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Choosy grazers: Influence of plant traits on forage selection by three cattle breeds

Caren M. Pauler[1,2,4] | Johannes Isselstein[2] | Matthias Suter[1] | Joel Berard[3] |
Thomas Braunbeck[4] | Manuel K. Schneider[1]

[1]Forage Production and Grassland Systems, Agroscope, Zurich, Switzerland

[2]Department of Crop Sciences, Georg-August-University, Goettingen, Germany

[3]AgroVet-Strickhof, Lindau, Switzerland

[4]Centre for Organismal Studies, Ruprecht-Karls-University, Heidelberg, Germany

Correspondence
Manuel K. Schneider
Email: manuel.schneider@agroscope.admin.ch

Abstract

1. Forage selection by herbivores is a major driver of plant diversity in pasture vegetation. Yet, we know relatively little about how plant traits influence decisions of different herbivore species and breeds to select or avoid a certain plant species on semi-natural pastures.

2. We quantified the influence of the traits leaf N and P content, leaf dry matter content (LDMC), specific leaf area (SLA) and physical defence mechanisms on plant species selection for three cattle breeds: high-yielding Angus × Holstein crossbreed, dual-purpose Original Braunvieh and undemanding Highland Cattle. The cattle grazed a series of adjacent paddocks in different alpine pastures. Plant species selection was quantified by assessing the difference in biomass proportions of all plant species in 66 vegetation subplots per breed before and after grazing. Plant traits and indicator values were extracted from the TRY database. Data on 152 plant species were analysed using a local mixed-effects model and a global multivariate hierarchical regression model.

3. Plant traits had a clear impact on forage behaviour. Plants with high SLA, leaf N and P contents were significantly selected, whereas plants with high LDMC (e.g. woody plants) and defence mechanisms (e.g. thistles) were generally avoided. Species with high forage quality indicator values as defined by Briemle et al. (2002) were significantly preferred. More importantly, significant differences between forage behaviour of cattle breeds were detected. Selection by less-productive Highland Cattle was much less influenced by plant traits than the selection by the two higher-yielding breeds.

4. Results indicate a clear impact of plant traits on forage selection and demonstrate breed-specific influences. Highland Cattle (and possibly other robust breeds) graze less selectively and impose less selective exclusion on plants. Thereby, they likely influence plant species composition of pastures in a different way than high-yielding breeds, thereby creating a distinct habitat.

KEYWORDS
alpine pastures, Bayesian statistics, cattle breeds, forage selection, plant traits, species diversity

1 | INTRODUCTION

If herbivores have an unrestricted access to forage, they favour certain plants over others according to their preference (Westoby, 1974). While grazing a pasture, herbivores make complex decisions about where and what to consume. These decisions influence forage intake and are important drivers of the long-term composition of pasture vegetation. Understanding the mechanisms of plant selection is therefore of high interest for pasture management, species diversity and conservation (Olff & Ritchie, 1998).

Unfortunately, *preference* is hard to measure because in almost every case, animals' preference, that is, their intrinsic desire to consume a certain plant, is influenced by other factors such as forage availability, small-scale composition of tasty and unattractive plants, spatial distribution of plants or fences that limit animal movement (Parsons, Newman, Penning, Harvey, & Orr, 1994). It is much easier to measure plant *selection*, that is, the actual consumption of plants as a result of consideration between preference and availability (Allen et al., 2011).

Numerous former studies analysed ruminants' selection in strongly controlled settings, mainly in stables, where only a few plants were offered to the animals and where forage selection can be evaluated by weighing the fodder before and after consumption (McInnis, Vavra, & Krueger, 1983). Field studies that allow for conclusions of animals' behaviour outdoors are rare and tend to cover sown grassland where zones with different plant species have been established. In these artificial environments, it is possible to count the bites taken or the time spent in each zone (Ganskopp, Myers, Lambert, & Cruz, 1997; Parsons et al., 1994).

It is much harder to quantify the consumed biomass of a certain plant species in semi-natural, alpine pastures, where many different species grow at small scales (Wilson, Peet, Dengler, & Pärtel, 2012) and heterogeneous patterns influence grazing decisions (Adler, Raff, & Lauenroth, 2001). From the millimetre to metre scale, managed, semi-natural grasslands are the most diverse plant communities of the world (up to 89 species on 1 m^2 in mountain grassland; Cantero, Pärtel, & Zobel, 1999). Due to the multifaceted choice options, these habitats are well suited to analyse general principles of forage selection by herbivores.

Alpine pastures deserve special attention for good reasons. Centuries of pasturing by domestic herbivores favoured plant species tolerant of trampling and defoliation (Díaz et al., 2007) and created plant associations of enormous species richness (Wilson et al., 2012). Besides climate and soil, the selective interaction between herbivores and plants has a substantial influence on the biodiversity of alpine pastures and other semi-natural grasslands (Ellenberg & Leuschner, 2010). It is important to understand the mechanisms of selection that created these species-rich, but vulnerable habitats.

In addition to understand the general mechanisms that influence forage selection, we wondered if selection differs among cattle breeds. Modern breeding has formed high-yielding animals with higher growth rate, adult body mass and demand in forage quality than traditional breeds not optimized for meat or milk production (Albertí et al., 2008; Derry, 2015). A recent study identified consistent differences in plant species composition between pastures grazed by production-oriented cattle and less-productive Highland Cattle under similar environmental and management conditions (Pauler, Isselstein, Braunbeck, & Schneider, 2019). The vegetation of Highland Cattle pastures contained fewer plant species adapted to grazing and trampling, fewer woody species, and a higher proportion of epizoochoric plants. Likely explanations for the differences in the observed vegetation are (a) the lower body weight of Highland Cattle resulting in lower trampling adaption and (b) a woollier fur favouring plant species specialized in distribution by animals. However, there is no obvious explanation for different adaptation to grazing or the cover of woody plants. Differences in forage selection among breeds, well known for different livestock species (Cuchillo-Hilario, Wrage-Mönnig, & Isselstein, 2017), may explain the development of breed-specific vegetation composition. We therefore hypothesize that cattle breeds differ in their selection of plant species and that they respond differently to plant traits.

In the present study, we aimed to investigate three different aspects related to the foraging behaviour of cattle breeds. First, we developed a field method that allows adequate assessment of plant species selection by cattle in species-rich, alpine pastures during different phases of the growing season and in contrasting vegetation types. Second, we quantified the impact of different plant traits on plant species selection and, ultimately, the difference in trait-depended selection among cattle breeds.

2 | MATERIALS AND METHODS

2.1 | Study area

A grazing experiment was conducted on heterogeneous alpine pastures of Alp Weissenstein in the eastern Swiss Alps (2,026 m a.s.l., 46.5816°N, 9.8002°E). This summer farm is ideal to study alpine grasslands because it is located on a geological contact zone, creating a mosaic of calcareous and crystalline bedrocks and a large diversity of vegetation types (Michna, Eugster, Hiller, Zeeman, & Wanner, 2013).

We selected three areas with contrasting vegetation, forming a gradient from high to low forage quality (Figure 1: areas 1–3): The first area (fertile pasture; 1.05 ha) was a nutrient-rich, flat pasture of the *Poion alpinae* type (classification of Delarze & Gonseth, 2008) rich in clover, mainly *Trifolium pratense* L., and broad-leaved grasses like *Trisetum flavescens* (L.) P. Beauv. and *Phleum rhaeticum* (Humphries) Rauschert. Most frequented herbs were *Ranunculus acris* L., *Carum carvi* L. and *Alchemilla xanthochlora* Rothm.

