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A quantitative index of land-use intensity in grasslands: Integrating mowing, grazing and fertilization

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Abstract

Land use is increasingly recognized as a major driver of biodiversity and ecosystem functioning in many current research projects. In grasslands, land use is often classified by categorical descriptors such as pastures versus meadows or fertilized versus unfertilized sites. However, to account for the quantitative variation of multiple land-use types in heterogeneous landscapes, a quantitative, continuous index of land-use intensity (LUI) is desirable. Here we define such a compound,

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[3] Equal contribution to overall design of study, analysis and writing.

[4] We dedicate this work to Elisabeth K.V. Kalko; it is with great disbelief and sadness as friends and colleagues that we had to accept her passing away while this work was reviewed.

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additive LUI index for managed grasslands including meadows and pastures. The LUI index summarizes the standardized intensity of three components of land use, namely fertilization, mowing, and livestock grazing at each site. We examined the performance of the LUI index to predict selected response variables on up to 150 grassland sites in the Biodiversity Exploratories in three regions in Germany (Alb, Hainich, Schorfheide). We tested the average Ellenberg nitrogen indicator values of the plant community, nitrogen and phosphorus concentration in the aboveground plant biomass, plant-available phosphorus concentration in the top soil, and soil C/N ratio, and the first principle component of these five response variables.

The LUI index significantly predicted the principal component of all five response variables, as well as some of the individual responses. Moreover, vascular plant diversity decreased significantly with LUI in two regions (Alb and Hainich).

Inter-annual changes in management practice were pronounced from 2006 to 2008, particularly due to variation in grazing intensity. This rendered the selection of the appropriate reference year(s) an important decision for analyses of land-use effects, whereas details in the standardization of the index were of minor importance. We also tested several alternative calculations of a LUI index, but all are strongly linearly correlated to the proposed index.

The proposed LUI index reduces the complexity of agricultural practices to a single dimension and may serve as a baseline to test how different groups of organisms and processes respond to land use. In combination with more detailed analyses, this index may help to unravel whether and how land-use intensities, associated disturbance levels or other local or regional influences drive ecological processes.

Zusammenfassung

Menschliche Landnutzung als wichtiger Treiber für die Biodiversität und Funktionen von Ökosystemen wird zunehmend in Forschungsprojekte einbezogen. Im Grünland wird die Landnutzung dazu meist durch kategoriale Variablen beschrieben wie etwa Weiden vs. Wiesen oder gedüngte vs. ungedüngte Flächen. Um jedoch die quantitative Variation in der Intensität der Landnutzung besser beschreiben zu können sind kontinuierliche Maße der Landnutzung wünschenswert. Wir führen einen quantitativen Index zur Beschreibung der Landnutzungsintensität (LUI; land-use intensity) in bewirtschaftetem Grünland ein. Der LUI Index standardisiert und addiert drei wesentliche Komponenten der Grünlandnutzung, die Beweidung, die Mahd und die Düngung. Die Effizienz des LUI Index in Bezug auf die Vorhersagefähigkeit einer Reihe landnutzungsabhängiger Variablen wurde im Rahmen des Projekts Biodiversitätsexploratorien am Beispiel von 150 Grünlandflächen in drei Regionen Deutschlands (Alb, Hainich, Schorfheide) geprüft. Die Prüfvariablen umfassten die Stickstoffzahl nach Ellenberg, die Stickstoff- und Phosphorkonzentrationen in der Biomasse, die Konzentrationen von pflanzenverfügbarem Phosphor im Oberboden, das Boden-C/N-Verhältnis sowie die erste Hauptkomponente einer Ordination dieser Variablen.

Während der LUI Index Änderungen in der ersten Hauptkomponente der Antwortvariablen sowie einiger Einzelvariablen signifikant vorhersagte, waren Regressionen mit einzelnen LUI Komponenten problematisch, da diese Komponenten wie die Düngungsintensität oder Mahdfrequenz miteinander korreliert und somit konfundiert sind. Das Management der Grünlandflächen variierte im Zeitraum 2006 bis 2008 von Jahr zu Jahr, insbesondere aufgrund von Änderungen in der Beweidungsintensität. Das Referenzjahr für die Berechnungen der LUI war daher sehr wichtig, während verschiedene Standardisierungsmethoden keinen großen Einfluss auf den Index hatten. Einige alternative Berechnungsmethoden der Landnutzungsintensität korrelierten stark mit der vorschlagenen Form des Index.

Der LUI Index reduziert die verschiedenen, miteinander korrelierten Dimensionen der menschlichen Landnutzung im Grünland zu einer kontinuierlichen Variable und kann dazu dienen, die Abhängigkeit verschiedener Organismengruppen und Prozesse von der menschlichen Landnutzung zu prüfen. In Verbindung mit detaillierten Analysen kann die Verwendung dieses Index helfen, die relative Bedeutung der menschlichen Landnutzung im Vergleich zu anderen lokalen oder regionalen Faktoren zu erkennen.

Keywords: Agro-ecosystems; Biodiversity exploratories; Grassland management; Land-use impacts; Livestock density; Meadows; Nitrogen; Pastures

Introduction

Anthropogenic land use is known to strongly affect biodiversity, ecosystem functioning and functional stability (Laliberté et al. 2010; Sala et al. 2000). Our study considers grassland systems, which represent widespread land-use types in most central European agricultural regions and often support a high proportion of the regional species pool in a given area (e.g. Bakker & Berendse 1999; Dahms et al. 2010). Formerly, grasslands have been managed at low intensities, but are now prone to different kinds of land-use intensification (Green 1990), and are increasingly converted to species-poor “bioenergy” producing arable systems (Campbell, Lobell, Genova, & Field 2008). Such changes in land-use intensity affect biological communities, and a better understanding of the effects of land-use intensity on grassland biodiversity and ecosystem functioning is a major task in ecological research (Sala et al. 2000).

However, quantifying land-use intensity is not a trivial issue. Different concepts and measures of land use are currently applied, many of them based on categorical classifications such as disturbed vs. undisturbed, grazed vs. mown or fertilized vs. unfertilized. Whereas such broad categorizations are suitable for certain comparisons across sites, or for designed experimental studies, they fail to account for quantitative variation in land-use intensities, e.g. the level of disturbance or fertilization (Klimek, Richter, Hofmann, & Isselstein 2007; Nevens & Rehuel 2003; Scott 2001). This may severely limit studies that attempt to quantify land-use effects across existing landscapes, especially when management regimes vary in space and time (e.g. Billeter et al. 2008; Vellinga & André 1999). Whereas quantifying a single factor such as fertilization may be straightforward, combining several components of land use is challenging because they often interact with each other, often non-linearly, across existing heterogeneous landscapes (Herzog et al. 2006).

We use the term land use synonymous with "management". Among various measures of land-use intensity, we need to distinguish input activities such as fertilization from output measures such as yield, which quantifies the consequences of land use rather than its intensity (Shriar 2000; Turner & Doolittle 1978). Herzog et al. (2006) considered four continuous local input measures, namely fertilization, livestock density, mowing frequency, and amount of pesticides, to develop a land-use intensity index applicable across numerous agro-ecosystems. This index allowed correlating the responses of different taxa to variation in overall land-use intensity (Hendrickx et al. 2007). In a different approach elsewhere, these four inputs plus four additional factors were scored and then combined to a management intensity index (Downie et al. 1999).

