Interactions between ecosystem properties and land use clarify spatial strategies to optimize trade-offs between agriculture and species conservation

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ABSTRACT
Species conservation and forage production are both important, yet conflicting components of sustainable grassland management. We modeled forage production and conservation value as dependent variables in a chain of responses and effects, starting with abiotic environmental conditions that affect the spatial distribution of land use and biotic ecosystem properties. We asked which relationships in this causal chain determine trade-offs between forage production and conservation value. Abiotic and biotic ecosystem properties were recorded on 46 plots in the coastal marshes of Northwest Germany. 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 structural equation model to determine responses and effects. Groundwater depth and salinity represent the ultimate causes for the spatial variation in sales and conservation value. The water gradient translated into more proximate causes, such as land-use intensity affecting aboveground net primary productivity, forage quality, and species richness. Plant species conservation and forage production were segregated along the water gradient, and both bird conservation and forage production depended on grassland management, albeit at different fertilization levels. Our study points to segregation and integration as two spatial strategies to react to trade-offs between services.

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).

The intensification of food production and the abandonment of extensive land use, such as seminatural grasslands, is due to an increasing prioritization of the provision of agricultural goods over species conservation. Many authors report that agricultural landscapes now host fewer species than in earlier centuries (e.g. 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, studies have called for a theoretical understanding of the multiple relationships between drivers of change and ecosystem services (e.g. Bennett et al. 2009). This requires a systems-based approach, addressing structural and functional relationships between environmental drivers of change, ecosystem properties, and corresponding 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). 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 can be intensified. Therefore, in a given landscape the relationships between the provisioning services and species conservation need to be linked to measured environmental conditions, land uses, and ecosystem properties.

Because trade-offs and synergies may occur on different scales (Lavorel & Grigulis 2012), research on the biophysical processes that drive ecosystem services is also essential for the implementation of successful land management schemes (Wong et al. 2015). However, such studies are still scarce. Seppelt
et al. (2011) found that few ecosystem service studies base their results on measured or observed data, and few identify interactions among ecosystem properties generating ecosystem services. Many studies also fail to indicate the uncertainty in their results, or to capture relationships between ecosystem services. Here, we investigate the potential trade-off between agricultural production and biodiversity conservation in coastal lowlands as a chain of interactions between the abiotic environment, biotic ecosystem properties and these services. At the landscape scale, soil and water resources drive the spatial distribution of land use and land abandonment, which collectively represent the drivers of change.

Globally, coastal lowlands are some of the most strongly threatened and modified landscapes (Huston 2014). These modifications comprise dikes to exclude storm surges, artificial drainage, agricultural intensification, settlements, and technical infrastructure construction, which together 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). Intensification of forage production by high levels of fertilizer application, more drainage, and the earlier onset of grazing and mowing may have led to an increased threat to plants and animals, as shown for floodplains (Krause et al. 2011; Wesche et al. 2012).

According to ecosystem service classifications (e.g. Haines-Young & Potschin 2013), the generation of sales from forage-based products falls into the category of provisioning services that can be translated into an economic value (de Groot et al. 2010). The value of conserving endangered plant species and breeding birds represents a nonuse existence, bequest or philanthropic cultural service. Each of them depends to some extent on biotic ecosystem properties such as biomass production and quality, species diversity, soil organic carbon (SOC) stocks, or biomass decomposition. In turn, these ecosystem properties depend not only on environmental conditions such as groundwater and nutrient availability, and soil aeration but also on the land uses that modify these properties (de Bello et al. 2008; Lavorel et al. 2011; Lavorel & Grigulis 2012).

In this study, we focused on the interactions between abiotic environment and biotic ecosystem properties that generate trade-offs or synergies between agricultural production and biodiversity conservation (Lavorel & Grigulis 2012; Wong et al. 2015). In addition, we are interested in the implications for spatial land management allocation resulting from these trade-offs or synergies (Bateman et al. 2013). We aim to identify the relevant predictors that determine the value of ecosystems for the provision of forage-based agricultural products and for the conservation of endangered plants and birds in coastal lowlands.