In area 2 (intermediate pasture; 1.83 ha), which was steeper than area 1, nutrient-rich *Poion alpinae* pastures were mixed with *Nardion*, with a higher share of fine-leaved grasses, primarily *Festuca rubra* L. and *Nardus stricta* L., and a dwarf shrub-dominated *Juniperion communis* L. community with *Erica carnea* L., *Calluna vulgaris* (L.) Hull and numerous different herbs.

While areas 1 and 2 were located on calcareous bedrocks, area 3 (wood pasture; 4.38 ha) was on impermeable, crystalline parent material. Therefore, the flat parts of area 3 were covered by a
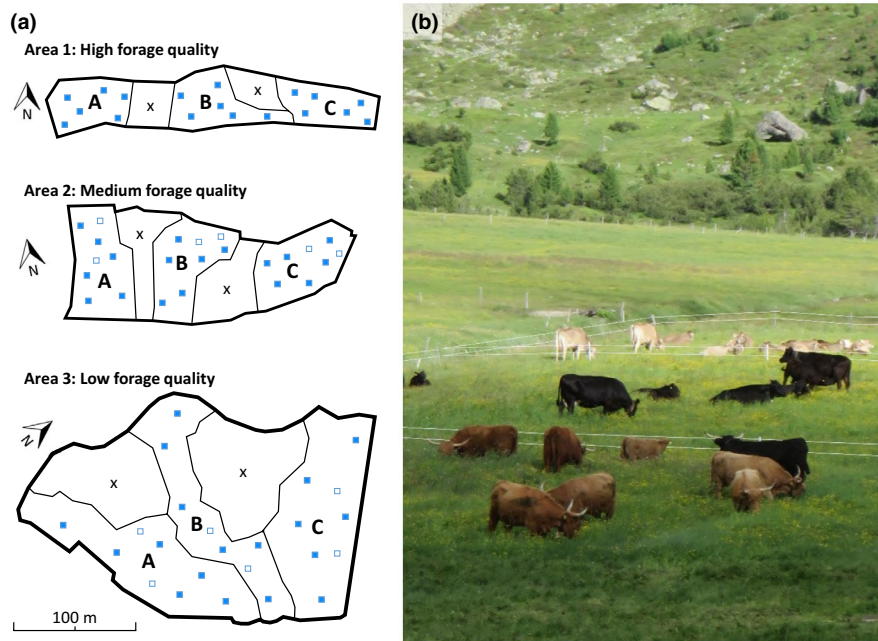
FIGURE 1 Study areas, paddocks and vegetation subplots of the grazing experiment. (a) The cattle were grazed in three areas with vegetation of different forage quality (areas 1–3). In each area, the pastures were subdivided into three paddocks of the same size (A–C). The paddocks of an area were grazed simultaneously by three herds of different breeds for 3 days. Each paddock was grazed once by each breed. This was repeated three times in a Latin square design. Supplementary sections (×) were added to paddocks grazed by A × H crossbreed and Braunvieh, but not to Highland Cattle paddocks, because of their lower body weight and forage demand. The vegetation was surveyed in six subplots of 3 × 3 m^2 (solid blue squares) per paddock before and after grazing. Two additional subplots (open squares) were established in areas 2 and 3 in the second and third rotations. Areas are drawn to the same scale, but north arrows are given for each area separately. (b) Impression of three adjacent paddocks with Highland Cattle (foreground), A × H (middle) and Braunvieh suckler cows (background) on the research station Alp Weissenstein in the Swiss Alps

Caricion fuscae fen dominated by moss and sedges like *Trichophorum cespitosum* (L.) Hartm., *Carex nigra* (L.) Reichard and *C. panicea* L. The surrounding steeper slopes were grown by open *Larici-Pinetum cembrae* forest with a canopy of scattered *Larix decidua* Mill. and *Pinus cembra* L. over *Vaccinium myrtillus* L., *V. gaultherioides* Bigelow and *Juniperus communis* L. in the shrub layer.

2.2 | Animals

Three different cattle breeds of suckler cows with calves were selected to evaluate their foraging behaviour. The first breed was a large-framed crossbreed of Angus, a high-yielding and heavy beef breed, and Holstein, the most productive and widespread dairy breed. On average, the Angus × Holstein cows (A × H) weighed 679 kg (*SD* = 40.4 kg). The second breed was Original Braunvieh, a traditional dual-purpose breed of the Swiss Alps with lower body weight (μ = 582 kg, *SD* = 59.3 kg). The third breed, Highland Cattle, is a less-productive and undemanding traditional breed. The Highland cows in our experiment weighed approximately half as much as the A × H cows (μ = 358 kg, *SD* = 57.4 kg).

Each breed was represented by three subgroups of three suckler cows with their calves, resulting in a total of nine cows and calves per breed. Subgroups were formed by breed-wise ranking of body weight and picking every third individual. Therefore, all three subgroups of a breed had about the same cummulated weight and were expected to have the same forage demand.

The animals originated of different mountain farms at 1,000–1,400 m a.s.l., where they had regular access to pastures in spring. All cows had experience of grazing at high elevation in preceding summers and were used to consume the relatively nutrient-poor alpine forage. More detailed information is given in Appendix S1.

2.3 | Study design

In each area, the pastures were subdivided into three equal-sized paddocks with similar site conditions and vegetation composition (Figure 1: A–C). The areas were grazed three times during the summer in June, July and August, representing three rotations. To avoid pseudoreplication regarding animals, a different subgroup of each breed was used for each rotation. In each rotation, areas were grazed one after the other. This was done so that the three paddocks of an area were grazed by one of the three different breeds for 3 days simultaneously; thereafter, the animals were transferred to the next area. Using a Latin square design, we allocated a different breed to each paddock in each rotation. Thereby, we ensured that each paddock was grazed once by each breed.

Since shortage in forage would reduce the ability to select plant species, the size of the paddocks was set to offer 4/3 of the calculated forage demand of the cattle based on their body weight. Because the two production-oriented breeds had a higher body weight and therefore a higher forage demand, in each rotation supplementary pasture

sections were added to the paddocks of A × H and Braunvieh cattle (marked by × in Figure 1). Further details on areas, stocking and calculation of paddock size are provided in Supporting Information S2.

2.4 | Vegetation survey

In each rotation, the vegetation was analysed before and after grazing in six randomly distributed subplots of 3 × 3 m^2 per paddock (Figure 1). The subplots were marked with wooden plugs that did not obstruct cattle access at any time during grazing. Two additional subplots were surveyed in the second and third rotation in areas 2 and 3, leading to a total of 186 surveys before and after grazing. On the days immediately before and after cattle were ranged to and from a pasture, we recorded all vascular plant species within the subplots according to Eggenberg, Möhl, and Wettstein (2013) and visually estimated their percent standing biomass (Cuchillo-Hilario et al., 2017). Estimated biomass proportions were validated against measured dry matter proportions of 50 plant species (Suter & Edwards, 2013). Estimated and measured data proved to be highly correlated (R^2 between .74 and .93; see Supporting Information S3). In 21 surveys, no sign of foraging was detected because animals did not graze there. For the statistical analysis, we only considered the 165 surveys with indications of grazing.