Here we developed and employed a continuous land-use index, called LUI index, for managed grasslands and tested its applicability in the framework of a large-scale multidisciplinary project in three model regions in Germany (Biodiversity Exploratories, Fischer et al. 2010). This LUI index accounts for different types of land use inputs, and will be used to test the relationship between land use and various measures of biodiversity or ecosystem processes.

In contrast to forests, where undisturbed natural forest stands can be used as a reference (Luyssaert, Hessenmöller, Lüpke, Kaiser & Schulze 2011), almost all Central European grasslands are anthropogenic habitats, which rely on some level of management to prevent bush encroachment and forest succession (Ellenberg 1996). The management intensity necessary to maintain grasslands depends on site characteristics such as soil fertility, but also on the productivity expectation by land users, which in turn are strongly influenced by socio-economical criteria (e.g. size of the farms, population density, regional income). This prevents the use of a simple reference for standardization.

Generally, we can distinguish two ways to test the effect of land use on biodiversity or ecosystem variables:

(1) Using the same, a priori defined LUI index as a common predictor that allows for an objective, unequivocal test of general hypotheses about effects of land-use intensity and for general comparisons between different groups of organisms.
(2) Using multiple regressions or related statistics to reveal which types and components of land use and which combinations among them are most relevant for a particular response variable. For such an a posteriori approach, different studies will yield different models and most likely highlight different components.

Here we emphasize the importance of (1) a general test of an a priori defined compound quantitative LUI index. This index simply summarizes the different land use inputs, irrespective of complex relationships between different inputs. For a more mechanistic understanding, a compound index may be split into its components, where multivariate approaches (2) may yield additional insights (e.g. Downie et al. 1999; Klimek et al. 2007). We suggest a simple compound LUI index (inputs) and test its performance to predict five response variables (outputs) for which we assume that they are sensitive to land-use intensity. We then examine the explanatory power of individual LUI components, and provide a stepwise analysis that may serve as an example for many kinds of other studies in managed grassland systems.

Methods

The biodiversity exploratory project

The biodiversity exploratories comprise three regions located across Germany, with the UNESCO Biosphere Reserve Schwäbische Alb and surroundings in the southwest of Germany, the National Park Hainich with surroundings in the centre, and the UNESCO Biosphere Reserve Schorfheide-Chorin in the northeast (henceforth termed Alb, Hainich and Schorfheide; for the general design, see Fischer et al. 2010). In each region, 50 grassland experimental plots were selected by stratified random sampling from over 500 grid points of which land-use information was available. The 50 selected plots per region span the whole range of land-use intensities from highly intensely used to hardly managed at all. Most grassland sites were managed commercially, but few plots were managed at low intensity for conservation purposes to prevent encroachment by shrubs and trees.

The grassland plots in the biodiversity exploratories were either mown for hay or silage production (meadows), grazed by livestock (pastures) or both (mown pastures), and were either unfertilized or fertilized to varying degree. Land use data were obtained from yearly interviews with farmers and land owners conducted between 2006 and 2008 (Fischer et al. 2010). The inquired information referred to the whole field, which was usually much larger than the actual plots, thus the precise level of fertilizer or grazing at the plot may differ to some extent from the average of the field.

Calculation of a land-use intensity index

We propose a compound, additive index in which different kinds of land uses contribute to an overall level of land-use intensity (LUI). This includes the intensity of fertilization, the frequency of mowing and the intensity of livestock grazing. No pesticides were applied to any plot and therefore not included.

Fertilization covered organic or inorganic fertilizer applied by farmers, but not excrements by grazing livestock, and was quantified by kg nitrogen (N) per hectare. Because of the low number of P-fertilized sites (Alt, Oelmann, Herold, Schrumpf, & Wilcke 2011) and inaccurate information on P-fertilization provided by farmers, we did not account for P fertilization. Similar low levels of P application did not significantly alter total P concentrations and P partitioning in soil in previous studies (Negassa & Leinweber 2009). Moreover, we used total N irrespective of differences in availability to plants between organic and mineral fertilizer; note that the lower availability in the former may be partly compensated for by higher P and K supply. When organic fertilizer was provided as volume (for 19 of the total 150 sites), we converted it to kg by multiplying with 3.2 kg nitrogen m^{-3} in case of cattle slurry and with 0.6 kg nitrogen m^{-3} in case of cattle manure (Timmermann and Siegfried, unpublished; see http://www.landwirtschaft-mlr.baden-wuerttemberg.de/servlet/PB/menu/1043361_l1/index.html). Grazing livestock included cattle, sheep and horses, which were converted to livestock units as presented by Fischer et al. (2010).

The compound LUI index adds fertilization plus mowing plus grazing intensities. Each individual LUI component (fertilization, mowing and grazing) was standardized relative to its mean within the corresponding model region. For each experimental plot i, the land-use intensity L_i is defined as

$$L_i = \frac{F_i}{F_R} + \frac{M_i}{M_R} + \frac{G_i}{G_R},$$

where F_i is the fertilization level (kg nitrogen ha^{-1} year^{-1}), M_i the frequency of mowing per year and G_i the grazing intensity, reflected by the density of livestock (livestock units days of grazing ha^{-1} year^{-1}) on each site i for a given year, and F_R, M_R and G_R their respective mean within its region R for that year (i.e. the mean across all 50 experimental plots in the Alb, Hainich or Schorfheide, respectively). Due to the standardization by ratios, L_i is dimensionless. To achieve a more even distribution and reduce the impact of outliers in regressions, a square-root transformation as $L_i' = \sqrt{L_i}$ was applied. This LUI index is conceptually similar to the index developed by Herzog et al. (2006) which included other factors (e.g. pesticide application) to cover also arable land. Their index was standardized by the maximum instead of the mean, which results in values between 0 and 1. However, since the maximum represents a measurement on a single site, we opted to standardize by the mean, which is much less variable among years and regions (see the section "Results"). We also explored Herzog's index and alternative approaches to define land-use intensity, e.g. using standardization by z-transformation. Moreover, differences between a regional standardization as above versus an inter-regional approach are explored. Detailed comparisons are provided in Appendix (A4), but conclusions are briefly highlighted in Discussion. For potential use and comparison with LUI measures in other regions, the inter-regional (subscript G for "global") mean values for the years 2006–2008 are: $F_G = 23.1$ kg N ha^{-1} year^{-1}, $M_G = 0.97$ cuts year^{-1}, and $G_G = 129.0$ livestock units d ha^{-1} year^{-1}. However, note that using such global instead of regional means within a different agricultural landscape context may lead to unbalanced contributions of the three LUI components to the aggregate index. Conceptual differences between regional and global references should thus be carefully considered in studies of land-use effects within or across regions, respectively.

