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Influence of Highland and production-oriented cattle breeds on pasture vegetation: A pairwise assessment across broad environmental gradients

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ABSTRACT

Highland cattle are lighter, slower-growing and less demanding on forage than most production-oriented cattle breeds, which may affect vegetation composition. This study aimed at identifying the importance of breed-dependent impact on the composition of pasture vegetation in comparison to well-investigated factors such as site properties and grazing management. Vegetation was investigated in 50 paired pastures at 25 locations ranging from Swiss mountain areas to lowlands in southern Germany. Pastures in a pair had been grazed by either Highland cattle or a more production-oriented cattle breed for at least 5 years. Plant species composition was assessed on 150 subplots, three per pasture in areas representing different grazing intensities. Generalized linear mixed-effects models, (partial) constrained correspondence analysis and structural equation models were used for data analysis. Despite similar site conditions between the paired pastures at each location, plants on pastures of Highland cattle showed significantly lower indicator values for grazing and trampling tolerance. Both, grazing and trampling were strongly connected and had a common negative effect on plant species diversity. Moreover, Highland cattle had a direct positive influence on diversity, likely due to reduced woody plant species cover and a higher cover of epizoochoric species. This resulted in significantly higher plant species richness (alpha and gamma) on pastures of Highland cattle than those of production-oriented breeds. The observed differences in plant species richness between pastures of different grazing breeds increased with duration of adaptation, *i.e.* the time a pasture was grazed by a certain breed. The study demonstrates a clear impact of cattle breed on vegetation, which is consistent with the phenotypical differences of the animals. Largely overlooked, cattle breed may explain some of the frequently contrasting responses of vegetation to grazing. The findings have important implications for management decisions and breeding endeavours which go beyond mere productivity objectives. They highlight the potential of low-production Highland cattle to sustain and promote ecosystem services on species-rich, semi-natural grasslands.

1. Introduction

Most semi-natural grasslands in Europe were formed by wild and domesticated herbivores after clearance by humans during centuries. Many plant species have migrated into this anthropo-zoo-genetic habitat and co-evolved (Ellenberg and Leuschner, 2010, chap. 3). Recent decades have brought about enormous changes in grazing livestock, which may affect the composition and functioning of grassland vegetation. In the 20th century, specialised breeding for productivity increased milk and meat yields of cattle, but also forage intake, growth rate and body mass (Derry, 2015). Because breeding traits are complex, the productivity gain often came at the price of lower body condition, reduced fertility and health status (Oltenacu and Broom, 2010).

In contrast, some cattle breeds were primarily selected for their adaptation to harsh environmental conditions and much less for productivity. A typical example of such slow-growing, robust breeds are Highland cattle, which perform well under the low-quality forage and rough climate of the Scottish Highlands. Due to robustness, undemanding foraging behaviour, tasty meat and relatively simple husbandry, Highland cattle have spread widely beyond Scotland and are the most commonly used low-production cattle breed in Switzerland, our main study country, today (SSCA, 2018).

Highland cattle are smaller, lighter and slower-growing than production-oriented beef cattle (Albertí et al., 2008). Compared to the popular breeds of Limousin, Simmentaler, Braunvieh, Angus and Charolais, cows of Highland cattle are 15% shorter at the withers,

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weigh 34% less and their daily average weight gain is 60% lower (SSCA, 2018). These phenotypical differences may change the animals' impact on vegetation. Trampling suppresses susceptible plants and indirectly causes the dominance of trampling-adapted species such as stoloniferous herbs and turf grasses (Briemle et al., 2002; Lezama and Paruelo, 2016; Cole, 1995). Therefore, we hypothesized that the lower weight reduces trampling pressure on Highland pastures and that this is reflected in a higher relative abundance of plant species susceptible to trampling.

The slow growth and low productivity of Highland cattle is associated with a small forage intake (Berry et al., 2002). It is currently unknown whether such lower demand results in less selective foraging, which would supress plant species with typical grazing traits such as a short, prostrate habit, a stoloniferous or rosette architecture, an annual life history and unpalatability (Díaz et al., 2007). While in wild herbivores small body weight is frequently associated with higher selectivity (Clauss et al., 2013), this may not be valid for domesticated grazers. Because their allometry was influenced by breeding decisions of humans and not by natural selection alone, farm animals with large body sizes and high growth rates may be more demanding on forage quality, which goes along with higher selectivity. The second hypothesis of our study was that, if Highland cattle are less demanding and they graze less selectively, their pastures will be less dominated by plant species adapted to grazing and by woody plants, which are usually avoided (Fraser et al., 2009). As a consequence of lower selective exclusion, plant species richness may be higher on Highland pastures.

Several past studies compared pasture vegetation grazed by different livestock species, but only a few examined the effect of the breed. A comparison of commercial and traditional breeds of cattle and sheep during three years only found marginal effects of breed on sward structure (Dumont et al., 2007) and plant diversity (Scimone et al., 2007). However, the traditional breeds used were not pronounced low-production breeds and vegetation presumably needs longer adaption time. Recent research by Spiegal et al. (2019) found larger home ranges and differences in space use for traditional Criollo cattle as compared to commercial Angus x Hereford crossbreeds.

Our aim was, therefore, to compare vegetation composition in pastures grazed by Highland cattle, with nearby pastures of similar environmental conditions grazed by a production-oriented breed. In order to account for the complex factors affecting plant composition in grasslands, the paired pastures were selected across broad environmental gradients. Furthermore, grazing history was recorded to investigate effects of the duration of adaptation.

2. Methods

2.1. Study locations and site selection

Fifty paired pastures were studied at 25 locations ranging from mountain areas in Switzerland to lowlands in southern Germany (Fig. 1). In each pair, one pasture was grazed by Highland cattle and the other by a production-oriented cattle breed. Furthermore, both pastures in a pair were (1) in close proximity of each other, (2) similar with respect to elevation, inclination, intensity of grazing and stocking method, (3) not recently mown, manured or fertilised, (4) grazed by the respective breed for at least five years, and (5) not subjected to supplementary feeding during grazing. To assess the duration of adaptation to a certain breed, all farmers were interviewed on the history of land use.

2.2. Cattle breeds

Highland cattle were compared to more production-oriented cattle breeds, mostly meat-oriented or dual-purpose breeds. No control was imposed on the exact type of the production-oriented breed, since this would have resulted in inadequate sample size. The production-oriented animals were purebreds or crossbreds of Limousin (22%), followed by Braunvieh and Simmental (20% each), Angus (15%), Charolais (6%) and a few animals of eight other breeds.

Because most Highland cattle were suckler cows, pastures grazed by production-oriented suckler cows were preferred. In order to maintain a reasonable sample size, Highland suckler cows were compared to production-oriented heifers at five locations, and Highland heifers were matched with production-oriented heifers at two locations.

