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Anatomical and behavioural differences among cattle breeds and their impact on pasture vegetation

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Für Konstantin

der seine Mama immer mit dieser Arbeit teilen musste

Previously published data

Chapters 3 and 4 of this thesis have already been published as the following peer-reviewed journal articles:

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The studies presented in this thesis were conducted, the data were analysed and text and figures were created by myself.

Contents

Abstract

Background: The species richness of semi-natural pastures, formed by grazing livestock over centuries, is endangered by the structural change in agriculture. In recent decades, human artificial selection formed cattle breeds with enhanced milk or meat production and these high-productive breeds account for a majority of cattle today. However, the increased productivity came along with increased requirements, for example a high nutritive demand. Therefore, high-productive cattle are reared on the agriculturally best pastures, whereas nutrient-poor, marginal grasslands are underused. Both, intensification as well as abandonment, reduce the biodiversity of marginal pastures. However, besides high-productive, modern cattle, there are traditional breeds nearly untouched by output-oriented breeding and thus, less productive. Apart from breeding aims easy to quantify, such as milk and meat yield, little attention was paid to breed characteristics which possibly co-evolved unnoticed during the breeding process, such as anatomy, movement and foraging behaviour. Such hidden traits could have a lasting effect on plant species composition of pasture vegetation.

This thesis, therefore, aimed at estimating differences between low- and high-productive cattle breeds, quantifying their long-term impact on pasture vegetation and analysing their suitability for the maintenance of species-rich, marginal grasslands.

Methods: Two different approaches were used: (1) An observational study along a broad environmental gradient from Southern Germany to the Swiss Alps examined the vegetation composition of highly comparable paired pastures, either grazed by high- or low-productive cattle breeds for years. (2) A controlled grazing experiment compared three cattle breeds representing a gradient from low to high productivity. On high-elevation summer pastures in the Swiss Alps, the drivers of forage selection were analysed at plant species level. In addition, anatomy, movement and foraging behaviour of cattle and their allometric relationships were evaluated. In all setups, Highland cattle were chosen as model for low-productive breeds. High-productive cattle were not restricted to a single breed in the observational study and represented by Original Braunvieh (intermediate productivity) and Angus×Holstein crossbreed cattle (high productivity) in the controlled grazing experiment. All experimental animals were suckler cows with calves.

Results: High- and low-productive breeds differed significantly in anatomy, movement and foraging behaviour as well as in their long-term impact on pasture vegetation:

(1) High-productive breeds were significantly heavier than low-productive breeds and their claws were relatively small. Subsequently, more body mass burdens the ground and promotes trampling-adapted plant species. Thereby, the vegetation composition was influenced: significantly more trampling adapted plant species were found on pastures grazed by high-productive breeds. Additionally, the trampling pressure of high-productive breeds was amplified by their movement behaviour: The more productive a breed was, the more it moved and thereby, the more frequently it exposed destructive kinetic energy to the ground.

(2) Forage selection was also influenced by productivity. The more productive a breed was, the more selective it foraged, i.e. the more it cared about plant traits: Plants protect themselves from being consumed by low nutrient content, physical and chemical defence mechanisms (e.g. spines and toxins) or woodiness. High-productive breeds preferred attractive forage plants and avoided unattractive plants more clearly than low-productive breeds. Since high-quality forage plants can be far from each other on heterogeneous pastures, highly selective cattle had to walk longer distances than low-productive cattle while foraging. Thereby, they consumed a diet of higher forage quality. The enhanced selectivity of high-productive breeds influenced plant species

composition: A higher share of grazing-adapted species spared by cattle were found on pastures of high-productive breeds.

(3) The enhanced trampling pressure and selectivity decreased plant species richness, because species highly adapted to trampling or grazing outcompete less resistant plants. Consequently, the species richness was lower on pastures of high-productive cattle breeds. The longer a pasture has already been grazed by low-productive Highland cattle, the clearer was the contrast to pastures of high-productive breeds. Additionally, vegetation grazed by low-productive Highland cattle for long, had a higher share of epizoochoric and lower abundance of woody species. Both contributed positively to the plant species richness.

(4) Although low-productive Highland cattle chose a diet of lower quality, they gained weight on the nutrient-poor alpine pastures, whereas the more productive breeds lost weight. The energy-saving movement behaviour and a presumably better conversion of fibre-rich fodder made them more efficient under harsh environmental conditions than so-called high-productive breeds.

Conclusion: Besides desired characteristics, modern breeding unintentionally changed hidden traits of cattle’s anatomy, movement and foraging behaviour. Thereby, breeding modified not only the cattle themselves, but also the vegetation grazed by these animals. Low-requirements and high efficiency give low-productive cattle breeds a key position in maintaining nutrient-poor, species-rich pastures.

Zusammenfassung

Hintergrund: Naturnahe, extensive Weideflächen entstanden durch jahrhundertelange, extensive Beweidung. Sie gehören zu den artenreichsten Pflanzengesellschaften Mitteleuropas, doch der anhaltende landwirtschaftliche Strukturwandel gefährdet ihre Vielfalt. Dazu tragen auch Entwicklungen in der Tierzucht bei. Durch künstliche Selektion entstanden innerhalb eines Jahrhunderts hochspezialisierte Rinderrassen mit herausragender Milch- oder Fleischleistung. Traditionelle Extensivrinderrassen, an denen die output-orientierte Züchtung nahezu spurlos vorübergegangen ist, sind deutlich leistungsschwächer. Die enorme Leistung der modernen, hochproduktiven Rassen hat dazu geführt, dass sie heute die überragende Mehrheit des Rinderbestandes stellen. Doch die gesteigerte Milch- oder Fleischleistung geht mit hohen Ansprüchen, beispielsweise an die Futterqualität, einher. Aus diesem Grund beweiden hochproduktive Rassen vor allem die landwirtschaftlich wertvollsten Weideflächen, während mageres, extensives Grünland immer weniger bewirtschaftet wird. Sowohl die Intensivierung in Gunstlagen als auch die Unternutzung von Grenzertragsstandorten bedrohen die Artenvielfalt von extensiven Weidenflächen.

Die moderne Leistungszucht hat ihren Fokus auf die Steigerung der Milch- und Fleischleistung gelegt – nicht zuletzt deshalb, weil diese Parameter einfach zu quantifizieren sind. Andere Merkmale wie Anatomie, Bewegungs- und Fressverhalten wurden dabei weitgehend außer Acht gelassen, obwohl es naheliegt, dass sie bei hochproduktiven Rassen im Verlauf der jüngeren Zuchtgeschichte unbemerkt co-evolvierten. Diese Eigenschaften könnten einen nachhaltigen Einfluss auf die Weidevegetation haben.

Das Ziel dieser Doktorarbeit war es deshalb, Unterschiede zwischen wenig produktiven und hochproduktiven Rassen abzuschätzen, den langfristigen Einfluss dieser Unterschiede auf die Weidevegetation zu quantifizieren und die Eignung von Extensivrindern für den Erhalt artenreicher Grenzertragsweiden zu untersuchen.

Methodik: Hierfür wurden zwei unterschiedliche Ansätze gewählt: (1) In einer Beobachtungsstudie wurde die Vegetation von 50 gepaarten Weideflächen an 25 Standorten über einen breiten ökologischen Gradienten von Süddeutschland bis zu den Schweizer Alpen verglichen. Die Weiden eines Paares waren in Bezug auf die Standort- und Bewirtschaftungsfaktoren vergleichbar, wobei die eine Weide seit mindestens fünf Jahren von wenig produktiven Extensivrindern, die andere von hochproduktiven Rinderrassen beweidet wurde. (2) In einem gelenkten Weideexperiment wurden wenig produktive Extensivrinder mit einer mittleren und einer hochproduktiven Rinderrasse verglichen. Hierfür wurde auf Almweiden in den Schweizer Alpen der Verzehr von Futterpflanzen auf Artniveau abgeschätzt. Außerdem wurden die Anatomie, das Bewegungs- und das Fressverhalten der Tiere sowie die allometrischen Beziehungen dieser Parameter auf dem Niveau des Individuums untersucht. Bei allen Ansätzen dienten Hochlandrinder als Modell für die wenig produktiven Extensivrinderrassen. Die produktiveren Rassen wurden in der Beobachtungsstudie nicht auf eine einzelne Rasse beschränkt. Im gelenkten Weideexperiment wurden sie von Original Braunvieh (mittlere Produktivität) und Angus×Holstein-Kreuzungstieren (hohe Produktivität) repräsentiert. Alle Versuchstiere waren Mutterkühe mit Kälbern.

Ergebnisse: Extensivrinder und hochproduktive Rinderrassen unterscheiden sich signifikant in ihrer Anatomie, ihrem Bewegungs- und ihrem Fressverhalten und haben langfristig einen unterschiedlichen Einfluss auf die Weidevegetation.

(1) Hochproduktive Rassen sind deutlich schwerer als wenig produktive Extensivrinder und ihre Klauen sind im Vergleich zum Gewicht relativ klein. Es lastet folglich mehr Gewicht auf der Auftrittsfläche und die Trittbelastung nimmt zu. Dadurch verändert sich langfristig die Zusammensetzung der Weidevegetation: Auf Flächen, die von hochproduktiven Rinderrassen beweidet wurden, fanden sich mehr trittangepasste Pflanzenarten. Das Bewegungsverhalten der hochproduktiven Rassen verstärkte die Trittbelastung zusätzlich: Je produktiver die Tiere waren, desto mehr und schneller bewegten sie sich und desto öfter und kraftvoller belasteten sie folglich den Untergrund.

(2) Auch die Futterselektion war abhängig von der Produktivität. Je produktiver die Rinder waren, desto selektiver fraßen sie und desto mehr wurde ihre Futterentscheidung von den Eigenschaften der Pflanzen beeinflusst: Pflanzen, die sich durch einen geringen Nährstoffgehalt, durch physikalische oder chemische Abwehrmechanismen (z.B. Stacheln oder Giftstoffe) oder durch Verholzung schützen, wurden von hochproduktiven Rassen viel deutlicher verschmäht als von anspruchslosen Extensivrindern. Hingegen nahm die Präferenz für attraktive Futterpflanzen mit der Produktivität der Rasse zu. Da auf heterogenen Bergweiden die guten Futterpflanzen häufig weit voneinander entfernt wachsen, mussten hochproduktive, hochselektive Rinder während des Fressens größere Distanzen zurücklegen. Sie wählten im Durchschnitt Futterpflanzen von besserer Futterqualität aus als die gleichmäßiger fressenden, wenig produktiven Extensivrinder. Diese Unterschiede in der Selektivität wirkte sich langfristig auf die Vegetation aus, denn je selektiver der Fraßdruck ist, desto größer ist der ökologische Vorteil weideangepasster Arten. Folglich wurde auf den Weiden hochproduktiver Rassen ein höherer Anteil von Pflanzen gefunden, die an regelmäßige Beweidung angepasst sind.

(3) Die erhöhte Trittbelastung und die forcierte Selektivität reduzierten die Artenvielfalt auf den untersuchten Weideflächen von hochproduktiven Rinderrassen: Pflanzenarten, die an Tritt und Fraß besonders gut angepasst sind, haben hier einen größeren Konkurrenzvorteil und verdrängen weniger spezialisierte Arten. Je länger eine Fläche bereits von wenig produktiven Rindern beweidet worden war, desto deutlicher war der Unterschied zu den Weiden der hochproduktiven Rassen. Außerdem besaßen Weideflächen von wenig produktiven Extensivrindern eine höhere Deckung epizoochorischer Arten und eine geringere Abundanz von Gehölzpflanzen. Beides beeinflusste die Artenvielfalt positiv.

(4) Obwohl die wenig produktiven Extensivrinder Futterpflanzen von geringerer Qualität auswählten, nahm ihr Körpergewicht auf den nährstoffarmen Almweiden zu, während die produktiveren Kühe Gewicht verloren. Auf diesen Grenzertragsstandorten waren die wenig produktiven Extensivrinder dank ihres energiesparenden Bewegungsverhaltens und einer möglicherweise besseren Verwertung von rohfaserreicher Nahrung effizienter als die sogenannten hochproduktiven Rassen.

Schlussfolgerung: Die moderne Zucht steigerte nicht nur gewünschte Merkmale, sondern veränderte unbemerkt auch bislang kaum beachtete Eigenschaften der Anatomie, des Bewegungs- und des Fressverhaltens von Rindern. Auf diese Weise beeinflusste die Zucht nicht nur die Tiere selbst, sondern auch die Weidevegetation. Aufgrund ihrer geringen Ansprüche und hohen Effizienz sind Extensivrinder der Schlüssel zum Erhalt des Artenreichtums extensiver Weiden in Grenzertragslagen.

1 Introductory remarks

From a farmer's point of view, the choice of cattle breed is essential. It is not only an important question of tradition and local identity, but also influences the entire farm, its strategy, management and economy: High-productive cattle, for example, require different infrastructure, housing conditions, forage supply and work processes than low-productive cattle. The productivity and thereby the requirements of breeds influence farmers' financial and labour input and cattle's output. Despite these obvious differences among cattle breeds, agronomists paid little attention to the impact breeds have on the grassland they graze. Discussions with farmers reporting different impact on plant species composition gave the impetus to analyse differences between high- and low-productive cattle breeds. The objective of this thesis was to analyse the breed-specific interactions of cattle and vegetation and to estimate the long-term effect of different breeds on plant species composition.

The thesis presented here concentrates on the grasslands of Central Europe and on the situation in the Swiss Alps and Prealps in particular, although many interactions of cattle and vegetation are universal and not bound to a certain region or country (Díaz et al., 2007). The region was chosen, because it still offered a reasonable number of semi-natural and extensively managed permanent grasslands. Nowadays, such farmland is mainly forced out of favourable areas of the lowlands and replaced by high-productive, sown grasslands or arable land (Poschlod, 2017). Permanent grasslands, which were of interest for this thesis, remain in mountainous and alpine regions. Switzerland still has a high share of permanent pastures, especially in the montane and the (sub-)alpine zone, and a long tradition of cattle farming (Mathieu et al., 2016). More than 70 % of the Swiss, agriculturally used land is covered by permanent grassland, including 31 % alpine summer pastures (Lüscher et al., 2019). In total, one third of Swiss territory is covered by pastures or meadows (Bosshard, 2016). Thereby, Switzerland perfectly met the requirements to conduct this study.

In the following, the term "alpine pasture" will not be used in a strict geobotanical sense as the zone between the natural tree line and the vegetation-free snow zone (Körner, 2003; Szerencsits, 2012). For practical reasons, it is used in a broader sense of nutrient-poor, marginal, open grasslands in the montane, sub-alpine and alpine zone. These are strongly influenced by elevation and associated factors such as low annual mean temperature, massive temperature fluctuations, long-lasting snow-cover, short vegetation period and intense solar radiation (Mertz, 2017).

All plant species mentioned exemplarily in the following were found on the pastures analysed for this thesis. The botanical nomenclature was obtained from Flora Helvetica (Lauber et al., 2018).

2 General introduction: About grasslands and herbivores

2.1 Impact of cattle on pasture vegetation

Semi-natural grasslands are the most diverse habitats in Europe. No other vegetation community hosts more plant species on one square meter (up to 89 according to Wilson et al., 2012) and many invertebrates rely on open grasslands (Lachat et al., 2010; Schneider and Walter, 2001). Hence, they play an essential role in biodiversity conservation (Huguenin-Elie et al., 2018; Mariotte and Kardol, 2014). Thereby, they provide productive, regulating, supporting and cultural ecosystem services for human well-being (Díaz et al., 2006; Rodríguez-Ortega et al., 2014).

The plant species composition and richness of grasslands is influenced by abiotic factors like temperature, precipitation, pH value, nutrient supply and their interactions. In contrast to meadows, the ecological niches of pastures are fundamentally influenced and thereby formed by the herbivores that graze it. In addition to the abiotic factors, grazing is a major driver of plant species composition and its impact increases with the amount of disturbance. Grazing is, in turn, able to modify other ecological factors like microclimate, pH value, light and soil nutrient content (Austin, 1986). Plant species which are well fitted to the conditions created by cattle or other grazers, become more abundant within the community. Vegetation response to grazing is well correlated with certain plant characteristics, so called traits (Cingolani et al., 2005; Díaz et al., 2007), on which this thesis focused.

Grazing is an entire complex of actions executed by herbivores. Among these are defoliation, selective foraging, trampling, nutrient translocation and diaspore dispersal. All these actions influence and shape pasture vegetation as they promote certain plant traits (**Figures 2.1 and 2.2**). Additionally, their impact depends on the date, frequency and duration of (first) grazing and the stocking density.