The type of land use and its intensity often varies across years therefore the year chosen as reference for the LUI index may strongly affect the result. In many cases, a long-term measure of land-use intensity may be desirable which integrates inter-annual variability. To obtain a more robust assessment, we thus summarized the land-use intensity data of three years 2006–2008. We defined $F_{R2006\text{–}2008}$, $M_{R2006\text{–}2008}$ and $G_{R2006\text{–}2008}$ as the regional mean across all three years to obtain the following three-year index that is applied as predictor variable in all our tests in this paper:

$$\begin{aligned} L_{i2006\text{–}2008} &= \frac{1}{3}\left(\frac{F_{i2006}}{F_{R2006\text{–}2008}} + \frac{F_{i2007}}{F_{R2006\text{–}2008}} + \frac{F_{i2008}}{F_{R2006\text{–}2008}}\right) \\ &+ \frac{1}{3}\left(\frac{M_{i2006}}{M_{R2006\text{–}2008}} + \frac{M_{i2007}}{M_{R2006\text{–}2008}} + \frac{M_{i2008}}{M_{R2006\text{–}2008}}\right) \\ &+ \frac{1}{3}\left(\frac{G_{i2006}}{G_{R2006\text{–}2008}} + \frac{G_{i2007}}{G_{R2006\text{–}2008}} + \frac{G_{i2008}}{G_{R2006\text{–}2008}}\right). \end{aligned}$$

Again, square-root transformation was applied to $L_{i2006\text{–}2008}$. Finally, we calculated the three components (fertilization, mowing and grazing) of $L_{i2006\text{–}2008}$ as F_i/F_R, M_i/M_R and G_i/G_R, averaged across the three years 2006–2008. The level of LUI was largely independent of soil types within each region (see Appendix A1).

Selected response variables

We chose five response variables to test the plausibility of the LUI index and to compare its performance with that of individual LUI components: (1) mean Ellenberg nitrogen indicator value for the plant community, (2) nitrogen and (3) phosphorus concentration in the aboveground plant biomass, (4) plant-available phosphorus concentration in the top soil and (5) C/N-ratio in the top soil. These five variables are assumed to be suitable to test land-use effects because we expect direct or indirect positive (1–4) and negative (5) responses to more intensive land use, particularly to fertilizer input. A review by Diekmann (2003) confirmed the usefulness of Ellenberg's indicator system to monitor land use and environmental change. The stoichiometry of N and P in plants is known to respond to grazing (Kleinebecker, Weber, & Hölzel 2011), as well as mowing and fertilization (Čop, Vidrih, & Hacin 2009). Plant-available N and P in soils also indicate land-use intensities in grasslands and have consequences for plant diversity (Alt et al. 2011; Dias, Malveiro, Martins-Loução, Sheppard, & Cruz 2011).

(1) Ellenberg's (1974) indicator values estimate the position of the realized niches of plant species on an ordinal scale and were determined for light, temperature, continentality, moisture, soil reaction, nutrient supply and salt tolerance for Central European plant species. An Ellenberg nitrogen indicator E_N of 1 indicates extremely nutrient-poor and one of 9 extremely rich occurrence sites, e.g. cattle resting places. We estimated the cover of all vascular plant species on relevés of 4 m × 4 m between 14/05 and 12/06/2009 and calculated mean nitrogen indicator value $\langle E_N \rangle$ weighted by the cover of each species ($N = 150$) (Diekmann 2003).

(2) Nitrogen (N) and (3) phosphorus (P) in plant biomass: Aboveground biomass of each plot was sampled on 1 m^2 at the same time as (1), and next to the vegetation relevés as mixed samples of four randomly placed quadrates ($N = 147$ plots). Biomass was dried immediately after harvesting for 48 h at 80 °C and thereafter ground to pass a 0.5-mm screen. Total N concentrations were determined by using an elemental analyzer (NA 1500, Carlo Erba, Milan, Italy). For the analyses of P, samples were digested in a microwave (MLS Start, Milestone, Bergamo, Italy) with concentrated nitric acid (65%) and hydrogen peroxide (35%). After digestion, P concentrations were determined by inductively-coupled plasma optical-emission spectrometry (ICP-OES analyses) (Vista-PRO Axial, Varian, Palo Alto, USA).

(4) For soil phosphorus (P) concentrations, one top soil sample was collected per plot during spring 2008 ($N = 140$ plots), sieved and dried for 48 h at 80 °C. Plant-available P concentrations were determined using $NaHCO_3$ as extractant (Hedley, Stewart, & Chauhan 1982). 0.5 g of air-dried soil have been extracted with 0.2 l of a 0.5 M $NaHCO_3$ solution (adjusted to pH 8.5 with 1 M NaOH) and shaken for 30 min before decantation and filtration (13 P Munktell & Filtrak GmbH, Bärenstein, Germany). In the extracts, plant-available P concentrations were determined with a continuous flow analyzer (Bran & Lübbe, Norderstedt, Germany) using the molybdenum blue method (Murphy & Riley 1962).

(5) For determination of C/N ratios, the upper 10 cm of the soil were sampled in 0.5 m distance to the plot centre in 2007 ($N = 133$ plots). The samples were sieved to <2 mm and ground. Subsequently, they were analyzed for total carbon and nitrogen with an elemental analyzer (Vario Max, Elementar Analysensysteme, Hanau, Germany). Inorganic C concentrations were determined after combustion of samples for 4 h at 550 °C. The organic C concentration was calculated as the difference between total C and inorganic C. The C/N ratio used here is thus the ratio of organic C to total N.

In addition to separate analyses, all five response variables were combined using principal component analysis (PCA), for which missing values (of response variables 2–5) in a plot were replaced by the overall mean of this variable. We used the first dimension (PC1), which explained 45.8% of the variance (eigenvalue 2.29) of the five response variables, with the following linear factor correlations: (1) $r = 0.86$, (2) $r = 0.36$, (3) $r = 0.85$, (4) $r = -0.53$, (5) $r = 0.64$.

As an example for biodiversity effects, we tested the relationship between LUI and vascular plant diversity. Shannon's diversity was calculated for the same plant surveys as used for Ellenberg's indicators described above.

Statistical analysis

Linear and non-linear regressions assessed the relationship between the LUI index and its individual LUI components (grazing, mowing and fertilization intensity) and the response variables for each of the three exploratories separately. We compared four different models:

(1) a linear regression: $\hat{y} = a \cdot x + b$, where a is the slope and b the intercept;

(2) an asymptotic Michaelis-Menten kinetic: $\hat{y} = (v_{\max} \cdot x)/(x + k_m)$, where $v_{\max}$ is the asymptotical maximum value of the response and k_m is the half-saturation constant;

(3) an asymptotic exponential model: $\hat{y} = a \cdot (1 - e^{-c(x-b)})$, with a being the asymptote, b the y-intercept and c the slope (constrained to $c > 0$) – this model allows for greater flexibility in fitting the shape than (2);

(4) a power function: $\hat{y} = a \cdot x^b + d$, constrained to $b > 0$ and $d > 0$.

For each model and exploratory, we computed the root mean square error (RMSE) and assessed the model's significance with an F-test. We also computed squared Pearson correlation coefficients between observed and fitted values (r^2-values) as a rough goodness-of-fit measure.

Multiple regression models were used to disentangle the potential contribution of the three LUI components to the combined response variable (principal component). The parameters (x) were included as linear ($\hat{y} = a \cdot x$) or non-linear terms ($\hat{y} = a \cdot x^b$), the latter only if non-linearity was evident and for $0 < b < 1$ to restrict the analyses to saturating functions. To account for the negative correlation between grazing and the other two components, we also split the data into pastures (grazed at least in one of the years) and meadows (ungrazed).

