

MS. VERENA BUSCH (Orcid ID : 0000-0001-5797-1375)

DR. STEFFEN BOCH (Orcid ID : 0000-0003-2814-5343)

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Will I stay or will I go? Plant species-specific response and tolerance to high land-use intensity in temperate grassland ecosystems

Running title: Plant- specific response to land-use intensity

Verena Busch¹, Valentin H. Klaus^{1,2}, Deborah Schäfer³, Daniel Prati³, Steffen Boch^{3,4}, Jörg Müller^{5,6},
Melanie Chisté⁷, Karsten Mody⁷, Nico Blüthgen⁷, Markus Fischer³, Norbert Hölzel¹, Till Kleinebecker^{1,8}

Correspondence

Verena Busch, Institute of Landscape Ecology, Westfälische Wilhelms-Universität Münster, 48149

Münster, Germany

verena.busch@uni-muenster.de

¹ Münster University, Institute for Landscape Ecology, Heisenbergstr. 2, 48149 Münster, Germany

² ETH Zürich, Institute for Agricultural Sciences, Universitätstrasse 2, 8092 Zürich, Switzerland

³ University of Bern, Institute of Plant Sciences, Altenbergrain 21, 3013 Bern, Switzerland

⁴ Swiss Federal Research Institute WSL, Zürcherstraße 111, 8903 Birmensdorf, Switzerland

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⁵ Institute of Biochemistry and Biology, University of Potsdam, D-14469

⁶ Heinz-Sielmann Foundation, Gut Herbigshagen, Duderstadt, D-37115

⁷ Technical University Darmstadt, Department of Biology, Schnittspahnstrasse 3, 64287 Darmstadt, Germany

⁸ Institute of Landscape Ecology and Resource Management, Justus-Liebig-University Gießen, Heinrich-Buff-Ring 26-32, D-35392 Gießen, Germany

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Abstract:

Aim: Intensification of land use strongly impacts plant communities by causing shifts in taxonomic and functional composition. Mechanisms of land-use induced biodiversity losses have been described for temperate grasslands, but a quantitative assessment of species-specific occurrence optima and maximum tolerance (niche breadth) to land-use intensity (**LUI**) in Central European grasslands is still lacking.

Location: Temperate, managed permanent grasslands in three regions of Germany.

Methods: We combined extensive field work with a null model-randomization approach, defined a 'habitat niche' for each plant species based on occurrence and abundance across 150 grassland sites differing in LUI (i.e. amount of fertilizer, mowing/grazing intensity and a compound index of these), and assessed their realized niche breadth (tolerance). Underlying mechanisms driving species' response to LUI were assessed by relating plant functional traits, Ellenberg indicator values (**EIV**), Grime's ecological strategies (**CSR**) and Briemle utilization numbers.

Results: Out of 151 plant species, 34% responded negatively, whereas 10% responded positively to high LUI. This pattern was mainly driven by species' response to fertilization and mowing frequency; grazing intensity response was less pronounced. Positively reacting species, displaying broader niches, were associated with competition-related functional traits, high EIV for nutrient supply and moisture and high mowing tolerance under spatiotemporally variable conditions. Negatively responding species, displaying relatively narrow niches confined to spatiotemporally homogeneous low LUI sites, were associated with a nutrient-retentive strategy, under nutrient poor, base-rich soil conditions.

Conclusion. Our analyses of individual species' reaction clearly demonstrate that species responding negatively to high LUI display little tolerance towards intensive fertilization and mowing, leading to plant diversity loss; whereas grazing partly thwarts these effects by creating new habitat niches and promoting ruderal species. Our approach can be applied to other habitat types and biogeographical regions in order to quantify local specific response or tolerance, adding to existing knowledge about local vegetation dynamics.

Keywords: Community composition, ecological strategies, Ellenberg indicator values, land-use intensity niche, plant functional traits, species-specific niche breadth, species-specific niche optima, temperate grasslands, vegetation dynamics

1. Introduction

Temperate semi-natural grasslands are among the most species-rich plant communities worldwide and provide a vast number of important ecosystem functions and services (Chapin et al., 2002; Hooper et al., 2005; Wilson et al., 2012). Though having emerged through anthropogenic land use, permanent grasslands in Central Europe have been in constant decline in quantity and ecological quality especially since the middle of the 20th century (Poschlod et al., 2005). Cessation, homogenization and intensification of traditional land use have led to a notable decrease in species

diversity (de Bello et al., 2010; Hodgson et al., 2005). Hence, current intensive anthropogenic land use has become a major threat for grassland biodiversity (Allan et al., 2014; Zechmeister et al., 2003).

Intensification of grassland management, like mowing and grazing, and altered soil fertility driven by increased fertilization, have been shown to affect vegetation dynamics and structure (Daufresne & Hedin, 2005; Fay et al., 2015); leading to severe changes in species diversity, abundance and overall community composition (Boch et al., 2016; Louault et al., 2005; Manning et al., 2015). Analogously affecting insect taxonomic groups, multitrophic interactions are negatively affected and the associations between plants and their specific pollinators, for example, are weakened. Non-random parallel losses of host plants and specific pollinators or herbivores may result in a biotic homogenization of high intensity grasslands (Manning et al., 2015; Weiner et al., 2014); translating to a large-scale decrease of ecosystem multifunctionality, a loss of high level ecosystem services (including provisioning services) and subsequently affecting the entire above-ground system (Allan et al., 2014, 2015; Manning et al., 2015). The identification of specific plant species' response to land-use intensity is hence crucial.

The assembly, coexistence and persistence of plant species along environmental gradients and the occupation of available ecological niches are based on the species' responses to disturbance and stress (Silvertown, 2004). These responses are, for instance, driven by species-specific life-history traits and ecological strategies for acquiring and using resources or for tolerating or avoiding disturbance (Busch et al., 2017; Devictor et al., 2010; Hodgson et al., 1999).

Thus, identifying environmental management filters and mechanisms that drive plant species reactions based on their functional traits and ecological strategies (Lavorel & Garnier, 2002; Westoby et al., 2002), will provide mechanistic insights into biodiversity and vegetation dynamics (Díaz et al., 2007; Hooper et al., 2005; Pfestorf et al., 2013). Knowledge of these drivers can help to predict species' tolerance towards land-use types and intensities, their response to interacting

abiotic factors and their reactions to land-use change. They may be used to conceive conservation strategies (Drobnik et al., 2011) and to predict the effectiveness of conservation management plans for threatened species and communities; or to operate sustainable, but economically profitable land-use practices under consideration of biodiversity conservation and development.