2.3. Vegetation analyses

In 2016, plant species composition was assessed on a total of 150 subplots. On each pasture, three subplots were located in zones of different intensity of grazing. The first subplot was established in a flat resting place, highly frequented by cattle. The second subplot was located in an intermediate area, showing the typical characteristics of the entire pasture with average inclination. The third subplot was set up in an area of steep slope with little signs of grazing or resting activity. Each subplot was 5×5 m. We recorded all vascular plant species within the subplot according to Eggenberg et al. (2013), visually estimated their absolute percent cover and the percent bare ground. For all available species, indicator values for grazing and trampling tolerance were extracted from Klotz et al. (2002), who attributed to each species a number between 1 (susceptible) and 9 (tolerant). Trampling tolerance was defined as the ability to grow under trampling pressure because of morphological and ecological adaptions. Grazing tolerance was specified as the ability to grow on regularly grazed pastures and includes forage avoidance strategies and trampling adaption (Briemle et al., 2002). Information about diaspore dispersal mechanisms and indicator values of nutrient requirements were taken from Landolt (2010), who extended the work of Ellenberg et al. (1992) for the Alps. Nutrient indicator values are given in numbers between 1 (low nutrient availability) and 5 (eutrophic areas). Dispersal mechanisms were included as categorial variable (1 = epizoochoric, 0 = not epizoochoric). Indicator values of each subplot were assembled to generate a cover-weighted mean.

2.4. Soil sampling

Soil was sampled by taking 9 cores per subplot (3 cm diameter, 10 cm depth) and pooled into a single sample. Plant-available phosphorus (P) and potassium (K) in sieved and dried soil were dissolved in an agent of calcium lactate, calcium acetate, acetic and water and measured by photometry after 90 min of incubation (VDLUFA, 2012, chap. A6.2.1.1). Plant-available magnesium (Mg) was quantified using a calcium chloride extractant and atomic absorption spectroscopy (VDLUFA, 2012, chap. A6.2.4.1) Soil pH was measured using electrometric assessment of H^+-ion activity in suspension (VDLUFA, 2012, chap. A5.1.1).

2.5. Calculation of normalized stocking rate

In order to account for differences in body weight between herds within a pair, a normalized stocking rate was calculated for each pasture. Farmer's information on the number of animals, their age and sex were multiplied by breed-specific age- and sex-dependent body weights and normalized to livestock units (LU) of 500 kg. Summed LU were divided by grazing duration and pasture size. For all breeds, data on body weight at various ages as well as the age at first calving was compiled from literature and personal information of different breeders and breeding societies. Average weights of male and female individuals were interpolated across different ages using a negative exponential function. Because of the large variation in weight among individuals of Highland cattle, herds were visually attributed to three sub-groups of small (suckler cows with an average body weight of around 450 kg), medium (500 kg) and large (550 kg) animals.

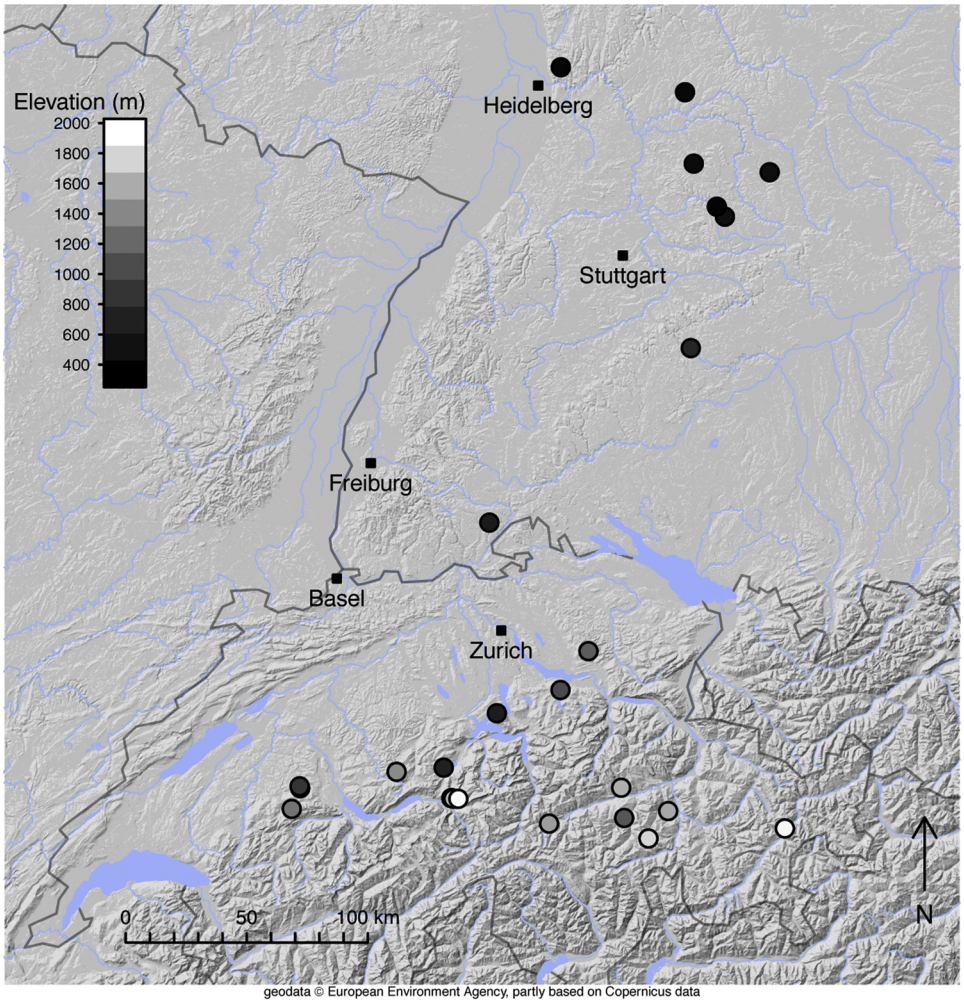

Fig. 1. Map of the study locations in Southern Germany and Switzerland. Each point represents a pair of pastures grazed by Highland Cattle on the one and a production-oriented cattle breed on the other.

2.6. Data analysis

All data were analysed in consideration of sampling structure, which involved the nesting of three vegetation subplots within paired pastures. An exception was the analysis of gamma richness per pasture, which was calculated by counting all plant species found in the three subplots and analysed in pasture pairs only. Values of P, K and stocking rate were log-transformed for normalization of variance.

