreviation
Farmers	Chairman	Farmers Association East Frisia	F1
	Director	Farmers Association East Frisia	F2
	Administrator	Chamber of Agriculture Lower Saxony	F3
	Farmer	-	F4
Conservationists	Head	Common Wadden Sea Secretariat	C1
	NGO member	Nature conservation station Fehntjer Tief	C2
	NGO member	NABU (Nature and biodiversity conservation union)	C3
	NGO	NABU (Nature and biodiversity conservation union)	C4
	Administrator	Lower Nature Conservation Authority	C5
	Administrator	Biosphere Authority Lower Saxony	C6
	Administrator	National Park Authority Lower Saxony	C7

Appendices Chapter 7

Appendix 7.1: Final model quality measures for latent variables. Abbreviations; WATER: Co-variation of salinity and groundwater levels: Nuts: Soil available nutrients.

Latent variable coefficients					
	PLANT GROWTH	SIZE AXIS	WATER	FORAGE QUALITY	Nuts.
Composite reliability	0.90	0.98	0.87	0.86	0.77
Average variances extracted (AVE)	0.83	0.94	0.77	0.76	0.54
R-Square	0,74	0,43		0,36	0,39

Appendices Chapter 8

Appendix 8.1: Correlation matrix for biotic ecosystem properties and values of final ecosystem services. Spearman' correlations. Significance: **: p<0.01 *p<0.05. N: 46. Abbreviations: CWM: Community-weighted means; NS: Non-significant correlation.

	SOC	AGB	Forage quality (Species-based CWM)	Decomposition	Forage sales	Breeding bird richness	Plant richness	Endangered plants	Endangered breeding birds
SOC									
AGB	NS								
Forage quality (Species-based CWM)	NS	NS							
Decomposition	NS	-0.53**	0.53**						
Forage sales	NS	-0.66**	NS	0.67**					
Breeding bird rich.	NS	NS	NS	-0.39**	-0.44**				
Plant richness	NS	-0.76**	NS	0.47**	0.53**	NS			
Endangered plants	NS	-0.30*	NS	NS	NS	NS	0.50**		
Endangered breeding birds	NS	NS	0.30*	0.38**	0.43**	0.30*	NS	NS	

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Curriculum Vitae

Personal infomation

Name:	Miguel Ángel Cebrián-Piqueras
Date of birth:	27 of July of 1979
Place:	Albacete, Spain

Academic background

06/2016-Ongoing	Research Fellow and Lecturer (Habilitation Process) Leibniz University of Hanover, Germany Institute of Environmental Planning
06/2011-02/2017	PhD in Landscape Ecology University of Oldenburg, Oldenburg, Germany Landscape Ecology Group Thesis supervisor: Prof. Dr. Michael Kleyer
02/2007-02/2009	MSc in Landscape Ecology (120 ECTS) University of Aarhus, Aarhus, Denmark Thesis supervisors: Jens. M. Olesen and Bo Dalsgaard Fieldwork in Monteverde Cloud Forest Preserve (Costa Rica)
09/2004-06/2005	Postgraduate program-Boreal Biota and Ecology (60 ECTS) University of Helsinki, Helsinki, Finland Department of Biological and Environmental Sciences Metapopulation Research Group; Ilka Hanski' Group.
09/1998-02/2006	Environmental Science Diploma (311 ETCS) University of Elche (UMH), Elche, Spain Thesis supervisors: Eduardo Minguez and Andreas Linden

Professional experience in landscape ecology and landscape planning

04/2009-05/2011	ECOMIMESIS; Almeria, Spain Environmental and landscape planning, nature conservation and environmental awareness
06/2009-10/2009	BERLIN BOTANICAL GARDEN; Berlin, Germany Seed bank procedures and monitoring of endangered plant species
09/2007-10/2008	ADIMAN; Cuenca, Spain Environmental and regional planning, nature conservation and environmental awareness
06/2006-01/2007	UMH University, Elche, Spain Landscape ecology, environmental impact assessment and endangered species monitoring
01/2004-01/2007	ELCHE CITY COUNCIL, Department of Environment and Nature Protection; Elche, Spain Nature conservation, species monitoring and environmental awareness

List of peer-review publications

Cebrián-Piqueras, M. A., Trinogga, J., Grande, C., Minden, V., Maier, M., & Kleyer, M. (2017). Interactions between ecosystem properties and land use clarify spatial strategies to optimize trade-offs between agriculture and species conservation. *International Journal of Biodiversity Science, Ecosystem Services & Management*, *13*(2), 53-66.

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Lewandowska, A. M., Biermann, A., Borer, E. T., **Cebrián-Piqueras, M. A**., Declerck, S. A., De Meester, L., ... & Harpole, W. S. (2016). The influence of balanced and imbalanced resource supply on biodiversity–functioning relationship across ecosystems. *Phil. Trans. R. Soc. B*, *371*(1694), 20150283.