A number of different approaches for studying and identifying mechanisms behind plant species distribution and assembly in response to environmental or large-scale management gradients have been established in ecological research. Plant functional traits, for instance, provide the basis for a general and mechanistic understanding of local changes in vegetation, biodiversity dynamics and ecosystem processes (e.g. Díaz et al., 2007; Garnier et al., 2007; Hooper et al., 2005; Laliberté et al., 2010; Pakeman, 2011). Defined as morpho-physio-phenological characteristics, they may either describe a physiological function or are a surrogate measure from which such a function may be derived (Hodgson et al., 1999; Weiher et al., 1999), and impact plant fitness via their effects on resource acquisition, growth, reproduction and survival (Violle et al., 2007).

Similarly, the CSR strategy scheme was initially introduced by Grime in 1974, and it is now a well-established ecological approach based on the assumption that multifaceted combinations of environmental stress, disturbance and competition are amongst the most important factors shaping plant species distribution and vegetation composition (Grime, 2006). Species are assigned to pursue different survival strategies or combinations thereof according to their abilities to cope with disturbance (R strategists), abiotic stress (S strategists) and competition (C strategists; Hodgson et al., 1999).

Likewise, Ellenberg indicator values represent the position of the realized ecological niche of plant species by indicating aspects of habitat quality such as light, temperature, soil moisture, soil pH value and nutrient availability (Diekmann, 2003; Ellenberg et al., 2001; Kleinebecker et al., 2017). However, though widely recognized and well-established, these indicator values are often based on expert knowledge rather than on measured data. Recent approaches, however, have taken another

step in understanding mechanisms and processes driving the ecological niche of a plant by characterizing Ellenberg indicator values functionally, morphologically or ecophysiologicaly (Bartelheimer et al., 2016). Similarly, Briemle utilization numbers (Briemle et al., 2002), are indicator values classifying grassland plant species according to their performance during agricultural use, i.e. their tolerance towards mowing, grazing and trampling (Briemle et al., 2002). They have been used to model future effects of land use on grassland dynamics for conservation-oriented grassland management (Siehoff et al., 2011).

A large amplitude of biotic and abiotic environmental factors need to be considered while studying drivers of vegetation dynamics. These include local landscape composition (habitat heterogeneity, distribution, fragmentation and interconnectability), climatic (precipitation, temperature), topographic (altitude, exposition, inclination), edaphic (soil type, soil depth, pH) and biotic factors (local species pool, inter- and intraspecific competition and facilitation, land use). All of them can have great impact on distribution, establishment and survival of grassland species (Allan et al., 2015; Díaz et al., 2007; Drobnik et al., 2011; Jongman 2002). However, a previous study showed that the effects of climatic, topographic and edaphic parameters on community weighted mean values of plant traits were shown to be less important, whilst land use and nutrient stoichiometry had the greatest impact (Busch et al., 2017).

Although research in the past decades has made great advances in assessing mechanisms driving species assembly and distribution along environmental and land-use gradients on a local, regional and even global scale (Bernhardt-Römermann et al., 2011; Boulangeat et al., 2012; Pierce et al., 2017; Shipley et al., 2017), it remains difficult to predict species responses and nearly impossible to reliably extrapolate gained knowledge (Drobnik et al., 2011; Lavorel et al., 1997; Vesik & Westoby, 2001). Furthermore, a detailed assessment of plant species-specific performance in response to current agricultural grassland use in Central Europe is widely missing; reliable tools for preserving

and promoting plant and, subsequently, overall biodiversity in agriculturally intensively used grasslands under consideration of indispensable and profitable farming, are still needed.

The aim of this study is hence to identify and characterize plant species responding positively or negatively to high land-use intensity in temperate, lowland to submontane grasslands in Central Europe. By employing a null model combined with a randomization approach (Chisté et al., 2016), we defined species-specific agricultural habitat niches and their corresponding niche breadth (i.e. tolerance range) based on species' occurrence and abundance across 150 grassland sites of variable land-use types and intensities over a six-year time period. In addition, we described these species' response-based characteristics employing their specific plant functional traits, Ellenberg indicator values and Briemle utilization numbers. Specifically, we assessed a) species' specialization under high land-use intensity; b) the relationship between species' specific response and niche breadth with regard to different land-use types; and c) how and which specific plant traits determine this individual response in relation to nutrient acquisition and retention, stress- and disturbance tolerance, competitiveness and productivity.

2. Materials and methods

2.1. Study area and design

This study took place within the framework of the Biodiversity Exploratories program, a large-scale and long-term functional biodiversity research project (Fischer et al., 2010; www.biodiversity-exploratories.de). The three Biodiversity Exploratories' study regions, the UNESCO Biosphere Reserve Schorfheide-Chorin, the Hainich National Park with the Dün and surroundings and the Biosphere Area Schwäbische Alb, reflect a gradient of increasing altitude and precipitation and decreasing annual mean temperatures from northeastern to southwestern Germany (**Table S.1**). Whilst sites in the Hainich-Dün and Schwäbische Alb region are all located on mineral, mostly calcareous soils, the northernmost region Schorfheide-Chorin also contains grasslands on drained

fen soils rich in organic matter. Each of the three regions comprises 50 relatively evenly distributed grassland plots. Selection of plots was based on a stratified random sampling design, along a land-use intensity gradient representative for large parts of Central European grasslands (for details, see Fischer et al. 2010). Whilst the three study regions of the Biodiversity Exploratories differ in landscape composition, climatic, geological and topographical conditions (Fischer et al., 2010), as well as in original species pools or current and past land-use history, the land-use intensity in these regions is comparable.

2.2. Land-use information

Study sites were located on permanent grassland plots that underlie low-intensity to high-intensity management, without being regularly resown or surpassing a management intensity of three cuts per year. The land use of the studied plots ranged from unfertilized sheep pastures and single-cut meadows to highly fertilized three-cut meadows, mown pastures – mown once per year and grazed by livestock in different densities within the same year – to intensively grazed grasslands (Fischer et al., 2010). Grazing animals were sheep, horses or cattle. Fertilizer was applied in either organic (e.g. slurry, manure) or mineral form (e.g. urea-N, ammonium nitrate-N, NPK) or a combination of both. Land-use information of each plot was obtained annually from 2009 to 2014 by using a standardized questionnaire provided to farmers and land owners, considering grazing intensity (livestock units \times days⁻¹ \times year⁻¹ \times ha⁻¹), mowing intensity (cuts per year) and amount of fertilizer applied (fertilization intensity; N kg \times ha⁻¹ \times year⁻¹). An index of compound land-use intensity (LUI) proposed by Blüthgen et al. (2012) was calculated for each year, including all three land-use components, to reduce the complexity of management to one dimension. For this, each land-use component (fertilization, mowing, grazing) was standardized to its mean across all regions and root-transformed for a more even distribution (Blüthgen et al., 2012). The land-use intensity index LUI is defined as:

$$LUI = (F_i \times F_M^{-1} + M_i \times M_M^{-1} + G_i \times G_M^{-1})^{0.5},$$

where F_i is the fertilization level, M_i the mowing frequency per year and G_i the grazing intensity on each site i for a given year; and F_M , M_M and G_M their respective mean for that year across all regions.