2.5 | Trait selection

Values of nine plant traits that reflect a wide range of plant characteristics and that are expected to influence forage selection in different

ways were extracted from the TRY database (Kattge et al., 2020; see Supporting Information S8 for detailed references) for all plant species for which they were available (Table 1): Leaf contents of phosphorus (P_{leaf}) and nitrogen (N_{leaf}) as well as the C:N ratio were chosen to measure the influence of cattle's nutrient requirement, with P_{leaf} and N_{leaf} assumed to increase and C:N ratio (C:N) assumed to decrease forage selection. The specific leaf area (SLA) as a proxy of physical digestibility was expected to increase consumption, whereas a reversed effect was expected for leaf dry matter content (LDMC) as a proxy of leaf toughness and therefore of ingestibility. A lower consumption was also assumed for plants with physical defence mechanisms (D), reducing ingestibility, too. Plant height (H) and woodiness (W) as substitutes for structural components and therefore for ingestibility and digestibility were supposed to reduce selection. The forage indicator value (FQ) is a rating of palatability to cattle (Briemle, Nitsche, & Nitsche, 2002) and was presumed to go along with positive plant selection.

Trait values obviously duplicated in the datasets were combined and six non-sense values were removed. We then calculated the median of all available values per species for all continuous traits. The trait plant height was limited to a maximum of 2 m because we assumed no effect of tree height on foraging above the range of cattle's mouth. The degree of physical defence (D) was reclassified into the five levels: glabrous, soft hairs, hairy, stiff hairs, spicules/spines according to Poschlod, Kleyer, Jackel, Dannemann, and Tackenberg (2003) and Eggenberg et al. (2013). The trait woodiness (W) was aligned to the Raunkiær plant life-forms as defined by Landolt and Bäumler (2010): All phanerophytes and woody chamaephytes (i.e. trees, shrubs and dwarf-shrubs) were classified as 'woody'. FQ, D and W were treated as continuous variables.

TABLE 1 Overview of plant traits: This table summarizes information about traits used in this study, including abbreviated trait names, units, descriptions, main relevance for grazing, ranges, medians and the number of species relevant to our study for which a certain trait was available (*n*)

Trait	Abbr.	Unit	Description	Relevance	Range	Median	*n*
Phosphorus	P_{leaf}	mg/g	Content of P per leaf dry mass	Nutrient supply	0.75–3.30	1.64	92
Nitrogen	N_{leaf}	mg/g	Content of N per leaf dry mass	Nutrient supply	10.80–52.35	22.03	105
C:N ratio	C:N		Ratio of C and N in leaf dry mass	Nutrient supply and digestibility	11.29–55.39	20.82	70
Leaf dry matter content	LDMC	g/g	Ratio of leaf dry matter to leaf fresh matter	Ingestibility	0.12–0.6	0.24	139
Height	H	m	Average plant height	Ingestibility and digestibility	0.04–2.00	0.21	146
Specific leaf area	SLA	mm^2/mg	Ratio of leaf area to leaf dry mass	Digestibility	6.07–50.23	20.54	105
Forage quality	FQ	–	Indicator value of forage quality: 1 = low quality 9 = high quality	Palatability	1–9	3	108
Physical defence	D	–	Degree of physical defence: 0 = no defence 4 = spines	Ingestibility	0–4	0	152
Woodiness	W	–	0 = herbs 1 = trees and shrubs	Ingestibility and digestibility	0–1	0	152

2.6 | Verification of pastures conditions

To evaluate homogeneity of the three paddocks within each area, mean trait values weighted by the biomass proportion of each species were calculated for each vegetation subplot prior to the first grazing. Differences among areas and among paddocks within areas were tested by two-sided Tukey range tests at 5% level, following an analysis of variance with the two factors areas and paddocks nested within areas (Bretz, Hothorn, & Westfall, 2016).

2.7 | Statistical modelling

Observed in the field were proportions p_i of each plant species i in the standing biomass of a vegetation subplot before and after grazing (Figure 2a). The observations were compositional because the biomass proportions of all plant species in each survey of a subplot summed to one. The estimated values in each survey were therefore transformed into centred logratio coefficients (Filzmoser, Hron, & Templ, 2018; see Supporting Information S4 for details). Selection was inferred from the difference d_i in biomass proportions before and after grazing. Plant species selected by the animals above average

decreased their proportion ($d_i < 0$), avoided species were left over and had $d_i > 0$ (Figure 2b).

We developed two statistical models with differing ecological interpretations. The first model was labelled the *local model* because it estimated the relationship between trait and selection locally but ignored the identity of plant species across surveys, assuming a cow only considers plants in the immediate proximity at a given moment (Figure 2c). We used a linear, mixed-effects model fitted by restricted maximum likelihood with d_i as the target variable, being regressed on trait values, breed, rotation, area and their interactions with trait as independent fixed effects. The sampling structure was represented by random effects for paddock, subplot and survey (details in Supporting Information S4).

The second model was labelled the *global model* because it accounted for the multivariate structure of the species dataset in a hierarchical manner, with all 152 plant species observed multiple times and in different subplots (Figure 2d). Ecologically, this assumes that cattle react to plant traits in global patterns beyond the local plant composition. Here, d_i was modelled as a breed-specific selection coefficient for each plant species plus random effects for subplot, paddock, area and rotation. The expected means of the selection coefficients across all observations were then regressed on trait values (if available) to estimate the global dependence of selection on each plant trait. To
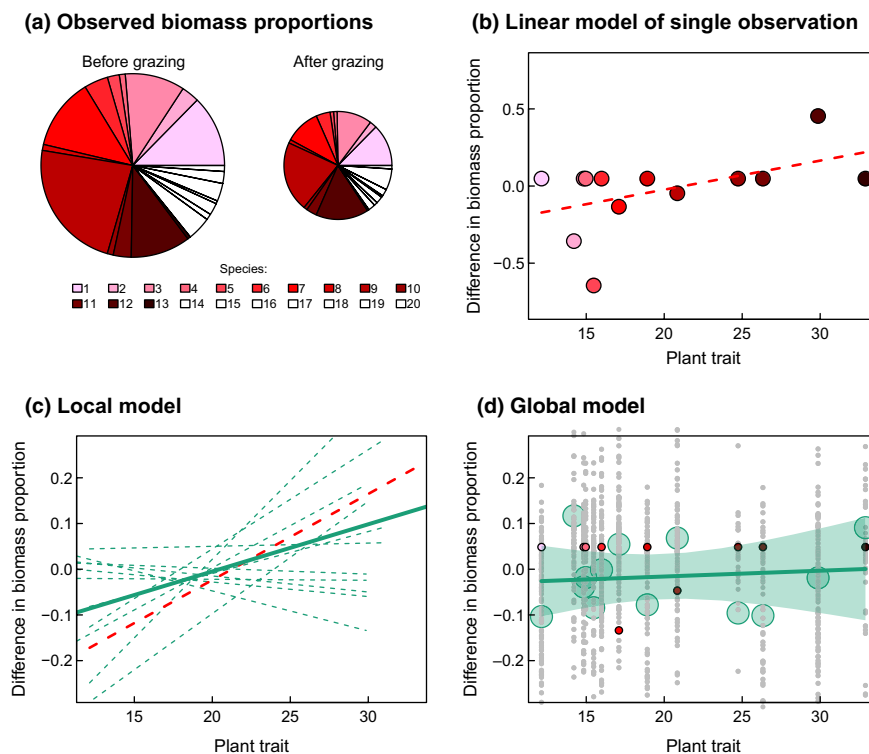