Univariate response variables (alpha and gamma plant species richness, cover-weighted indicator values and percent cover of woody and epizoochoric species) were analysed using generalized linear mixed-effects models (GLMMs). Random effects were estimated for pasture pairs and subplots within pairs and the likelihood distribution was chosen according to the sampling process of the data: Species numbers were over-dispersed count data, and a negative binomial likelihood with logarithmic link function was used. Percentage of woody and epizoochoric species was bounded between 0 and 1 and modelled by a beta likelihood with logit link. Because the beta distribution does not include 0, all 0 values were considered potentially undiscovered and replaced by very small values according to Smithson and Verkuilen (2006, p. 55). A normal likelihood was used for cover-weighted indicator values, since they were normally distributed and well away from 0. After checking for heteroscedasticity and multicollinearity, all models were estimated for the same set of fixed and random effects. The significance of fixed effects was tested by omitting them from the model individually and calculating the likelihood ratio to the full model, which approximately follows a χ^2 distribution (Zuur et al., 2009). Quadratic relationships of all continuous variables were checked but not included in the final model due to non-significance. Marginal and conditional R^2 were calculated according to Nakagawa (2017), except for the beta models, for which these are not available. Differences in site properties between breeds or subplots were tested using linear mixed-effects models of an individual site property depending on breed and subplot, followed by Tukey´s post-hoc test.

Species composition as a multivariate dataset was analysed using constrained correspondence analysis (CCA), either globally across all locations and subplots or after partialling out the effects of location and subplot (Legendre and Legendre, 2012, chap. 11). Variables included in the CCA were descriptors of location, site and management properties, but not of vegetation structure. Additional vegetation indices were fitted to ordination axes thereafter.

Causes and effects between breed, site and management conditions and vegetation were analysed using a piecewise structural equation model (SEM), a local estimation method allowing for the consideration of random effects (Lefcheck, 2016). In brief, we constructed a conceptual model including all ecologically meaningful paths between breed, site and management conditions and species diversity as moderated by trampling, grazing and soil fertility (Fig. S1). Stocking rate, P-concentration and species richness were log-transformed. Trampling and grazing were represented by indicator values for trampling and grazing. Soil P concentrations and species richness were used as proxies for soil fertility and species diversity, respectively. Directional

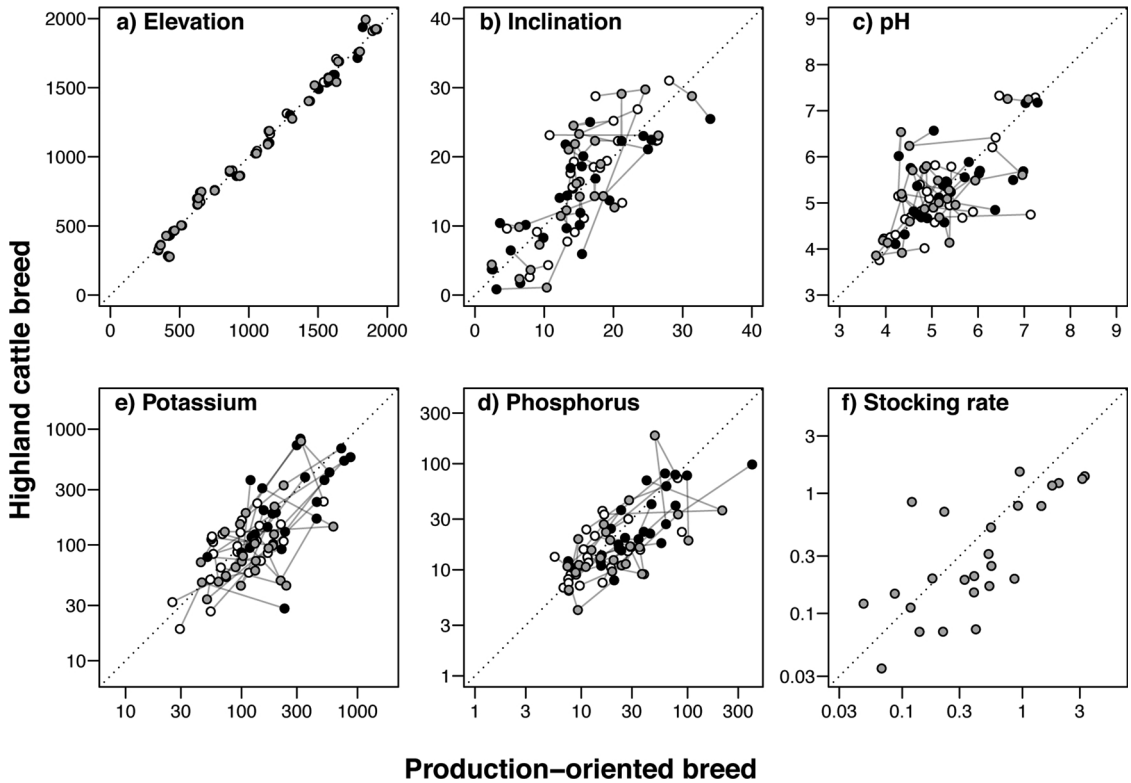

Fig. 2. Environmental location variables of paired pastures grazed by Highland cattle or production-oriented breeds: elevation in m asl. (a), inclination in degree (b), soil pH (c), plant-available potassium (d) and phosphorus (e) in mg kg^{-1} soil and normalized stocking rate in livestock units ha^{-1} yr^{-1} (f). For each pasture, the three subplots with a high (black), medium (grey) and low intensity of grazing (white) are connected by a grey line, except for stocking rate, which is the same for the three subplots.

relationships were described by a list of linear mixed-effects models with random effects for pastures within sites. Because the relationship between soil pH and stocking rate had no clear direction, it was included as a correlation. More complex models including nutrient indicator values or the cover of woody plants were also tested but resulted in a higher Akaike information criterion (AIC). Finally, we scaled regression coefficients by the standard deviation of the variables involved in order to receive standardized path coefficients (SC) as unitless measures of association.

All analyses were carried out in R 3.4.3 (R Core Team, 2017) using packages lme4 for normal and negative binomial likelihoods (Bates et al., 2015), glmmADMB for beta likelihoods (Fournier et al., 2012), emmeans for post-hoc tests (Lenth, 2018), vegan for multivariate analyses (Oksanen et al., 2017) and piecewiseSEM for structural equation modelling (Lefcheck, 2016).

3. Results

3.1. Site and management properties

The sample locations covered a broad gradient in site conditions (Fig. 2a–f): elevation ranged from 300 to 2000 m asl., inclination from flat to 33° and stocking rate from 0.04 to 3.3 LU yr^{-1} ha^{-1}. More detailed information about site characteristics are given in Table S1.

Although there was a large range of conditions across locations, both pastures within one pair were highly comparable to one another: The average difference in elevation (Fig. 2a) within a pair was 36 m (range: 0.5-143 m; standard deviation (SD): 34 m) and inclination (Fig. 2b) was almost the same in corresponding subplots (Tukey´s post-hoc-test: +0.30°, $p = 0.76$). The least grazed subplots were significantly steeper than the intermediate (+1.76°, $p < 0.001$) and the highly used subplots (+2.35°, $p < 0.0001$) on both breed's pastures.