For further calculations, the LUI and its components were averaged over all sampling years in order to obtain a robust mean value of land-use intensity.

2.3. Vegetation samples

Vegetation was sampled annually from May to June from 2009 to 2014. In an area of 4 m × 4 m all vascular plant species were recorded and the percentage cover of each species was estimated. By averaging vegetation records over the six-year sampling period, we obtained a stable 'mean vegetation record' covering a total number of 254 vascular plant taxa. Nomenclature of vascular plants follows Wisskirchen & Haeupler 1998.

2.4. Data analysis

2.4.1. Niche modelling

For the following analysis, we excluded all woody species in order to avoid great data distortions in life-history traits of grassland species. Moreover, by deleting all species with less than eight occurrences in the total dataset we aimed at excluding spatio-temporally randomly occurring species and thus generating a robust dataset, resulting in a total of 151 plant species. To define the land-use niches of each plant species, abundance-weighted means ($_{AW}Means$) of land-use intensity and its components were calculated analogously to Chisté et al. (2016):

$$_{AW}Mean_i = \sum_{s=1}^{150} \sum_{y=2009}^{2014} p_{i,s,y} \times L_{s,y}$$

where $p_{i,s}$ is the proportion of cover of species i found in site s averaged over all years in relation to its abundance across all sites ($\sum_s \sum_i p_{i,s} = 1$) and L_s is the land-use intensity on site s averaged over all years. Proportions concern the species' total cover averaged over all years. L_s was calculated for the compound land-use intensity and its components fertilization, mowing and grazing separately for each year. Intensity values were subsequently averaged across the years 2009 to 2014 to avoid repeated consideration of sites. The species' $_{AW}Mean$ was likewise computed from the mean of all sites, which resulted in one value for each species. As a proxy for the niche breadth of a plant species, the cover-weighted standard deviation ($_{AW}SD$) was calculated (see Galassi et al., 2009), analogously weighted by the species cover:

$$_{AW}SD_i = \sqrt{\frac{\sum_{s=1}^{150} \sum_{y=2009}^{2014} p_{i,s,y} (L_{s,y} - \bar{L}_{s,y})^2}{(N-1) \sum_{s=1}^{150} \sum_{y=2009}^{2014} p_{i,s,y}}}$$

Where $\bar{L}_{s,y}$ is the land-use intensity averaged over all sites and years; $\sum_s \sum_i p_{i,s}$ is a species' abundance across all sites, which is equal 1; and N is the number of non-zero weights. For statistical analysis of particularly high and low $_{AW}Means$ indicating species responding positively, respectively negatively to high land-use intensity, we chose a null model approach that calculates theoretical $_{AW}Mean$ values for each species based on the randomized occurrence of a species the plots according to Chisté et al. (2016). The null model for each species chooses LUI, mowing, grazing or fertilization intensities of random sites, considering the number of sites where this species occurs, and calculates a theoretically expected value of the $_{AW}Mean$ for each species after 10,000 iterations. The proportion of randomized $_{AW}Means$ with greater or smaller values than the observed $_{AW}Mean$ value for each species provides significance p -values ($\alpha = 0.05$). Species with significantly smaller observed $_{AW}Means$ than expected were considered as species being responding negatively under high LUI, adapted to low intensity, whereas those that had a significantly higher $_{AW}Mean$ than expected were classified as species responding positively to high LUI. Species that could neither be

classified as 'responding negatively' nor 'responding positively' were defined as neutrally responding species. The calculations described in this section were performed using the package 'SDMTools' (Version 1.1-221) implemented in R (R Version 1.0.143, R Development Core Team, 2016).

2.4.2. Relating the land-use niche to species-specific functional and ecological traits

We aimed at describing species responding positively, neutrally or negatively to high LUI by relating their specific niche value ($_{AW}Mean$) and their niche breadth ($_{AW}SD$) to specific functional traits, CSR ecological strategy types sensu Grime (1974), Ellenberg indicator values (Ellenberg et al., 2001) and Utilization numbers sensu Briemle (Briemle et al., 2002; Dierschke & Briemle, 2002).

We chose five different vegetative and generative plant traits reflecting responses to disturbance, competition, reproduction and dispersal (see **Table S.2**). As vegetative traits, **Plant height**, **Specific leaf area** (SLA) and **Leaf dry matter content** (LDMC) were chosen. Plant height reflects the trade-off between competition capacity and immediate resistance to mowing and grazing disturbance due to durable, tough tissue (Bernhardt-Römermann et al., 2011; Weiher et al., 1999; Westoby et al., 2002). SLA and LDMC both describe aspects of leaf economy, being associated with flexible responses to variable light, fertilization, resource utilization of plants and defoliation (e.g., Pfestorf et al., 2013; Westoby et al., 2002). **Seed mass** and **seed number** were chosen as generative traits; both being closely linked to dispersal, reproduction and establishment/regeneration success (Westoby, 1998). All traits related to vegetative growth were obtained from the TRY database (Kattge et al., 2011). Missing entries and life-history traits concerning seed characteristics were compiled from the open source trait databases LEDA and BIOLFLOR (Kleyer et al., 2008; Klotz et al., 2002). For species recorded as aggregates (e.g. *Poa pratensis* agg.) and, in cases of subspecies where no information was available, traits of the superordinate species (e.g. *Poa pratensis*) were compiled. Missing values

in these databases were either selected from other literature or, if not obtainable otherwise, extrapolated using the mean of the genus in the overall species pool of both databases.

CSR strategy types for each species were extracted from Grime et al. (2007; see **Table S.2**).

Established strategy types were converted into numerical values by a system of linear interpolation in three dimensions similar to Hill et al. (2002) by assuming that the sum of all strategy types per species equals 1: competitors (1,0,0); stress tolerant (0,1,0); ruderal (0,0,1); stress tolerant - ruderals (0, 0.5, 0.5), completely intermediate types (0.33, 0.33, 0.33), etc. Missing values were left blank, corresponding to 4% of all entries.

In order to link species' $_{AW}Means$ and $_{AW}SDs$ to environmental site conditions, we chose Ellenberg indicator values for moisture (**M indicator**), soil reaction (**R indicator**) and nutrients (**N indicator**).

These indicator values reflect the realized ecological niche and the ecological behavior of species (Diekmann et al. 2003; Kleinebecker et al. 2018), following an ordinal twelve-point scale in the case of M indicator, and a nine-point scale in the case of R indicator and N indicator (see **Table S.2**).

Missing values or those indicating an indifferent reaction of a species to one environmental condition were left blank, corresponding to 25.8%, 49.7% and 20.5% of all entries of M indicator, R indicator and N indicator, respectively.

We selected **Briemle utilization numbers** (Briemle et al., 2002; Dierschke & Briemle, 2002) for mowing (M tolerance), trampling (T tolerance) and grazing tolerance (G tolerance). These reflect the ecological behaviour or tolerance of species to mechanical disturbances caused by agricultural land use, following a nine-point scale (see **Table S.2**). Missing values were left blank, corresponding to 10.6% of all entries.