Grazing promotes fast-growing plant species

Cattle remove biomass. Vegetation regularly grazed by cattle or other herbivores, is dominated by fast-growing plant species with a short life cycle. They are in a better position to regenerate cropped stems, leaves, flowers and seeds. Fast-growing annuals (e.g. *Poa annua* L., *Capsella bursa-pastoris* (L.) MEDIK.) are more dominant on pastures than slow-growing perennials, as a global synthesis proved (Díaz et al., 2007). In addition, there is an advantage of early bloomers (e.g. *Bellis perennis* (L.), *Crocus albiflorus* Kit., *Primula veris* L., *Ranunculus ficaria* L.) which complete (most of) their life cycle before the first grazing in spring. Similarly, late bloomers can grow undisturbed after last grazing in autumn, like *Colchicum autumnale* L. which is additionally protected by highly toxic colchicum (see 1.3.).

Grazing promotes short plant species

Cattle forage what they are able to reach. Plant height is the most important limit of grazing. Cattle normally graze with their tongue: the tongue wraps and grasps the forage plants and plucks them relatively far above the ground (according to personal inspection up to 10 cm), whereas sheep, goats, horses, deer and fallow deer can forage much closer to the ground, as they pluck the plants with their lips. Subsequently, tall and erect grasses and herbs are damaged more than short and prostrate ones, which are promoted indirectly (Cingolani et al., 2005; Díaz et al., 2001). Prostrate plants are harder to reach for cattle's tongues. Thus, many species frequently growing on cattle pastures carry the creeping habitus in the epitheton of their scientific names (lat. *repere* = to creep; e.g. *Elymus repens* (L.) GOULD, *Potentilla reptans* L., *Ranunculus repens* L., *Trifolium repens* L.).

An exception of this rule are adult trees. Their leaves are out of cattle's mouth range and consequently cannot be foraged. However, under appropriate stocking, most woody plants are destroyed already in the seedling stage – either by foraging or by trampling.

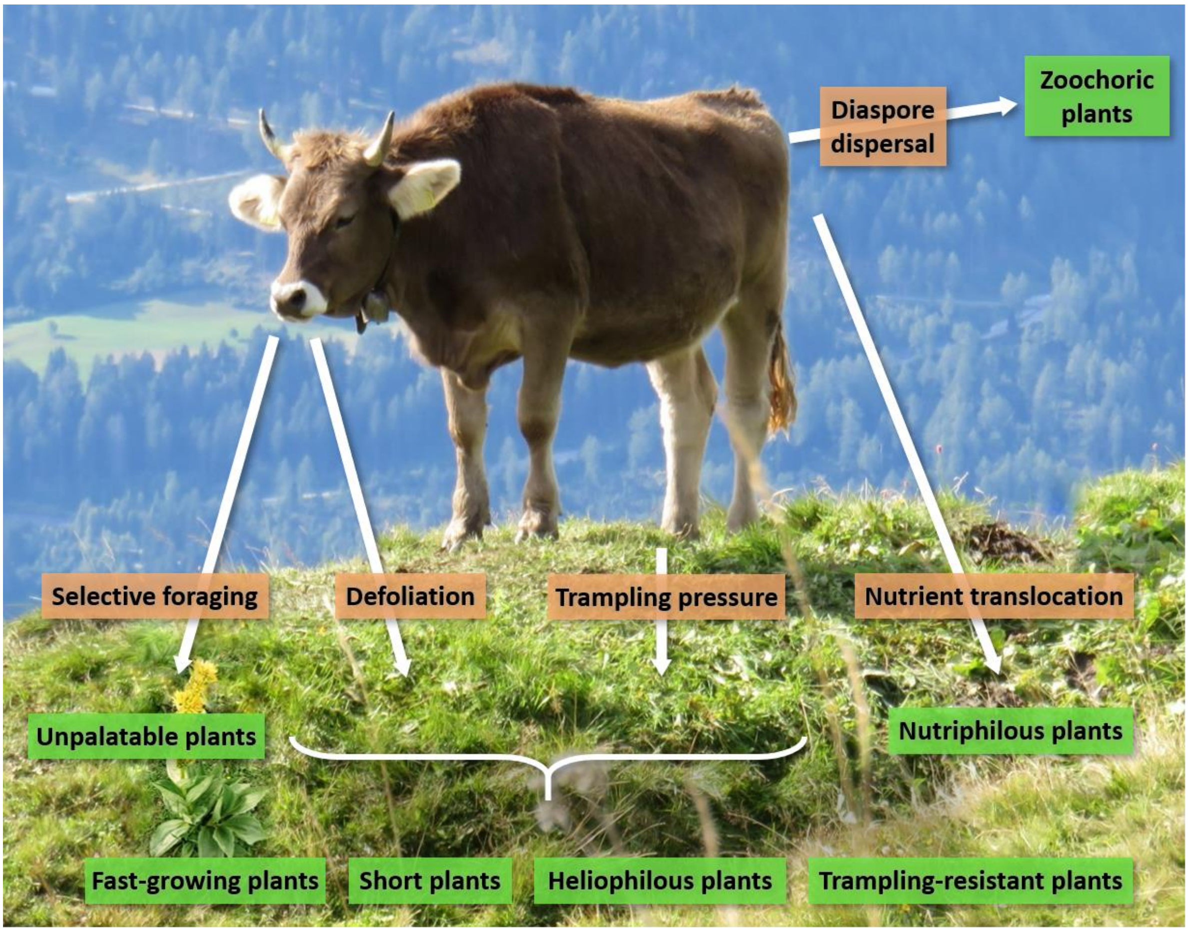


Figure 2.1 | Schematic illustration of cattle actions on pastures (orange) and the plant traits favoured by these actions (green).

Grazing promotes unpalatable plant species

If herbivores removed biomass evenly, plant species composition of pastures would hardly differ from meadows. However, in contrast to mechanical defoliation by mowing, which does not discriminate among plant species, cattle and other herbivores forage selectively. Plant species avoided by cattle have a competitive advantage over plants regularly foraged. Therefore, unpalatable plants become more abundant in grazing systems with long herbivory history (Díaz et al., 2007) and can be agronomically problematic if they overgrow desired forage plants. In other words: Grazing favours what is not favoured by grazers. There are different aspects that influence plant palatability for cattle (**Table 2.1**).

Table 2.1 | Overview of plant traits which reduce palatability for cattle.

Trait	**Specification**	**Example for unpalatable species**
Leaf traits	Specific leaf area	*Juniperus communis* L. *Calluna vulgaris* (L.) HULL *Deschampsia cespitosa* (L.) P. BEAUV.
	Leaf dry matter content	*Rhododendron ferrugineum* L. *Carex nigra* (L.) REICHARD *Carex pallescens* L.
Nutrient content	Ratio of carbon to nitrogen	*Nardus stricta* L. *Festuca ovina* L. *Vaccinium vitis-idaea* L.
	Content of phosphor or minerals	*Antennaria dioica* (L.) GAERTN. *Luzula sudetica* (WILLD.) SCHULT. *Rhinanthus minor* L.
Chemical defence mechanisms	Toxins	*Aconitum napellus* L. (alkaloid aconite)
	Bitter substances	*Gentiana lutea* L. (gentianopicrin)
	Acids	*Rumex acetosa* L. (oxalic acid)
	Ethereal oils	*Mentha longifolia* (L.) HUDS.
Physical defence mechanisms	Woodiness	Trees and (dwarf) shrubs
	Thorns	*Crataegus monogyna* JACQ.
	Spines	*Rosa canina* L.
	Prickled leaves	*Cirsium acaule* SCOP.
	Stinging hairs	*Urtica dioica* L.
	Dense hairs	*Hieracium pilosella* L.

Roughly spoken, cattle prefer soft, broad and thin leaves, easy to crop, with high water, nitrogen and phosphor content and without any defence mechanisms, whereas small, hard, thick, leathery leaves with high tensile strength, high fibre content or effective defence mechanisms are avoided (Cingolani et al., 2005; Díaz et al., 2001). The higher the stocking density on a pasture, the less cattle are able to make a decision on forage plants (WallisDeVries et al., 1999). In intensively managed rotational systems, the impact of grazing is similar to mowing. But on continuously grazed grasslands managed less intensively, such as extensive alpine pastures, herbivores' forage decisions are among the most important ecological factors. *Deschampsia caespitosa* (L.) P. BEAUV., for example, can build obstructive tufts which replace better forage plants on low-intensively managed pastures, but nearly disappears under high grazing pressure (Briemle et al., 2002).

Grazing promotes trampling-resistant plant species

Cattle impose physical pressure by walking, standing or lying on plants. Plants which are not able to deal with this force will be diminished on pastures. Subsequently, plants that are adapted to trampling have an ecological advantage and become the more dominant the higher the trampling impact is (Lezama and Paruelo, 2016). There are numerous strategies to cope with trampling: Short plants with caespitose, matted or rosette architecture (e.g. *Juncus effuses* L., *Polygonum aviculare* L., *Plantago major* L.) and with elastic tissue are less damaged than tall, erected plants. Prostrate or stoloniferous species with rooting stems or stolons can regrow from intact parts after trampling (Cole, 1995; Díaz et al., 2007). Plants which are able to reproduce vegetatively can disperse without seed production and save time before being trampled. Species with high regenerative capacity rebuild damaged parts fast. Early bloomers avoid being trampled by finishing their life cycle before the first grazing in spring. Among shrubs, those species with elastic branches (e.g. *Vaccinium myrtillus* L., *Vaccinium vitis-idaea* L., *Helianthemum nummularium* (L.) MILL.) are promoted (Briemle et al., 2002). Trampling pressure densifies the soil, decreases microbial activities and nutrient turnover (Kissling et al., 2009). Thus, plants which are able to deal with these conditions are promoted.

The impact of trampling on vegetation composition depends on its intensity and frequency. In areas of highest trampling pressure such as paths and resting places, ruderal plant species (e.g. *Chenopodium bonus-henricus* L., *Aegopodium podagraria* L., *Capsella bursa-pastoris* (L.) MEDIK.) benefit from open soil for germination (Stančić et al., 2008). Less trampling pressure goes along with higher plant species richness (Jägerbrand and Alatalo, 2015; Pickering and Growcock, 2009).

Grazing promotes nutriphilous plant species adapted to high nutritive supply

Cattle do not use the space of the pasture evenly. During grazing, cattle visit a much higher share of the pasture than during resting or ruminating, which are restricted to a few flat and shady places only (Homburger et al., 2015). That means, that they remove nutrients all over the pasture, but excrete them mainly on a small area. Subsequently, most resting places are highly eutrophicated. Plant species that can make use of the high nutritive supply most effectively (e.g. *Plantago major* L., *Rumex acetosa* L., *Anthriscus Sylvestris* (L.) HOFFM., *Heracleum sphondylium* L.) overgrow less specialised plants and decrease biodiversity.

Grazing promotes heliophilous plant species and changes the microclimate

In addition to the direct effects of herbivores on vegetation, there are indirect impacts. Grazing and trampling especially destroy tall plants. After removal of these, sunlight reaches plants which had been shadowed before. Thereby, grazing cattle create an ecological niche for light demanding plant species in the understory (e.g. *Helianthemum alpestre* (JACQ.) DC., *Euphrasia minima* SCHLEICH., *Poa supina* SCHRAD.). The patchiness of light availability is a major driver of species richness of pastures (Borer et al., 2014; Grieme, 1979).

Furthermore, the removal of biomass changes the microclimate within the vegetation, because the sward becomes less dense, which results in higher thermal loss, larger temperature fluctuation and increasing evaporation. Species that are able to deal with these conditions have a competitive advantage and become more dominant on pastures (e.g. *Ranunculus acris* L., *Trifolium montanum* L., *Sesleria caerulea* (L.) ARD.).

Grazing promotes zoochoric plant species

Finally, some plant species profit from livestock as a dispersal vector. Because the diaspores of *endo*zoochoric plants are able to survive foraging and digestion, they are spread within the faeces of herbivores. The diaspores of *epi*zoochoric species (e.g. *Arctium lappa* L., *Galium aparine* L., *Geum urbanum* L.) are transported by attachment to animals' fur. Nowadays, the number of animals grazing outdoors decreases as livestock husbandry is more and more reallocated into stables, and migratory herding and transhumance become less important. Thereby, remote habitats lose an important connection and the biotope network is weakened (Poschlod et al., 1996). Zoochoric species miss their main dispersal vector and subsequently, many of them are in current decline (Ozinga et al., 2008; Poschlod et al., 1998).

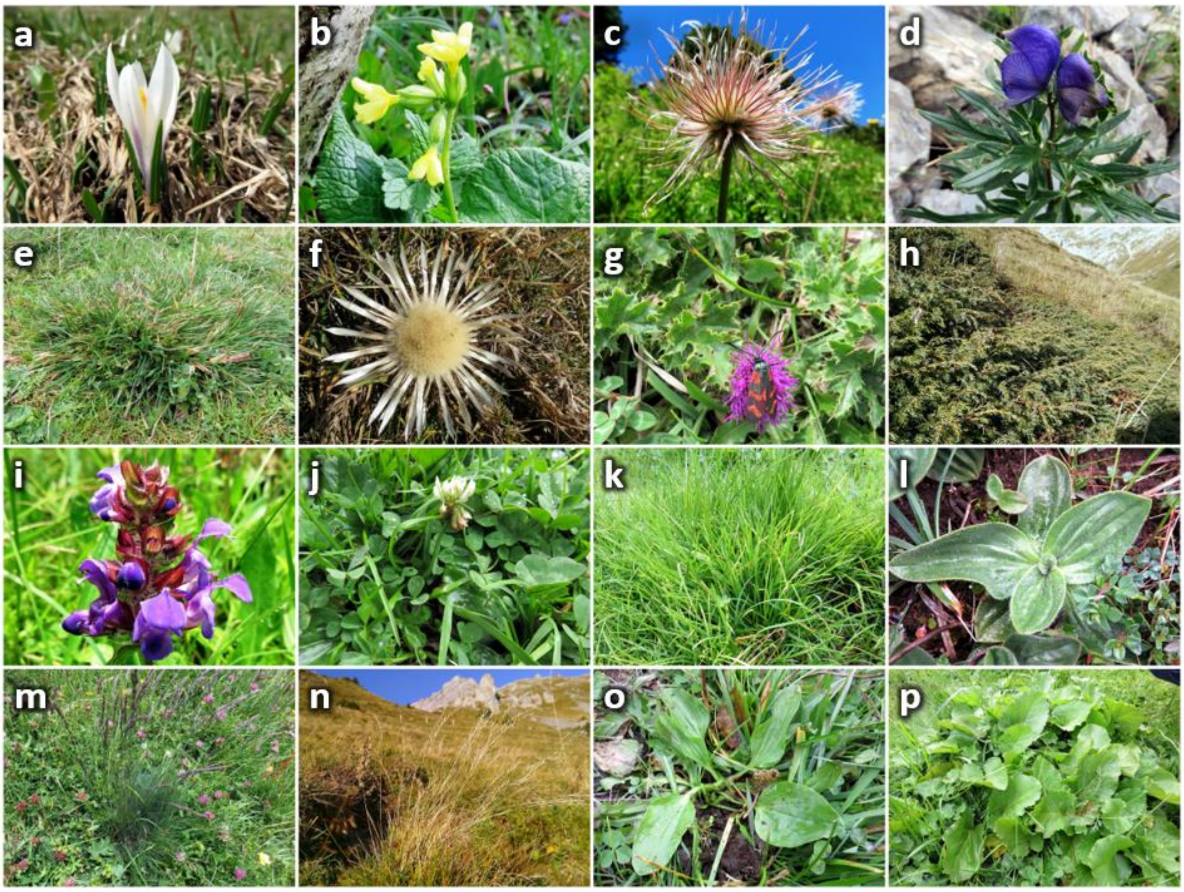


Figure 2.2 | Exemplary plant species adapted to grazing on alpine pastures of the study area in the Swiss Alps. On pastures there is a competitive advantage of early bloomers (**a** *Crocus albiflorus* KIT., **b** *Primula veris* L.), zoochoric species (**c** *Pulsatilla alpina* (L.) DELARBRE), plants that are unpalatable because of chemical defence mechanisms, such as toxins (**d** *Aconitum napellus* L.), because of unattractive structure, such as rough, hard and thick leaves with high tensile strength (**e** *Deschampsia caespitosa* (L.) P. BEAUV.), because of physical defence mechanisms (**f** *Carlina acaulis* L., **g** *Cirsium acaule* SCOP., **h** *Juniperus communis* L.), species which are trampling resistant because of creeping habitus and rooting stolons (**i** *Prunella vulgaris* L., **j** *Trifolium repens* L.), because of short height and high regenerative capacity (**k** *Poa supina* SCHRAD.), because of rosette (**l** *Plantago media* L.) or caespitose architecture (**m** *Festuca ovina* L.), species which are avoided by cattle because of high fibre and low nutrient content (**n** *Nardus stricta* L.) and finally, fast-growing nitrophilous species promoted by eutrophication (**o** *Plantago major* L., **p** *Rumex alpinus* L.).

Relevance for the thesis

The composition of pasture vegetation is importantly influenced by herbivores' (selective) foraging, trampling, nutrient translocation and diaspore dispersal. The interaction of grazing animals and growing plants is a finely balanced relationship.

What are the long-term effects of cattle grazing on pasture vegetation?