Soil pH (Fig. 2c) was not influenced by breed (−0.048, $p = 0.75$), but by subplots, with lower pH values in the intermediate (−0.2, $p = 0.003$) and the highly used subplot (−0.76, $p < 0.0001$) than in the least grazed one.

Differences in nutrient concentrations within a pair were marginal compared to the overall concentrations. K concentrations (Fig. 2d) in soil were about the same (+0.16 mg kg^{-1}, $p = 0.15$), P concentrations (Fig. 2e) were marginally higher in pastures grazed by production-oriented breeds (+0.23 mg kg^{-1}, $p = 0.08$) and significantly higher in the highly used subplot than in the intermediate (+0.5 mg kg^{-1}, $p < 0.0001$) and the least used (+0.76 mg kg^{-1}, $p < 0.0001$).

Normalized stocking rates (Fig. 2f), only available at pasture scale, were higher on production-oriented breeds' pastures (+0.38 LU ha^{-1} yr^{-1}, $p = 0.03$).

3.2. Bodyweight of cattle breeds

Weight and weight-gain differed enormously between cattle breeds (Fig. 3). The compiled data indicated that all production-oriented breeds were generally heavier than Highland cattle. Only a few Hinterwaelder breed cattle, which were part of a herd of heavier breeds and not really production-oriented, had similar sizes to Highland cattle.

3.3. Vegetation indices

Plant species richness per subplot (alpha richness) was significantly different between breeds (Fig. 4a; Table 1). On average, 16.1% more vascular plant species were found on pastures grazed by Highland cattle ($p_{\chi^2} < 0.0001$). Apart from grazing breed, alpha richness was positively affected by elevation ($p_{\chi^2} = 0.01$) and inclination ($p_{\chi^2} = 0.005$) and negatively by soil P ($p_{\chi^2} = 0.001$). In addition, alpha richness differed between the three subplots within each pasture, if other location factors

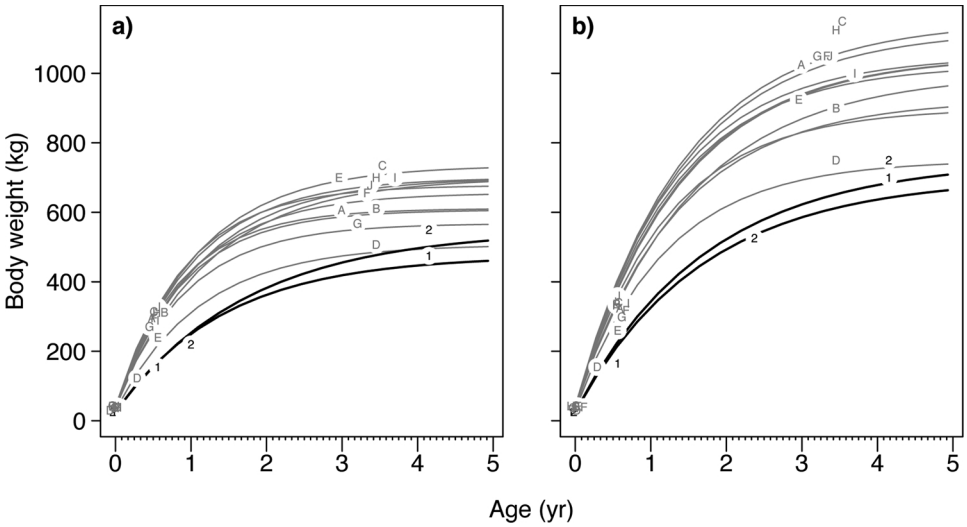

Fig. 3. Estimated age dependency of body weight of female (a) and male (b) animals of all cattle breeds involved in the study: small-framed Highland cattle (1), large-framed Highland cattle (2), Angus (A), Braunvieh and Original Braunvieh (B), Charolais (C), Hinterwaelder (D), Holstein Friesian (E), Limousin (F), Luing (G), Pinzgauer (H), Salers (I), Simmentaler (J). Labels are set at points of known data from various sources. For display, random jitter was added to data points at times 0 and 205 days (standard weighing day).

were disregarded ($p_{\chi^2} = 0.004$). Highest plant species richness was found in the least grazed subplot, which contained 5.7% and 15.1% more species than the intermediate and the highly frequented subplot, respectively. If the model included breed, elevation, inclination, soil P and subplot, stocking rate or its interaction with breed did not have a significant effect on plant species richness.

In line, species richness at the scale of paired pastures (gamma richness) was significantly increased by Highland cattle ($p_{\chi^2} = 0.0004$; Table 1) and elevation ($p_{\chi^2} = 0.001$), but unaffected by mean soil P concentration or stocking rate. Pielou's evenness of species abundance (Fig. 4b) was not influenced by breed, normalized stocking rate or subplot, but by elevation ($p_{\chi^2} = 0.004$), inclination ($p_{\chi^2} = 0.001$) and soil P ($p_{\chi^2} = 0.0006$).

The cover of woody species was lower in pastures grazed by Highland cattle ($p_{\chi^2} = 0.02$), but many pastures were completely free of woody plants (Fig. 4c). Most subplots with a substantial cover of woody species were subplots at higher elevation, which were grazed at intermediate or low intensity. As a consequence, elevation ($p_{\chi^2} = 0.02$) and subplot ($p_{\chi^2} = 0.004$) significantly affected woody species cover. Because of the broad environmental gradient, many different woody species occurred. Seedlings of *Picea abies* and *Alnus glutinosa* were most frequently recorded and common shrubs were *Vaccinium myrtillus* and *Calluna vulgaris*.

Vegetation used by production-oriented breeds contained a higher share of grazing- and trampling tolerant species compared to that of Highland cattle (Fig. 4d). Grazing and trampling indicator values were