FIGURE 2 Schematic illustration of the modelling process: (a) displays a selected example survey of the biomass proportions of 20 plant species before and after grazing. Species, for which trait values are available, are coloured; (b) is the resulting relationship between the difference in biomass proportion and an exemplary plant trait for the selected observation; (c) depicts the local model, in which only the relationship between the differences in biomass proportion and the trait in each observation is considered. The dashed red line is the linear regression of the selected observation, thin dashed lines are other observations and the bold line represents the fitted linear mixed estimate of the relationship for all observations; (d) represents the global model, in which multiple observations of many plant species are considered. Small red dots represent the data of the example survey, small grey dots are the data of other surveys, green dots are the modelled selection coefficients of each plant species and the solid green line is the global dependence of selection on the plant trait with its credibility interval

make calculations computationally feasible, random effects were represented using the latent variable approach presented by Warton et al. (2015) and parameters were estimated in a Bayesian framework using Markov Chain Monte Carlo (for details, see Supporting Information S4). All calculations were done in R 3.6.1 (R Core Team, 2018).

3 | RESULTS

3.1 | Characterization of areas and paddocks

The comparison of biomass-weighted means of plant traits within the subplots showed that the vegetation was similar in the three paddocks in an area, but differed among areas (Figure 3). Tukey post-hoc tests identified significant differences in traits among most areas, but no significant differences among paddocks within an area.

The average P_{leaf} and N_{leaf}, forage indicator value and specific leaf area were highest in the fertile pasture (area 1), less in the intermediate pasture (area 2) and lowest in the wood pasture (area 3). The C:N ratio, LDMC and woodiness showed the opposite trend. The traits of

observed plant species were not independent, but there were only few strong correlations among them (see Supporting Information S5).

3.2 | Local trait-dependent selection

The local model demonstrated significant effects of all plant traits on differences of biomass proportions before and after grazing as a proxy for forage selection (Figure 4). Irrespective of cattle breed, differences in biomass proportion significantly decreased with higher P_{leaf}, N_{leaf}, SLA and forage quality indicator values (p_{trait} < .001 each), meaning that plants with high values of these traits were foraged above average. In contrast, plants with high C:N ratio (p_{trait} = .004), LDMC (p_{trait} < .001), plant height (p_{trait} = .001) and strong physical defence (p_{trait} = .02) were avoided by cattle and therefore, their biomass proportion increased during grazing.

Besides these general trends, breeds significantly differed in their forage selection behaviour (for six traits $p_{trait \times breed}$ < .05). The strength of forage selection, indicated by the steepness of the regression lines, decreased in the order A × H, Original Braunvieh, Highland
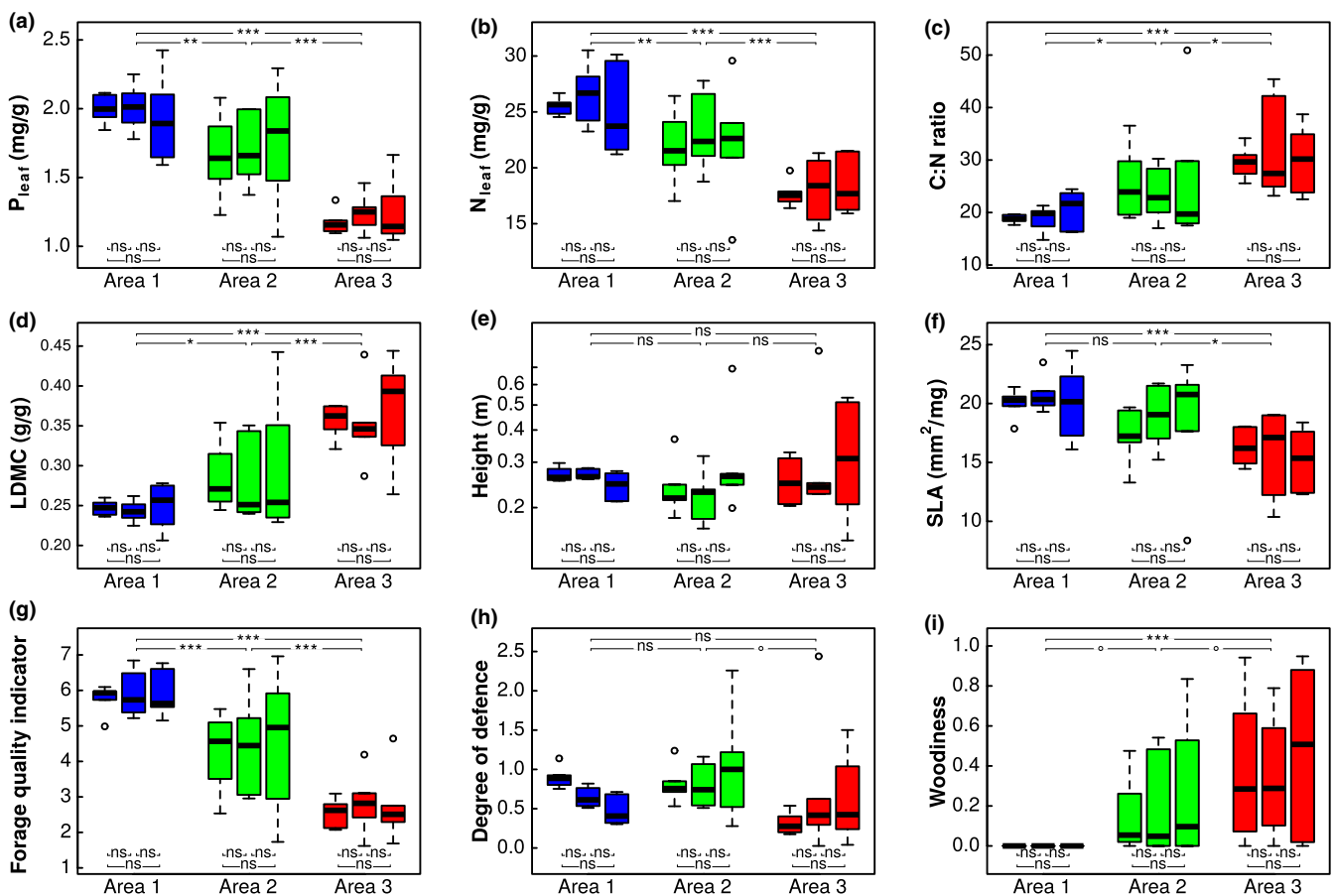