2.2 Adapting vegetation to human needs: History and structural change of grassland in Central Europe

2.2.1 The origin of semi-natural grasslands

Central Europe is covered by a cultural landscape and there is almost no habitat unaffected by humans. One of the most far-reaching processes of landscape transformation was the introduction of ruminant livestock into natural ecosystems (Veen et al., 2009).

At the end of the Würm glaciation, the last glacial period 12 000 years ago, temperature increased and glaciers moved back. Hazelnut forests emerged on the defrosted land and were successively replaced by birch, pine and finally beech and oak trees (Mathieu et al., 2016). It is debated whether large, wild herbivores, such as mammoth, deer, wild horse and aurochs, already created open glades within dense woodlands (Ellenberg and Leuschner, 2010; Vera, 2000). Either way, Central Europe was mostly covered by forest for millennia.

In the Neolithic about 7000 years ago, humans, who were hunters with little influence on vegetation until then, settled down. Ruminant livestock, mainly goats (*Capra aegagrus hircus*), sheep (*Ovis aries*) and cattle (*Bos taurus*), which had already been domesticated about 4000 years earlier in the Fertile Crescent of the Near East, accompanied the settlers. Thus, they made the woodland agriculturally utilisable for humans (Jochim, 2008; Poschlod, 2017). The forests around the settlements were opened up by livestock foraging leaves, foliage and seedlings of trees as well as the understory. Humans, who cut and dried foliated branches as winter fodder and likely used fire for forest clearance for pastoral activities contributed to this development (Thierry et al., 2009). In the Alps, natural alpine grassland was available and used for summer farming, so-called transhumance. By grazing activities and woodcutting for cheese dairies, the natural tree line was lowered (Ellenberg and Leuschner, 2010; Körner, 2003).

Subsequently, a multitude of different extensive, semi-natural, anthropo-zoogenic, open grasslands evolved under humans’ influence. The novel habitats hosted a broad spectrum of plant and animal species, which built totally new ecological communities. The new habitats were populated by (1) plant species migrating from the few naturally unforested local habitats such as fens, alluvial zones, dry grassland and alpine matts above the natural tree line (Dierschke and Briemle, 2002; Klötzli et al., 2010); (2) plant species migrating from distant vegetation zones with higher share of open grasslands, such as the Mediterranean region or salt marshes in coastal areas; some of these species adapted to the novel conditions, for example by polyploidisation (Landolt, 1970); (3) plant species newly developed (e.g. *Festuca ovina* L., *Alchemilla vulgaris* L.) or formed by crossing of two native species (e.g. *Lotus corniculatus* L. = *L. alpinus* (DC.) RAMOND × *L. tenuis* WILLD., *Trifolium pratense* L. = *Trifolium pratense nivale* (W.D.J. KOCH) CES. × *T. diffusum* EHRH.; (Schreiber et al., 2009).

In the Bronze Age (1800-800 BC) the scythe was developed, but mainly used for grain crop. In the Roman times the scythe was widely introduced for mowing (Leube, 2003). Thereby, open grasslands were expanded and perpetuated (Ellenberg and Leuschner, 2010). Romans also invented the targeted, selective breeding of livestock and crop plants. Subsequently, the productivity of both increased (Dierschke and Briemle, 2002).

Since the Neolithic, forests, pastures, meadows and arable land had been seen as a permeable continuum of agricultural use. However, in the Middle Ages they were more and more differentiated in clearly distinct units. Since then, forest pastures were successively given up and finally disappeared in modern times (with some noteworthy exceptions in alpine regions where cattle still graze woodlands today, like the chestnut forests in the Ticino). Medieval farmers increased productivity of agricultural land by sowing nitrogen fixating legumes, mainly *Trifolium pratense* L. (Poschlod, 2017). Thus, the nutrient-richer fodder allowed the breeding of larger animals and to increase the number of livestock. In the Late Middle Ages, the higher fodder requirements and massive forest clearance for charcoal production led to the greatest extent of open grasslands ever (Schreiber et al., 2009).

2.2.2 Structural change: Intensification and industrialisation of favourable grasslands

Ruminant farming and pastoral land use became less important in the Modern Era. The grasslands of Central Europe, formed over ages, were deeply transformed by the technical achievements of the industrialisation. Mechanisation, herbicides, drainage of wet habitats and fens, irrigation of dry habitats, sowing of improved, high-productive varieties of forage plants, increasing stocking density, land consolidation and removal of small-scale structure created high-productive, uniform and species-poor grasslands (Dierschke and Briemle, 2002; Ewald and Klaus, 2010; Isselstein et al., 2005; Sabatier et al., 2015).

Moreover, the invention of mineral fertilizer (e.g. Thomas process in 1876, Haber-Bosch reaction in 1913, Odda process in 1927) led to an intensive application of nitrogen, phosphorus and potassium. This brought a decisive change in the productivity and the biodiversity of agricultural land – unfortunately in opposite directions: Fertilisation and high nutrient availability are among the most important drivers of species loss (Humbert et al., 2016; Vitousek et al., 1997), because a few specialised plant species adapted to high nutritive supply outcompete the multitude of less adapted plant species.

Moreover, industrialisation caused a decreasing energy efficiency of agriculture and a poor ratio of energy input and output. While ancient farmers invested nothing more than the power of their draft animals and their own, today, cultivating one hectare of agricultural land in Switzerland consumes about 1400 l diesel equivalents (Latsch and Anken, 2015). The current agricultural system is more effective than ever in regard to the output, but for one food kilocalorie earned by industrialised Swiss agriculture, 2.5 kilocalories of external energy are invested (Bosshard, 2016). The poor efficiency may, inter alia, be reinforced by modern livestock breeds, which require nutrient-rich fodder and cannot deal with nutrient-poor grassland. On the other hand, low-intensive, grassland-based agricultural systems could be an efficient, cost-effective and sustainable way of management (Gazzarin et al., 2011; Goliński et al., 2008; Thomet et al., 2002).

However, in grasslands, the increasing productivity came at the price of species and habitat loss: Most nutrient-poor pastures and meadows were intensified and transformed into more productive grassland. From 1960 to the end of the last millennium, the pasture and meadow yield increased by 60 % (Dierschke and Briemle, 2002), but plant species adapted to nutrient-poor grasslands declined significantly (Peter et al., 2009), because they lost their habitat: 90 % of nutrient-poor calcareous grasslands (*Meso*- or *Xerobrometum*) and 95 % of nutrient-poor, dry sand grasslands in Southern Germany disappeared, as they depend on low-intensive management (Baumann et al., 2005; Poschlod et al., 1998).

Finally, the industrialisation implied a geographical segregation of arable and grassland-based farming: With modern transport systems, the cheap goods from the lowlands were brought into mountainous and alpine regions. Subsequently, arable farming became uneconomical in the mountain regions and subsistence farming was given up (Schreiber et al., 2009). Instead, grassland-based livestock production was intensified to supply the lowland population with meat and dairy products (Mathieu et al., 2016).

2.2.3 The other side of the coin: Abandonment of unfavourable grasslands

The majority of remaining valuable, species-rich grasslands nowadays is found in the montane and (sub-)alpine zone (Walter et al., 2013), but grassland-based farming was also intensified there in the last century. Relatively flat and fertile pastures and meadows, accessible by agricultural machines and easy to cultivate were intensified in mountain regions, similarly to arable land in the lowlands. But since the 1950s, there was (and still is) an opposite trend: Unfavourable, marginal land, which was too steep, wet, dry, rocky or remote to cultivate economically, was underused or even abandoned. Due to the decreasing stocking rate, the competitive conditions change. Grazing-adapted, stress-tolerant plant species are less promoted and tall plants get a competitive advantage. On the fallow land, open grasslands are successively replaced by tall forb communities, shrubs, pioneer forest and finally dense forest (Dierschke and Briemle, 2002). In Switzerland, the forest area has increased by 30 to 100 % in the last 150 years, depending on the region (Stöcklin et al., 2007). Although there is a temporary increase of diversity after the invention of shrubs, in the long term, the species richness of semi-natural grasslands disappears as the later succession stages are normally less diverse, especially at large scale, and rare species diminish first (Spiegelberger et al., 2006).

2.2.4 Legal situation

Agricultural subsidies of the European Union were linked to the production output since the Treaty of Rome 1957. They led to massive intensification and overproduction (Rodgers, 2004). The EU agricultural reform in 1992 brought a first departure from mass production, because subsidies now depended on the size of the cultivated area and additional support was paid for environmentally friendly management (Thomas et al., 2009). The aims were to reduce the negative effects of industrialised agriculture and to sustain the rare remaining species-rich habitats by making ecological responsible farming economically more lucrative. In 2005, a second agricultural reform established the “second pillar” that rewards, for example, biodiversity protection and organic farming. Thereby, habitat and species loss are slowed down but not stopped. The preservation of the remaining diverse grasslands is supported but not yet guaranteed (Hampicke, 2013).

In Switzerland, direct payments are linked to ecological management since 1996. The less intensively a site is managed, the higher the payments. In 2014, the European Union spent 387 € subsidies per hectare agricultural land, whereas Switzerland supported farmers with 3535 CHF (≈ 3000 €) per hectare and thereby created a larger financial scope to protect biodiverse, semi-natural habitats (Bosshard, 2016; Dietschi et al., 2007). Nevertheless, even in Switzerland the extinction of vulnerable habitats and species is going on.

Relevance for the thesis

The development of species-rich grasslands was an unintended by-product of traditional agriculture. Similarly, the loss of species richness is an unintended by-product of modern agriculture. The objective of nature conservation is to sustain the remaining valuable habitats, but it is faced with a double challenge: These habitats are threatened by increasing as well as decreasing management intensity.

To maintain the species richness of nutrient-poor, marginal grasslands, low-intensive but regular grazing or mowing is necessary. Under such management, only marginal investments are needed (e.g. no fertiliser, sowing, irrigation, herbicides). Therefore, costs are minimal, but the fodder produced on these pastures and meadows is of low quality and quantity. Modern high-yielding breeds are not able to fulfil their genetic potential under these challenging conditions.

Are there cattle breeds whose low requirements allow for an efficient use of nutrient-poor, marginal grasslands in order to sustain their species richness?

2.3 Adapting cattle to human needs: History and implications of breeding

2.3.1 History of breeding

The domestication of the aurochs (Beja-Pereira et al., 2006) and its adaptation to human needs over millennia formed the recent cattle breeds. Without the knowledge of heredity, ancient farmers unintentionally bred the first cattle by sorting out aggressive and tall animals to protect themselves. Thereby, the first domesticated cattle were bred towards ease of handling and small body size (Kretchmer and Fox, 1975; Price, 2002). Fertile individuals were favoured (Setchell, 1992). Apart from this early human artificial selection cattle had to survive under near-natural conditions and therefore, natural selection still defined cattle.

Improved grassland management and housing conditions reduced the impact of natural selection since the Roman Age (Poschlod, 2017). Regional breeds were slowly formed by mostly intuitive decisions and preferences of farmers and by adaptation to the local conditions. The formation of distinct breeds was enforced where natural borders like valleys (e.g. Simmental) or islands (e.g. Jersey) prevented the genetic exchange with external cattle. Anyway, for a long time, breeds were not seen as fixated classes but as a fluid continuum (Derry, 2015).

This changed in the 19th century, when breeding societies established herdbooks for single breeds. They aimed at creating a uniform, clearly defined type of cattle and at increasing certain characteristics (Bieleman, 2005). The idea of purebreeding was born. In order to choose the best performing cattle for reproduction, breeding societies applied structured artificial selection methodology. Thereby, former multiple-purpose breeds used for dairy, beef, leather and wool production and as draft animals were transformed into specialised single-purpose breeds.

In the late 19th and early 20th century, the breeding process, first implemented rather intuitively, was refined by a scientific fundament: The rediscovery of Mendel’s laws brought a basic understanding of the mechanisms behind heredity, the Darwinistic idea made clear that artificial selection works like natural selection and is able to alter characteristics of a population and finally, biometry explained the distribution of performance characteristics within breeds (Derry, 2015).

On the technical side, artificial insemination and freezing semen has increased the number of siblings and the spatial range of the best performing bulls. Subsequently, much more bulls could be sorted out and the breeding potential has increased in male cattle. Progeny tests enabled to estimate the genotypic quality of bulls and thereby, to breed more effectively toward desired characteristics (Fleming et al., 2019). For progeny tests, consequent documentation within the entire population was established, for example centralised milk recording (Derry, 2015).

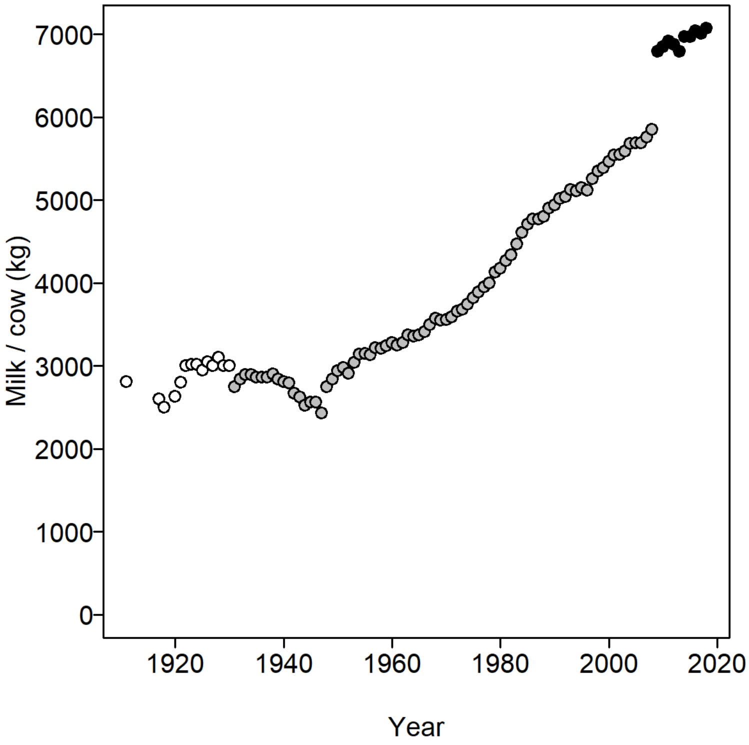
Other reproductive technologies like embryo transfer after multiple ovulation, cloning and transgenic animals never made a breakthrough in cattle, because they were too expensive or poorly accepted by consumers (Derry, 2015). Today, marker assisted selection enables to test for single alleles that code for hereditary diseases, for example. Furthermore, selection via DNA mapping and single-nucleotide polymorphism has the potential to revolutionize or even replace traditional selection via progeny testing (Brito et al., 2019).

2.3.2 Implications of breeding

Artificial selection has enormously increased productivity. The downside of this development is a decreasing genetic diversity and an increasing level of homozygosity (Fleming et al., 2019). The lower the genetic diversity, the lower is the ability to adapt to changing conditions and the higher is the risk of inbreeding and hereditary diseases (Oldenbroek, 2019). In 2005, 30 % of the American Holstein gen pool stemmed from only two bulls (Hansen et al., 2005). Modern high-productive breeds are closely related – not only within breeds, but also amongst breeds. However, traditional low-productive breeds like Highland cattle still differ genetically from other breeds significantly (Wiener et al., 2004).

The effect of production-oriented breeding focusing on only a few traits is most obvious in the development of milk yield of dairy cattle (**Figure 2.3**): Within one century, modern breeding and farming methods increased the average annual milk production per cow from less than 3000 kg in 1911 to more than 7000 kg in 2018 in Switzerland (data were gathered from all annual milk statistic reports of the Swiss farmers association between 1911 to 2018). Average cows of the most common and most productive dairy breed Holstein even produce more than 9000 kg annually (Holstein Association Switzerland, 2020) and thereby tripled the amount of milk produced 100 years ago. However, the increase of productivity came along with declining fertility, longevity and health status of cattle (Oltenacu and Broom, 2010).

Figure 2.3 | Average annual milk production per cow in Switzerland in the last century. Data were gathered from the Swiss annual milk statistic reports in the period from 1911 to 2018. Until 1931 (white dots), the milk production was estimated without considering the lower milk production on alpine summer farms. Therefore, estimates are lower after correction (grey dots). Since 2009 (black dots), the values represent dairy cows only and exclude suckler cows, resulting in an abrupt rise. Except for both (post-)war periods, during which productivity stagnated or declined, milk production per cow has increased continuously.



In beef cattle (**Figure 2.4**), on which this thesis focuses, the breeders put less emphasis on the milk yield, but on daily weight gain, muscle characteristics and carcass weight. Thereby, a specialised beef type was formed. Generally spoken, beef cattle are shorter, but heavier and more muscular than dairy cattle.