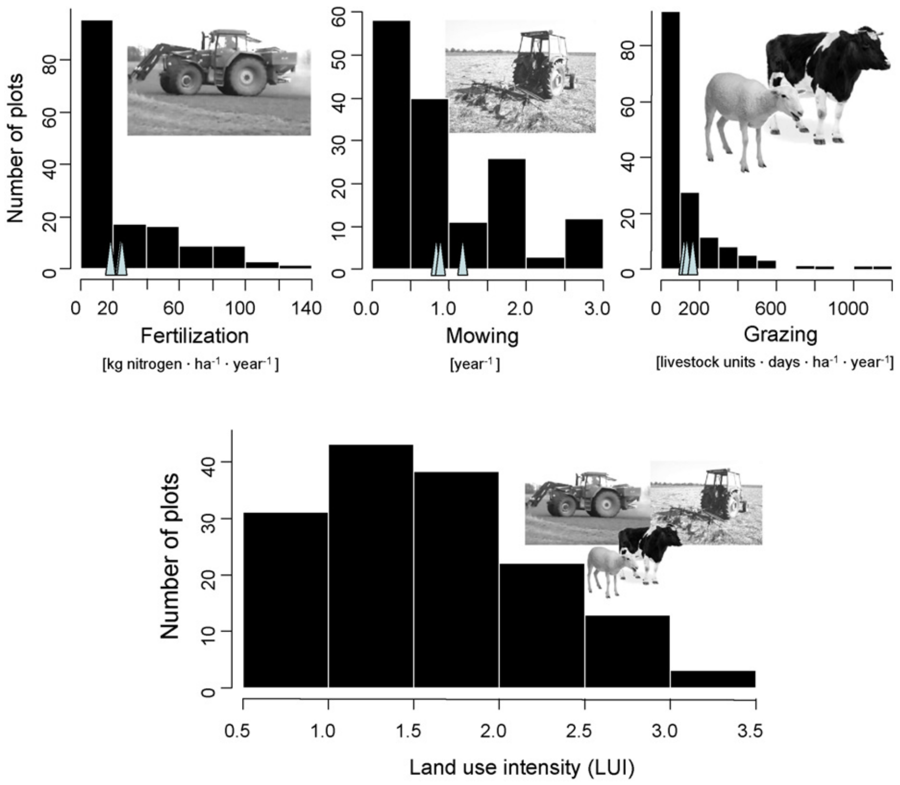

Fig. 1. Distribution of land-use intensity components. Fertilization, mowing and grazing intensity for each plot as mean value over three years (2006–2008), and the combined land-use intensity index across these three years are shown (total $n = 150$ experimental grassland plots). Mean values in each region which were used to standardize the LUI index are shown with triangles.

All analyses were carried out using R, version 2.12.1 (R Development Core Team 2010).

Results

General patterns and dynamics of land use

Of the 150 grassland sites investigated, all were used by land owners between 2006 and 2008 (LUI index > 0). However, 84 sites had not been fertilized, 52 not been mown and 38 not been grazed by livestock within this three-year period. The distributions of LUI components were thus strongly right-skewed, with modes being zero or close to zero (Fig. 1). Only when all three components were combined as LUI index, the distribution was more symmetric and did not differ from a normal distribution when square-root transformed (L_i'; Kolmogorov-Smirnov test, $p > 0.2$) (Fig. 1). Fertilization and mowing intensities were positively correlated across sites (Fig. 2). In contrast, grazing and fertilization intensities were negatively related, often exclusive: 70 (47%) of the pastures were unfertilized. The same was true for grazing and mowing intensities, since 54 (36%) of the pastures were not mown (Fig. 2).

In most sites, the type or intensity of the three LUI components (fertilization, mowing and grazing) changed over the years. Qualitative variation was particularly notable and would represent a problem for categorical analyses. A total of 22 sites (15%) were grazed in one year but not in one of the others, the incidence of mowing varied in 16 sites (11%) and that of fertilization in nine sites (6%). Even for sites with persistent land-use types, quantitative variation was high across the three years (Fig. 3; see also Appendix A3: Fig. S1).

Relationship between land use and response variables

The first principal component (PC1), combining the five response variables (nitrogen indicator, nitrogen and phosphorus in plant biomass, soil phosphorus and soil C/N ratio), was strongly related to the LUI index in each of the three regions (Table 1, Fig. 4). Overall, the combined PC1 was more closely related to the LUI index than any of the individual response variables except for Ellenberg's nitrogen indicator in two regions and showed a consistent and significant relationship in each of the three regions.

The LUI index was significantly related to all five response variables in the Alb, and to three response variables in the Hainich, namely nitrogen indicator, plant phosphorus and soil C/N ratio. In the Schorfheide, only a marginally significant trend for plant phosphorus was found. All trends were in the predicted direction (increasing with LUI except C/N ratio) (Table 1, Fig. 5).

Table 1. Univariate relationships between land-use intensity and five response variables and their combined principal component, as well as plant diversity.

Region	N	LUI index				Fertilization intensity				Mowing intensity				Grazing intensity			
		Type	R^2	RMSE	p	Type	R^2	RMSE	p	Type	R^2	RMSE	p	Type	R^2	RMSE	p
Combined response (principal component)																	
Alb	50	E	0.61	1.25	**<0.0001**	L	0.38	1.57	**<0.0001**	E	0.42	1.52	**<0.0001**	L	0.01	1.99	0.57
Hainich	50	E	0.44	0.87	**<0.0001**	L	0.15	1.08	**0.0062**	L	0.18	1.06	**0.0024**	L	0.09	1.11	**0.039**
Schorfheide	50	L	0.11	0.85	**0.020**	L	0.10	0.85	**0.025**	L	0.02	0.89	0.36	L	0.001	0.90	0.77
Ellenberg nitrogen indicator																	
Alb	50	E	0.65	0.87	**<0.0001**	L	0.32	1.24	**<0.0001**	E	0.35	1.22	**<0.0001**	L	0.03	1.49	0.29
Hainich	50	E	0.55	0.49	**<0.0001**	L	0.13	0.68	**0.010**	L	0.26	0.63	**0.0001**	L	0.03	0.72	0.23
Schorfheide	50	L	0.03	0.63	0.22	L	0.07	0.62	0.0545	L	0.05	0.63	0.14	L	0.03	0.63	0.26
Plant nitrogen concentration																	
Alb	49	E	0.24	0.37	**0.0003**	L	0.21	0.37	**0.0008**	E	0.23	0.37	**0.0026**	L	0.01	0.42	0.94
Hainich	49	L	0.08	0.30	0.053	L	0.00	0.31	0.71	L	0.01	0.31	0.45	L	0.11	0.29	**0.017**
Schorfheide	49	L	0.05	0.62	0.13	L	0.10	0.60	**0.029**	L	0.16	0.58	**0.0048**	L	0.06	0.61	0.08
Plant phosphorus concentration																	
Alb	49	M	0.44	0.06	**<0.0001**	L	0.31	0.07	**<0.0001**	E	0.42	0.06	**<0.0001**	L	0.00	0.08	0.73
Hainich	49	E	0.22	0.06	**0.0034**	L	0.04	0.06	0.18	L	0.06	0.06	0.08	L	0.08	0.06	0.15
Schorfheide	49	E	0.10	0.05	0.08	L	0.01	0.05	0.49	L	0.01	0.05	0.63	L	0.04	0.05	0.16
Soil plant-available phosphorus concentration																	
Alb	49	E	0.45	9.50	**<0.0001**	E	0.49	9.09	**<0.0001**	L	0.17	11.64	**0.0030**	L	0.02	12.69	0.38
Hainich	42	L	0.10	14.12	0.053	L	0.08	14.11	0.06	L	0.04	14.45	0.21	L	0.02	14.58	0.34
Schorfheide	49	M	0.00	18.87	0.70	L	0.00	18.89	0.78	L	0.00	18.90	0.93	E	0.00	18.87	0.91
Soil C/N-ratio																	
Alb	49	M	0.29	0.79	**0.0004**	L	0.15	0.87	**0.0062**	L	0.13	0.88	**0.010**	L	0.02	0.93	0.38
Hainich	47	M	0.27	0.68	**0.0010**	L	0.17	0.73	**0.0044**	L	0.10	0.76	**0.027**	L	0.01	0.80	0.48
Schorfheide	37	L	0.06	1.25	0.14	L	0.07	1.25	0.11	L	0.12	1.21[a]	0.039	L	0.10	1.22	0.05
Plant diversity																	
Alb	50	L	0.25	0.34	**0.0002**	L	0.20	0.35	**0.0011**	L	0.09	0.37	**0.031**	L	0.03	0.38	0.23
Hainich	50	M	0.45	0.34	**<0.0001**	L	0.32	0.38	**<0.0001**	L	0.28	0.39	**<0.0001**	L	0.01	0.45	0.60
Schorfheide	50	M	0.00	0.28	0.49	L	0.00	0.30	0.69	L	0.01	0.28	0.61	L	0.03	0.28	0.24