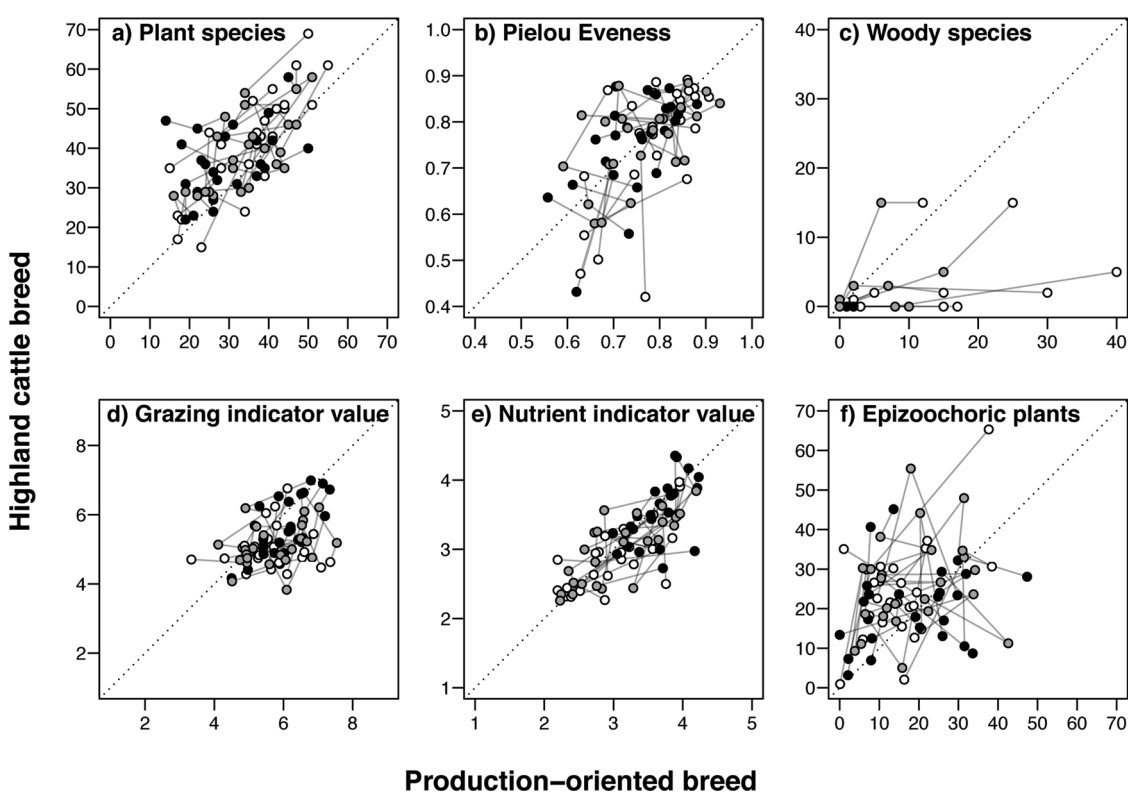

Fig. 4. Vegetation indices of paired pastures grazed by Highland cattle or production-oriented breeds: Number of plant species per subplot (a), Pielou's eveness (b), cover of woody species in % (c), cover-weighted mean of grazing (d) and nutrient indicator values (e) as well as cover of epizoochoric plants in % (f). For each pasture, the three subplots with a high (black), medium (grey) and low intensity of grazing (white) are connected by a grey line.

Table 1
Estimated fixed effects (χ^2) of cattle breed and site and management conditions on vegetation indices together with their significance (p) and direction (+/−). For the subplot, the direction shows the effect of the two higher used subplots compared to the least used one. Marginal and conditional coefficients of determination (these are not available for beta models) are shown together with details on the specification of generalized linear mixed-effects models. Gamma plant species richness was analysed based on an aggregated dataset with mean site variables for the three subplots.

		Plant species richness			Pielou's Eveness			Woody species cover			Grazing indicator value		
	Df		χ^2	p		χ^2	p		χ^2	p		χ^2	p
Highland breed	1	+	16.6	<0.0001	−	2.14	0.14	−	5.92	0.02	−	12.14	0.0005
Elevation	1	+	6.33	0.01	+	8.38	0.004	+	5.88	0.02	−	0.47	0.49
Inclination	1	+	7.78	0.005	−	10.65	0.001	−	2.27	0.13	−	0.14	0.71
Phosphorus	1	−	10.13	0.002	−	11.65	0.0006	−	0.54	0.46	−	0.81	0.37
Stocking rate	1	−	0.63	0.43	−	0.03	0.86	−	1.65	0.2	+	3.06	0.08
Subplot	2	−	0.92	0.63	+	0.68	0.71	−	11.09	0.004	+	18.76	<0.0001
		−			+			−			+		
Marginal R^2			0.51			0.49			n.a.			0.26	
Conditional R^2			0.62			0.57			n.a.			0.54	
N			150			150			150			150	
Likelihood			Neg. binominal			Gaussian			Beta			Gaussian	
Link function			log			identity			logit			identity	

	Trampling indicator value			Nutrient indicator value			Epizoochoric plants			Gamma plant species richness		
		χ^2	p		χ^2	p		χ^2	p		χ^2	p
Highland breed	−	3.96	0.047	−	2.57	0.11	+	10.54	0.001	+	12.51	0.0004
Elevation	−	0.45	0.5	−	20.23	<0.0001	+	1.03	0.31	+	10.27	0.001
Inclination	+	0.25	0.62	+	0.24	0.63	+	1.32	0.25	+	3.06	0.08
Phosphorus	−	2.93	0.09	+	8.8	0.003	+	0	1	−	2.31	0.13
Stocking rate	+	4.07	0.044	+	0.14	0.71	−	5.97	0.02	−	0.73	0.39
Subplot	+	21.87	<0.0001	+	62.24	<0.0001	+	3.8	0.15		n.a.	
	+			+			+					
Marginal R^2		0.23			0.64			n.a.			0.67	
Conditional R^2		0.6			0.73			n.a.			0.8	
N		150			150			150			50	
Likelihood		Gaussian			Gaussian			Beta			Neg. binominal	
Link function		identity			identity			logit			log	

significantly higher on production-oriented breeds' pastures (p_{χ^2} = 0.0005 and 0.047, respectively) and significantly increased from the least to most frequented subplot (p_{χ^2} < 0.0001). Both indicator values increased at higher stocking rate (p_{χ^2} = 0.08 and 0.044, respectively).

Additionally, pastures grazed by production-oriented breeds contained more bare ground than those grazed by Highland cattle (p_{χ^2} = 0.02). Since almost no vegetation-free soil was found in less grazed subplots, only subplots grazed at intermediate and high frequency were analysed. Overall, trampling indicator values and the proportion of open soil were correlated (r = 0.21, p = 0.01).

Nutrient indicator values (Fig. 4e) were not affected by breed (p_{χ^2} = 0.11). They depended mainly on elevation (p_{χ^2} < 0.0001) and plant available phosphorus (p_{χ^2} = 0.003) and significantly differed between subplots (p_{χ^2} < 0.0001).

The cover of epizoochoric plant species (Fig. 4f) was higher in pastures grazed by Highland cattle (p_{χ^2} = 0.001) and increased with stocking rate (p_{χ^2} = 0.02).

3.4. Effects of adaptation time

All pastures had a long-term history of grazing (5-25 years for Highland cattle; Fig. 5). Even sites grazed by Highland cattle for 5 years had been grazed before, mostly by a production-oriented cattle breed. However, the time during which vegetation had been grazed by a particular cattle breed, had a clear impact on the difference within paired pastures. The longer a pasture had been grazed by Highland cattle, the more distinct was the difference in plant species richness compared to the pasture of production-oriented cattle (p = 0.0001; Fig. 5a). Grazing indicator values tended to decrease with adaptation time (p = 0.08; Fig. 5b). There was, however, no correlation between adaptation time and the P concentration in soil nor the nutrient indicator value of vegetation (data not shown).