Minden, V., Scherber, C., **Cebrián-Piqueras, M. A.,** Trinogga, J., Trenkamp, A., Mantilla-Contreras, J., ... & Kleyer, M. (2016). Consistent drivers of plant biodiversity across managed ecosystems. *Phil. Trans. R. Soc. B*, *371*(1694), 20150284.

Cebrián-Piqueras, M. A. et al. Plant functional traits respond to environmental gradients and explain trade-offs and synergies between multiple ecosystem services. *In preparation.*

Grande, C., Stahl, J., Maier, M., **Cebrián-Piqueras, M.A.**, Trenkamp, A., Trinogga, J., Kleyer, M. Direct and indirect effects of land management on threatened birds in coastal habitats. *Submitted.*

Participation in conferences

09/2014	GFÖ annual meeting conference, Hildesheim, Germany *"Drivers of ecosystem services variation in coastal grasslands"*
09/2014	NRG-BESS conference, Southampton, UK *"Ecosystem services provision in coastal grasslands "*
09/2013	Open Landscapes conference, Hildesheim, Germany "*Sustainable management in coastal grasslands: Trade-offs and synergies"*
09/2013	GFÖ annual meeting conference, Potsdam, Germany "*Trade-offs and synergies between ecosystem services in coastal habitats*"
10/2013	CEW, Coastal Ecology Workshop, Spikeroog, Germany "*Stakeholders' perceptions about ecosystem services provision in a temperate coastal marsh landscape"*
09/2012	Sustainable Development Network Workshop, Cozumel, Mexico *"Scaling up from plant functional traits to ecosystem services"*
04/2009	ECOFLOR, Santiago de Compostela, Spain "*Modularity of a pollination network in a tropical cloud forest "*

Authors' contributions

Chapters 1; 2; 3; 4 and 8 were conceived and written by Miguel A. Cebrián-Piqueras.

Chapter 5: *Interactions between ecosystem properties and land use resolve trade-offs between forage production and species conservation in coastal lowlands*

Authors: Miguel Ángel Cebrián-Piqueras (MC), Juliane Trinogga (JT), Celia Grande (CG), Vanessa Minden (VM), Martin Maier (MM) and Michael Kleyer (MK)

MK conceived the study; MC performed vegetation surveys; MC collected and measured part of the abiotic parameters on the field; MC collected biomass samples to calculate disturbance; MC collected biotic properties on the field and supervised lab processing; MC conducted farmers' surveys about land use; JT conducted the analysis of plant nutrients' content on the lab; CG conducted the bird surveys, VM conducted part of the soil nutrients analysis; MM managed the database and provide the required data; MK conducted the soil parameters' analysis. MC analysed the data, MC wrote the initial draft of the manuscript; all authors contributed to the final version of the manuscript.

Chapter 6: *Coupling stakeholder assessments of ecosystem services with biophysical ecosystem properties reveals importance of social contexts*

Authors: M.A. Cebrián-Piqueras (MC), L. Karrasch (LK) and M. Kleyer (MK).

MC and MK conceived the study, LK conducted the stakeholders' surveys; MK conducted the soil parameters analysis; MC collected and measured part of the abiotic and biotic ecosystem properties data; MC analysed the data, MC wrote the initial draft of the manuscript; all authors contributed to the final version of the manuscript.

Chapter 7: *Plant functional traits respond to environmental gradients and explain trade-offs and synergies between bundles of ecosystem properties and services*

Author: M.A. Cebrián-Piqueras (MC)

MK conceived the study; MC, VM, JT, Silke Eilers, Anastasia Trenkamp and Camilla Fløjgaard collected and measured the plant traits. MK conducted the soil parameters' analysis; MC collected and measured part of the abiotic and biotic ecosystem properties data; MC analysed the data, MC wrote the manuscript; MK commented and corrected the manuscript. MM managed, updated the database and provide the require data.

Selected Pictures


OCEAN

Erklärungen gemäß der Promotionsordnung

Erklärungen gemäß der Promotionsordnung der Fakultät für Mathematik und Naturwissenschaften der Carl von Ossietzky Universität Oldenburg vom 21.03.2013

Hiermit erkläre ich, dass

• die vorliegende Dissertation von mir selbständig verfasst wurde und ich die benutzten Hilfsmittel vollständig angegeben habe.

• die vorliegende Dissertation weder in ihrer Gesamtheit noch in Teilen einer anderen wissenschaftlichen Hochschule zur Begutachtung in einem Promotionsverfahren vorliegt oder vorgelegen hat.

• der Grad eines Doktors verliehen werden soll.

• ich die Leitlinien guter wissenschaftlicher Praxis an der Carl von Ossietzky Universität Oldenburg befolgt habe.

• ich im Zusammenhang mit dem Promotionsvorhaben keine kommerziellen Vermittlungs- oder Beratungsdienste (Promotionsberatung) in Anspruch genommen habe.

Oldenburg, den 30 September 2016

Miguel Ángel Cebrián-Piqueras