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

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) (Figure 1). It has a mean annual temperature of 9.4°C and receives a mean annual rainfall of 823 mm. A single large seawall 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 seaward of the dike, and crop fields lie in a narrow, elevated strip of a few kilometers width behind the seawall. 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 has been abandoned. Forty-six plots located

![Figure 1. Map of the study area. Fields in white color, grassland and water courses in dark grey color, settlements in light grey color; left side: Wadden Sea. Map layout: Christian Aden, map source: LGN Lower Saxony.](image-url)
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.

2.1. Ecosystem properties, land-use intensity, and ecosystem services

There are different and sometimes controversial conceptual models, frameworks, and classifications of the relationships between land management, ecosystem functions, and services available (e.g. de Groot 1992; Costanza et al. 1997; MEA 2003; TEEB 2010; Potschin & Haines-Young 2011). Here, we rather pragmatically define all parameters as ecosystem properties that can be expressed in physical, chemical, or biological units (except nature protection status and grassland utilization indicator values, see below). The economic and normative values of ecosystems for the generation of sales of forage-based agricultural products and the conservation of endangered plants and birds are seen as indicators for services, although some authors categorized the former as good or of benefit value that derives from services (e.g. UK NEA 2011). Sales better reflect the agronomic value of forage, as compared to the simple mass of produced forage.

2.2. Abiotic ecosystem properties

For each soil horizon on each plot down to a depth of 80 cm, 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 biweekly during the vegetation period between March and October 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, and as a proxy for salinity, groundwater electrical conductivity was measured with WTW ph/Cond340i/SET using a Tetracon 325 electrode (see Table 1 for variable descriptors).

2.3. Land use

We assessed land-use regulation according to German official 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), 3 (nature reserve, 13 plots), or 5 (national park, 19 plots). Other legal categories such as nature park and biosphere reserve

Table 1. Variable descriptors and abbreviation names. N: 46.

| Variable | Abbreviation | Units | Min. | Max. | Mean or median |
|----------|--------------|-------|------|------|----------------|
| (a) Abiotic ecosystem properties | | | | | |
| Plant available soil potassium content* | K | g/m$^2$ (80 cm. depth) | 9.57 | 837.79 | 417.81 |
| Plant available soil phosphorous content* | P | g/m$^2$ (80 cm. depth) | 5.66 | 134.55 | 47.21 |
| Plant available soil nitrogen* | N | g/m$^2$ (30 cm. depth) | 8.40 | 157.10 | 53.20 |
| Mean groundwater conductivity** | Salinity | mS/cm | –100 | –7.6 | –42.9 |
| Cation exchange capacity** | CEC | cmol+/kg | 0.00 | 37.32 | 13.20 |
| Inorganic fertilization | Fertilization | kg of N /ha/year | 0.00 | 250.00 | 29.04 |
| Nature protection status index | Nature protection Index | 0 | 5 | 2 |
| Biomass removal | Biomass removal % | 0.00 | 91.94 | 32.89 |
| (c) Biotic ecosystem properties | | | | | |
|*** Utilization indicator value (CWM) | Utilization value | Index | 3 | 9 | 5 |
|**Native biomass decomposition rate | Decomposition | %/day | 0.01 | 0.45 | 0.26 |
| Plant species richness | Plant richness | Counts of Species/Plot | 1 | 15 | 7 |
| Soil organic carbon stock | SOC | kg/m$^3$ (30 cm depth) | 3.46 | 119.97 | 25.88 |
| Aboveground net primary productivity | ANPP | g/day/m$^2$ | 0.79 | 13.66 | 5.68 |
| Breeding bird species richness | Breeding bird richness | Counts of Species /ha/Patch | 0 | 9 | 4 |
| (d) Services | | | | | |
| Sales of forage-based agricultural products | Forage sales | €/ha/year | 0.00 | 4400.00 | 912.83 |
| Conservation value of endangered birds | Endan. plants conservation index | 0 | 22 | 4 |
| Conservation value of endangered plants | Endan. birds conservation index | 0 | 8 | 0 |

*Variables which are used as indicator variables (observed) for ‘NUTRIENTS’ (latent, nonobserved variable). **Indicator variables used for the latent variable ‘WATER’. ***Variables used as indicator variables for the latent variable ‘FORAGE QUALITY’. CWM: Community weighted mean. Means were replaced with medians for ordinal indices or counts.
would fall between these ranks (2 and 4, respectively), but were not applicable in the study area.