Although breeding improved the production output of many breeds, some breeds remained nearly untouched by the developments of the last century and were neither bred towards high milk yield nor towards enhanced beef production. Especially the traditional British breeds Dexter, Highland cattle and Galloway, which were formed under harsh environmental conditions, preserved their original character. Unfortunately, the breeding development of beef cattle is not as well documented as the milk yield increase of dairy cattle, but comparing recent production-oriented, intensified breeds on the one with traditional, hardly modified breeds on the other hand, clearly points out that breeding transformed beef cattle considerably:

Production-oriented beef breeds like Charolais, Blond d'Aquitaine or the double-muscled Piemontese are substantially heavier (**Figure 2.5a**) and taller (**Figure 2.5b**) than the traditional breeds. For the breeding parameters weight and height, there is a continuum from light to heavy and from small to tall breeds reflecting the level of breeding intensity. In other parameters, traditional breeds are clearly distinct from more productive breeds: Calves of production-oriented breeds have a considerably higher birth weight (**Figure 2.5c**) and grow much faster (**Figure 2.5d**). On the contrary, in intensive fattening systems traditional breeds like Highland cattle perform poorly (Albertí et al., 2008). **Figure 2.6** displays the close, positive correlation of typical productivity parameters (weight, height, birth weight and daily weight gain; $r^2 = 0.79\text{-}0.94$), which were improved simultaneously by breeding, and highlights the exceptional position of traditional Highland cattle, the overarching model breed of this thesis. The age of first calving (**Figure 2.5e**) and the calving interval (**Figure 2.5f**) – two economically most important factors – are particularly large (i.e. economically disadvantageous) in Highland cattle.

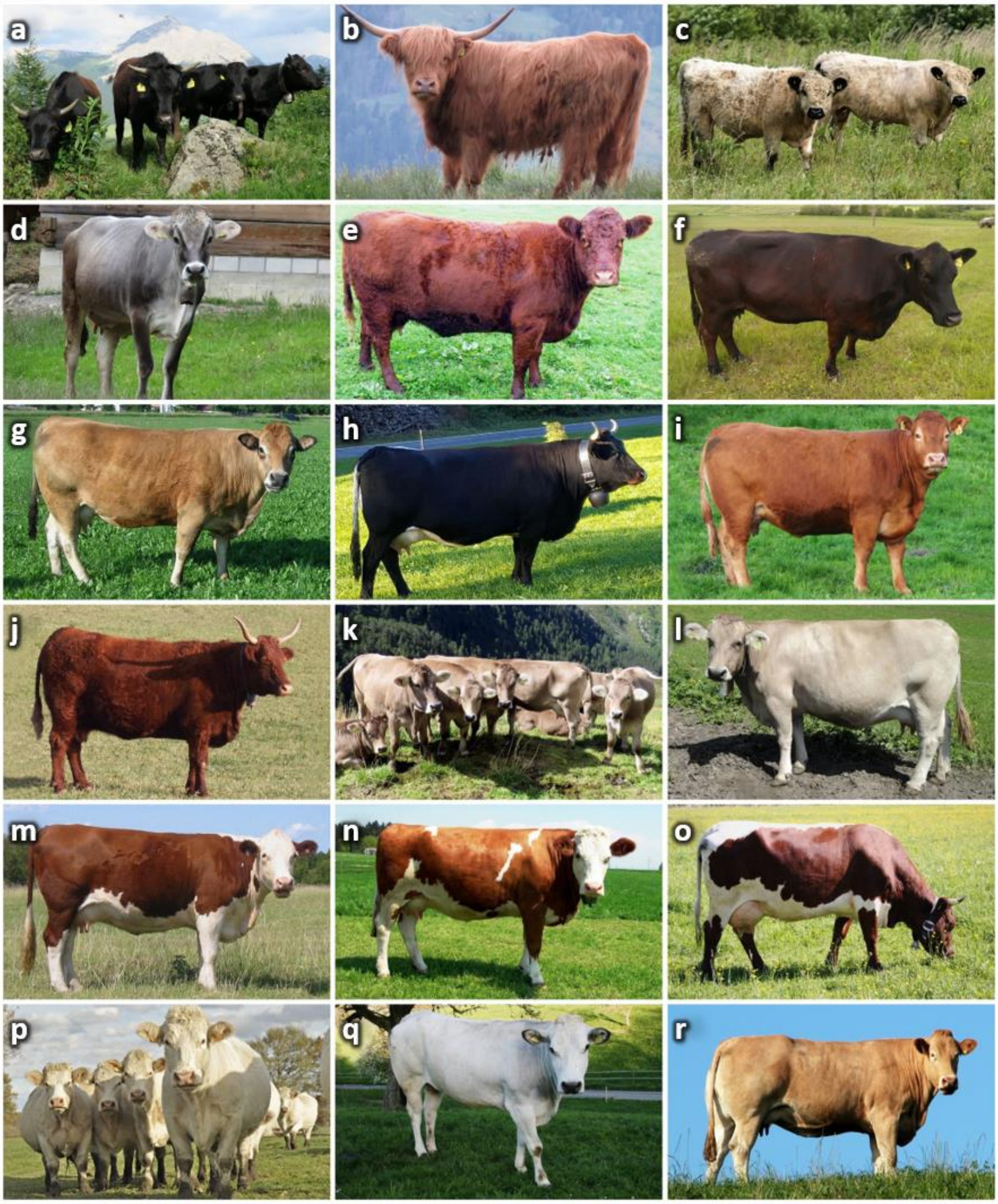


Figure 2.4 | Images of the 17 most common beef cattle breeds in Switzerland, increasingly arranged according to cows' adult body weight: **a** Dexter, **b** Highland cattle (the overarching model breed of this thesis, **c** Galloway, **d** Grauvieh, **e** Luing, **f** Angus, **g** Aubrac, **h** Tux-Zillertal, **i** Limousin, **j** Salers, **l** Braunvieh, **m** Hereford, **n** Simmental, **o** Pinzgauer, **p** Charolais, **q** Piemontese, **r** Blonde d'Aquitaine. Data are presented for all breeds affiliated in the Swiss suckler cow association with more than 100 cows registered in the herd book (Mutterkuh Schweiz, 2020). For the sake of completeness, Original Braunvieh (a less intensified sub-population of high-productive Braunvieh) was added to the display (**k**), as it was part of the study on Alp Weissenstein.

Photos by M. Schneider (a), C. Pauler (b,d,f,k), K. Büscher (c), Mutterkuh.ch (e,g-o,q,r), C. de France (p).

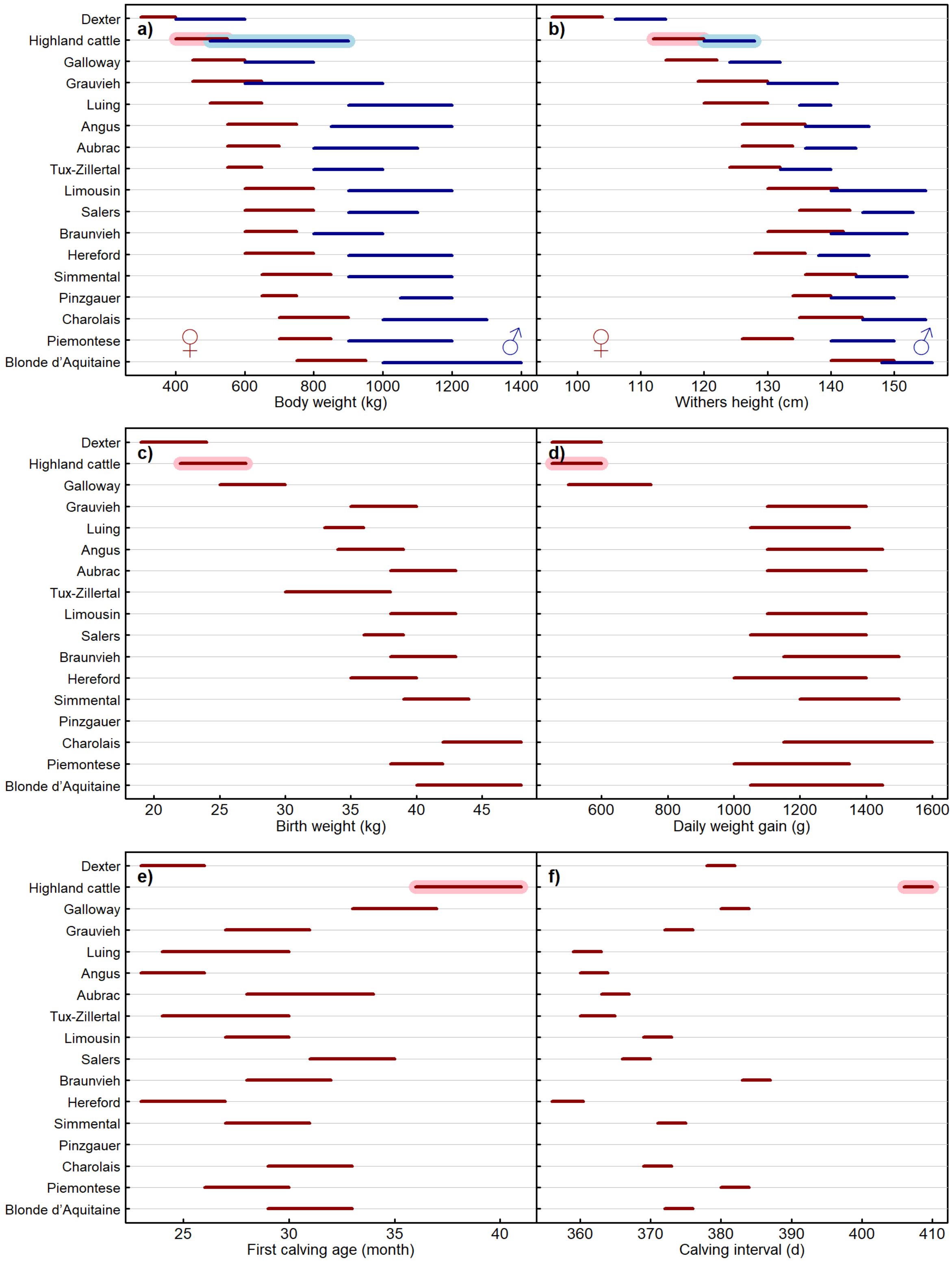


Figure 2.5 | Breeding parameters of the 17 most common beef cattle breeds in Switzerland as defined by the breeding associations: **a** body weight in kg and **b** height at withers in cm of cows (red) and bulls (blue), **c** calves birth weight in kg, **d** the daily weight gain until the slaughter in g, **e** the age of first calving in month and **f** the interval of calving in days. Data are presented for all breeds affiliated in the Swiss suckler cow association with more than 100 cows registered in the herd book. Breeds are ordered by cows' minimum body weight (Mutterkuh Schweiz, 2020). Values of Highland cattle, the overarching model breed of this thesis, are highlighted.

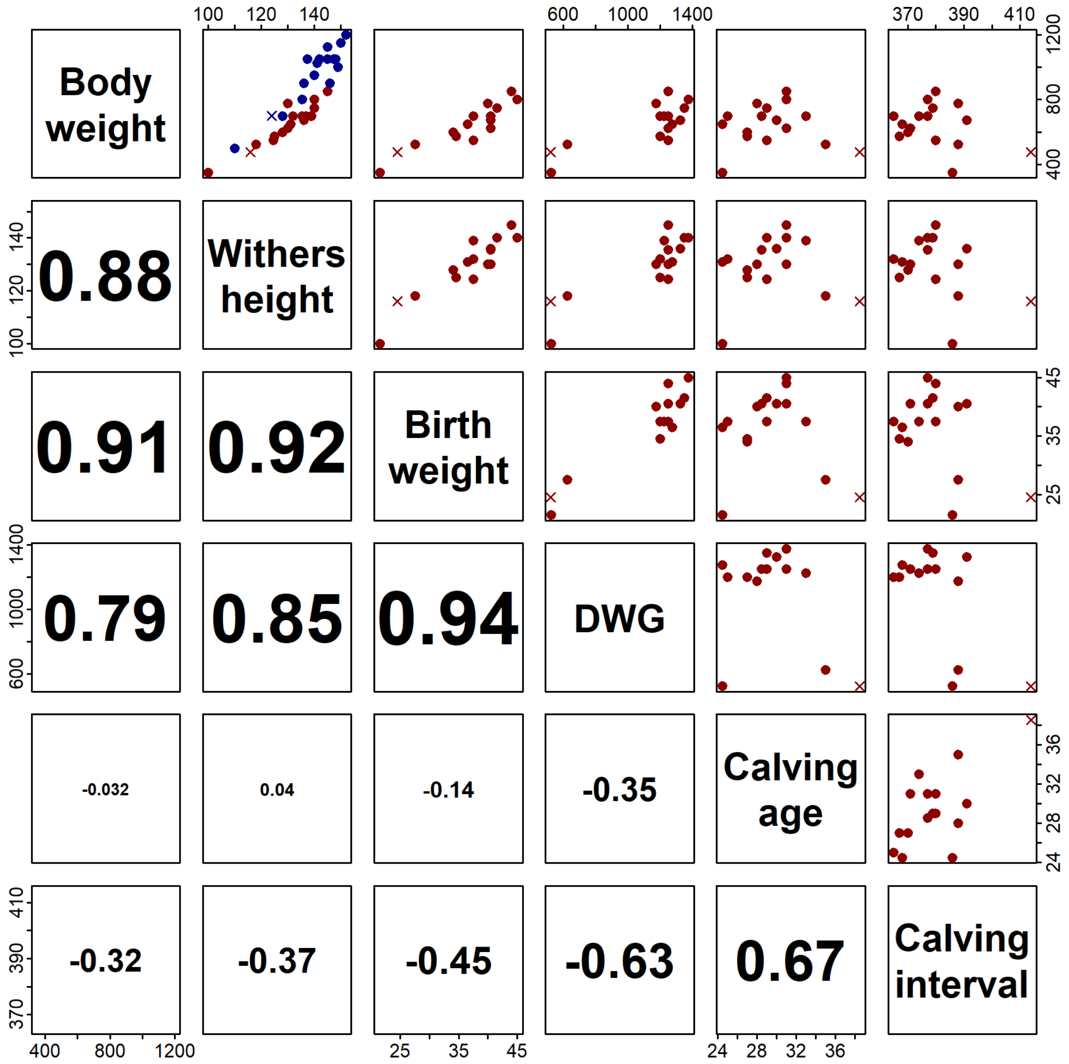


Figure 2.6 | Pearson correlation coefficients (lower triangle) and scatterplots (upper triangle) for eight averaged breeding parameters as defined by the breeding associations (Mutterkuh Schweiz, 2020): body weight in kg and height at withers in cm of cows (red) and bulls (blue), calves birth weight in kg, the daily weight gain until the slaughter (DWG) in g, the age of first calving in month and the interval of calving in days. Highland cattle, the overarching model breed of this thesis, are depicted by ×, other breeds by dots. The font size is scaled by the absolute values of the correlation coefficients.

Considering the poor productive performance of traditional breeds, it is not surprising that they were outcompeted and replaced by modern breeds with superior productivity. Therefore, many traditional breeds are endangered nowadays (FAO, 2015) or already extinct (e.g. Oberpfälzer Rotvieh and Freiburger Rind). It is remarkable that, on the other hand, some low-productive breeds like Galloway or Highland cattle are still in use and even wide-spread over the world. They are appreciated for their robustness and undemanding requirements.

Relevance for the thesis

Recent cattle breeds cover a broad spectrum of productivity. Their outward appearance and performance were modified by breeding. Many breeding societies intended to alter certain productivity traits (e.g. milk yield or body weight) but gave little attention to potentially co-evolving characteristics. Some of these overlooked traits (e.g. fertility, health and longevity) came back in mind in the 1990s when, despite an increasing annual productivity, the lifetime production and economic return of cows decreased (Fleming et al., 2019). Other potentially co-evolved characteristics stayed still unnoticed: An elevated nutrient demand, for example, allowing for fast growth, has the potential to influence foraging behaviour on pastures as well as movement behaviour. Much emphasis was put on increasing body mass, but little attention was paid to the claws on which this mass burdens and the question if their size increased to the same extend. These changes have the potential to affect the long-lasting and finely balanced interaction between grassland and grazing cattle.

Did the changes, that intentionally formed modern cattle breeds, come along with unintended anatomical and behavioural modifications? If so, do high-productive cattle breed influence pasture compositions in different ways than low-productive breeds?

2.4 Outline

The thesis is organized in the temporal order in which results were generated and published: **Chapter 3** addresses the question, whether the composition and diversity of pasture vegetation in the long term depends on the productivity level of the cattle breed by which it is grazed. **Chapter 4** analyses the mechanisms of forage selection and how these mechanisms differ among breeds. **Chapter 5** traces back differences among individuals in anatomy, movement and foraging behaviour to the productivity level of their breed. Finally, **Chapter 6** evaluates the methodological challenges, points out overarching ecological consequences and highlights practical implication as well as open research questions.

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

This chapter has already been published as the following journal article:

Pauler, C.M., Isselstein, J., Braunbeck, T., Schneider, M.K., 2019. Influence of Highland and production-oriented cattle breeds on pasture vegetation: a pairwise assessment across broad environmental gradients. Agriculture, Ecosystems & Environment 284, 1–11. https://doi.org/10.1016/j.agee.2019.106585

The study was conducted, the data were analysed and text and figures were created by myself.