For each case, the model with the best fit (RMSE) of four types of univariate models is shown, including (*L*) linear regression, (*M*) an asymptotic Michaelis–Menten kinetic, and (*E*) an asymptotic exponential model (corresponding to equations given in Methods and curves in Figs. 4–6, S3 and S4). Number of sites (*N*) is shown for each response. Model fit is expressed as Pearson correlation coefficient (R^2) and root mean square error (RMSE), in addition to significance level (*p*) where significant fit ($p < 0.05$) was marked boldface.

[a] Negative correlation between mowing intensity and C/N in the Alb and Hainich, but opposite trend in the Schorfheide.

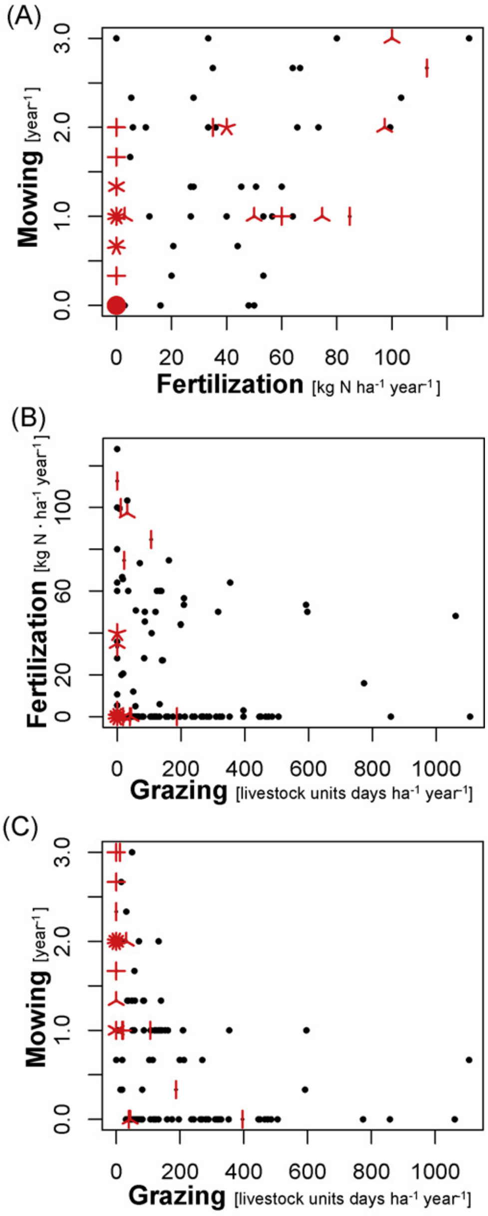

Fig. 2. Relationship between individual land-use intensity components: fertilization, mowing and grazing intensity. Spearman rank correlations for (A) $r_S = 0.61$, (B) $r_S = -0.22$, and (C) $r_S = -0.68$, all $p < 0.001$, $n = 150$ plots. Number of lines around points indicates overlapping data (starplots).

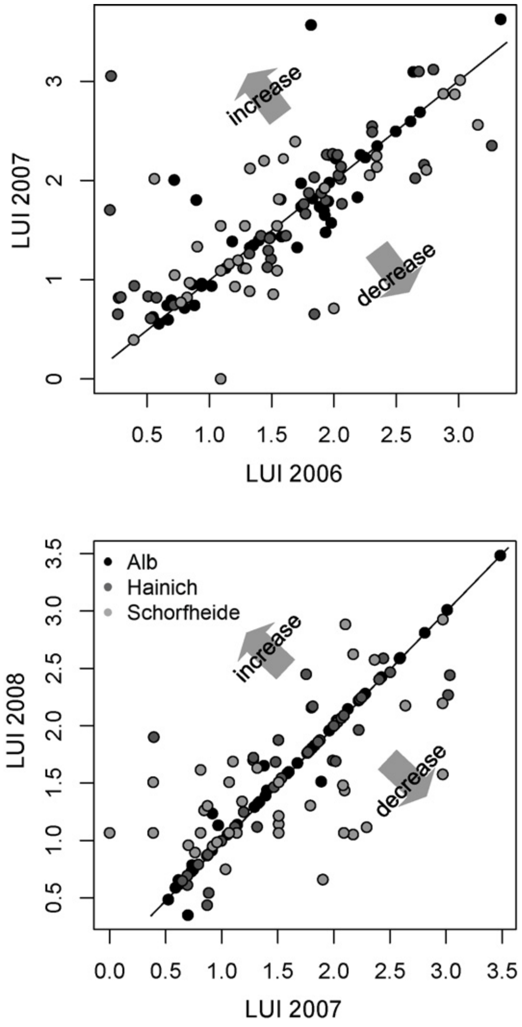

Fig. 3. Dynamics of the annual land-use intensity (LUI) indices over three years (2006–2008). For this comparison, the LUI index for 2007 was standardized against the regional means of 2006 for each of the three LUI components, and the LUI index for 2008 against the respective means of 2007. Points along the diagonal show sites that did not change in their LUI, whereas sites above the lines increased and below the lines decreased in intensity.

The compound LUI index was generally more closely related to the response variables than any one of the three individual LUI components alone. Across the five response variables in the three regions, the explanatory power of the LUI index performed similar to, or better than, the best single LUI component (lower root mean square error RMSE) (Table 1). Since fertilization and mowing intensities were positively correlated, both significantly predicted the same response variables in the same regions (eight cases), whereas grazing intensity was a significant predictor in only two cases (Table 1) and even showed a negative trend for some responses (see Appendix A5: Fig. S3).