Land-use intensity was described by two continuous parameters: biomass removal and fertilization. Biomass removal was quantified using fenced enclosures of 4 m², where grazing or mowing was not possible. During peak vegetation, we collected the community aboveground biomass on a subplot with a size of 0.5 m² inside and outside each enclosure (de Leeuw et al. 1990). The samples were sorted according to live and dead biomass, oven-dried at 70°C for 72 h, and then weighed. The percentage of biomass removal (hereafter disturbance) was calculated from the difference between both samples. Biomass values were normalized to 1 m². The amount of applied inorganic fertilizer (kg of applied nitrogen per hectare and year) was obtained by interviewing farmers and landowners managing the different plots during 2012. Most plots were fertilized with calcium ammonium nitrate (27% N and 10% Ca).

2.4. Biotic ecosystem properties

Plant species composition and abundance was recorded by frequency analysis at each plot in the summer of 2012, using a 1 × 1 m grid of 100 cells (each 10 × 10 cm). Breeding bird species were surveyed according to Südebeck et al. (2007) on nine visits during each breeding season over 3 years (2011–2013), while recording territorial or breeding behavior in homogeneous 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 BIOFLOR database (http://www2.ufz.de/bioflor/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. SOC was measured for the first 30 cm as the difference between CaCO₃ and total carbon values.

Calcium carbonate (CaCO₃) 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 h.

From the abovementioned biomass samples, we obtained aboveground net primary productivity (ANPP). 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 h 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/m²/day (Scurlock et al. 2002; Garnier et al. 2007)).

2.5. 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 per hectare and year in Euros during 2012.

The conservation value of endangered plants was calculated as an index. Every plant species was assigned a value according to the German Red List (www.floraweb.de), translated to the International Union of Conservation of Nature (IUCN) levels of conservation concern as follows: not evaluated and lesser concern: 0; near threatened: 1; vulnerable: 2; endangered: 3; critically endangered: 4. Subsequently, the final conservation value of endangered plants was calculated as the sum of all values of the species occurring in a plot.

The conservation value of endangered breeding birds was calculated according to the method used by Behm and Krüger (2013). Based on the German red list status of a species (Südebeck et al. 2007), points were given per breeding pair and 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 threatened species categories (vulnerable, endangered, and critically endangered) were included in the index.

2.6. Statistical analysis

The structural equation modeling approach requires the development of an initial model that comprises all hypothesized relationships between environmental, ecosystem, and service variables, based on the available literature. This initial model is then tested against a dependence model, to assess which relationships are significant. We used partial least square analysis (PLS-SEM; Hair Jr et al. 2013) to
test the initial model, which is explained below in more detail (see also Figure 2). PLS-SEM has been extensively used in the social sciences and recently introduced into ecological studies (Pepppler-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 does, however, allow the introduction of latent variables, which are non-observed variables aggregating the information of several correlated observed variables, similar to the scores of the 1st axis of a principal components analysis. Using Spearman correlation coefficients and a two-tailed significance test, correlated observed variables were identified prior to the modeling. The following latent variables were created from 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 2 and Figure 2). 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 (Table 2 and Figure 2), because they were not significant (Hair et al. 2011).

2.7. Initial model

For better visualization, the initial model was divided into four graphs, one for biophysical processes (Figure 2(a)) and one for each ecosystem service (Figure 2(b–d)). The model assumed that abiotic ecosystem properties influence land-use intensity and that both determine biotic ecosystem properties, which together affect sales and conservation value of endangered plants and birds. To represent a potential trade-off, we assumed a negative correlation between the latter (Figure 2(c,d)) (Kleijn et al. 2006; Zhang et al. 2007).

Environmental relationships (Figure 2(a)): Soil texture and water conditions often determine the allocation of land uses in space (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 seawater 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 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 variables that are not explained by other variables. All other variables were considered endogenous and with measurement error.

Relationships among ecosystem properties (Figure 2(a)): Vegetation forage quality (latent variable ‘FORAGE QUALITY’) should increase with nutrient availability, CEC, and fertilization (Lavorel & Grigulis 2012). SOC should increase with nutrient availability and ANPP (Bateman et al. 2013; Conti & Diaz 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).