Abstract

1. 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.

2. 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 (SEM) were used for data analysis.

3. 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.

4. 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.

Keywords: biodiversity, grazing, Highland cattle, indicator value, pasture, structural equation model, vegetation

3.1 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 (Mutterkuh Schweiz, 2020).

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 and weigh 34 % less and their daily average weight gain is 60 % lower (Mutterkuh Schweiz, 2020). 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; Cole, 1995; Lezama and Paruelo, 2016). 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.

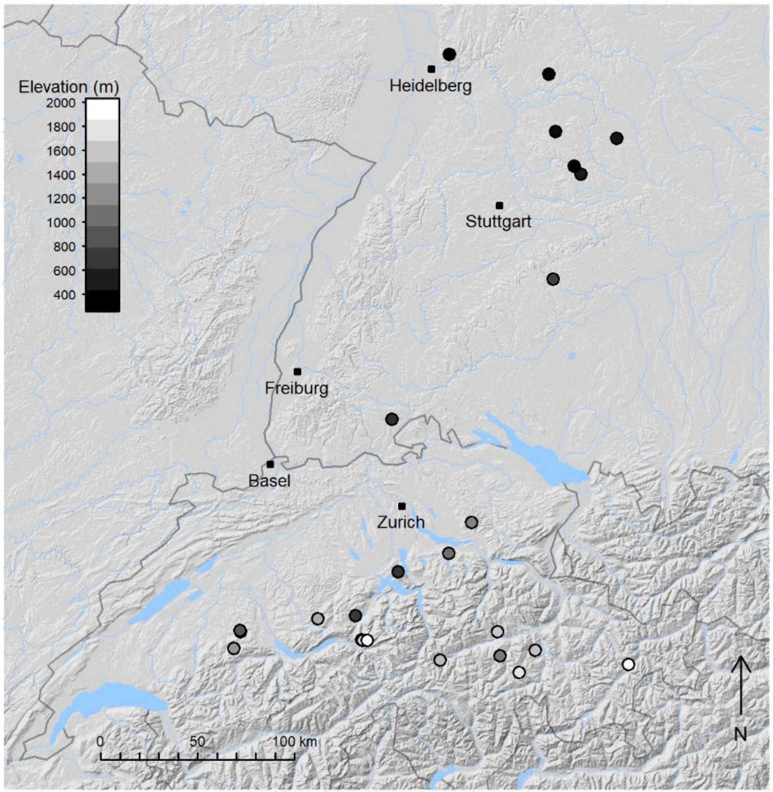
Several past studies compared pasture vegetation grazed by different livestock species, but only a few examined the effect of the breed. A comparison of commercial and traditional breeds of cattle and sheep during three years only found marginal effects of breed on sward structure (Dumont et al., 2007b) 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 compare 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 along broad environmental gradients Furthermore, grazing history was recorded to investigate effects of the duration of adaptation.

3.2 Material and methods

3.2.1 Study locations and site selection

Fifty paired pastures were studied at 25 locations ranging from mountain areas in Switzerland to lowlands in southern Germany (**Figure 3.1**). 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.



geodata © European Environment Agency, partly based on Copernicus data

Figure 3.1 | 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.

3.2.2 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.

3.2.3 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.

3.2.4 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 minutes 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).

3.2.5 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) framed animals.

3.2.6 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 & Verkuilen (2006). 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). 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 (**Figure S3.1**). 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 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).

3.3 Results

3.3.1 Site and management properties

The sample locations covered a broad gradient in site conditions (**Figure 3.2, a-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 S3.1**.

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 (**Figure 3.2a**) within a pair was 36 m (range: 0.5-143 m; standard deviation (SD): 34 m) and inclination (**Figure 3.2b**) 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 (**Figure 3.2c**) 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 (**Figure 3.2d**) in soil were about the same (+0.16 mg kg^{-1}, $p = 0.15$), P concentrations (**Figure 3.2e**) 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 (**Figure 3.2f**), only available at pasture scale, were higher on production-oriented breeds' pastures (+0.38 LU ha^{-1} yr^{-1}, $p = 0.03$).

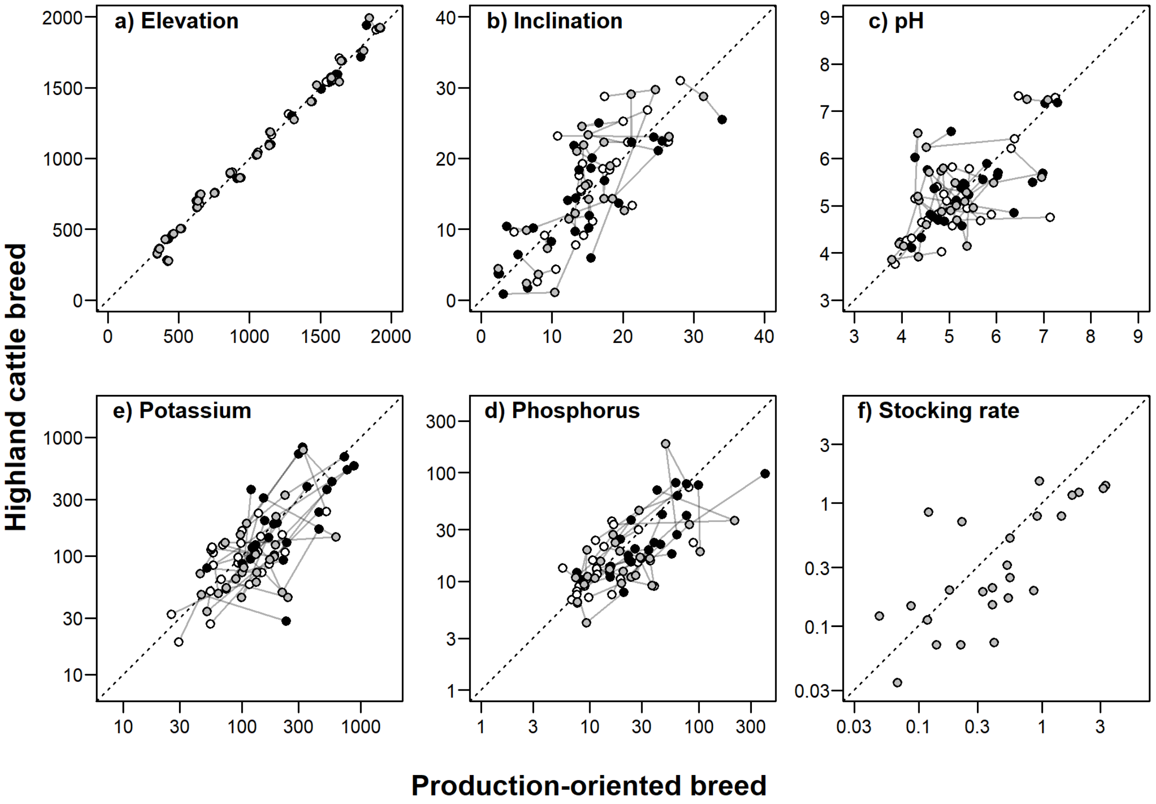


Figure 3.2 | Environmental location variables of paired pastures grazed by Highland cattle or production-oriented breeds: **a** elevation in m asl., **b** inclination in degree, **c** soil pH, **d** plant-available potassium and **e** phosphorus in mg kg^{-1} soil and **f** normalized stocking rate in livestock units ha^{-1} yr^{-1}. For each pasture, the three subplots with a high (black), medium (grey) and low intensity of grazing (white) are connected by a grey line.

3.3.2 Bodyweight of cattle breeds

Weight and weight-gain differed enormously between cattle breeds (**Figure 3.3**). 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.

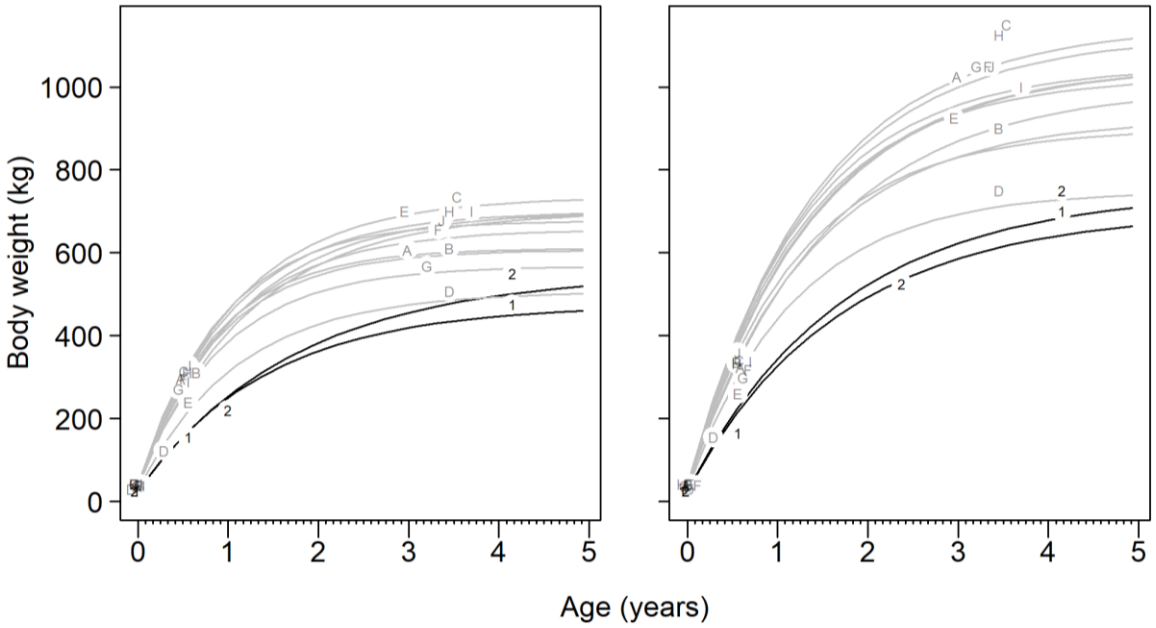


Figure 3.3 | Estimated age dependency of body weight of **a** female and **b** male animals of all cattle breeds involved in the study: 1 small-framed Highland cattle, 2 large-framed Highland cattle, A Angus, B Braunvieh and Original Braunvieh, C Charolais, D Hinterwaelder, E Holstein Friesian, F Limousin, G Luing, H Pinzgauer, I Salers, J Simmentaler. 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).

3.3.3 Vegetation indices

Plant species richness per subplot (alpha richness) was significantly different between breeds (**Figure 3.4a; Table 3.1**). 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 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 3.1**) and elevation ($p_{\chi^2} = 0.001$), but unaffected by mean soil P concentration or stocking rate. Pielou's evenness of species abundance (**Figure 3.4b**) 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 (**Figure 3.4c**). 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 (**Figure 3.4d**). Grazing and trampling indicator values were significantly higher on production-oriented breeds' pastures ($p_{\chi 2}$ = 0.0005 and 0.047, respectively) and significantly increased from the least to most frequented subplot ($p_{\chi 2} < 0.0001$). Both indicator values increased at higher stocking rate ($p_{\chi 2}$ = 0.08 and 0.044, respectively).

Additionally, pastures grazed by production-oriented breeds contained more bare ground than those grazed by Highland cattle ($p_{\chi 2}$ = 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 (**Figure 3.4e**) were not affected by breed ($p_{\chi 2}$ = 0.11). They depended mainly on elevation ($p_{\chi 2} < 0.0001$) and plant available phosphorus ($p_{\chi 2}$ = 0.003) and significantly differed between subplots ($p_{\chi 2} < 0.0001$).

The cover of epizoochoric plant species (**Figure 3.4f**) was higher in pastures grazed by Highland cattle ($p_{\chi 2}$ = 0.001) and increased with stocking rate ($p_{\chi 2}$ = 0.02).

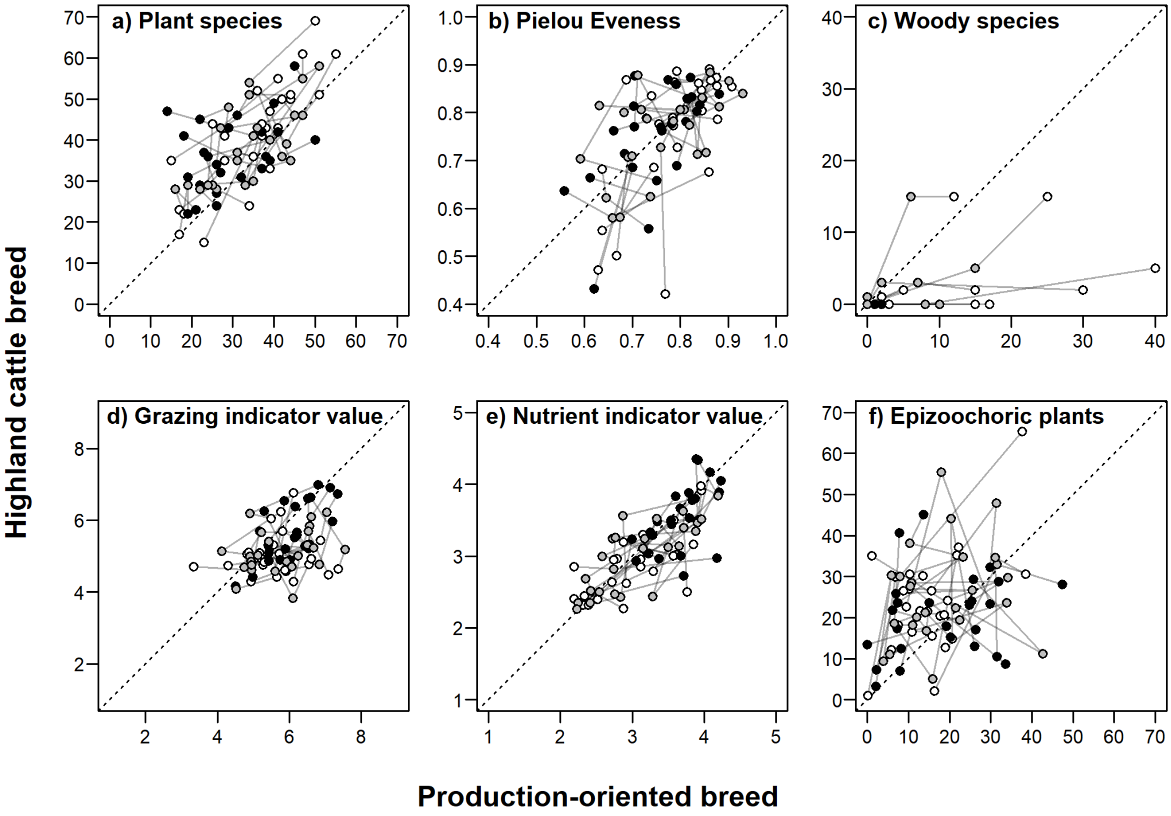


Figure 3.4 | Vegetation indices of paired pastures grazed by Highland cattle or production-oriented breeds: **a** Number of plant species per subplot, **b** Pielou's eveness, **c** cover of woody species in %, **d** cover-weighted mean of grazing and **e** nutrient indicator values as well as **f** cover of epizoochoric plants in %. 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 3.1 | 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 was analysed based on an aggregated dataset with mean site variable for the three subplots.

		Plant species richness			**Pielou's Eveness**			**Woody species cover**			**Grazing indicator value**			**Trampling indicator value**			**Nutrient indicator value**			**Epizoochoric plants**			**Gamma plant species richness**		
	Df		χ^2	p		χ^2	p		χ^2	p		χ^2	p		χ^2	p		χ^2	p		χ^2	p		χ^2	p
Highland breed	1	+	16.60	<0.0001	-	2.14	0.14	-	5.92	0.02	-	12.14	0.0005	-	3.96	0.047	-	2.57	0.11	+	10.54	0.001	+	12.51	0.0004
Elevation	1	+	6.33	0.01	+	8.38	0.004	+	5.88	0.02	-	0.47	0.49	-	0.45	0.50	-	20.23	<0.0001	+	1.03	0.31	+	10.27	0.001
Inclination	1	+	7.78	0.005	-	10.65	0.001	-	2.27	0.13	-	0.14	0.71	+	0.25	0.62	+	0.24	0.63	+	1.32	0.25	+	3.06	0.08
Phosphorus	1	-	10.13	0.002	-	11.65	0.0006	-	0.54	0.46	-	0.81	0.37	-	2.93	0.09	+	8.80	0.003	+	0.00	1.00	-	2.31	0.13
Stocking rate	1	-	0.63	0.43	-	0.03	0.86	-	1.65	0.20	+	3.06	0.08	+	4.07	0.044	+	0.14	0.71	-	5.97	0.02	-	0.73	0.39
Subplot	2	-	0.92	0.63	+	0.68	0.71	-	11.09	0.004	+	18.76	<0.0001	+	21.87	<0.0001	+	62.24	<0.0001	+	3.80	0.15	n.a.		
		-			+			-			+			+			+			+			n.a.		
Marginal R²		0.51			0.49			n.a.			0.26			0.23			0.64			n.a.			0.67		
Conditional R²		0.62			0.57			n.a.			0.54			0.60			0.73			n.a.			0.80		
N		150			150			150			150			150			150			150			50		
Likelihood		Neg. binominal			Gaussian			Beta			Gaussian			Gaussian			Gaussian			Beta			Neg. binominal		
Link function		log			identity			logit			identity			identity			identity			logit			log		

3.3.4 Effects of adaptation time

All pastures had a long-term history of grazing (5-25 years for Highland cattle; **Figure 3.5**). 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; **Figure 3.5a**). Grazing indicator values tended to decrease with adaptation time (p = 0.08; **Figure 3.5b**). There was, however, no correlation between adaptation time and the P concentration in soil nor the nutrient indicator value of vegetation (data not shown).