In a multiple regression model of the three LUI components aiming to predict the combined response (PC1), only mowing and grazing intensity remained as a significant predictor, but not fertilization intensity (Table 2a). Only for sequential models where fertilization intensity was selected as the first predictor, this factor became significant. Following a separate analysis for pastures (grazed at least in one of the years) and meadows (ungrazed), grazing and mowing intensities were again confirmed as significant terms for pastures (Table 2b), and only mowing intensity for meadows, but not fertilization intensity, (Table 2c). These results correspond well with the positive correlation between fertilization and mowing intensity.

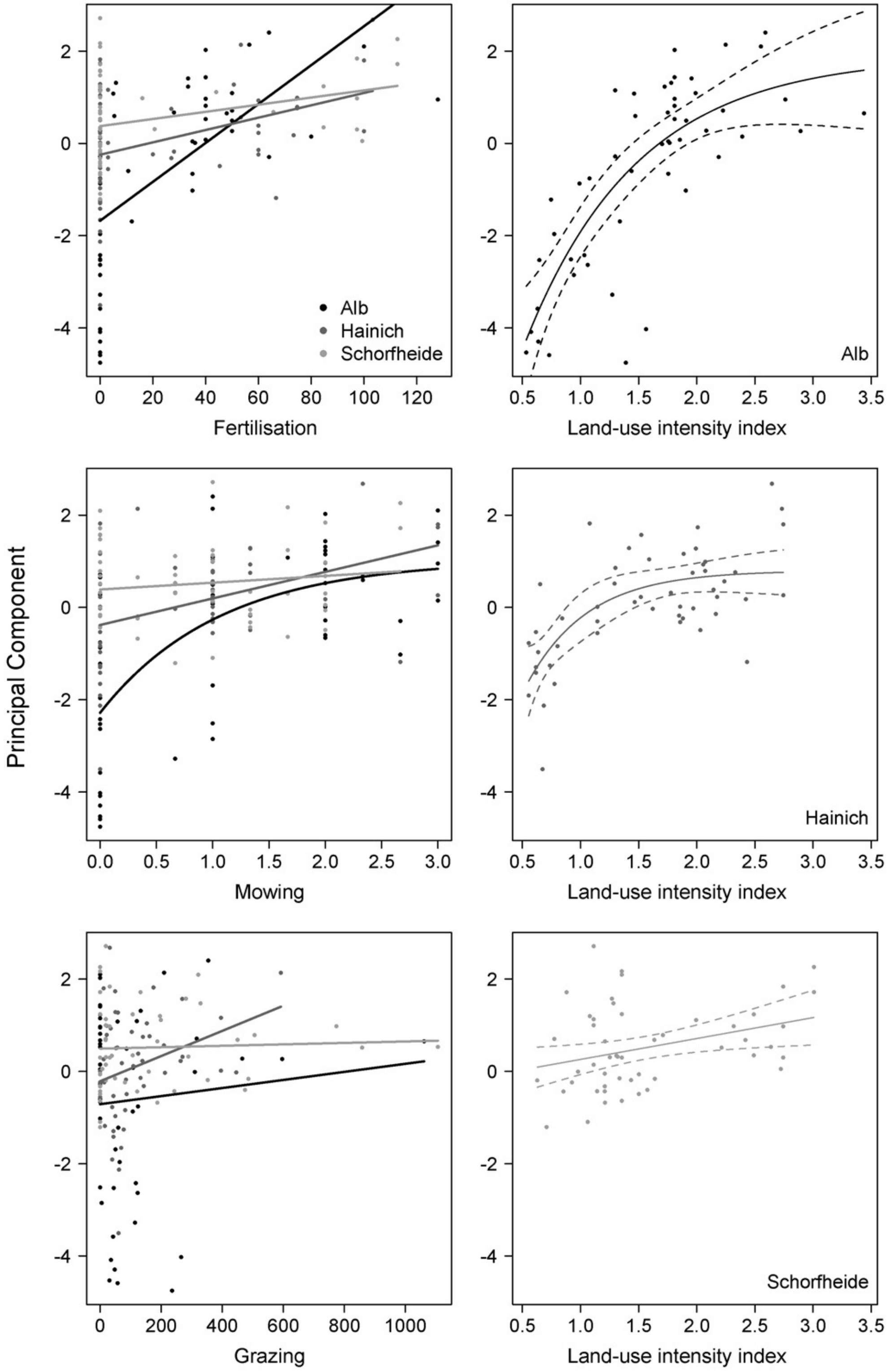

Fig. 4. Relationship between land-use intensity (LUI) and the first principal component of all five response variables (PC1, see the section "Methods"). Individual LUI components (left panel) were much less predictive than the compound LUI index, right panel). The strongest predictive power of the LUI was found in the Alb, an intermediate level in the Hainich followed by the Schorfheide.