3.5. Interactions between breed, site conditions and vegetation

Ecological interactions within pastures were complex. In compliance with the GLMMs, the SEM (Fig. 6) showed that plant species diversity was significantly influenced by site properties and grazing breed. Species diversity increased with higher elevation (SC = 0.27), but also with steeper inclination (SC = 0.20), and decreased at high soil fertility (SC = −0.23). The higher the grazing impact, the lower was the diversity (SC = −0.36). Grazing effect itself was strongly strengthened by trampling (SC = 0.67). The remaining direct effect of trampling on diversity was positive (SC = 0.31). Furthermore, trampling was positively influenced by soil pH (SC = 0.19). Highland cattle pasturing decreased grazing and trampling (SC = −0.15 and −0.21, respectively) and had a direct positive effect on diversity (SC = 0.18), independent of grazing and trampling. There was no significant relationship between breed and soil fertility (p = 0.31, SC = −0.04). The subplots, included in the model to represent the study design, showed small but significant effects: The subplots of the highly frequented areas positively influenced grazing and trampling indicator values (SC = 0.11 and 0.17, respectively) and soil fertility (SC = 0.26), whereas the rarely frequented areas had a negative impact on soil fertility (SC = −0.15). Stocking rate was strongly reduced by elevation (SC = −0.68) and moderately by Highland cattle (SC = −0.15) but did not have significant effects on other variables. All other ecological links included in the conceptual model (Fig. S1), didn't show significance. The model reproduced the data well (C_{10} = 7.29, p = 0.70) and the predictors explained substantial variation of the response variables stocking rate (R^2 = 0.86), grazing (R^2 = 0.69), trampling (R^2 = 0.60), soil fertility (R^2 = 0.68) and diversity (R^2 = 0.61). The R^2 of the SEM diverge from R^2 in Table 1 because they were calculated by different models. Regression coefficients and more detailed information about R^2 of the SEM are given in Tables S2 and S3.

3.6. Plant species composition

The CCA indicated that plant species composition across all locations was mainly explained by geographic location and site properties (Fig. 7a). The first and second correspondence axis were aligned to longitude (X), latitude (Y), elevation (Z) and stocking rate. Axis 1 represented an altitudinal gradient from the lowlands of Southern Germany to the Swiss Alps, which was closely aligned to decreasing stocking rates. Axis 2 was an East-West gradient. Site properties were located between the two main axis with sites rich in soil P and Mg in the lower left quadrant and nutrient-poor sites with more acidic soils and steeper slopes in the upper right. These general patterns are corroborated by typical plant species located within each of the four quadrants of the ordination. The habitat of *Polygonum viviparum* and *Sesleria caerulea,* for example, were high altitude pastures. *Helianthemum nummularium*, *Vaccinium myrtillus* and *Homogyne alpine* were often found on steep subplots with acidic soil conditions. In contrast, *Capsella bursa-pastoris* and *Agropyron repens* are typical residents of nutrient-rich and disturbed areas.

If location and subplot were partialled out of the ordination, plant species composition differed between breeds' pastures (Fig. 7b). The remaining variation in species composition was primarily explained by soil acidity (axis 1), Mg content and inclination (axis 2). Acidity was the

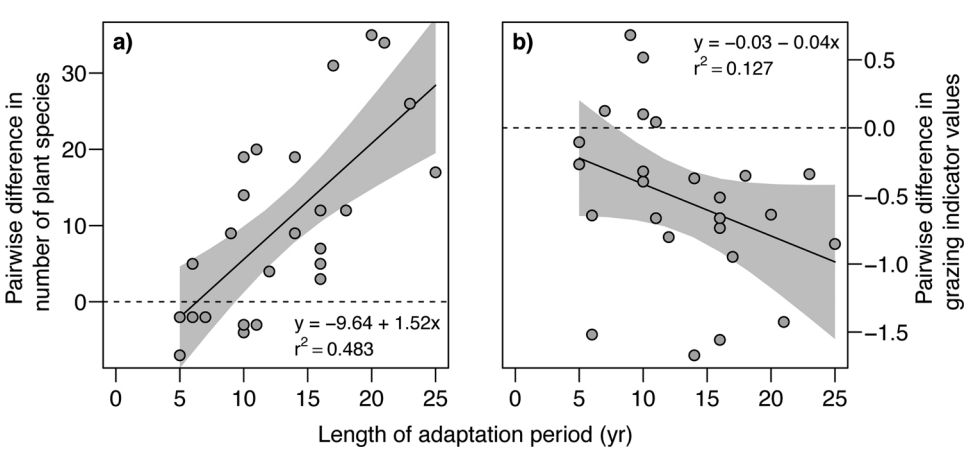

Fig. 5. Effect of the duration of adaptation on the pairwise difference between pastures grazed by Highland cattle and production-oriented breeds with regards to (a) aggregated plant species richness per pasture (gamma richness) and (b) grazing indicator values. Positive values represent higher values for pastures of Highland cattle. The grey areas depict the 95% confidence intervals.

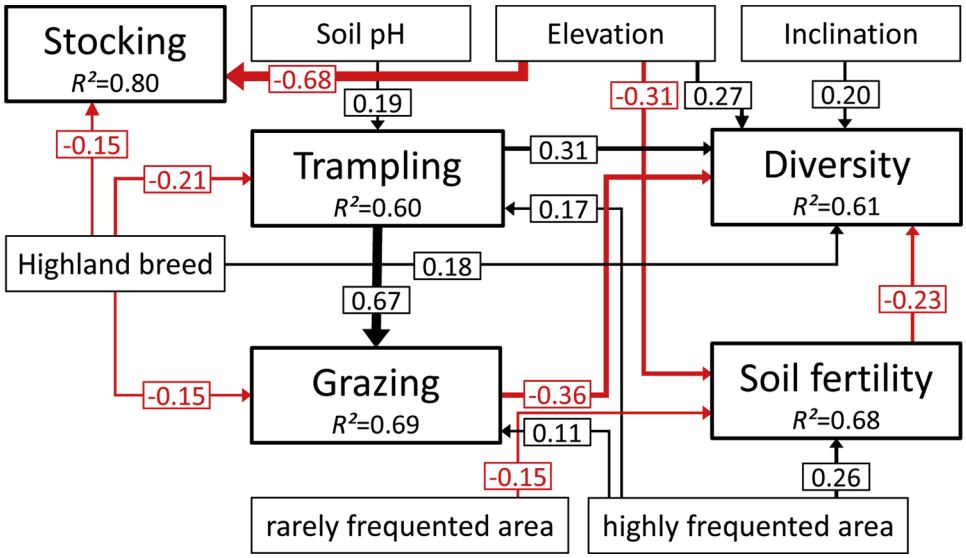

Fig. 6. Structural equation model of vegetation in response to grazing and site and management properties. Only significant links between the five response variables stocking (= normalized stocking rate), trampling (= trampling indicator value), grazing (= grazing indicator value), diversity (= number of plant species) and soil fertility (= plant available P) and the predictors (Highland cattle breed, soil pH, elevation, inclination and the two study design-dependent predictors of rarely and highly frequented subplots) are shown. Red arrows denote negative, black arrows positive relationships. Arrow width is scaled according to the standardized regression coefficient indicated in the associated box. Conditional R^2s for component models are provided in the boxes of response variables. For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.