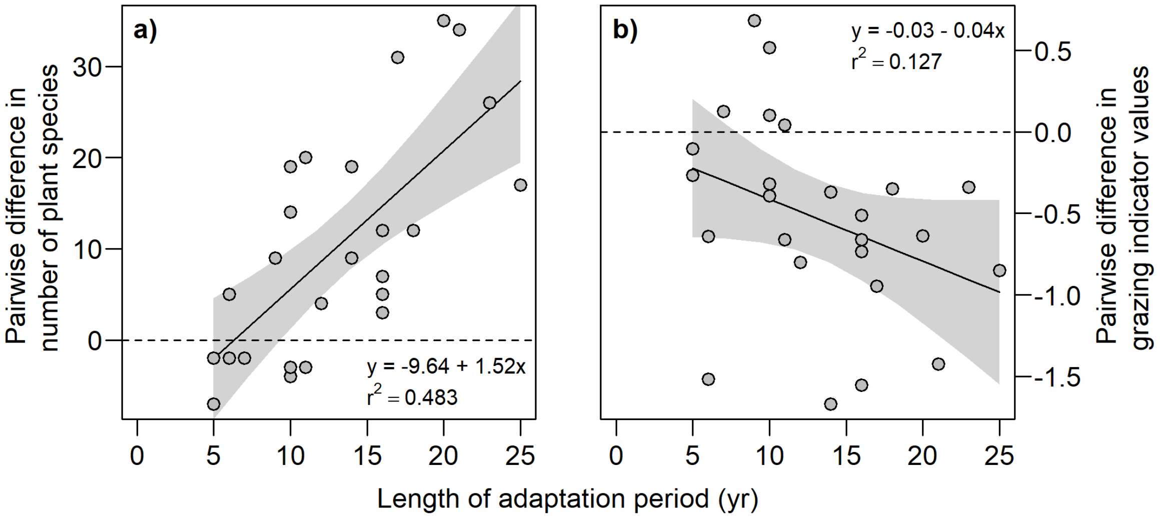


Figure 3.5 | Effect of the duration of adaptationon the pairwise difference between pastures grazed by Highland cattle and production-oriented breeds with regards to **a** aggregated plant species richness per pasture (gamma richness) and **b** grazing indicator values. Positive values represent higher values for pastures of Highland cattle. The grey area depicts the 95 % confidence interval.

3.3.5 Interactions between breed, site conditions and vegetation

Ecological interactions within pastures were complex. In compliance with the GLMMs, the SEM (**Figure 3.6**) 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 (**Figure S3.1**), 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 3.1** because they were calculated by different models. Regression coefficients and more detailed information about R^2 of the SEM are given in **Tables S3.2** and **S3.3**.

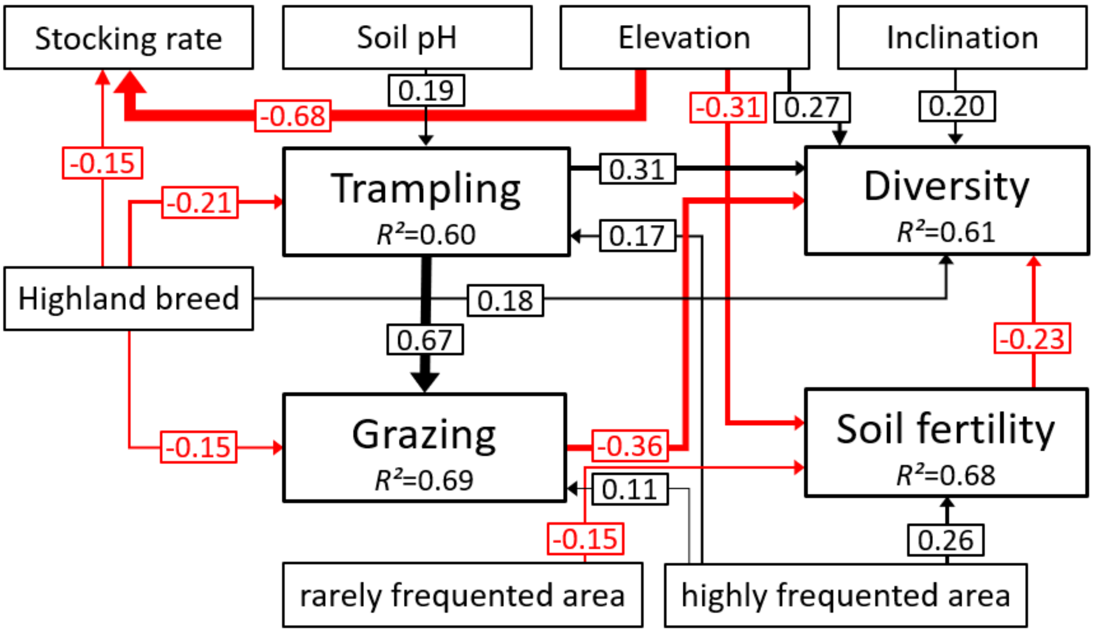


Figure 3.6 | Structural equation model of vegetation in response to grazing and site and management properties. Only significant links between the five response variables stocking (= normalized stocking rate), trampling (= trampling indicator value), grazing (= grazing indicator value), diversity (= number of plant species) and soil fertility (= plant available P) and 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.

3.3.6 Plant species composition

The CCA indicated that plant species composition across all locations was mainly explained by geographic location and site properties (**Figure 3.7a**). 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 (**Figure 3.7b**). The remaining variation in species composition was primarily explained by soil acidity (axis 1), Mg content and inclination (axis 2). Acidity was the 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.

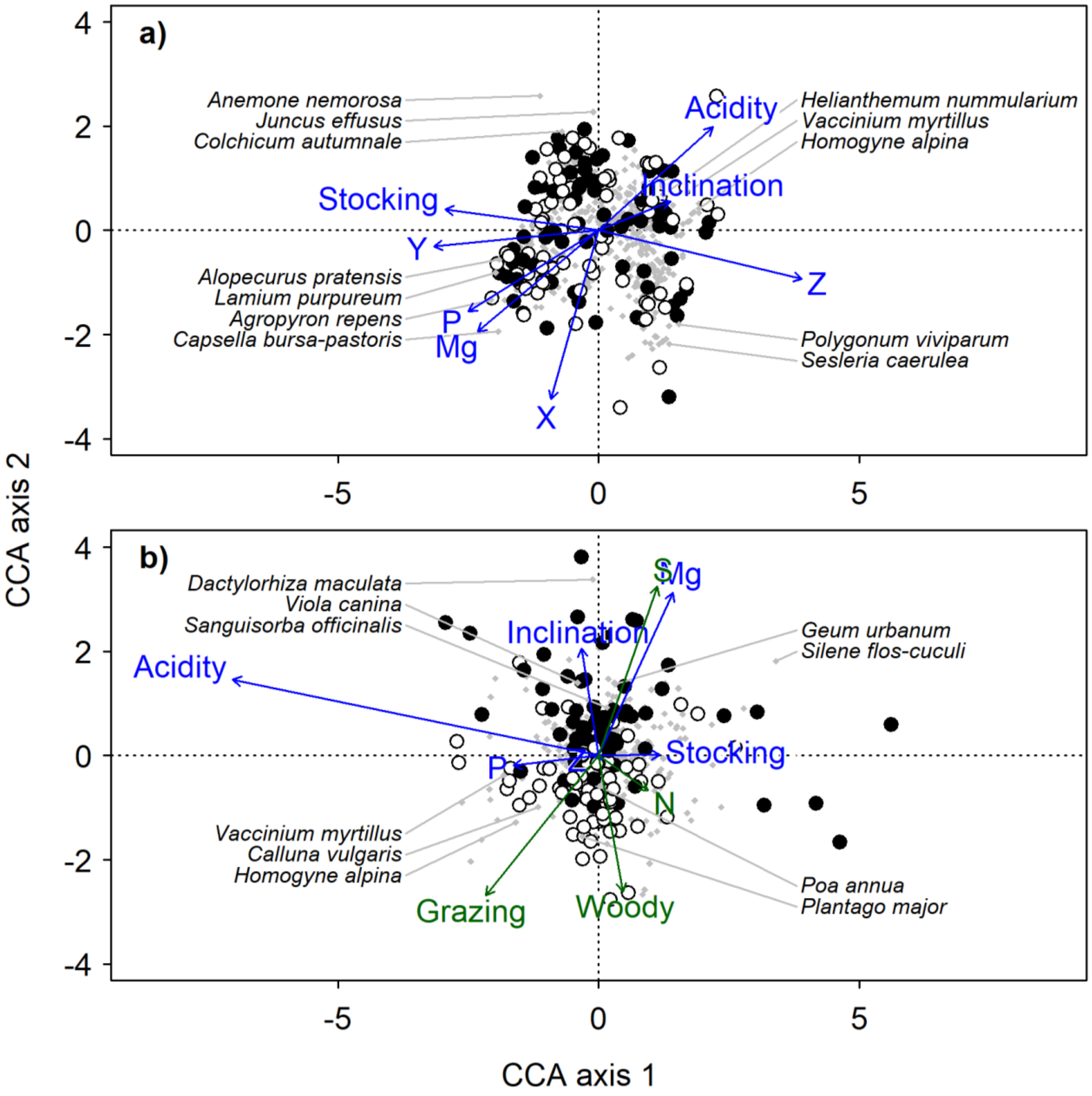


Figure 3.7 | Constrained correspondence analysis of plant species composition in pastures grazed by Highland cattle (black circles) and production-oriented breeds (white circles) in response to geographic location (longitude (X), latitude (Y), elevation (Z)) and site properties (acidity (inverse pH), 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 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).

3.4 Discussion

3.4.1 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 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., 2007b; 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.

3.4.2 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., 1998). 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.

3.4.3 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 (**Figure 3.3**; 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.

3.4.4 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.

3.5 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 surprisingly 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 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.

3.6 Supporting Information

Additional supporting information is provided in the appendix (S3)

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

This chapter has already been published as the following journal article:

Pauler, C.M., Isselstein, J., Suter, M., Berard, J., Braunbeck, T., Schneider, M.K., 2020. Choosy grazers: influence of plant traits on forage selection by three cattle breeds. Functional Ecology 34, 980–992. https://doi.org/10.1111/1365-2435.13542

The study was conducted, the data were analysed and text and figures were created by myself.

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

4.1 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 and Ritchie, 1998).

Unfortunately, *preference* is hard to measure because in almost every case, animals' preference, i.e. 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 et al., 1994). It is much easier to measure plant *selection*, i.e. 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 et al., 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 et al., 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 et al., 2012) and heterogeneous patterns influence grazing decisions (Adler et al., 2001). From the millimetre to meter scale, managed, semi-natural grasslands are the most diverse plant communities of the world (up to 89 species on 1 m² in mountain grassland; Cantero, Pärtel, and 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 promoted 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 and 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 et al., 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 (1) the lower bodyweight of Highland cattle resulting in lower trampling adaption and (2) a woollier fur promoting plant species specialised 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 et al., 2018), 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 of all, 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. Secondly, we quantified the impact of different plant traits on plant species selection and, ultimately, the difference in trait-depended selection among cattle breeds.

4.2 Material and methods

4.2.1 Study area

A grazing experiment was conducted on heterogeneous alpine pastures of Alp Weissenstein in the eastern Swiss Alps (2026 m asl., 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 et al., 2013).

We selected three areas with contrasting vegetation, forming a gradient from high to low forage quality (**Figure 4.1**: 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 and Gonseth, 2008) rich in clover, mainly *Trifolium pratense* L., and broad-leafed 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 *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* in the shrub layer.

4.2.2 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, a 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 1000-1400 m asl., 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 consuming the relatively nutrient-poor alpine forage. More detailed information is given in the Appendix S4.1 in Supporting Information.

4.2.3 Study design

In each area, the pastures were subdivided into three equal-sized paddocks with similar site conditions and vegetation composition (**Figure 4.1**: 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 three 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.

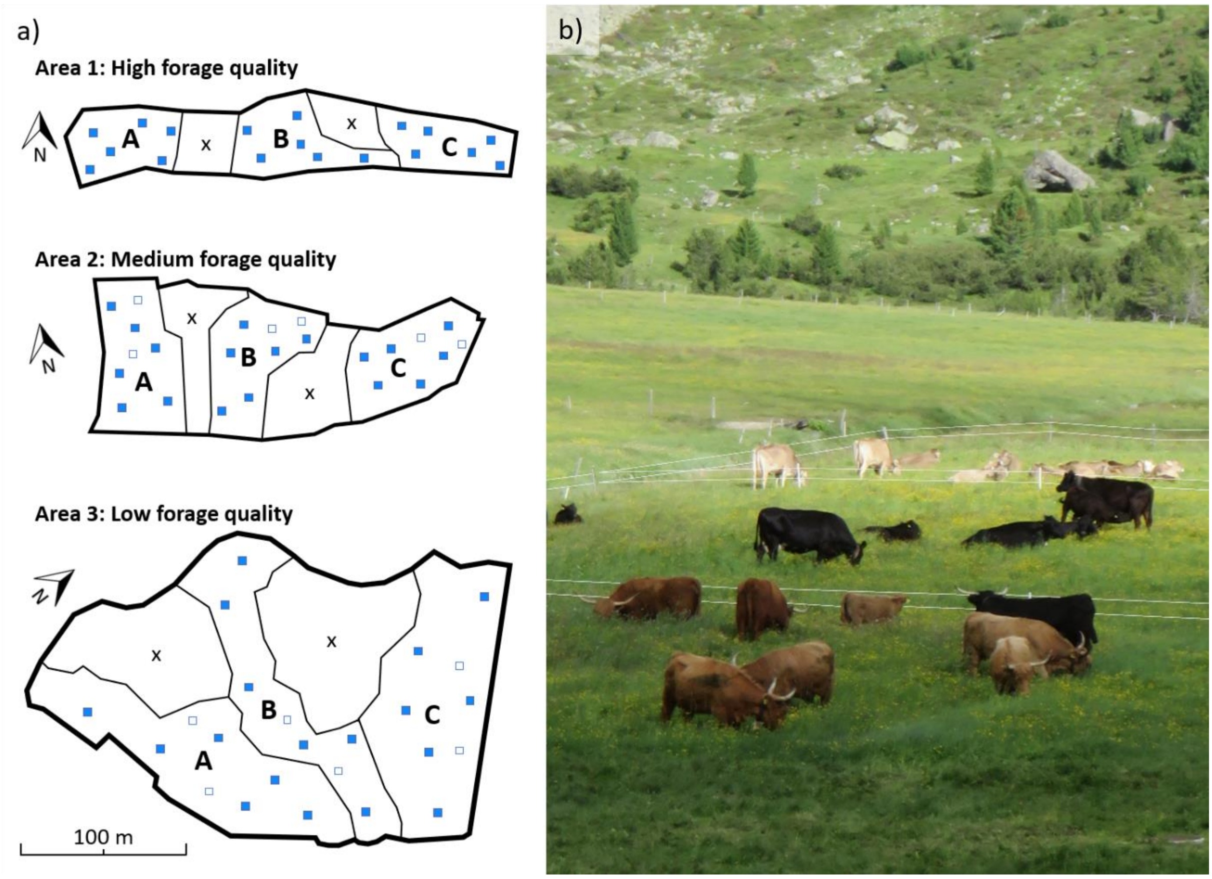


Figure 4.1 | Study areas, paddocks and vegetation subplots of the grazing experiment. **a** The cattle were grazed in three areas with vegetation of different forage quality (areas 1-3). In each area the pastures were subdivided into three paddocks of the same size (A-C). The paddocks of an area were 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 (x) 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 (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.

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 × **Figure 4.1**). Further details on areas, stocking and calculation of paddock size are provided in the supplement S4.2.

4.2.4 Vegetation survey

In each rotation, the vegetation was analysed before and after grazing in six randomly distributed subplots of 3×3 m per paddock (**Figure 4.1**). 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 a pasture, we recorded all vascular plant species within the subplots according to Eggenberg et al. (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 and Edwards, 2013). Estimated and measured data proved to be highly correlated (R^2 between 0.74 and 0.93; see supplement S4.3). 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.