FIGURE 3 Initial status of vegetation traits within areas and paddocks: Each boxplot shows the distribution of biomass-weighted means of the n = 6 vegetation subplots in each of the three paddocks per area before the first grazing. Area 1 (blue): fertile pasture, area 2 (green): intermediate pasture with shrubs, area 3 (red): nutrient-poor wood pasture. Plant traits are (a) P_{leaf} and (b) N_{leaf} content per dry mass in mg/g, (c) C:N-ratio, (d) leaf dry matter content (LDMC) in g/g, (e) plant height in m, (f) specific leaf area (SLA) in mm²/mg, (g) forage quality indicator value, (h) degree of physical defence and (i) woodiness. Symbols on top show significances of Tukey range tests of differences among areas, symbols at the bottom indicate differences among paddocks within areas (∘p < .1; *p < .05; **p < .01; ***p < .001; ns, not significant)
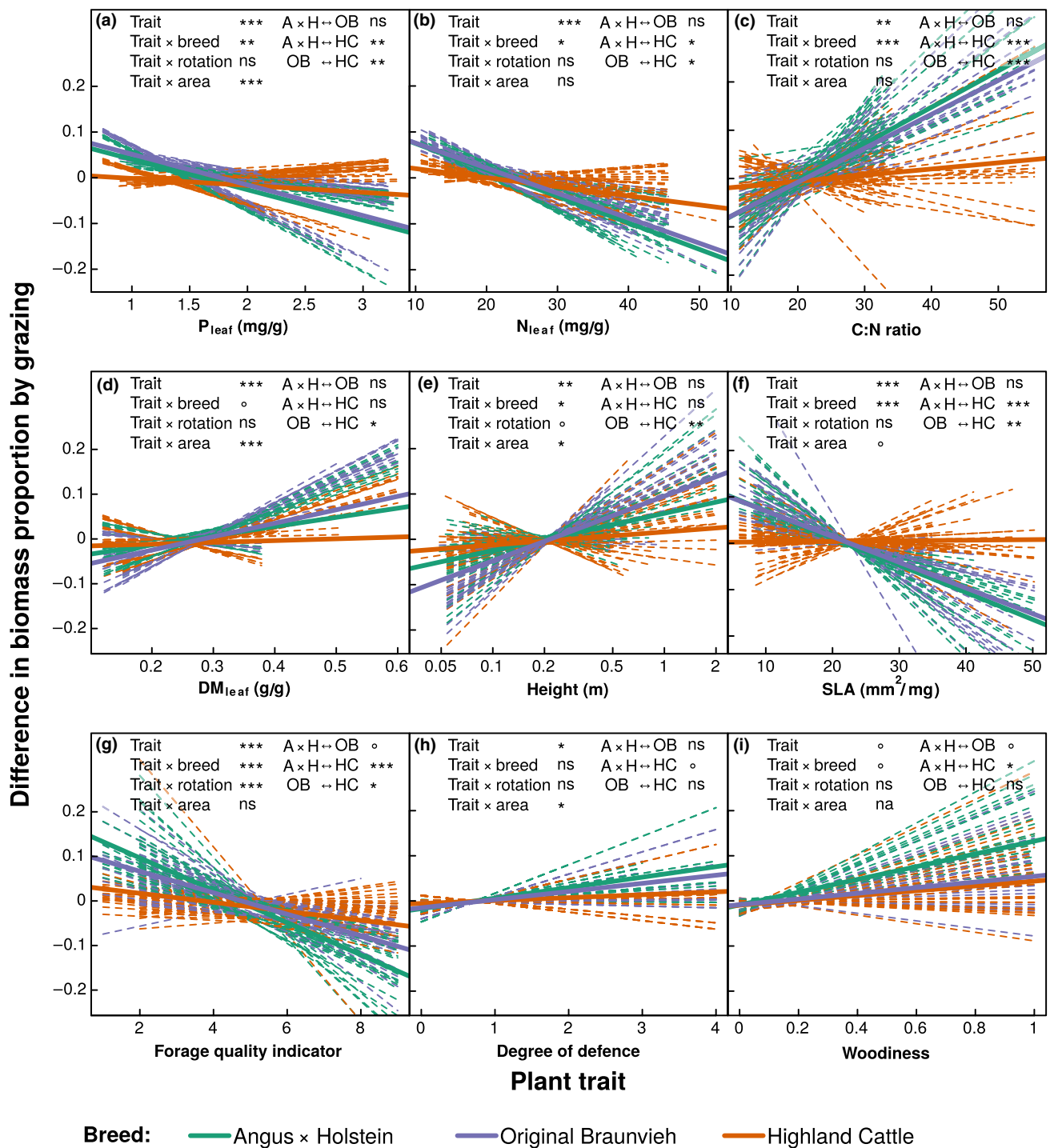
FIGURE 4 Effect of plant traits on the differences in biomass proportions before and after grazing as estimated by the local model: Continuous bold lines are predicted mean effects for the three cattle breeds A × H (green), Original Braunvieh (blue) and Highland Cattle (orange). Dashed lines show the predicted relationship for the 165 surveys (the variation around the fixed mean). Plant traits are (a) P_{leaf} and (b) N_{leaf} content per dry mass in mg/g, (c) C:N-ratio, (d) leaf dry matter content (LDMC) in g/g, (e) plant height in m, (f) specific leaf area (SLA) in mm^2/mg, (g) forage quality indicator value, (h) degree of physical defence and (i) woodiness. A declining regression line represents a positive influence of the trait on biomass consumption, that is, selection of species with high trait values. An inclining line represents a negative effect on consumption, that is, avoidance. Significances of the trait effect and its interactions with breed, rotation and area, as well as the differences among breeds are given in each panel ($\circ p < .1$; $^*p < .05$; $^{**}p < .01$; $^{***}p < .001$; ns, not significant; na, not available)

Cattle. The A × H and Original Braunvieh only differed slightly from each other and Highland Cattle differed clearly from the other two breeds. This was inversely related to the productivity of the breeds.

Forage decision was rarely influenced by season, as indicated by largely absent interactions of trait × rotation. Only the influence of plant height and forage quality on selection behaviour differed

among seasons. At the beginning of the season, cattle avoided tall plants slightly less ($p_{\text{trait} \times \text{rotation}}$ = .07) and favoured plants with a high forage quality indicator more clearly ($p_{\text{trait} \times \text{rotation}}$ < .001).

Likewise, the vegetation type affected the influence of some plant traits on selection behaviour, as indicated by the interaction term of trait and area. The preference of plants with high P_{leaf} was significantly higher in the wood pasture ($p_{\text{trait} \times \text{area}}$ < .001), whereas plants with high LDMC ($p_{\text{trait} \times \text{area}}$ < .001), large height ($p_{\text{trait} \times \text{area}}$ = .05) and degree of defence ($p_{\text{trait} \times \text{area}}$ = .04) were avoided more strongly there. The interaction of woodiness and area could not be tested because the nutrient-rich area 1 lacked woody species. Other traits did not interact significantly with area: Although traits differed among the areas, they influenced foraging behaviour equally. For example, N_{leaf} was significantly higher on the fertile than on the wood pasture, but plants with a high N_{leaf} were equally favoured over nitrogen-poor plants in both areas.