In order to determine the different drivers and their relative strength of niche location ($_{AW}Mean$) and breadth ($_{AW}SD$) of each species, linear regression models (LMs) were calculated. Using the `lm` function implemented in R (package 'stats', R Version 1.0.143, R Development Core Team, 2016),

$_{AW}Mean$ and $_{AW}SD$ of the compound land-use intensity (LUI) and each land-use component (fertilization, mowing, grazing) were defined as a function of each single environmental or ecology-strategic parameters listed above.

In order to approach normal distribution of residuals, $_{AW}Mean$ Fertilization, $_{AW}SD$ LUI and $_{AW}SD$ Grazing were square-root transformed, $_{AW}Mean$ Grazing was log transformed and $_{AW}Mean$ LUI was squared. $_{AW}Mean$ Mowing, $_{AW}SD$ Fertilization and $_{AW}SD$ Mowing were left unchanged. Model assumptions were checked using the summary function implemented in R, the Shapiro-Wilk test for normality of residuals and diagnostic plots for controlling linearity and heteroscedasticity. Furthermore, to check for inter-correlation among variables, a Spearman rank correlation to the full data set was calculated. Pairwise comparisons between plant species reactions along the different land-use intensity gradients were performed using Mann-Whitney-U tests, with a Bonferroni-adjustment for $k=3$. All statistical analyses listed above were performed using packages 'base', 'stats', 'graphics' implemented in R (R Version 1.0.143, R Development Core Team, 2016). Nonparametric analyses were performed in SPSS (IBM SPSS Statistics 24).

3. Results

The studied grasslands showed great variation in their land-use, vegetation and ecological characteristics as well as in their abundance-weighted land-use niche ($_{AW}Mean$) and the respective niche breadth ($_{AW}SD$) averaged over all sites, species per site or groups per site (for detailed information see **Table S.3**). The gradient in land-use intensity, averaged over a six-year period, is reflected by the compound land-use intensity (LUI), ranging from 0.49 to 3.56, and by its components fertilization level (ranging from 0–208.12 kg N \times ha⁻¹ \times year⁻¹), mowing frequency (0–3 times per year) and grazing intensity (0–1084.4 livestock units \times grazing days⁻¹ \times ha⁻¹ \times year⁻¹). Averaged plant species richness ranged from 13 to 63 species per 16 m².

3.1. Niche optimum and niche breadth modelling

Generally, our analyses showed that the number of species responding negatively to high land-use intensity was considerably larger than the amount of species responding positively to it. However, species' response to high land-use intensity varied between LUI and its components (**Figs. 1A-D**).

34% of all species were identified as responding negatively under high LUI, whereas only 11% turned out as responding positively to it (**Fig. 1A**). The niche breadth of those species responding negatively to high LUI was the narrowest, whereas niche breadths of species being promoted by it were the broadest (**Table S.6**). Neutrally responding species had significantly narrower niches than those responding positively. The intensity of fertilization and mowing affected 41% and 40% of all species negatively, whereas 7% and 13% responded positively to higher fertilization intensity and mowing frequency, respectively (**Figs. 1B and C**). Species responding negatively to fertilization and mowing intensity had the narrowest niche, whereas those responding positively had on average the largest niche. The amount of species responding negatively to high grazing intensity was slightly lower than those responding positively (13% and 15%, respectively; **Fig. 1D**). Positively responding species had the largest average grazing niche breadth.

Inconsistent species-response patterns between types of land-use intensity were revealed. When looking at the compound land-use intensity or at each of the single components, most positively responding species varied in their response between responding positively to high land-use intensity and responding neutrally to it (e.g. *Carum carvi*, *Dactylis glomerata*). On the other hand, most species that responded extremely negatively to high land-use intensity, such as *Euphrasia rostkoviana*, reacted negatively irrespective of land-use type (either compound land-use intensity, fertilization, mowing or grazing. For a full overview, see **Table S.4**).

3.2. Niche characterization employing species-specific functional and ecological traits

The niche optima for the LUI, as well as for its two components amount of fertilizer and mowing frequency were associated with taller growing species with higher SLA and lower LDMC values (**Table 1**) which associated with species being promoted by high LUI (**Figs. S.1a, b**). The degree of decreased stress tolerance and Ellenberg indicator values for moisture and nutrients (M indicator, N indicator) increased with increasing $_{AW}Mean$ in LUI, fertilization intensity and mowing frequency (**Figs. S.3a, c**). The species' LUI niche optimum was positively associated with mowing tolerance (M tolerance). Niche breadths of compound land-use intensity were positively associated with M indicator and M tolerance (**Table 1**); whilst niche breadths of fertilization intensity and mowing frequency were positively associated with SLA and negatively with LDMC values and the degree of stress tolerance (**Table 1**). M indicator and N indicator values both increased with increasing niche breadth in fertilization intensity and mowing frequency (**Figs. S.3b, d**), as did M tolerance (**Figs. S.4b, d**). Additionally, niche breadth along the fertilization intensity gradient was positively associated with species height and competitive strategy.

Grazing intensity displayed rather different results. With increasing grazing $_{AW}Mean$, plant height and LDMC values decreased (**Table 1**). All three are characteristics displayed by species responding positively to high LUI (**Fig. S.1i**). Increased $_{AW}Means$ in grazing intensity were negatively associated with Ellenberg indicator values for soil reaction (**Fig. S.3e**); whereas both G tolerance (**Table 1**) and T tolerance were positively associated (**Fig. S.4e**). With increasing niche breadth in grazing intensity, LDMC values (**Table 1**) and the degree of stress tolerance decreased (**Fig. S.2c**), whereas N indicator values (**Table 1**) as well as M, G and T tolerance increased (**Fig. S.3f**).

4. Discussion

4.1. Species-specific response and response characterization to land-use intensity

Our analyses indicate that it is not simple to classify species into groups of land-use intensity (species responding positively to intensification, henceforth 'Winners'; and species responding negatively to it, henceforth 'Losers'), as the ecophysiological characteristics determining the species' specific reactions vary depending on the type of land use. However, overall patterns of species specialization (i.e. niche breadth) under all land-use types were discernible. The characteristics of 'Winners' (and hence, those of 'Losers' as well) of high compound land-use, fertilization and mowing intensity were fairly similar. However the characteristics of 'Winners' (and 'Losers' respectively) of high grazing intensity differed considerably. Therefore, we will discuss our results in sections below, focusing on overall patterns first and then addressing the results according to land-use type. However, it is important to bear in mind, two aspects. First: our land-use components are partly strongly correlated (fertilization and mowing ($\rho = 0.67$, $p < 0.001^{***}$), fertilization and grazing ($\rho = -0.32$, $p < 0.001^{***}$), mowing and grazing ($\rho = -0.71$, $p < 0.001^{***}$)). Second: mathematically speaking, a species' niche position and its respective niche breadth are not independent. They both give insight, however, into different interesting aspects of species response to land-use type and intensity, and will thus be discussed together in each section.