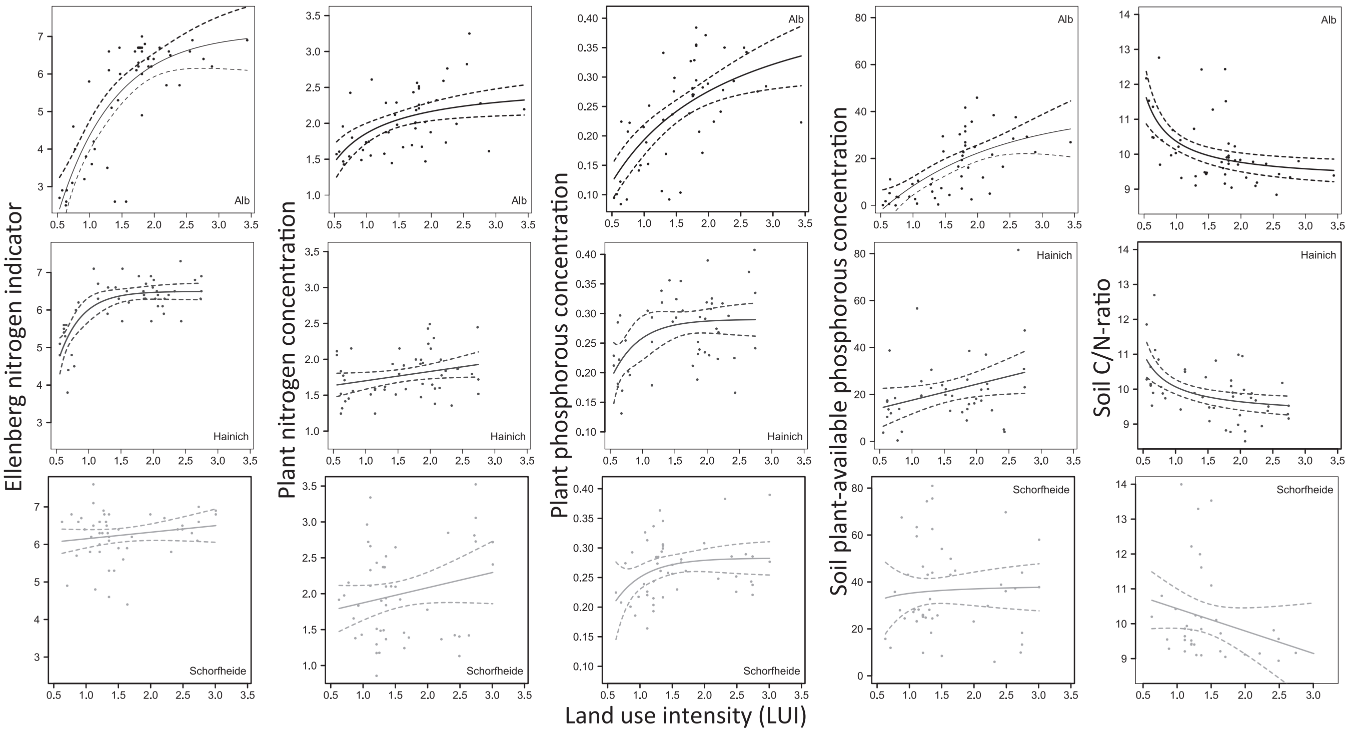

Fig. 5. Relationship between land-use intensity (LUI) and five response variables: the weighted mean plant nitrogen indicator value of Ellenberg's indicator system, nitrogen and phosphorus concentration in the vegetation biomass, plant-available soil phosphorus concentration and soil carbon:nitrogen (C:N) ratio. Each curve (±95% CI) corresponds to the selected model in Table 1.

Table 2. Multivariate relationships between land-use intensities and the summarized response variable *y* (PC1, see the section "Methods").

(a) All 150 grasslands: $y = 0.11\ F + 1.4^{***}\ M^{0.52(*)} + 0.80^{*}\ G^{0.61}$		
Fertilization intensity (*F*)	$t = 1.3$	$p = 0.19$
Mowing intensity (*M*)	$t = 5.8$	$p < \mathbf{0.0001}$
Grazing intensity (*G*)	$t = 4.8$	$p < \mathbf{0.0001}$
Whole model:	$R^2_{adj} = 0.30$, $p < \mathbf{0.0001}$	
(b) 112 pastures (grazing): $y = 0.10\ F + 1.44^{***}\ M^{0.44*} + 1.44\ G^{0.40}$		
Fertilization intensity (*F*)	$t = 0.9$	$p = 0.37$
Mowing intensity (*M*)	$t = 4.7$	$p < \mathbf{0.0001}$
Grazing intensity (*G*)	$t = 4.4$	$p < \mathbf{0.0001}$
Whole model:	$R^2_{adj} = 0.29$, $p < \mathbf{0.0001}$	
(c) 38 meadows (no grazing): $y = 0.13\ F + 0.91^{*}\ M$		
Fertilization intensity (*F*)	$t = 1.0$	$p = 0.31$
Mowing intensity (*M*)	$t = 2.4$	$p = \mathbf{0.02}$
Whole model:	$R^2_{adj} = 0.32$, $p < \mathbf{0.001}$	

Non-linear or linear model equation, *t*-value and significance levels (*p*, marked boldface when significant) for each single land-use intensity component and adjusted multiple fit (R^2_{adj}) and significance of the whole model are shown (type III). Where no evidence for saturated effects was found for a single component, it was included as a linear term. Significant estimates in equation are marked as follows: *** for $p < 0.001$, ** for $p < 0.01$, * for $p < 0.05$, and (*) for $p < 0.1$.

The LUI index proposed here was standardized against the mean value of each LUI component in each region. However, taking the grand mean across regions as reference led to very similar values (linear correlation with LUI index, $R^2 = 0.97$, $p < 0.0001$), since the means for most LUI components were similar across the regions. Other approaches to define LUI such as standardization by the maximum (Herzog et al., 2006), *z*-transformation and other modifications were all strongly linearly correlated with L_i ($0.79 \leq R^2 \leq 0.95$, see Appendix A4: Fig. S2).

Plant species diversity declined significantly with increasing LUI in the Alb and Hainich, but not in the Schorfheide where the diversity level was generally low (Fig. 6). Again, the compound LUI index was a better predictor than its individual components (Table 1; Appendix A5: Fig. S4).

Discussion

To test the effects of land use on biodiversity and ecosystem functioning, two alternative options involve either categorical analyses based on different land-use types or intensity classes, or the use of one or more continuous intensity variables. For grasslands, the former approach has a clear limitation in that different types ignore any quantitative variation within types, and different types (e.g. meadows vs. pastures) do not necessarily correspond to different

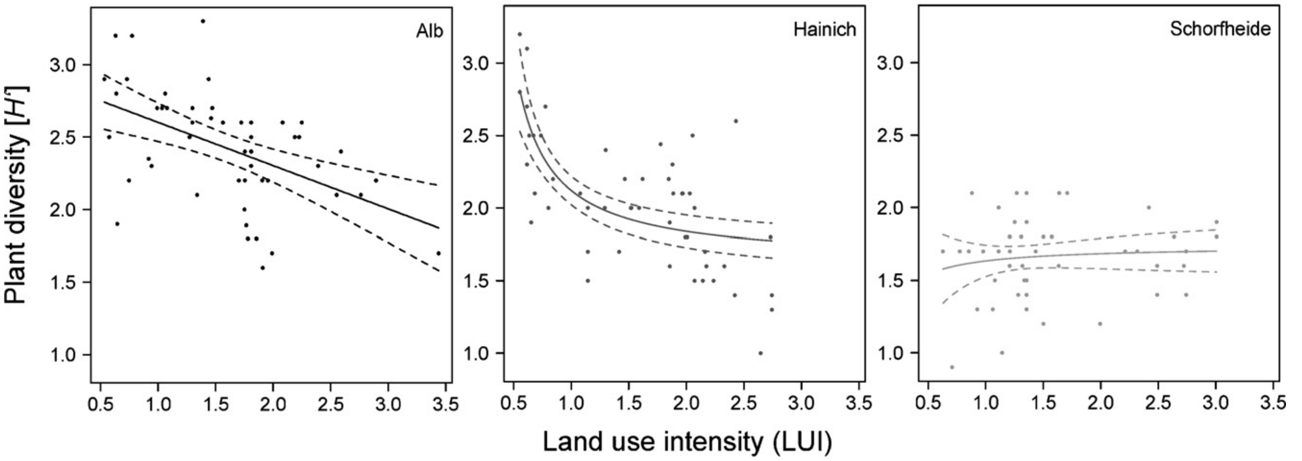

Fig. 6. Vascular plant diversity declined with land-use intensity (LUI) in the Alb and Hainich, but not in the Schorfheide (Shannon diversity index *H*′).

intensities. Moreover, pronounced qualitative changes between grazed vs. ungrazed, fertilized vs. unfertilized and mown vs. unmown regimes represent a severe problem for defining categories. Therefore, categorical approaches may require additional mixed categories if land use varies among several years, whereas a continuous variable can account for such changes. We have found a high level of both qualitative and quantitative changes in a three-year period for the grasslands investigated, confirming the need to capture the dynamics of land-use intensity.

Agricultural grasslands are mown, grazed or both with variable intensity, and fertilized to different degrees, and these different inputs are not independent. For example, meadows mown for silage and hay are particularly profitable if the yield can be optimized by fertilization, which consequently occurs at a higher level than in pastures. In contrast, infertile low-productive grasslands are often used as pasture, e.g. by sheep grazing and with support of agri-environmental schemes (Kleinebecker et al. 2011).