3.3 | Global trait-dependent plant species selection

The trends of selection and avoidance and their differences among breeds were also evident at the plant species level (Figure 5). Certain species, such as clover (*Trifolium repens* L., *T. pratense* L.), some composites (*Leontodon hispidus* L., *L. helveticus* Mérat) or

Plantago alpina L., were consistently preferred by all three breeds, whereas others were generally avoided, for example, shrubs (*Calluna vulgaris* (L.) Hull, *Juniperus communis* L., *Pinus mugo* Turra), thistles (*Cirsium acaule* Scop., *Carlina acaulis* L.), grasses of low forage quality (*Nardus stricta* L.) and some toxic species (*Ranunculus acris* L., *R. montanus* Willd.). The higher magnitude of effects on the x- than on the y-axis indicates that Highland Cattle avoided these species less strictly than A × H. Some species of high forage quality like graminoids (*Poa pratensis* L., *Alopecurus pratensis* L.), legumes (*Lotus corniculatus* L., *Trifolium badium Schreb.*) or herbs (*Taraxacum officinale Weber*) were selected by A × H, but not by Highland Cattle, and some plants positively selected by A × H were even avoided by Highland Cattle (*Poa alpina* L., *Agrostis capillaris* L.). On the contrary, unattractive species like *Deschampsia cespitosa* (L.) P. Beauv. or *Carex caryophyllea* Latourr. were selected by Highland Cattle and avoided by A × H.

In heterogeneous pastures, avoidance or consumption depends not on traits of a single plant species but also on the traits of the surrounding plants. The palatability of a forage plant is relative. Therefore, the global model estimated the overall effect of plant traits on species selection as expressed by the difference in biomass proportion before and after grazing (Figure 6). Trait effects were mostly similar to the local estimates, but the global model indicated a
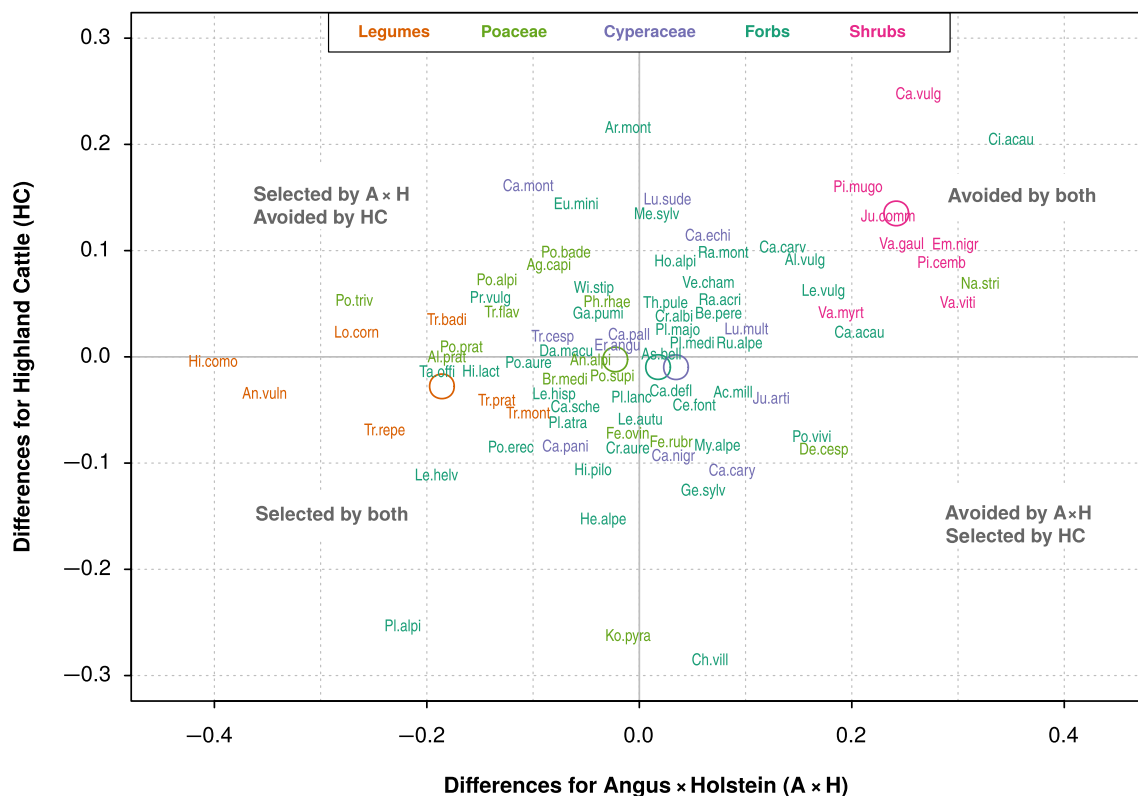

FIGURE 5 Selection and avoidance of plant species by two cattle breeds: Observed differences in biomass proportions before and after grazing by Angus × Holstein (A × H; x-axis) and Highland Cattle (HC; y-axis). Positive values indicate an increase in biomass proportion and hence deselection by the animals, negative values indicate selection. All plant species observed more than 10 times are presented and coloured according to five functional groups. Circles indicate the mean values for each group across the entire dataset. A list with the abbreviated and full names, number of observation and available traits as well as figures displaying A × H versus OB and HC versus OB are provided in Supporting Information S6. The positions of 20 species were slightly modified to avoid overlapping labels
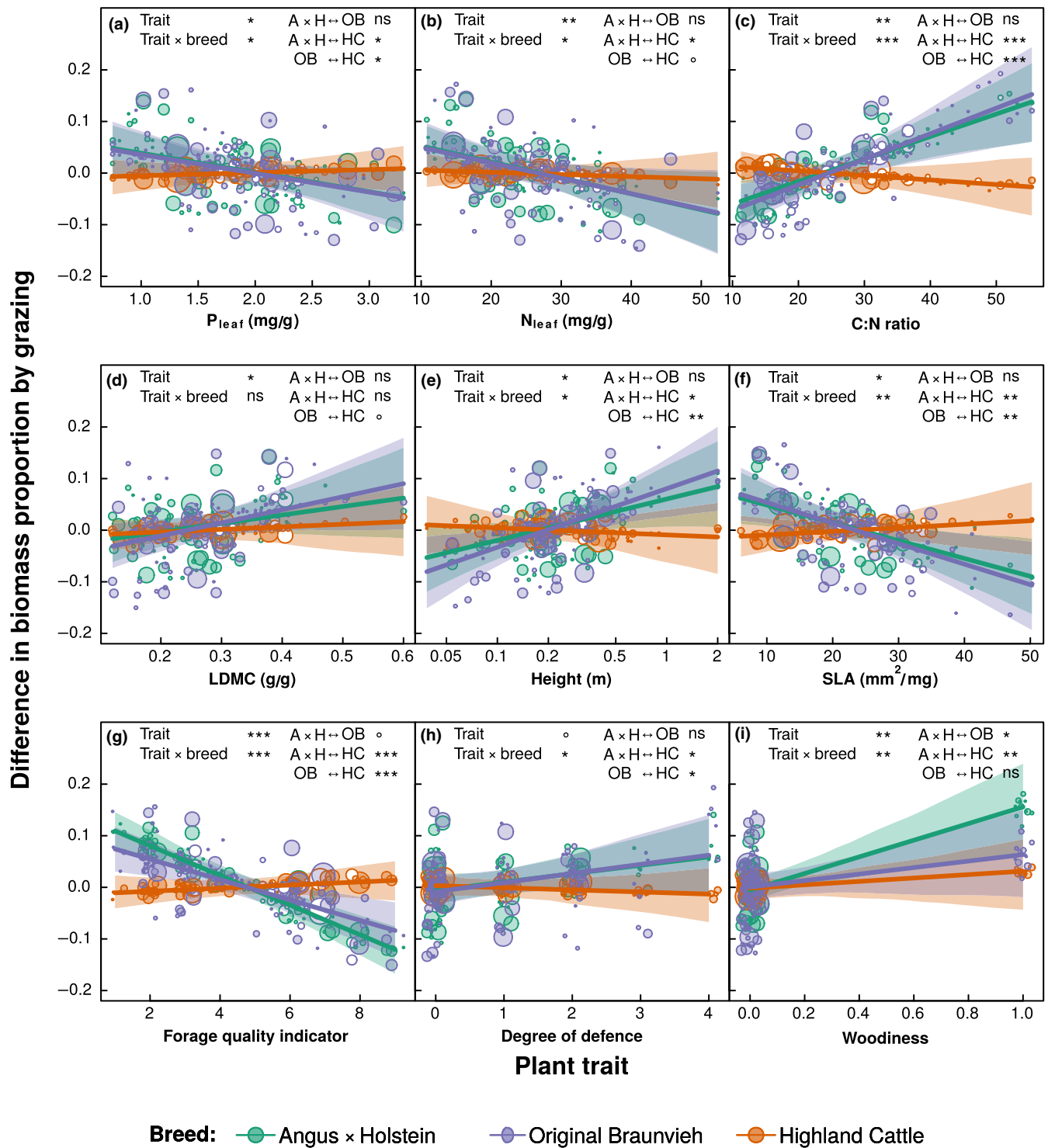
FIGURE 6 Effects of plant traits on differences in biomass proportion by grazing as estimated by the global model: Solid lines represent estimated effects of plant traits with their 95% credibility interval (shaded areas) for three cattle breeds A × H (green), Braunvieh (blue) and Highland Cattle (orange) for the nine traits: (a) P_{leaf} and (b) N_{leaf} content per dry mass in mg/g, (c) C:N-ratio, (d) leaf dry matter content (LDMC) in g/g, (e) plant height in m, (f) specific leaf area (SLA) in mm²/mg, (g) forage quality indicator value, (h) degree of physical defence and (i) woodiness. A declining regression line stands for a positive influence of the trait on biomass removal, that is, selection of species with high trait values. An inclining line represents a negative effect on consumption and represents avoidance of plants. Circles show the modelled selection coefficients before and after grazing for each plant species. Radii are scaled by number of observations of each species. Plants, for which a trait value was not available in the database but inferred from observed consumption, are represented by open circles. Probabilities that the trait effect and its interaction with breed are equal to zero are given in each panel, along with the differences of trait effects among breeds ($\circ p < .1$; $*p < .05$; $**p < .01$; $***p < .001$; ns, not significant)