4.1.1. Species' specialization under high land-use intensity

When comparing species' response between land-use types, it was discernible that niche breadth was strongly associated with species' specific reaction: 'Loser' species were generally associated with relatively narrow niches and remained 'Losers' irrespective of land use, whereas 'Winners' had the broadest niches and varied between positive and neutral response to high land-use intensity.

Niche breadth of a species has been associated with its specialization under specific habitat conditions (Boulangéat et al., 2012; Chisté et al., 2016; Devictor et al., 2010), with wide-niched

generalists rather evolving in temporally and spatially heterogeneous habitats, whilst specialists with narrow niches develop under spatio-temporally homogeneous conditions (Dostál et al., 2017). In grasslands, for instance, plant species with wide niches are usually common grassland species adapted to anthropogenic land use, dominating in intensively used, temporally heterogeneous grasslands. These can cope more readily with the varying environmental conditions such as climate change or land use induced stresses and disturbances (Allan et al., 2014; Thuiller et al., 2005). Species with narrow niches, such as rare, ecophysiologicaly delimited species with specific environmental requirements and associated with grasslands managed at low intensities, are only able to adapt within a small margin (Boulangéat et al., 2012; Zechmeister et al., 2003) and disappear once the tolerated margin is surpassed.

4.1.2. Compound land-use, fertilization and mowing intensity

Our analyses revealed a clearly larger number of plant species responding negatively to high compound land-use, fertilization and mowing intensity than species responding positively. This is in line with the overall loss of species richness along increasing gradients of compound land-use ($\rho = -0.415$, $p < 0.001$), mowing ($\rho = -0.399$, $p < 0.001$) and fertilization intensity ($\rho = -0.285$, $p < 0.001$). Many studies corroborate our results, showing plant species richness decreasing strongly especially due to the intensification of fertilization (e.g. Kleinebecker et al., 2018; Zechmeister et al., 2003), mowing or combined effects (Busch et al., 2017; Socher et al., 2012).

'Winners' of high compound land-use, fertilization and mowing intensity were highly competitive, productive species. These were fast-growing with high SLA and low LDMC values, including graminoids such as *Arrhenatherum elatius*, *Lolium perenne* or *Phleum pratense* or umbelliferous herbs such as *Anthriscus sylvestris* or *Heracleum sphondylium* (see also Zechmeister et al., 2003). These are usually nutrient-acquisitory species with high Ellenberg values for nutrient availability and moisture (Bartelheimer et al., 2016; Dostál et al., 2017; Wesche et al., 2012), which are characteristics that can be translated into the production of high quality biomass and a quick

resprouting after disturbance events through flexible responses to nutrient and light availability (Bernhardt-Römermann et al., 2011; Louault et al., 2005). Mowing at low intensities, a nonselective disturbance, may promote species richness by continuously setting above-ground competition parameters to zero through opening space and thus allowing less competitive species to complete their life-cycle (Müller et al., 2014). In contrast, fertilization and the combination of mowing and fertilization mainly favours highly productive species, which outgrow and displace others, leading to decreased species richness (Zechmeister et al., 2003). ‘Winner’ species also show increased tolerance to shade and defoliation events due to mowing or fertilization (Westoby et al., 2002), as they are able to quickly absorb available nutrients, invest them in the production of photosynthetically active biomass and overgrow other species on the one hand, or to quickly regrow after a defoliation event on the other hand. Hence, they are characterized through the interplay of competitive ability and disturbance tolerance.

Our analyses indicate that species responding positively to high land-use intensity were rather less tolerant to stress (rarely S strategists). In combination with or under fertilization alone, however, they were highly competitive (C strategists), such as nitrophilous species like *Heracleum sphondylium* and *Anthriscus sylvestris*. These typically occur in sites with high nutrients under high land-use intensity, but respond less well to high grazing pressure. These results are in line with predictions from Grime (2006), who pointed out that in agriculturally used habitats stress tolerant species or intermediate strategists (SR, SC) are most prone to be lost. Accordingly, C, CR and R strategists can be expected to increase under high compound land-use intensity (Grime, 2006). Boulangeat et al. (2012) showed that C strategists are mostly generalists, with wide niches and thus greater capacity to cope with agricultural management, whilst S or CS strategists represent species with a higher degree of specialization and a narrower niche (Boulangeat et al., 2012). Their decreased capability to adapt to increased land use-induced disturbances subsequently leads to loss under high land-use intensity, corresponding to our results. Accordingly, ‘Losers’ of high compound land-use intensity, of mowing, fertilization or a combination thereof tend to be small-growing

species with nutrient-retentive strategies, rather investing acquired nutrients in tough, durable tissues than in fast regrowth. These species are rather specialized, narrow-niched and stress-tolerant species, and are found in low-intensity grasslands. These often occur on shallow, calcareous soils, which are characterized by high temperatures, low moisture and nutrient availability (Bartelheimer et al., 2016).

4.1.3. Grazing

Contrasting to our results discussed above, species' response to grazing showed slightly more 'Winner' than 'Loser' species; and grazing intensity did not affect species richness significantly ($\rho = -0.099$, $p = 0.226$). Generally, studies focussing on the effect of grazing intensification have produced rather ambiguous, partly even contradictory results. Some showing positive, some negative and some inconclusive effects on species diversity. These results strongly depend – of course also caused by differing points of departure in each study – on grazing intensity, defined through stocking rates, residence time or herbivore type and size (Dupré & Diekmann, 2001; Olf & Ritchie, 1998; Vesik & Westoby, 2001), its nature of being a selective disturbance, or the surrounding environmental context in combination with grazing (de Bello et al., 2006; Pakeman, 2004).

In our study, 'Winners' of high grazing intensity were small growing species with low LDMC values, like *Viola arvensis* or *Plantago lanceolata*. We could show that these species favoured high nutrient availability, but were also rather connected to calcareous soils (high Ellenberg values for nutrient availability and soil reaction). Usually, species on calcareous soils are adapted to low-nutrient soil conditions and extensive grazing management (Bartelheimer et al., 2016); with nutrient-retentive characteristics translating into retaining nutrients and transferring them to tough, rather unpalatable and durable tissue instead of fast growth and the production of photosynthetic active biomass (Díaz

et al., 2007; Weiher et al., 1999; Westoby et al., 2002). These species are usually light-loving species (Drobnik et al., 2011) and characterized by an interplay of stress tolerance and stress avoidance.