The additive index of land-use intensity (LUI) proposed here combines these inputs in a very simple way and defines a gradient that increases from zero (no land use) to high levels when one or several types of land use are applied. In accordance with our expectation, the LUI index showed a close relationship to nitrogen indicators and nutrient levels in the plant biomass and the soil, confirming the suitability of this index to evaluate ecosystem responses to land-use intensity. Significant relationships between the LUI index and the five response variables only occurred in the Alb and the Hainich, but not in the Schorfheide where plant diversity was also consistently low. Drainage of the dominant peat soils in the Schorfheide may lead to mineralization and thus release of nutrients independent of fertilizer application (Lamers, Smolders, & Roelofs 2002); Ellenberg's nitrogen indicators and soil phosphorous levels are particularly high in this region across many sites. This effect may explain the lack of clear relationships between LUI and responses in the Schorfheide (see also Fischer et al. 2010; Klaus et al. 2011).

Among the five selected response variables, Ellenberg nitrogen indicators showed the strongest relationship with the LUI index, followed by phosphorous concentrations in aboveground plant biomass and C/N ratios of the top soil, whereas nitrogen in the plant biomass and plant-available phosphorous concentrations in the soil showed a close relationship with the LUI index only in the Alb. Combining the five variables in their first principal component revealed the closest relationship with land-use intensity which was even significant in the Schorfheide, showing the value of this combination of variables as a potential indicator of land-use intensity applied. Furthermore, the LUI adequately reflects the regional variation in land-use intensity observed in the individual response variables.

For a more detailed understanding of land-use effects, comparisons within a single land-use type may focus on a single LUI component such as grazing intensity across pastures or fertilization intensity across meadows. We performed this exercise for the first principal component summarising the five response variables. Since land-use intensity variables are negatively correlated or substituted, e.g. the absence of grazing often corresponds to frequent mowing and heavy fertilization and vice versa, analyses based on single LUI components unlike the compound LUI index should be viewed with caution. For instance, fertilization intensity that is likely to cause changes in soil and plant nutrient levels was not a significant predictor in multiple regression models due to its positive correlation with mowing frequency. Moreover, a poor predictive power of actual fertilization intensities may also reflect an unknown underlying heritage of fertilizer resides, especially phosphorous, from former intensive management. Drainage and subsequent effects on soil mineralization add another source of variation, particularly to peat soils in the Schorfheide.

Why did we choose the particular compound LUI index outlined above in favour of alternative approaches? Due to the lack of precise measurements, some alternative measures of LUI are based on ranks (Laliberté et al. 2010; Machado

2004), with obvious statistical limitations. If several quantitative measurements are available, or when mixtures of nominal and continuous variables apply, ordination techniques may serve to reduce the number of variables to one or few continuous variables, for example using principal component analyses (PCA) (e.g. Atkinson et al. 2005). However, such procedures do not lead to a single *unidirectional intensity gradient* when the LUI components have complex relationships as in our dataset (see Appendix A4). The use of the maximum (as in Herzog et al. 2006) has the advantage that each LUI component is scaled between 0 and 1, but is disadvantageous in our case because it relies on a single site, which is often represented by an atypically high value. LUI components for single sites vary considerably among years and among regions, and such variation would strongly affect all LUI index values when the maximum is taken as a reference. Temporal variation of the regional maxima of the LUI components was relatively large (coefficient of variation CV: mean ± sd 15.8 ± 14.6%) compared with variation in the mean values (CV: 9.4 ± 5.3%). Nevertheless, Herzog's index and several other alternative indices were highly correlated with the one defined in this paper, suggesting that the type of standardization does not affect the general conclusions about land-use effects. This is also true for the decision to use the regional or the 'global' mean across regions ($R^2 = 0.97$) in our study, since the regional means were similar. In studies where different regions are combined in a single model, one might prefer global over regional references, but this decision will be at the cost of imbalances in the relative contributions of the LUI components within a region when regional standards vary. Whereas different standardization methods led to similar LUI levels in our study, the variation of the LUI index among years is more pronounced (mean $R^2 = 0.75$). This finding emphasizes that the selection of an appropriate temporal reference can be crucial for the outcome of a study. For organisms or processes studied that respond slowly to land use and its intensity, an integrated measure across several years may be particularly suited, such as $L_{i2006\text{–}2008}$ chosen here to test the response in plant species composition (indicator values) and various fertility measures.

Outlook

Defining a land-use index that integrates different land-use types (here: mowing, grazing, fertilization intensity) allows a generalized approach, which integrates the real-world complexity but disregards specific causes of the patterns found. The advantage of getting a general picture under real world conditions trades-off with a more mechanistic understanding of causal factors as it is usually possible in experimental single-factor studies. Hence, both strategies have their merits. A further limitation of an integrative index is that potential interactions among different land-use types may be hidden (see Tylianakis, Didham, Bascompte, & Wardle 2008).

In the simple LUI index presented here, fertilization, mowing, and grazing intensity are weighted equally in their contribution to define the gradient, although they might contribute to a different extent. For specific target responses in a study, the relative contribution of each LUI component can be fitted post hoc, but there is no unequivocal way to a priori define their relevance to all kinds of organisms or ecosystem processes. A better mechanistic understanding would be desirable for an improved LUI index, e.g. how the quantitative effect of more continuous grazing by specific livestock compares to discrete mowing events, or how deposition of cattle dung and urine compares to organic or inorganic fertilization in terms of short-term nutrient availability. Moreover, mowing and grazing differ in type and level of disturbance that they cause which could be quantified. A major problem in this context is to define land-use intensity independently of its desired effects or of possible feedbacks, e.g. the harvest (biomass removal) that reflects the overall productivity, which is the target of land use in meadows and influenced by abiotic site conditions, e.g. soil properties. As in any land use of heterogeneous landscapes, various confounding factors may apply such as soil types and other environmental conditions.

The three components chosen to describe the intensity of land use in grasslands, namely fertilization, mowing, and grazing intensity, may require further refinement for more detailed studies of impacts, including quantitative measurements of nutrients other than nitrogen, and other effects of livestock such as the rotation system of grazing, seasonality and resting places. Similarly, mowing differs among machineries used, e.g. whether conditioners are included or not, and in the cutting height, which likely affects the survival of insects differently (Humbert, Ghazoul, Richner, & Walter 2010). For many animals, grazing and mowing represent a reduction of shelter, plant resource quantity and heterogeneity of fodder. More productive grasslands are often mown earlier in the season and more frequently. In contrast, mown pastures are typically cut once at the end of the season, mainly to reduce unpalatable species such as thistles, often without removing plant biomass. Spatial and temporal variation in timing of these events during the season can be important for its impacts, especially in mobile organisms (Johst, Drechsler, Thomas, & Settele 2006). Vegetation recovery time after mowing events may additionally depend on site conditions and fertilization. Hence, further studies may quantify not only the frequency as proposed in the LUI index, but also the timing of the management activities during the season. Moreover, the interplay between local land-use intensity applied to the particular site versus the naturalness of the surrounding types of land use may be important for species composition and ecosystem processes (Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies 2005). Local intensity levels can be weighted by per cent area in a given landscape, an approach often applied for catchment areas to quantify inputs from different land-use types (Brown & Vivas 2005).

We thus suggest using the LUI index in combination with other local and regional land-use descriptors and more detailed analyses of individual LUI components to evaluate responses of different organisms and ecosystem functions to land use.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.baae.2012.04.001.

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