only remaining site condition not controlled for in the study and explained variability after removal of all the other factors. The distinction between pastures grazed by Highland cattle and other breeds was mainly associated with axis 2. In line with the univariate relationship described earlier, grazing and nutrient indicator values and cover of woody species pointed in the direction of production-oriented breeds. Differences in vegetation composition between pastures grazed by Highland and other breeds were also illustrated by typical plant species located in the quadrants of the ordination. *Plantago major* and *Poa annua* have high indicator values of grazing tolerance; *Calluna vulgaris* and *Vaccinium myrtillus* are shrubs. Both groups were associated with production-oriented breeds. In contrast, *Geum urbanum*, a typical epizoochoric plant, and *Dactylorhiza maculata, Viola canina* and *Sanguisorba officinalis*, species with very low grazing and trampling tolerance, were associated with Highland pastures.

4. Discussion

4.1. Pastures in a pair are similar in environmental conditions

Despite the broad environmental gradient, the available descriptors confirm that the two sampled pastures in each pair were similar with

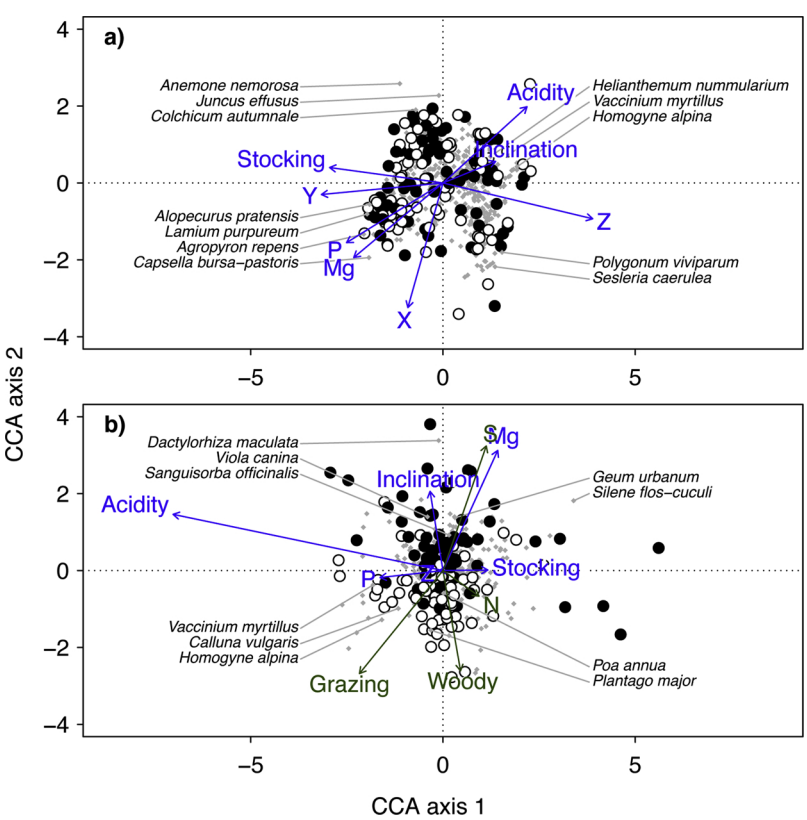

Fig. 7. Constrained correspondence analysis of plant species composition in pastures grazed by Highland cattle (black circles) and production-oriented breeds (white circles) in response to geographic location (longitude (X), latitude (Y), elevation (Z)) and site properties (acidity (inverse pH), inclination, stocking rate, soil phosphorus (P) and magnesium (Mg)).
Panel a) displays the global ordination across all locations, panel b) the ordination after partialling out the effects of location and subplot. Grey dots show the scores for individual plant species. Selected characteristic species are labelled by names. Blue arrows show the direction of association of explanatory variables with the ordination axes. Green arrows show the association of additional vegetation properties (indicator values for grazing and nutrient (N), number of plant species (S) and cover of woody species) with the ordination axes.

regards to site conditions. Of course, low-production, robust cattle tend to graze on marginal agricultural land and production-oriented breeds on more productive grassland. However, the decision for one or another breed is mostly made because of the structure of the entire farm and not because of an individual pasture field. In line, adaptation time (*i.e.* the period for which Highland cattle grazed a pasture) did not depend on the productivity of the investigated pasture. Therefore, the *farms* to which the two paired pastures belong, may differ enormously at some locations, but the two investigated *pastures* were similar in the measured site conditions.

The fact that differences in plant species richness and grazing indicator values between breeds increased with adaptation time, corroborates that these differences were not caused by site selection. If they were, we may expect a systematic difference independent of adaptation time.

The data also demonstrated that vegetation needs many years to adapt to grazing by a particular breed. This may explain some of the weak differences between breeds found in earlier experimental studies involving three or four years of pasturing (Dumont et al., 2007; Jerrentrup et al., 2015; Scimone et al., 2007).

Because differences in grazing pressure may confound the effect of breed on vegetation (*e.g.* Porensky et al., 2017), considerable effort was undertaken to normalize the stocking rate by the live weight, both in terms of breed and age. Nevertheless, stocking rate can only be quantified for the entire pasture field, in which it may vary considerably, and thus not reflect the grazing intensity of individual subplots (Homburger et al., 2015). Normalized stocking rate was lower for Highland cattle and therefore included as a covariate in GLMMs, SEM and CCA. Across all locations, stocking rate did not have a significant effect on species richness (alpha and gamma), grazing indicator values or woody species cover. One explanation may be that the study was explicitly designed to prevent confounding effects of stocking rate by carefully selecting pasture pairs with similar site conditions and by sampling subplots with contrasting use intensity. Furthermore, stocking rate was strongly collinear to elevation and soil P concentrations. We assume that these variables overwrote most effects of stocking rate. Finally, our estimates of stocking rate are based on summed body weights only and therefore very conservative. Differences in stocking rate between breeds may therefore overestimate real differences in vegetation impact.