Ecosystem effects on services (Figure 2(b,c,d)): Sales of forage-based products should increase with forage quality, NUTRIENTS, and fertilization. ANPP per se is unlikely to affect sales, because unmanaged reeds produce even higher amounts of biomass than fertilized pastures. The probability of finding both plant and bird species with higher conservation value 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
Figure 2. Initial model with expected responses and effects between ecosystem properties and services. Rectangles represent measured variables (‘observed variables’), ovals represent latent variables: ‘NUTRIENTS’ (available phosphorus, potassium and nitrogen); ‘WATER’ (mean groundwater level and salinity); ‘FORAGE QUALITY’ (native biomass decomposition and grassland utilization indicator value) (see Table 1). (a) Expected relationships between abiotics, land-use and biotic ecosystem properties. (b), (c), and (d) Expected direct effects on forage sales, endangered breeding bird conservation, and endangered plant conservation, respectively. Note that (a), (b), (c), and (d) are all part of the same model and were only separated for better visualization. Expected positive links are shown with solid black arrows and negative links with dashed black arrows. ESP: Ecosystem properties. Further abbreviations, see Table 1.
on sufficient prey for precocial chicks and for adults (Beintema et al. 1991). We were not able to collect data on prey abundance and prey energy content. 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, an increased number of mowing events, a more uniform sward, and with a lower biomass of grassland invertebrates, should therefore decrease the conservation values of endangered birds and plants (Vickery et al. 2001; Newton 2004).

### 3. Results

The structural equation model (separated into several sections in Figure 3) was consistent with the initial model; only 6 out of 29 paths were not significant and were removed from the final model. 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 (Hair et al. 2011) (Table 4).

The most relevant deviation from the initial model was that there was no direct trade-off between sales of forage-based products and the habitat value for bird or plant conservation (Figure 3, Table 3). However, a separate bivariate correlation analysis showed that sales of forage-based products was positively related to the conservation value of endangered breeding birds ($r_{\text{Spearman}} = 0.43; p < 0.05$). Furthermore, the following paths were removed because they were not significant: CEC $\rightarrow$ NUTRIENTS, fertilization $\rightarrow$ conservation value of endangered plants, conservation value of endangered birds, ANPP $\rightarrow$ breeding bird richness. As a consequence, breeding bird richness was unrelated to any environmental, land-use, or ecosystem property parameter (Figure 3 and Table 2). Since it still explained the conservation value of endangered birds, it became the third exogenous variable (together with WATER and CEC).

According to the standardized regression coefficients of the direct, indirect, and total effects (Figure 3 and Table 5, 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 had been abandoned, so correlations with disturbance and fertilization were negative. SOC strongly increased with biomass removal.

The following paths were weaker, yet also significant: Fertilization of landward grasslands increased nutrient availability. Biomass removal 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 (Figure 3, Table 5). Plant species richness decreased with increasing ANPP.

### Table 2. Bootstrapping analysis, N: 46. 5000 runs. T values higher than 1.96 are significant at 5% (Hair et al. 2011). Only significant pathways (→) were left in the final model.