However, in our study 'Winners' of high grazing intensity were shown to be less stress tolerant – but rather ruderal species (R strategists) like *Capsella bursa-pastoris*, *Chenopodium album* and *Polygonum aviculare*, which also displayed tolerance mechanisms related to mowing or to animal herding like grazing and trampling tolerance (i.e.. small-growing, creeping species such as *Ranunculus repens* and *Trifolium repens*) and a preference for high nutrient availability. These patterns coincide with Grime (2006), who predicted a clear preference of ruderals rather than of stress tolerants under intensive grazing. Hence, an increase of R, CR and SR strategists may be expected, whereas C, SC and S strategists should decrease (Grime, 2006). Ruderal species, often annuals, are promoted, as these avoid stress by taking advantage of favourable growing conditions caused by selective biomass removal, the creation of vegetation gaps and patches of open soil (Bartelheimer et al., 2016; Drobnik et al., 2012; Müller et al., 2014; Olf & Ritchie, 1998). These sites are free of inter-specific competition, enabling ruderal species to quickly uptake nutrients, invest them in growth and the production of biomass (hence presenting with low LDMC values) and effectively reproduce in frequently disturbed habitats such as intensively grazed sites (Bartelheimer et al., 2016). This is often associated with an overall increase in species richness. However, also other non-ruderal grassland species may be promoted under high-intensity grazing, such as nutrient-acquisitive, fast-growing and resprouting species with low LDMC values such as grasses like *Dactylis glomerata* and *Lolium perenne* (Zechmeister et al., 2003). The 'Losers' of high grazing intensity, however, again clearly correspond to those expected to be found on low-intensity grasslands on calcareous soils: stress-tolerant species with nutrient-retentive strategies adapted to low nutrient conditions and expressing survival strategies rather related to disturbance avoidance (Díaz et al., 2007).

Our results add statistical evidence to existing knowledge for explaining and predicting community assembly and species coexistence in response to current land-use practices in temperate, lowland to submontane grasslands in Central Europe. More importantly, our statistical approach can be used by scientists working in other managed habitat types from other biogeographical regions for quantifying the specific response or tolerance of plant species to explain local vegetation dynamics and offering the possibility to develop compromises of conserving and restoring species rich, multifunctional grasslands and economically reasonable grassland use at the same time.

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Author's contributions

VK, TK conceived the idea for the manuscript; VB, TK defined the final analyses; MC, KM, NB developed the used statistical model; VB and VK analyzed the data and outlined previous versions of the manuscript; VB, VK, DS, DP, SB, JM, NH, MF contributed data; and all authors contributed on the finalization of the manuscript.

Data accessibility

Data used in this study will be made publicly available via the webpage of the database of the Biodiversity Exploratories project: <https://www.bexis.uni-jena.de>

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Tables and Table legends:

Tables:

Table 1: Summary of single linear regression models (LMs) abundance-weighted mean niches ($_{AW}Mean$) and abundance-weighted niche breadths ($_{AW}SD$) over all species, corresponding to the intensity of compound land-use (LUI), fertilization, mowing and grazing with plant functional traits, CSR ecological strategy types, Ellenberg indicator values and Briemle utilization numbers. Land-use type $_{AW}Means$ and $_{AW}SDs$ over all 151 species under study (dependent variables) were modelled as functions of each parameter listed (independent variables). Multiple R^2 values expressing the fraction of variability of each dependent variable explained by each linear model are given. Asterisks and letters indicate respective model significance values: $p > 0.05 = n.s.$; $0.05 > p > 0.01 = *$; $0.01 > p > 0.001 = **$; $0.001 > p = ***$.

Appendix Table S.1: Main geographic and environmental characteristics of the Biodiversity Exploratory Regions.

Table S.1: Main geographic and environmental characteristics of the three regions of Biodiversity Exploratories. In each region the respective 50 studied grassland sites are relatively evenly distributed. Modified from Fischer *et al.*, 2010.

Appendix Table S.2: Ecological relevance of selected life history traits and ecological strategy types.

Table S.2: Selected vegetative and generative traits, CSR ecological strategy types, Ellenberg indicator values and Briemle utilization numbers and their ecological relevance. Abbreviations: RGR = Relative growth rate. Further name abbreviations and their units, as well as respective online trait databases and additional literature are indicated.

Appendix Table S.3: Exploratory statistic values of all analysed variables and parameters over all species and sites.

Table S.3: Mean values, respective standard errors as well as minimum and maximum values of the analysed variables and parameters over all species and/or sites; calculated for a time period of six years. Plant species richness was calculated excluding woody species taller than 2m. In order to provide an overview over the data margin of fluctuation, all values below for 'Land use and vegetation' were averaged over all sites; the values for abundance-weighted mean niches ($_{AW}Mean$), and abundance-weighted niche breadth ($_{AW}SD$) and 'Life-history traits' were averaged over all species and sites; the values for 'CSR ecological strategy types' were averaged over all groups and sites. We used the following abbreviations: MV = Mean value; SE = Standard error, MIN = Minimum value, MAX = Maximum value; Ellenberg indicator values: M indicator = Moisture; R indicator = Soil reaction; N indicator = Nutrients;. Units: Compound land-use (LUI) = none; Fertilization = $N \text{ kg} \times \text{ha}^{-1} \times \text{year}^{-1}$; Mowing = cuts per year; Grazing = $\text{livestock units} \times \text{days}^{-1} \times \text{year}^{-1} \times \text{ha}^{-1}$; Plant height = cm;

Specific leaf area = mm²/mg; Leaf dry matter content = mg/mg; Seed mass = mg; Seed number = none.

Appendix Table S.4: Complete list of plant species-specific abundance weighted niche values and abundance weighted niche breadths.

Table S.4: : Complete list of analyzed plant species, the number of sites they occurred on, species-specific abundance weighted niche values ($_{AW}Mean$) and abundance weighted niche breadths ($_{AW}SD$) and their specific reaction (SpReaction), depending on land use (compound land-use or LUI, fertilization, mowing and grazing). In cases of species' aggregates the eponymous species name is given.

Table S.4 (continued):

Appendix Table S.5: Correlation analysis of all analyzed parameters with abundance-weighted mean niches and abundance-weighted niche breadth.

Table S.5: Spearman correlation matrix of all analyzed parameters with abundance-weighted mean niches ($_{AW}Mean$) and abundance-weighted niche breadth ($_{AW}SD$) over all species, corresponding to the intensity of compound land-use (LUI), fertilization, mowing and grazing, with plant functional traits, CSR ecological strategy types, Ellenberg indicator values and Briemle utilization numbers. Ellenberg indicator values: M Indicator = Moisture; R Indicator = Soil reaction; N Indicator = Nutrients. Coefficient ρ and p -values are given. Asterisks and letters indicate respective significance values: $p > 0.05 = n.s.$; $0.05 > p > 0.01 = *$; $0.01 > p > 0.001 = **$; $0.001 > p = ***$.

Appendix Table S.6: Exploratory statistic values of species responding negatively, neutrally and positively to high intensity land-use.