significant effect of woodiness on species selection and only a marginal effect of plant defence mechanisms.

In accordance with the local model, the selection behaviour of the three breeds differed consistently, with A × H showing the most distinct selection behaviour and Highland Cattle being the least selective with respect to the investigated traits. The interaction between breed and trait was significant for all traits except LDMC. Both A × H and Original Braunvieh preferred plants with higher C:N ratio less than Highland Cattle, while better forage quality increased removal of biomass in A × H and Original Braunvieh relative to Highland Cattle ($p_{trait \times breed}$ < .001 each).

4 | DISCUSSION

4.1 | Assessing forage selection in species-rich pastures

Alpine pastures and other semi-natural, low-productive grasslands are important hotspots of biodiversity (Wilson et al., 2012). Their species richness offers innumerable opportunities for grazing ruminants to select plant species. At the same time, their large heterogeneity and diversity make it more difficult to evaluate the actual forage consumption than in sown grasslands. Nevertheless, it is crucial to analyse the mechanisms of selection to understand the drivers forming the botanical composition of these habitats.

We therefore developed a method to assess the joint selection of many plant species by grazing cattle. Unlike former studies (e.g. Katjiua & Ward, 2006; Sanon, Kaboré-Zoungrana, & Ledin, 2007), we did not observe grazing animals directly because many alpine plant species are unrecognizable from afar. We did, however, assess consumption of species, not only vegetation types (e.g. Wallis de Vries & Daleboudt, 1994) and estimated biomass change on a continuous scale rather than by classes (Iussig, Lonati, Probo, Hodge, & Lombardi, 2015; Meisser et al., 2014; Mládek et al., 2013). Moreover, we considered it difficult and erroneous to estimate consumption based on something that is no longer present. We therefore assessed what was left over (i.e. the biomass of each species) and compared it to what was recorded before grazing.

This method was applied during different phases of the growing season and for different cattle breeds. The nested study design with replications for areas, paddocks, vegetation subplots and herds, fulfilled the intended requirements: The three areas reflected contrasting vegetation types and differed significantly with respect to most traits, whereas the three paddocks within each area provided similar conditions. This allowed for the simultaneous grazing of the three cattle breeds under similar conditions. Confounding effects were minimized by grazing each breed in each paddock once. Furthermore, each of the three rotations was conducted with different cows to avoid pseudoreplication.

Finally, we analysed trait effects on plant species selection using two statistical models, which have different ecological interpretations. The local model assumes that cattle mainly select plants

locally, that is, they select the tastiest of all reachable species even if they are relatively unattractive compared to spatially distant plants. The global model assumes that cattle move to patches with a high share of tasty species and select the tastiest there. Our data show a good agreement between both models, indicating that similar trait effects operate both locally and globally, at least within the technical limits of a controlled grazing experiment.

4.2 | Plant traits have an impact on forage selection

We tested the impact of a wide spectrum of traits, and found that both the chemical composition and physical characteristics of a plant affect the foraging behaviour of cattle. Both models showed a clear preference for plant species with high N_{leaf} or P_{leaf}. This is not surprising because these nutrients are important for the production of milk and muscles. In grass diets, particularly nutrient-poor alpine pastures, these nutrients are, however, commonly in short supply. To meet their demand, cattle naturally select plants with high N or P content (Woodward & Coppock, 1995). The local model showed that plants with high C:N ratio and LDMC (typically plants with high investment in leaf structural tissue resulting in a large share of cellulose and lignin) are avoided. In a pasture diet, there is usually no shortage of C, but high fibre content increases the time spent foraging and digesting. The total amount of exploitable nutrients therefore decreases with increasing fibre content (Katjiua & Ward, 2006). Accordingly, Pakeman (2014) reported that animals' productivity is highly correlated to the LDMC of their diet. Cattle's response to N_{leaf} and P_{leaf} was opposite to C:N ratio and LDMC. This contrast was also reflected by the negative correlation of these traits (Supporting Information S5) and exemplifies the different strategies of nutrient-rich, fast-growing competitive ruderals and nutrient-poor, long-lived stress-tolerant species (Pierce, Ceriani, de Andreis, Luzzaro, & Cerabolini, 2007; Pyankov, Ivanov, & Lambers, 2001).

Besides the chemical properties, plants' physical texture and dimensions influence foraging decisions. In agreement with Cingolani, Posse, and Collantes (2005) and Mládek et al. (2013), we found a positive effect of SLA on species selection. The thinner a leaf is, the more it is selected, because of ease in cropping, ingestion and digestion. The positive selection of species with high SLA is intensified by the positive correlation with nutrient contents.