4.2.5 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 detailed references can be found in the online version of this article) for all plant species for which they were available (**Table 4.1**): 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 reduce selection. The forage indicator value (FQ) is a rating of palatability to cattle (Briemle et al., 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 et al. (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.

4.2.6 Verification of pastures conditions

In order 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 et al., 2016).

4.2.7 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 4.2a**). 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 et al., 2018a); see supplement S4.4 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 4.2b**).

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 4.2c**). 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 supplement S4.4).

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 4.2d**). 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 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 supplement S4.4).

All calculations were done in R 3.6.1 (R Core Team, 2018). Data and code to reproduce results are provided on https://github.com/mkschneider/trait-selection.

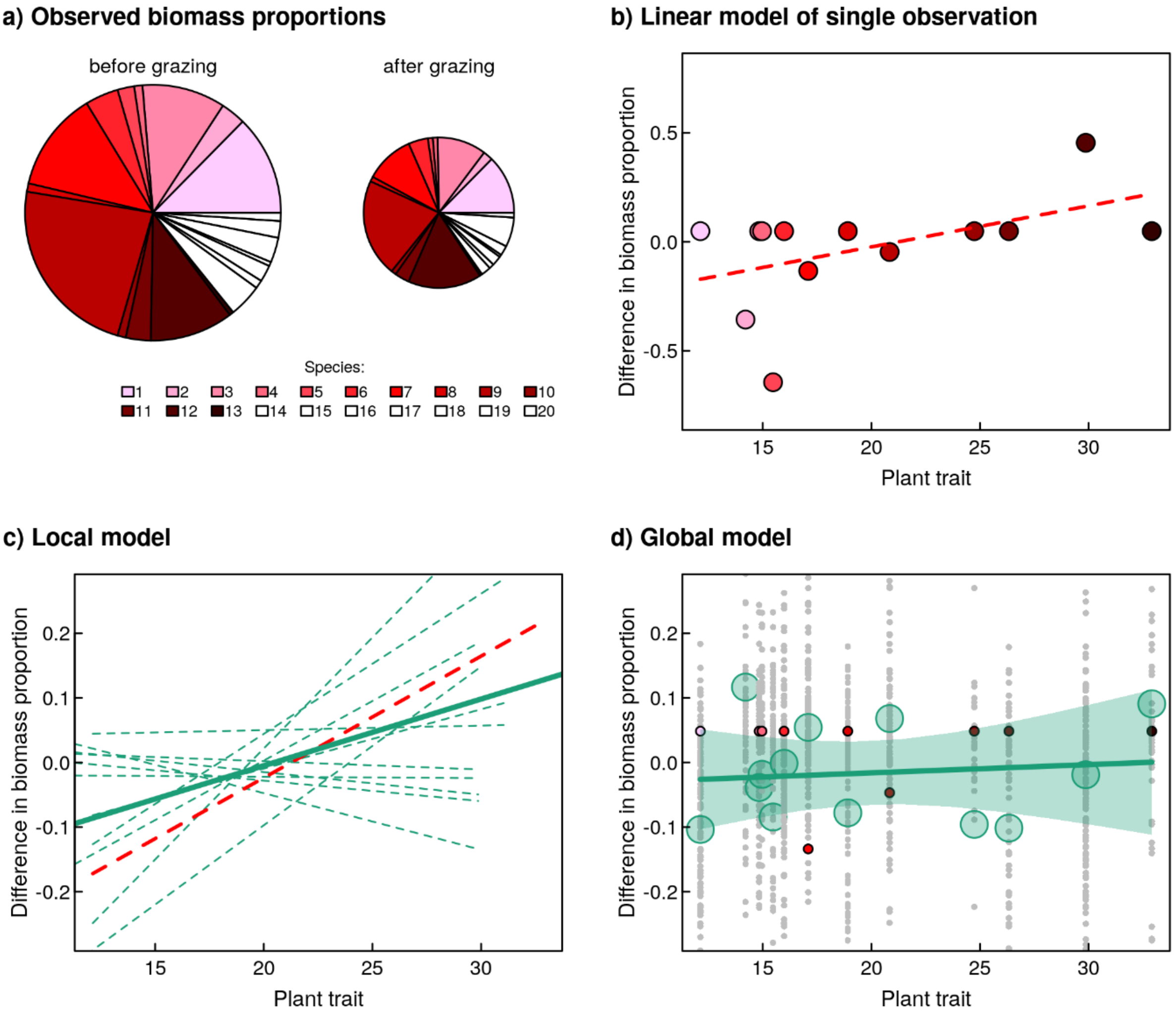


Figure 4.2 | Schematic illustration of the modelling process: **a** displays a selected example survey of the biomass proportions of 20 plant species before and after grazing. Species, for which trait values are available, are coloured; **b** is the resulting relationship between the difference in biomass 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.

4.3 Results

4.3.1 Characterisation 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 4.3**). 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). C_{leaf}, C:N ratio 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 supplement S4.5).

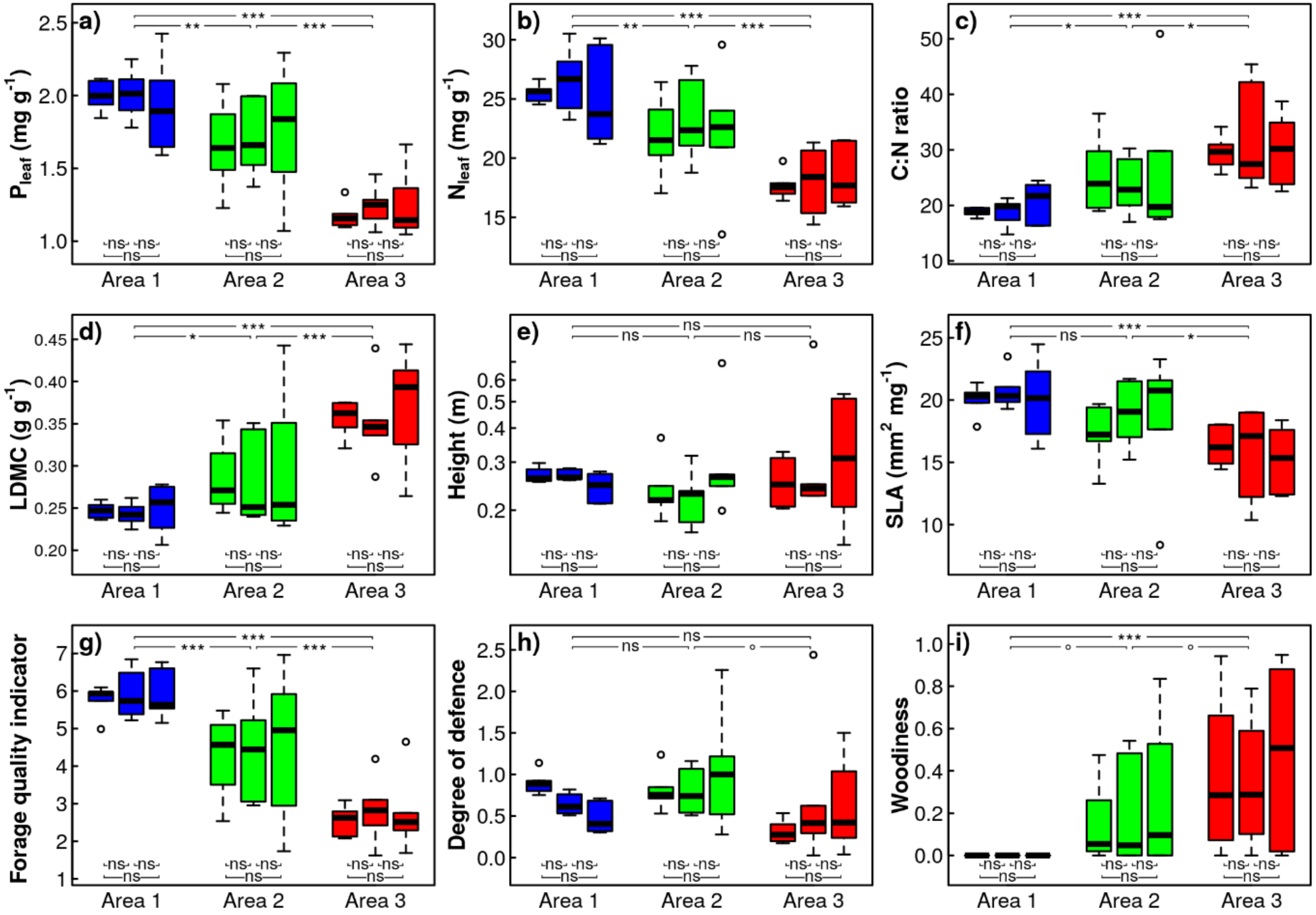


Figure 4.3 | Initial status of vegetation traits within areas and paddocks: Each boxplot shows the distribution of biomass-weighted means of the n = 6 vegetation subplots in each of the three paddocks per area before the first grazing. Area 1 (blue): fertile pasture, area 2 (green): intermediate pasture 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^{-1}, **c** C:N-ratio, **d** leaf dry matter content (LDMC) in g g^{-1}, **e** plant height in m, **f** specific leaf area (SLA) in mm^2 mg^{-1}, **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 ($\circ$ $p < 0.1$, $*$ $p < 0.05$, $**$ $p < 0.01$, $***$ $p < 0.001$, ns not significant).

4.3.2 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 4.4**). Irrespective of cattle breed, differences in biomass proportion significantly decreased with higher P_{leaf}, N_{leaf}, SLA and forage quality indicator values ($p_{trait} < 0.001$ each), meaning that plants with high values of these traits were foraged above average. In contrast, plants with high C:N ratio ($p_{trait} = 0.004$), LDMC ($p_{trait} < 0.001$), plant height ($p_{trait} = 0.001$) and strong physical defence ($p_{trait} = 0.02$) 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 $p_{trait \times breed} < 0.05$). The strength of forage selection, indicated by the steepness of the regression lines, decreased in the order A×H, Original Braunvieh, Highland 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 ($p_{trait \times rotation} = 0.07$) and favoured plants with a high forage quality indicator more clearly ($p_{trait \times rotation} < 0.001$).

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 ($p_{trait \times area} < 0.001$), whereas plants with high LDMC ($p_{trait \times area} < 0.001$), large height ($p_{trait \times area} = 0.05$) and degree of defence ($p_{trait \times area} = 0.04$) 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.

4.3.3 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 4.5**). 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, while 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, unattractiv species like *Deschampsia cespitosa* (L.) P. BEAUV. or *Carex caryophyllea* LATOURR. were selected by Highland cattle and avoided by A×H.

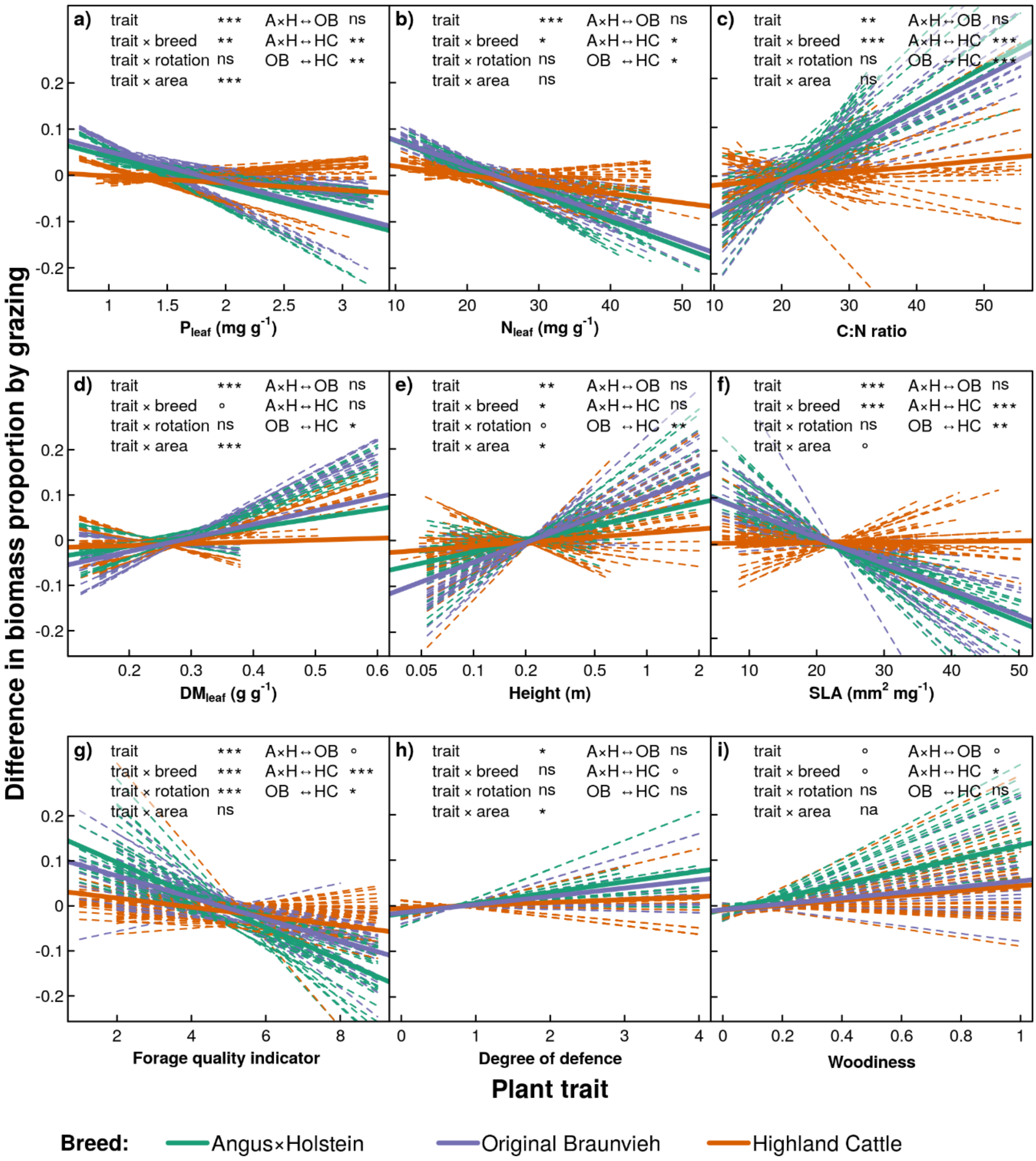


Figure 4.4 | Effect of plant traits on the differences in biomass proportions before and after grazing as estimated by the local model: Continuous bold lines are predicted mean effects for the three cattle breeds A×H (green), Original Braunvieh (blue) and Highland cattle (orange). Dashed lines show the 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^{-1}, **c** C:N-ratio, **d** leaf dry matter content (LDMC) in g g^{-1}, **e** plant height in m, **f** specific leaf area (SLA) in mm^2 mg^{-1}, **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, i.e., selection of species with high trait values. An inclining line represents a negative effect on consumption, i.e., 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 ($\circ$ $p < 0.1$, $*$ $p < 0.05$, $**$ $p < 0.01$, $***$ $p < 0.001$, ns not significant, na not available).