| Path                                      | Original sample (O) | Sample mean | Standard deviation | Standard error (STERR) | T statistics (|O/STERR|) |
|-------------------------------------------|---------------------|-------------|--------------------|------------------------|-----------------|
| ANPP $\rightarrow$ FORAGE QUALITY         | -0.4150             | -0.4106     | 0.1203             | 0.1203                 | 3.4486          |
| ANPP $\rightarrow$ Plant species richness| -0.7023             | -0.7008     | 0.0593             | 0.0593                 | 11.8419         |
| ANPP $\rightarrow$ SOC                    | 0.4044              | 0.3910      | 0.1712             | 0.1712                 | 2.3614          |
| Breeding bird richness $\rightarrow$ Bird conservation | 0.4161 | 0.4215 | 0.1267 | 0.1267 | 3.2848 |
| CEC $\rightarrow$ Bird conservation       | 0.4143              | 0.3770      | 0.2020             | 0.2020                 | 2.0508          |
| CEC $\rightarrow$ FORAGE QUALITY          | 0.3049              | 0.2998      | 0.1169             | 0.1169                 | 2.6078          |
| Biomass removal $\rightarrow$ ANPP         | -0.5515             | -0.5517     | 0.0846             | 0.0846                 | 6.5203          |
| Biomass removal $\rightarrow$ Bird conservation | 0.5080 | 0.5305 | 0.1629 | 0.1629 | 3.1191 |
| Biomass removal $\rightarrow$ SOC          | 0.8726              | 0.8731      | 0.1290             | 0.1290                 | 6.7618          |
| Fertilization $\rightarrow$ Bird conservation | -0.3536 | -0.3313 | 0.1372 | 0.1372 | 2.5774 |
| Fertilization $\rightarrow$ FORAGE QUALITY | 0.3630 | 0.3676 | 0.1221 | 0.1221 | 2.9724 |
| Fertilization $\rightarrow$ Forage sales   | 0.6567              | 0.6295      | 0.0959             | 0.0959                 | 6.8462          |
| Fertilization $\rightarrow$ SOC            | -0.3386             | -0.3200     | 0.1146             | 0.1146                 | 2.9555          |
| FORAGE QUALITY $\rightarrow$ Forage sales  | 0.2184              | 0.2256      | 0.0705             | 0.0705                 | 3.0992          |
| Nature protection $\rightarrow$ Biomass removal | -0.7481 | -0.7471 | 0.0632 | 0.0632 | 11.8445 |
| Nature protection $\rightarrow$ Fertilization | -0.6068 | -0.5989 | 0.0886 | 0.0886 | 6.8457 |
| NUTRIENTS $\rightarrow$ Forage sales       | -0.2969             | -0.3033     | 0.0767             | 0.0767                 | 3.8715          |
| NUTRIENTS $\rightarrow$ SOC                | 0.4410              | 0.4326      | 0.1065             | 0.1065                 | 4.1365          |
| Plant species richness $\rightarrow$ Plant conservation | 0.5982 | 0.6050 | 0.0763 | 0.0763 | 7.8430 |
| WATER $\rightarrow$ Plant conservation     | 0.5420              | 0.5476      | 0.0666             | 0.0666                 | 8.1365          |
| WATER $\rightarrow$ FORAGE QUALITY         | 0.2780              | 0.2725      | 0.1389             | 0.1389                 | 2.0021          |
| WATER $\rightarrow$ Nature protection      | 0.7221              | 0.7242      | 0.0556             | 0.0556                 | 12.9881         |
| WATER $\rightarrow$ NUTRIENTS              | 0.6563              | 0.6807      | 0.0720             | 0.0720                 | 9.1189          |
Figure 3. Structural equation model for (a) biotic and abiotic ecosystem properties and (b) sales of forage-based agricultural products, (c) conservation value of endangered breeding birds and (d) conservation value of endangered plants. Note that (a), (b), (c), and (d) are all part of the same model and were only separated for better visualization. Arrow thickness represents standardized regression coefficients for both positive (solid) and negative values (dashed). The explained $R^2$ is shown by the contour thickness (see legend). Rectangles represent measured variables ('observed variables'), ovals represent latent variables. ESP: Ecosystem properties; Latent variables: 'NUTRIENTS' (N (+), P (+) and K (+)); 'WATER': Groundwater level (+) and salinity (+); 'FORAGE QUALITY' (Native biomass decomposition (+) and grassland utilization indicator value (+)). Further abbreviations, see Table 1.
Table 3. Total, indirect, and direct links (TE, IE, and DE respectively) between ecosystem properties and services.