Table S.6: Mean values, respective standard errors as well as minimum and maximum values of species responding negatively ('Losers'), neutrally ('Neutrals') and positively ('Winners'), defined with respect to their expected niche optimum ($_{AW}Mean$) and their niche breadth ($_{AW}SD$) over all species, corresponding to the intensity of compound land-use (LUI) and its components (fertilization, mowing, grazing). Letters indicate results of comparative Mann-Whitney-U tests with Bonferroni-correction. All pairwise comparisons were highest significantly different ($p < 0.0003, ***$), with the exception of $_{AW}SD$ Fertilization Neutrals vs. Winners (highly significant ($p < 0.003, **$)) and $_{AW}SD$ LUI Neutrals vs Winners, $_{AW}SD$ Mowing Neutrals vs Winners, $_{AW}SD$ Losers vs Neutrals (not significant ($p < 0.17, n.s.$)). Abbreviations: MV = Mean value; SE = Standard error, MIN = Minimum value, MAX = Maximum value.

Figures and Figure Legends:

Figure 1:

Land-use niches of selected plant species, displaying grassland sites in which these species most frequently occur. Abundance weighted means (niche position) and their respective abundance weighted standard deviation (niche breadth) of A) compound land-use intensity (LUI), B) fertilization intensity ($\text{N kg} \times \text{ha}^{-1} \times \text{year}^{-1}$), C) mowing intensity (0 to 3 cuts per year), D) grazing intensity ($\text{livestock units} \times \text{days}^{-1} \times \text{year}^{-1} \times \text{ha}^{-1}$). Uppermost circles and dashed lines indicate the overall mean intensity for compound land-use (LUI) and each of its components fertilization, mowing and grazing; averaged over six years. Open circles represent abundance-weighted means and their abundance-weighted standard deviation of species repressed by high land-use intensity ('Losers'). Black filled circles represent abundance-weighted means and their abundance-weighted standard deviation of land-use levels of species promoted by high land-use intensity ('Winners'). The number of sites where each species occurs on are shown in parentheses behind species names. Due to better visualization purposes, 'Neutrals' species have been omitted from this figure, leading to different amounts of species shown depending on the land-use component. In cases of species' aggregates the eponymous species name is given.

Appendix Figure S.1: Distribution of plant functional traits among "Winner", "Neutral" and "Loser" species along a land-use gradient.

Figure S.1:

Distribution of plant functional traits among species responding positively ('Winners'), neutrally ('Neutrals') and negatively ('Losers') to high land-use intensity, along land-use gradients. Along a mowing gradient, distribution of a) Plant height in m, b) Specific leaf area in $\text{mm}^2 \times \text{mg}^{-1}$, c) Ellenberg Indicator value for nutrients (N indicator). Along a grazing gradient, distribution of e) Plant height in m, f) Leaf dry matter content in $\text{mg} \times \text{g}^{-1}$. Along a mowing gradient, d) proportion mean of the C strategy types (Competitors, as found in C, CR, CS, CSR strategists). Along a grazing gradient, g) Ellenberg indicator value for soil reaction (R indicator), h) proportion mean of the R strategy types (Ruderals, as found in R, CR, SR, CSR strategists). Errorbars indicate a standard error (SE); outliers are shown as black dots. Dark grey filled boxplots and big circles represent 'Winners', unfilled ones represent 'Neutrals', light grey filled represent 'Losers'.

Appendix Figure S.2: Relationships between abundance weighted mean niches of species in response to high land-use intensity, and their ecological strategies.

Figure S.2:

Relationships between abundance weighted mean niches ($A_W\text{Mean}$) of species responding positively ('Winners'), neutrally ('Neutrals') and negatively ('Losers') to high land-use intensity, and their ecological strategies as competitors (C strategists), stress-tolerants (S strategists) and ruderals (R

strategists). C strategists and a) $_{AW}Mean$ fertilization niche, b) $_{AW}Mean$ mowing niche; S strategists and c) $_{AW}Mean$ fertilization niche, d) $_{AW}Mean$ mowing niche; R strategists and e) $_{AW}Mean$ grazing niche, f) $_{AW}Mean$ mowing niche. Significance and strength of Spearman rank correlations (ρ) are given. Asterisks and letters indicate respective values: $p > 0.5 = n.s.$; $0.5 > p > 0.1 = *$; $0.01 < p = ***$. A trendline was added for better visualization of data correlation.

Appendix Figure S.3: Relationships between abundance weighted mean niches and abundance weighted niche breadth of species in response to high land-use intensity, and Ellenberg indicator values.

Figure S.3:

Pairwise Spearman rank correlations between abundance weighted mean niches ($_{AW}Mean$) and abundance weighted niche breadth ($_{AW}SD$) of species responding positively ('Winners'), neutrally ('Neutrals') and negatively ('Losers') to high land-use intensity, and Ellenberg indicator values. Nutrients (N indicator) and a) $_{AW}Mean$ fertilization niche, b) $_{AW}SD$ fertilization niche breadth; Moisture (M indicator) and c) $_{AW}Mean$ mowing niche, d) $_{AW}SD$ mowing niche breadth; Soil reaction (R indicator) and e) $_{AW}Mean$ grazing niche, f) $_{AW}SD$ grazing niche breadth. Significance and strength of Spearman rank Correlations (ρ) are given. Asterisks and letters indicate respective significance values: $0.05 > p > 0.01 = *$; $0.001 > p = ***$. A trendline was added for better visualization of data correlation.

Appendix Figure S.4: Relationships between abundance weighted mean niches and abundance weighted niche breadths of species in response to high land-use intensity, and Briemle's utilization numbers.

Figure S.4:

Pairwise correlations between land-use abundance weighted mean niches ($_{AW}Mean$) and abundance weighted niche breadths ($_{AW}SD$) of species responding positively ('Winners'), neutrally ('Neutrals') and negatively ('Losers') to high land-use intensity, and Briemle's utilization numbers. Mowing tolerance and a) $_{AW}Mean$ fertilization niche, b) $_{AW}SD$ fertilization niche; trampling tolerance and c) $_{AW}Mean$ mowing niche, mowing tolerance and d) $_{AW}SD$ mowing niche; trampling tolerance and e) $_{AW}Mean$ grazing niche, f) $_{AW}SD$ grazing niche. Strength and significance of Spearman rank Correlations (ρ) are given. Asterisks and letters indicate respective significance values: $0.05 > p > 0.01 = *$; $0.01 > p > 0.001 = **$; $0.001 > p = ***$. A trendline was added for better visualization of data correlation.