On the contrary, plants aim at reducing herbivore impact by developing defence structures such as hairs, thorns or spines (Gong & Zhang, 2014; Laca, Shipley, & Reid, 2001). We detected a negative response to physical defence mechanisms, but it was less pronounced than expected. This may be due to the low overall number of species with physical defence structures, in contrast to semi-arid regions where the share of armoured species is much higher (Woodward & Coppock, 1995). Chemical defence mechanisms (e.g. terpens, alkaloids and tannins) likely cause a similar response, but the effect is hard to analyse because of missing data for many alpine species. Woodiness is a special case of defence, making a plant unattractive by the storage of lignin. Cattle generally avoid woody plants (Fraser, Theobald,

Griffiths, Morris, & Moorby, 2009) because of the hard structure and poor digestibility. The low overall number of foraged woody species minimized the effect size in the local model, but it was clearly significant in the global model. Still, some parts of a woody plant may be tasty (e.g. fresh leaves or buds). Our estimation of the entire biomass did not account for the selection of particular plant parts. Plant height had an effect on selection, with short species preferred, which is consistent with Cingolani et al. (2005). As a synopsis of the traits described above, we examined the explanatory power of the forage indicator value (Briemle et al., 2002) as an educated rating of palatability based on observation and experience. We congruently identified it as a reliable predictor for cattle's plant species selection, as Mládek et al. (2013) did for sheep in mesic grassland.

Trait effects were mostly consistent across areas and rotations, with some noteworthy exceptions. First, in compliance with Iussig et al. (2015), who found that goats select forage plants more strictly in forestland than in grassland, the cattle of our study preferred plants with high P_{leaf} and avoided plants with high LDMC more clearly in the wood pasture than in the two nutrient-richer areas. In the wood pasture, the excessive supply of nutrient-poor leaf structural tissue (i.e. high LDMC) that goes along with a shortage of P, forces cattle to forage more selectively to cover their nutritional demand. Second, plants with high forage quality were selected more strictly at the beginning of the grazing season than in late summer (trait × rotation interaction, Figure 4g), which is in agreement with Mandaluniz, Aldezabal, and Oregui (2011). The explanation may be that the difference in quality, and therefore the driver of selection, is higher in juvenile than mature plants, or it may be a function of the condition of the cattle at the end of their winter housing.

4.3 | The impact of plant traits differs among breeds

Production-oriented, nutrient-demanding A × H and Original Braunvieh cattle showed strongly selectively grazing. In contrast, less-productive, undemanding Highland Cattle selected their forage less strictly, as indicated in both models and consistently for all traits.

A × H and Original Braunvieh selected positively for traits associated with high forage quality: Nutrient-rich plants (i.e. high N_{leaf} and P_{leaf} content), plants easily ingestible and digestible (high SLA) and those rated to have a high forage indicator value, were more clearly preferred by the two production-oriented breeds than by Highland Cattle. In contrast, traits of low forage quality (i.e. high C:N ratio, LDMC, height, defence mechanisms) had less negative impact on foraging by Highland Cattle. Especially productive A × H cattle need fodder with high nutrient density to meet their demand for genetically defined weight gain and milk production. Hence, they avoided unattractive and favoured tasty plant species most clearly according to most traits.

In contrast, Highland Cattle grow slower, their calves demand less milk and they presumably have a better feed conversion (Berry, Jewell, Sutter, Edwards, & Kreuzer, 2002). They consume proximal forage without exerting effort to search and thereby save legwork and energy by being less selective. This is in line with previous studies showing that heritage cattle graze more evenly in space (Peinetti et al., 2011) and less selectively (Koczura et al., 2019) than modern breeds. For single traits such as woodiness, differences in forage selection among breeds have been detected by some previous studies (Orr, Tallowin, Griffith, & Rutter, 2014; Winder, Walker, & Bailey, 1995) that reported higher shrub consumption by less-productive breeds, whereas others found traditional cattle avoiding shrubland (Spiegal et al., 2019).

Original Braunvieh showed an intermediate selectivity between productive A × H and undemanding Highland Cattle. It is a traditional dual-purpose breed that has undergone the less intensive breeding transformations than Brown Swiss, a high-productive dairy breed from the same original population. On the other hand, and in contrast to Highland Cattle, Original Braunvieh has not been unaffected by modern breeding, and the efficiency has increased moderately. Therefore, Original Braunvieh cattle are slightly less productive, heavy and fast growing than A × H, but much more productive than Highland Cattle. This intermediate position is also reflected in forage behaviour of Original Braunvieh. The local model showed an intermediate selection behaviour of Original Braunvieh regarding seven out of nine traits, but in most cases, their foraging behaviour was much closer to A × H than to Highland Cattle. Therefore, in either model, selection behaviour did not significantly differ between the two productive breeds for most traits, but clearly differed compared to Highland Cattle.

The marginal differences between modern A × H and traditional Original Braunvieh may explain why some previous studies detected breed effects on forage selection and others did not. Where relatively low-productive traditional breeds are compared to each other (Braghieri, Pacelli, Girolami, & Napolitano, 2011) just as little difference was found as where relatively high-productive breeds were compared among themselves (Dumont et al., 2007; Scimone, Rook, Garel, & Sahin, 2007). The more similar two breeds are in terms of productivity, the less discernible the difference in forage selection.

In agreement with previous work (Pauler et al., 2019), we found that cattle breeds exhibit consistent forage selection behaviour—not only regarding single traits but also for a wide spectrum of traits— and that the difference in the breeds' foraging preferences for these traits increases with the degree of breeding-induced increase in productivity.

5 | CONCLUSIONS

The comparison of biomass proportions before and after grazing is an appropriate method to analyse the plant species selection of large generalist herbivores like cattle in species-rich heterogeneous grasslands. Our analysis using a local and a global model showed that forage selection by grazing cattle depends on plant traits. Nutrient-rich plant species of high forage quality with relatively thin and tall leaves were preferred, whereas shrubs, tall and armoured plants as well as species rich in fibre were avoided. Besides these general foraging preferences, cattle breeds responded differently to plant traits,

depending on their productivity. The least demanding Highland Cattle demonstrated less strict plant selection than the two more production-oriented breeds, which sought out high-quality forage to cover their breed-specific demand.

AUTHORS' CONTRIBUTIONS

C.M.P., J.I., J.B., T.B. and M.K.S. conceived the ideas and designed the methodology; C.M.P. and M.K.S. collected the data; C.M.P., M.S. and M.K.S. analysed the data; and C.M.P. and M.K.S. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data and code to reproduce the main results are provided in zenodo https://zenodo.org/record/3629561 (Pauler et al., 2020).

ETHICAL APPROVAL

This research complied with all legal requirements (authorization GR2018_12 of veterinary office of Grisons).

ORCID

Caren M. Pauler (iD) https://orcid.org/0000-0002-7872-2711
Johannes Isselstein (iD) https://orcid.org/0000-0002-8010-9238
Matthias Suter (iD) https://orcid.org/0000-0003-2747-4524
Joel Berard (iD) https://orcid.org/0000-0002-7222-632X
Thomas Braunbeck (iD) https://orcid.org/0000-0002-1785-6759
Manuel K. Schneider (iD) https://orcid.org/0000-0002-3842-2618

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SUPPORTING INFORMATION

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