| Variable           | Forage sales ($R^2$: 0.76) | Endan. bird conservation ($R^2$: 0.49) | Endan. plant conservation ($R^2$: 0.49) |
|--------------------|----------------------------|---------------------------------------|---------------------------------------|
|                    | TE | IE | DE | TE | IE | DE | TE | IE | DE |
| NUTRIENTS          | −0.30 | NS | −0.30 | 0.41 | 0.41 | 0.42 | −0.12 | 0.54 |
| CEC                | −0.50 | −0.50 | −0.23 | −0.23 | −0.35 | −0.35 | −0.17 | −0.17 |
| WATER              | 0.74 | 0.08 | 0.66 | −0.35 | 0.70 | 0.20 | 0.50 | 0.23 | 0.23 |
| Fertilization      | −0.50 | −0.50 | −0.17 | −0.17 | −0.17 | −0.17 | −0.17 | −0.17 | −0.17 |
| Nature protection  | 0.08 | 0.08 | 0.70 | 0.20 | 0.50 | 0.23 | 0.23 | 0.23 | 0.23 |
| Biomass removal    | 0.22 | 0.22 | 0.42 | 0.42 | 0.6 | 0.6 | 0.6 | 0.6 | 0.6 |
| FORAGE QUALITY     | −0.09 | −0.09 | −0.42 | −0.42 | −0.42 | −0.42 | −0.42 | −0.42 | −0.42 |
| ANPP               | 0.29 | 0.27 | 0.30 | 0.30 | 0.30 | 0.30 | 0.30 | 0.30 | 0.30 |
| Breeding bird richness | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 |
| Plant richness     | 0.55 | 0.78 | 0.43 | 0.43 | 0.43 | 0.43 | 0.43 | 0.43 | 0.43 |
| Soil organic carbon| 1.00 | 1.00 | 0.39 | 0.39 | 0.39 | 0.39 | 0.39 | 0.39 | 0.39 |
| WATER              | 0.75 | 0.86 | Empty cell | Empty cell | Empty cell | Empty cell | Empty cell | Empty cell | Empty cell |

The values represent the standardized regression coefficients. All relationships are significant at $p < 0.05$. NS: not significant. Total effects are the sum of direct and indirect effects. Abbreviations see Table 1.

Table 4. 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 (Hair et al. 2011).

| Variable          | AVE | Composite reliability | $R^2$ |
|-------------------|-----|-----------------------|-------|
| ANPP              | 1.0 | 1.00                  | 0.30  |
| Breeding bird richness | 1.00 | 1.00 | 0.48 |
| CEC               | 1.0 | 1.00                  | 0.56  |
| Plant conservation| 1.0 | 1.00                  | 0.49  |
| Biomass removal    | 0.76 | 0.86 | 0.52 |
| Fertilization      | 1.0 | 1.00                  | 0.37  |
| Nature protection  | 1.0 | 1.00                  | 0.52  |
| NUTRIENTS         | 0.55 | 0.78 | 0.43 |
| Forage sales       | 1.0 | 1.00                  | 0.76  |
| Nature protection  | 1.0 | 1.00                  | 0.52  |
| NUTRIENTS         | 0.55 | 0.78 | 0.43 |
| Plant richness     | 1.0 | 1.00                  | 0.49  |
| SOC               | 1.0 | 1.00                  | 0.39  |
| WATER             | 0.75 | 0.86 | Empty cell |

3.1. Service responses to ecosystem properties and land use

Sales of forage-based agricultural products were largely well explained by the model (Figure 3 and Table 3). In accordance with our initial model (Figure 2), sales of forage-based products were associated with FORAGE QUALITY, though not strongly. Both intensive grasslands landward of the seawall and salt marshes seaward of the seawall featured relatively high FORAGE QUALITY. However, the salt marshes did not provide any sales from forage due to conservation regulations that led to the abandonment of mowing and grazing (Villbrandt et al. 1999). Sales increased with fertilization and decreased with WATER, which points to the intensively managed, clayey, and well-drained grasslands landward of the seawall, where most forage was produced. In contrast, both ANPP, which was higher in reeds, and NUTRIENTS, which was highest in the salt marshes, were negatively associated with sales.

The conservation value of endangered breeding birds were moderately well explained (Figure 3 and Table 3) and responded positively to biomass removal and potential CEC, but negatively to fertilization and also indirectly and negatively to the water gradient (Table 3). Contrary to our expectations, SOC did not affect the occurrence of endangered breeding birds.

The conservation value of endangered plants was moderately well explained by WATER and plant species richness (Figure 3 and Table 3). We also found indirect positive effects of biomass removal, as well as indirect negative effects of nature protection and ANPP. This result points to seaward salt marshes and to landward wet meadows, which all host relatively high numbers of endangered plants, but the wet meadows are not protected.

Table 5. Total effects between environment, land-use parameters, and biotic ecosystem properties. The values represent the standardized regression coefficients. NS: Not significant.

| ANPP | FORAGE QUALITY | NUTRIENTS | Plant richness | SOC |
|------|----------------|-----------|----------------|-----|
| −0.44| 0.58           | 0.42      | 0.42           | 0.65|
| −0.44| −0.37         | −0.17     | −0.32          | −0.34|
| 0.16 | 0.16           | 0.68      | −0.23          | 0.10|

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 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, SOC, plant diversity, and forage quality. Finally, sales of forage-based products and endangered species were dependent on the water gradient, potential CEC, land-use intensity, and species richness.