In addition, plants with high nutrient indicator values were not significantly more frequent on pastures of production-oriented breeds, K concentrations in soil were similar and P concentrations were only slightly higher. Consequently, the higher plant species richness on pastures of Highland cattle cannot be sufficiently explained by stocking rate or nutrient availability alone, but may be attributed to other differences between breeds.

4.2. Highland cattle cause vegetation with different traits

Plant species richness is higher on pastures grassed by Highland cattle and a number of Highland cattle's special characteristics are mirrored in plant composition:

First, Highland cattle promote the abundance of epizoochoric plant species. These species rely on dispersal by animals and several among them are in current decline (Ozinga et al., 2008; Poschlod et al., 2009). Because the fur of Highland cattle is longer and woollier than that of most other breeds, it is likely that diaspores adhere better to it. Consequently, epizoochoric species have a reproductive advantage on Highland cattle pastures, become more abundant and add to species richness. Epizoochory may be one important component of the direct positive impact of Highland cattle on diversity, as identified in the SEM.

Second, because of slower growth rate and lower demand with regard to forage mass and quality (Berry et al., 2002), Highland cattle may remove less biomass by defoliation and select their forage less strictly than other breeds. Both mechanisms result in vegetation that carries less of the typical aspects of pastures (Adler et al., 2001; Díaz et al., 2001) and that is reflected in the grazing indicator values. All model types tested, GLMMs, SEM and CCA, show a significant negative influence of Highland cattle on grazing indicator values, which is the strongest driver of plant species richness. Reduced selectivity by low-production breeds was also shown by Sæther et al. (2006), who found that a high-yielding dairy breed selected a more nutrient-rich diet than a non-production-oriented, traditional breed, although Rook et al. (2004) stated that differences in foraging behaviour between breeds have received relatively little attention and evidence about breed and background effects on diet selection is patchy.

Forage avoidance is another mechanism structuring pasture communities. Plants with typical strategies of forage avoidance are thistles (genera *Carduus*, *Carlina* and *Cirsium*), which were found four times less frequently on Highland cattle pastures.

Besides foraging strategies, movement behaviour and spatial distribution of cattle also have an impact on pasture vegetation. For example, Spiegal et al. (2019) reported that production-oriented Angus x Herford cattle settled more often at the same hotspot areas than low-production Criollo cattle and visited less different locations on the pasture. This goes along with our findings that there are less overused nutrient-rich resting places on Highland cattle pastures.

4.3. Highland cattle impose less physical pressure on vegetation

Trampling is an important selective force in pasture vegetation (Cole, 1995). On the one hand, trampling is determined by the frequency of steps. Hence, GLMM and SEM consistently showed that there were higher trampling indicator values in the highly frequented subplots.

On the other hand, trampling impact is influenced by the weight of animals and therefore the pressure imposed by each step (Lezama and Paruelo, 2016). Highland cattle are substantially lighter than most other breeds (Fig. 3; Albertí et al., 2008). Moreover, comparing different independent assessments of claw dimensions suggest that claws of Highland cattle are not smaller than claws of other breeds, despite their lower body weight (Nuss et al., 2014; Nuss and Paulus, 2006). Hence, they exert much less pressure on vegetation with each step taken. All three statistical techniques suggest that these physical differences lead to a consistently detectable signal in plant species composition. Trampling reduces plant height and increases soil density, which reduces microbial activity and nutrient turnover (Kissling et al., 2009). The partial CCA (*i.e.* after removal of location effects on species composition) highlighted several species adapted to trampling as characteristic for pastures grazed by production-oriented breeds. In contrast, plant species susceptible to trampling were associated with Highland pastures.

Univariate models show that, because plant species richness is negatively correlated to trampling indicator values ($r = -0.19$, $p = 0.024$), less trampling goes along with higher richness (Jägerbrand and Alatalo, 2015; Pickering and Growcock, 2009). The SEM showed in more detail, that Highland cattle pasturing reduces trampling indicators in vegetation ($SC = -0.21$), which contributes to the grazing effect ($SC = 0.67$). Lezama and Paruelo (2016) found interacting effects of simulated trampling and defoliation on plant species composition. In line, Briemle et al. (2002) specified grazing tolerance as the ability to grow on regularly grazed pastures and partly included trampling tolerance. Since grazing has a negative impact on species diversity, trampling also exerts an indirect negative effect on it. Beyond that, the SEM indicated that trampling has an additional positive effect on diversity, which may be attributed to open soil for germination.

4.4. Highland cattle have a distinctive effect on vegetation structure

A special case of foraging behaviour is the consumption of woody plants, which are usually avoided (Meisser et al., 2014). Woody plants were less abundant in pastures grazed by Highland cattle and the

partial CCA associated several woody species with production-oriented breeds. It is remarkable that woody species are repressed on Highland pastures, despite the fact that their normalized stocking rate tended to be lower, which is commonly thought to cause higher woody species cover (Celaya et al., 2010; Lezama and Paruelo, 2016). However, the current study was not explicitly designed to address the question of woody plant cover. Therefore, the total number of locations with woody species was small, and the clear statistical signal was based on a limited number of observations.

Shrubs and emerging tree seedlings positively contribute to biodiversity but can cause problems on semi-natural pastures with low stocking rate. Since most grazing animals tend to avoid woody plant parts (Fraser et al., 2009), pastures become overgrown with shrubs and plant diversity declines (Kesting et al., 2015; Pornaro et al., 2013). Highland cattle may contribute to prevention of woody plants encroachment on semi-natural pastures and thereby sustain plant species richness. Moreover, Highland cattle can maintain or even create habitats for susceptible plant species, which are under pressure by intensive grazing in modern agricultural systems.

5. Conclusions

Several well-known mechanisms in pasture ecosystems were confirmed by the data presented, for example a decrease in plant species richness at higher grazing pressure or nutrient availability. In addition to site properties, these parameters have the strongest impact on plant diversity and botanical composition. The SEM highlights the complexity of these mechanisms. Trampling, for example, has an indirect negative effect on species diversity via grazing impact and a positive one by increased soil disturbance.

The data also demonstrated an additional and often overlooked driver of vegetation composition: the breed grazing a pasture. Despite controlling for effects of site properties, grazing intensity and ruminant species, general patterns across grazing studies are often surprisingly hard to detect. Breed may at least partially explain the large variation in grazing impact on vegetation (Díaz et al., 2007) and on ecosystem services such as C sequestration (McSherry and Ritchie, 2013).

The presence of a genetic component in grazing impact opens up new opportunities for targeted breed choice or livestock breeding towards multiple management objectives beyond productivity. Matching grazing breed and vegetation may not only be beneficial for the animal but also for vegetation. These findings show that Highland cattle help prevent undesired shrub encroachment on semi-natural grassland, provide habitat for grazing-susceptible and epizoochoric plants, and therefore have the potential to sustain and promote biodiversity.

Declaration of Competing Interest

None.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agee.2019.106585.

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