Table 1: Summary of single linear regression models (LMs) abundance-weighted mean niches (AWMean) and abundance-weighted niche breadths (AWSD) over all species, corresponding to the intensity of compound land-use (LUI), fertilization, mowing and grazing with plant functional traits, CSR ecological strategy types, Ellenberg indicator values and Briemle utilization numbers. Land-use type AWMeans and AWSDs over all 151 species under study (dependent variables) were modelled as functions of each parameter listed (independent variables). Multiple R ² values expressing the fraction of variability of each dependent variable explained by each linear model are given. Asterisks and letters indicate respective model significance values: p > 0.05 = n.s.; 0.05 > p > 0.01 = *; 0.01 > p > 0.001 = **; 0.001 > p = ***.																				
Simple Linear Regression																				
	AWMean Compound land-use					AWMean Fertilization					AWMean Mowing					AWMean Grazing				
	Mult R ²	Intercpt	Estimate	t value	sign.	Mult R ²	Intercpt	Estimate	t value	sign.	Mult R ²	Intercpt	Estimate	t value	sign.	Mult R ²	Intercpt	Estimate	t value	sign.
Plant functional traits																				
Plant height	0.03	1.96	0.65	2.11	*	0.06	3.14	1.98	3.05	**	0.09	0.52	0.59	3.89	**	0.04	4.95	-0.38	-2.41	*
Specific leaf area	0.16	-0.64	0.60	5.33	**	0.15	1.10	0.12	5.00	**	0.14	0.09	0.03	4.88	**		4.81	0.00	0.08	n.s.
Leaf dry matter content	0.11	3.13	-3.74	-4.08	**	0.05	5.32	-5.60	-2.81	**	0.03	1.00	-0.96	-1.98	*	0.04	5.08	-1.21	-2.42	*
Seed number		2.24	0.00	0.63	n.s.		3981.00	0.00	0.69	n.s.		0.77	0.00	1.27	n.s.		4.79	0.00	0.44	n.s.
Seed mass		2.27	-0.02	-0.50	n.s.		4.03	-0.03	-0.42	n.s.		0.73	0.02	0.98	n.s.	0.03	4.86	-0.00	-2.10	*

																			4	4	
Ecological Strategy types																					
Competitors		2.04	0.41	1.82	n.s.	0.05	3.29	1.33	2.83	**	0.06	0.59	0.35	3.09	**		4.89	-0.19	-1.55	n.s.	
Ruderals		2.18	0.20	0.80	n.s.		4.13	-0.50	-0.95	n.s.		0.82	-0.17	-1.33	n.s.	0.05	4.68	0.37	2.85	*	
Stress-tolerants	0.17	2.61	-2.19	-5.33	** *	0.09	4.54	-3.47	-3.83	** *	0.08	0.90	-0.79	-3.61	** *		4.87	-0.45	-1.92	n.s.	
Ellenberg indicator values																					
Moisture	0.13	0.91	0.28	4.14	** *	0.17	0.67	0.68	4.77	** *	0.19	-0.08	0.18	5.03	** *		4.99	-0.04	0.38	n.s.	
Soil reaction		2.81	-0.11	-1.18	n.s.		3.36	0.05	0.27	n.s.		0.65	0.01	0.19	n.s.	0.08	5.55	-0.12	-2.60	*	
Nutrient supply	0.41	0.72	0.31	9.02	** *	0.30	1.13	0.56	7.13	** *	0.27	0.11	0.13	6.68	** *		4.59	0.04	1.83	n.s.	
Briemle utilization numbers																					
Mowing tolerance	0.21	0.73	0.27	5.86	** *	0.23	0.65	0.59	6.37	** *	0.17	0.08	0.12	5.27	** *		4.57	0.04	1.52	n.s.	
Grazing tolerance		2.01	0.04	0.84	n.s.		4.02	-0.03	-0.32	n.s.		0.94	-0.04	-1.79	n.s.	0.14	4.32	0.09	4.67	*	
Trampling tolerance		1.89	0.07	1.54	n.s.		3.88	0.00	0.01	n.s.		0.92	-0.04	-1.73	n.s.	0.19	4.29	0.11	5.53	*	

	AWSD Compound land-use					AWSD Fertilization					AWSD Mowing					AWSD Grazing					
	Mult R ²	Interc ept	Estimate	t value	sig n.	Mult R ²	Interc ept	Estimate	t value	sig n.	Mult R ²	Interc ept	Estimate	t value	sig n.	Mult R ²	Interc ept	Estimate	t value	sig n.	
Plant functional traits																					
Plant height		0.63	0.05	1.80	n.s.	0.04	22.41	12.70	2.52	*		0.62	0.13	1.51	n.s.		11.04	0.26	0.31	n.s.	
Specific leaf area		0.64	0.00	0.49	n.s.	0.11	8.95	0.81	4.16	**		0.09	0.38	0.01	3.78	**		10.19	0.04	1.30	n.s.
Leaf dry matter content		0.67	-0.07	-0.72	n.s.	0.05	38.06	-42.30	-2.75	**		0.06	0.87	-0.81	-3.05	**	0.04	12.63	6.08	2.41	*
Seed number		0.65	0.00	0.40	n.s.		27.53	0.00	0.83	n.s.		0.67	0.00	1.17	n.s.		11.06	0.00	0.75	n.s.	
Seed mass		0.66	-0.01	-1.66	n.s.		28.54	-0.50	-0.86	n.s.		0.69	-0.01	-0.54	n.s.		11.39	0.14	1.55	n.s.	
Ecological Strategy types																					
Competitors		0.63	0.04	1.67	n.s.	0.03	23.67	7.87	2.14	*		0.62	0.11	1.65	n.s.		10.93	0.42	0.69	n.s.	
Ruderals		0.65	-0.02	-0.73	n.s.		27.50	0.50	0.12	n.s.		0.67	0.02	0.26	n.s.		10.81	1.04	1.57	n.s.	
Stress-tolerants		0.66	-0.08	-1.95	n.s.	0.13	32.85	-31.38	-4.56	**		0.09	0.75	-0.46	-3.81	*	0.12	11.95	4.89	4.32	**
Ellenberg indicator values																					
Moisture	0.05	0.57	0.02	2.28	*	0.15	3.48	4.94	4.40	**	0.08	0.37	0.06	3.02	**		9.73	0.3	1.5	n.	

										*								1	6	s.	
Soil reaction		0.65	0.00	-0.22	n.s.		28.37	-0.46	-0.33	n.s.		0.78	-0.02	-0.79	n.s.		13.60	-0.41	-1.67	n.s.	
Nutrient supply		0.62	0.00	1.13	n.s.	0.27	6.89	4.09	6.62	** *		0.27	0.31	0.07	6.57	** *	0.15	8.67	0.50	4.57	* *
Briemle utilization numbers																					
Mowing tolerance	0.07	0.57	0.01	3.15	**	0.19	4.28	4.17	5.67	** *		0.18	0.28	0.07	5.48	** *	0.09	8.54	0.46	3.56	* *
Grazing tolerance		0.63	0.00	1.11	n.s.		23.66	0.66	0.99	n.s.		0.57	0.02	1.61	n.s.		0.05	9.69	0.27	2.50	* *
Trampling tolerance		0.63	0.00	1.14	n.s.		23.25	0.84	1.20	n.s.		0.60	0.01	1.18	n.s.		0.09	9.31	0.40	3.54	* *