Contrary to our expectations, the potential CEC did not have a significant effect on nutrient availability, because the import of nutrients to salt marshes from seawater (Rozema et al. 2000) outweighed the effect of CEC, which was lower in salt marshes than in the more clayey inland soils. Additionally, breeding bird richness did not depend on ANPP. We attribute this to the fact that the 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, in salt marshes with intermediate ANPP and in 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. The conservation value of endangered breeding birds was unrelated to 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 is a poor predictor of prey availability (Scheckerman & Boele 2009). Even more so, our assumption that SOC would be informative on prey supply was probably too simplistic to capture the relationship between birds and their habitat requirement resources.

Most importantly, we did not find a direct trade-off between forage sales and conservation value, 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 is optimized at the landscape scale. The water gradient, ranging from rain-fed, well-drained sites 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. Proximate causes for the generation of forage sales 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 forage sales. 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, 2015). Salt marsh forage quality was similar to the inland pastures, but nature protection precluded the generation of sales of forage-based products from the resource. This is reflected in the opposed paths from NUTRIENTS to FORAGE QUALITY and sales of forage-based products.

On the landward, rain-fed marshes, the trade-off between plant species protection and forage sales 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. The spatial division of the coastal landscape into a landward part optimized for agricultural production and a seaward part for plant species conservation is indicated by the direct and indirect effects of the water gradient. It is also responsible for the fact that the trade-off between both services did not surface in our model.

In contrast to plants, the conservation value of endangered birds depended on the same direct and indirect predictors as the sales of forage-based agricultural products, 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 sales increased with fertilization. Lower fertilization accompanied less drainage and lower stocking rates, facilitating successful reproduction of meadow birds (Newton 2004; Kentie et al. 2013).

In summary, trade-offs between species protection and sales of forage-based products on inland marshes have 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, forage production was optimized at the expense of species protection. Decisions to increase income from less intensively used grasslands might thus put their protection service at risk (Kremen & Miles 2012).

5. Conclusion
Some studies have focused on spatial aspects of multiple ecosystem service provisioning (e.g. Chan et al. 2006). Our study points to two spatial strategies to
optimize potential trade-offs among ecosystem services. The first is the 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 seawall are optimized to provide agricultural production. Seaward of the dike, all land use has been abandoned and strict nature protection applied. This has resulted in two adjacent monofunctional landscapes explained by the water gradient. The segregation approach appears to be promising for nature conservation, as farming can be 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. The more widespread fertile, mesic landscapes are reserved for maximizing provisioning services, leading to strong impoverishment of their species pools (Walker et al. 2004).

In contrast to the segregation of forage production and the protection of endangered plants, 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 restored wetlands and moderately managed grasslands that enable breeding of meadow birds, while other grasslands should be optimized for income from forage. The integrated approach has the potential to reconcile the conservation of plants and birds within the cultivated landscape. It has a long history in spatial planning (e.g. Haber 1973) and requires sensitive management both at the catchment and the local scale, both to conserve endangered species and yield farming income in the same landscape (de Groot et al. 2010; Maes et al. 2012; Gonthier et al. 2014). Lower sales of forage-based products due to reduced management intensity are now often compensated by state subsidies (van Noordwijk et al. 2014). The spatial arrangement of land-use intensities may, however, not necessarily be static in time. In fact, former land uses were 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 & Voïnov 2003; Polasky et al. 2008; Schröter & Remme 2015).

Recent reviews called for a better understanding of the direct and indirect causes for variations in ecosystem services in order to improve landscape management. Here, we modeled multiple ecosystem services in a coastal landscape as dependents of a chain of responses and effects, starting with environmental conditions affecting land uses and ecosystem properties, which in turn affect services. 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 services. Direct negative interactions between the 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 synergy between meadow bird conservation and forage production, both depending on grassland management, albeit at different fertilization levels. Identifying the most relevant determinants of services improves action planning in management schemes. For instance, different levels of biomass removal, ANPP, and fertilization need to be allocated in space in order to both conserve endangered birds and to generate sales of forage-based products. 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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