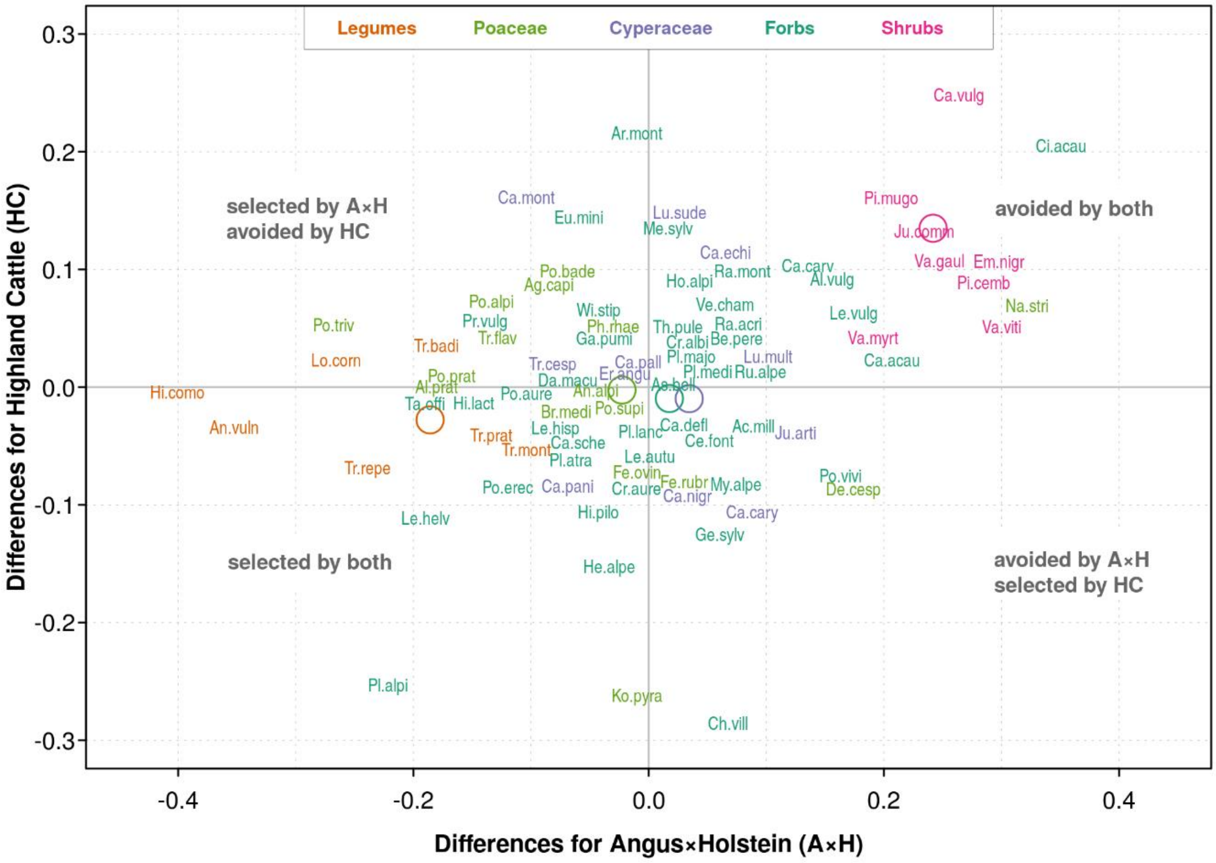


Figure 4.5 | Selection and avoidance of plant species by two cattle breeds: Observed differences in biomass proportions before and after grazing by Angus×Holstein (A×H; x-axis) and Highland cattle (HC; y-axis). Positive values indicate an increase in biomass proportion and hence deselection by the animals, negative values indicate selection. All plant species observed more than ten 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 vs OB and HC vs OB are provided in the supplement S4.6. The positions of 20 species were slightly modified to avoid overlapping labels.

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 plants 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 4.6**). Trait effects were mostly similar to the local estimates, but the global model indicated a 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 ($p_{\text{trait} \times \text{breed}} < 0.001$ each).

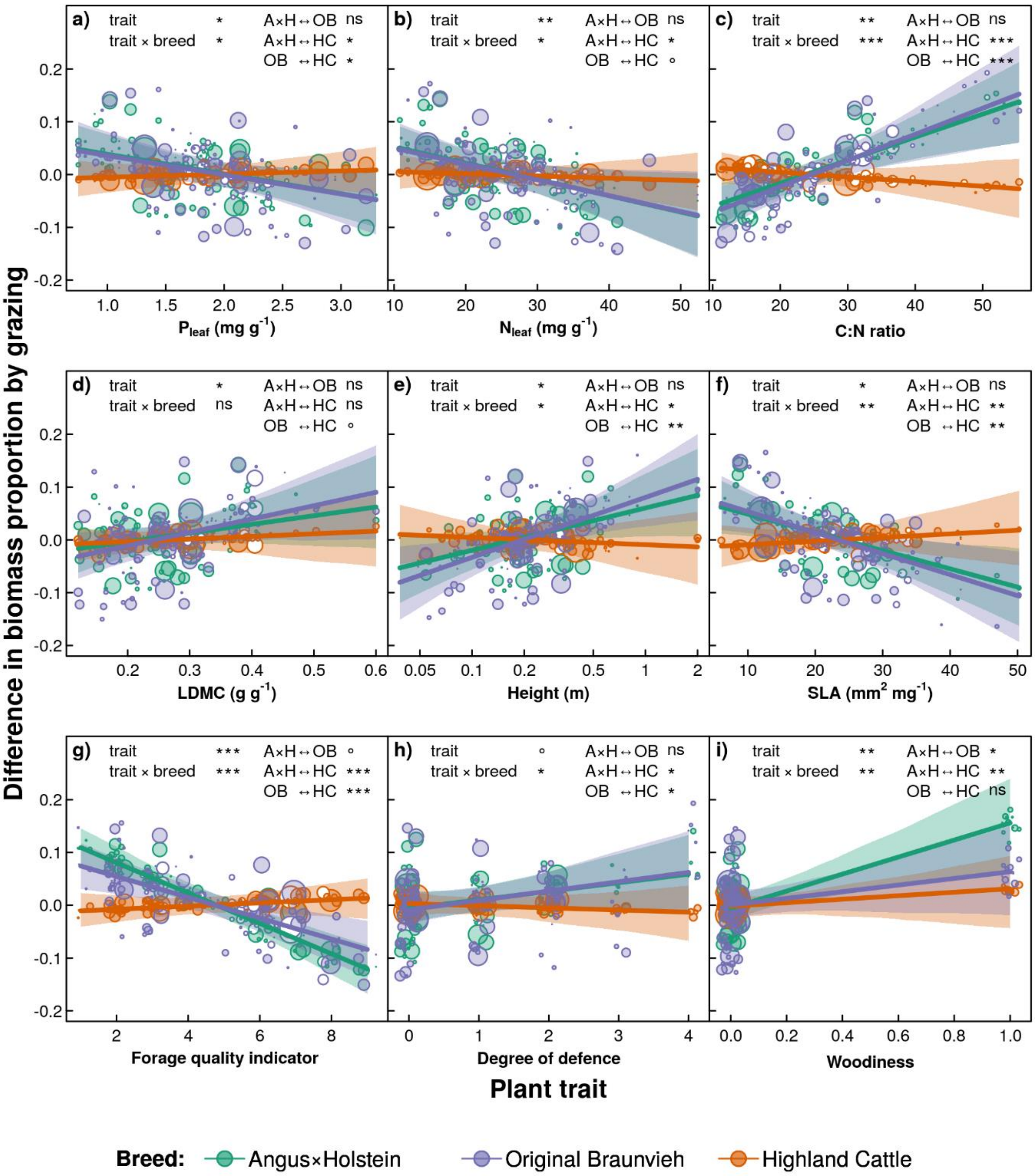


Figure 4.6 | Effects of plant traits on differences in biomass proportion by grazing as estimated by the global model: Solid lines represent estimated effects of plant traits with their 95 % credibility interval (shaded areas) for three cattle breeds A×H (green), Braunvieh (blue) and Highland cattle (orange) for the nine traits: **a** P_{leaf} and **b** N_{leaf} content per dry mass in mg g^{-1}, **c** C:N-ratio, **d** leaf dry matter content (LDMC) in g g^{-1}, **e** plant height in m, **f** specific leaf area (SLA) in mm^2 mg^{-1}, **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, i.e., 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 ($\circ$ $p < 0.1$, $*$ $p < 0.05$, $**$ $p < 0.01$, $***$ $p < 0.001$, ns not significant).

4.4 Discussion

4.4.1 Assessing forage selection in species-rich pastures

Alpine pastures and other nutrient-poor, semi-natural 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 in order 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 (Katjiua and Ward, 2006; Sanon et al., 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 and Daleboudt, 1994) and estimated biomass change on a continuous scale rather than by classes (Iussig et al., 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, i.e. 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.

4.4.2 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 $\mathbf{N_{leaf}}$ or $\mathbf{P_{leaf}}$. 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 and 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 and 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 (supplement S4.5) and exemplifies the different strategies of nutrient-rich, fast-growing competitive ruderals and nutrient-poor, long-lived stress-tolerant species (Pierce et al., 2007; Pyankov et al., 2001).

Besides the chemical properties, plants' physical texture and dimensions influence foraging decisions. In agreement with Cingolani et al. (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 and Zhang, 2014; Laca et al., 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 and 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 et al., 2009) because of the hard structure and poor digestibility. The low overall number of foraged woody species minimised 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. Secondly, plants with high forage quality were selected more strictly at the beginning of the grazing season than in late summer (trait×rotation interaction, **Figure 4.4g**), which is in agreement with Mandaluniz et al. (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.

4.4.3 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 et al., 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 et al., 2014; Winder et al., 1995), that reported higher shrub consumption by less-productive breeds, while 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 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 et al., 2011) just as little difference was found as where relatively high-productive breeds were compared among themselves (Dumont et al., 2007a; Scimone et al., 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 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.

4.5 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.

4.6 Supporting Information

Additional supporting information is provided in the appendix (S4).

5 Grazing allometry: anatomy, movement and foraging behaviour of three cattle breeds of different productivity

This chapter is under consideration for publication at the time of thesis submission:

Pauler, C.M., Isselstein, J., Berard, J., Braunbeck, T., Schneider, M.K., in revision. Grazing allometry: anatomy, movement and foraging behaviour of three cattle breeds of different productivity. Frontiers in Veterinary Science, Ruminant grazing behavior: a tool to improve product quality and ecosystem services.

The study was conducted, the data were analysed and text and figures were created by myself.

Abstract

1. Modern breeding has formed a multitude of cattle breeds ranging from undemanding, but low-productive traditional breeds to high-productive, specialized dairy or beef cattle. The choice of cattle breed has important implications for farm management, but its impact on pasture vegetation and biodiversity is underestimated. Cattle breeds differ not only in appearance and productivity, but likely also in anatomy, movement and foraging behaviour.

2. In order to quantify the importance of these factors, three cattle breeds, grazing three types of heterogenous alpine pastures, were simultaneously investigated: (1) low-productive Highland cattle, (2) traditional, dual-purpose Original Braunvieh, and (3) high-productive Angus×Holstein crossbreed. We measured body weight and claw base of nine cows per breed, recorded the step frequency by pedometer and space use evenness by GPS, and visually observed forage behaviour. Forage selectivity and quality were calculated for every cow's diet. Allometric relationships were analysed by fitting standardized major axes.

3. Body weight was found to scale with claw base, but there were significant differences between breeds: the relatively large claws of Highland cattle presumably reduce physical pressure and erosion on pastures compared to other breeds. Step frequency scaled with forage selectivity: the more productive a breed was, the higher the forage selectivity and step frequency. For example, woody species and thistles were more frequently foraged by low-productive Highland cattle than by high-productive Angus×Holstein crossbreed cattle. The latter also walked longer distances to select higher-quality diet, while low-productive Highland cattle used the space more evenly. Irrespective of breed, vegetation composition influenced cattle: on pastures of low forage quality animals walked more, selected their diet more strictly and used space less evenly.

4. In conclusion, the observed breed-specific differences deserve greater consideration in breeding decisions, pasture management and grassland conservation.

Keywords: alpine pastures, cattle breeds, claws, forage selection, GPS, movement behaviour, pedometer

5.1 Introduction

The domestication of wild aurochses (*Bos primigenius*) created a plethora of cattle breeds (*Bos taurus*) with different characteristics (Ajmone-Marsan et al., 2010). While the aurochs slowly evolved to cope with environmental conditions (Edwards et al., 2010), human breeding decisions enormously accelerated genetic transformation of these animals to meet agricultural needs, but not necessarily the environment (Mason, 1984). During the mid-nineteenth century, different breeds emerged from pure-breeding, as motivated by ideas of Darwinism, Mendelism and biometry. In recent years, productivity has been enhanced by artificial insemination, quantitative genetics and molecular markers (Derry, 2015). Such breeding has enhanced traits favoured by humans, particularly milk yield, body weight, forage intake and growth rate. Records of historical livestock production in Austria indicate that at the beginning of nineteenth century cows weighed about 250 kg and produced 1300 kg of milk per year (Krausmann, 2008). Today, target weights for breeding specialized beef cattle, such as Charolais or Blonde d'Aquitaine, range from 700 to 950 kg (Mutterkuh Schweiz, 2020), and specially bred dairy cows, such as Holstein Friesian, produce, on average, more than 9000 kg of milk annually (Holstein Association Switzerland, 2020). In addition to these favoured traits, for which breeding is controlled, there are numerous uncontrolled characteristics not accounted for in selection decisions and therefore may have co-evolved unnoticed. Some of these traits that have long been ignored have recently gained awareness, such as robustness (Calus et al., 2013), while others, such as claw size, movement, and foraging behaviour, remain unresearched.

Such profound transformations of cattle are likely to have an impact on the vegetation of the sites they graze. Open grasslands, which belong to the most diverse habitats on earth (Wilson et al., 2012), were created by centuries of low-intensity grazing with low-productive animals (Ellenberg and Leuschner, 2010). What happens to these pastures, if the animals which formed them, undergo tremendous modifications within a few decades? After a recent study highlighted differences in vegetation when pastures are grazed by breeds of different productivity (Pauler et al., 2019), a follow-up study was designed to quantify the drivers of these differences. Strong changes in body weight, for example, may exert more pressure to the ground with negative consequences for vegetation, soil properties and claw health. This characteristic is particularly interesting because the claw base that the animal mass burdens was not considered in breeding decision and is, therefore, presumably disproportionately underdeveloped. Additionally, higher body weight, growth rate and milk yield probably altered movement and foraging behaviour. If modern cattle walk more, use the pasture differently, or forage other plants than their lower-productive ancestors, this could influence vegetation composition, as suggested by Pauler et al. (2020).

Unfortunately, it is not possible to compare modern, high-productive cattle directly to their low-productive ancestors, which grazed pastures centuries ago, before production-oriented herdbook breeding began. However, modern, low-productive breeds exist, such as Highland cattle, that are less intentionally bred for productivity. Mason (1984) postulated little difference between modern Highland cattle and sculptures of cattle made by ancient Etruscans. While other breeds annually broke records of beef and milk production, the main breeding aim of Highland cattle was to thrive under harsh environmental conditions and on the low forage quality of the Scottish Highlands. Consequently, animals are lighter, slower growing, but at the same time more robust and less demanding than high-productive breeds (Albertí et al., 2008). Therefore, along the productivity gradient, Highland cattle are ideal for comparison with Angus×Holstein cattle, which represent the high-productive end of the breeding spectrum in our study. In-between Highland cattle and Angus×Holstein, Original Braunvieh was added as a traditional mountain breed, moderately altered by breeding.

If productivity of cattle influences pasture vegetation, there are far-reaching consequences for habitat conservation of nutrient-poor, marginal grasslands, which host many vulnerable and endangered plant species (Klötzli et al., 2010; Peter et al., 2009; Wilson et al., 2012). These species may be negatively affected by grazing with high-productive cattle breeds, as suggested by Pauler et al. (2019): Species resistant to selective foraging, such as thistles or shrubs, and species adapted to trampling become dominant on pastures of high-productive breeds, decreasing biodiversity (Pauler et al., 2019; Zehnder et al., in revision). Moreover, in contrast to Highland cattle, high-productive animals are insufficiently alimented by the forage present in nutrient-poor grasslands (Berry et al., 2002).

Therefore, the objectives of our study were (1) to relate the productivity of a cattle breed to its anatomy, movement and foraging behaviour, (2) to analyse if differences among animals are explained by individual variation alone or if there is a breed effect, and, finally, (3) to quantify the allometric relationship between anatomy, movement and foraging behaviour of cattle.

5.2 Material and methods

5.2.1 Three breeds: low-, medium- and high-productive

We investigated anatomy, movement and foraging behaviour of three cattle breeds, representing a gradient from low to high productivity. The lower end of this gradient was represented by Highland cattle (HC), an undemanding and low-productive traditional breed, bred to thrive in the harsh environmental conditions of the Scottish Highlands, but widespread over the world. Cattle of medium productivity were represented by Original Braunvieh (OB), a traditional dual-purpose breed of the Swiss Alps, with body weight and growth rate considerably higher than that of Highland cattle (Mutterkuh Schweiz, 2020). The Original Braunvieh is not to be confused with Brown Swiss, a high-productive, but genetically less diverse dairy breed selected from the same original population (Bhati et al., 2020). The most productive breed in our experiment was Angus×Holstein crossbreed (AH), which combines the large-framed, heavy body of Angus beef cattle with the elevated milk production of Holstein dairy cows.

Three groups of three suckler cows and their calves were formed for each of the breeds studied, for a total of 54 animals. The groups were developed by breed-wise ranking cows based on specific body weights and joining every third individual (1 heavy, 1 middle weight, 1 light cow per group). Anatomy and behaviour were quantified for the 27 cows, but not for the calves. All cows were familiar with mountainous grasslands, as they originated from mountain farms and had experience grazing high-elevation, alpine pastures in preceding summers. Cows were aged between 2.8 and 10.3 years. We tested all variables for correlations with age, but found only weak relationships ($R^2 = 0.08 - 0.31$).

5.2.2 Study areas: three types of alpine pastures

Movement and forage behaviour were observed on three types of alpine pastures on Alp Weissenstein in the eastern Swiss Alps (2026 m asl., 46.5816°N, 9.8002°E, **Figure 5.1**).

The three pastures differed in plant species composition, forage quality and bedrock material (**Tables 5.1 and 5.2**). We calculated the expected forage demand for all individuals based on their body weights. A total forage demand of 1800 kg dry matter was expected for each of the three pastures during the experiment. The actual biomass of the study area was measured by a rising plate meter and pasture size was set to provide excessive forage compared to the estimated forage demand (Pauler et al., 2020): The pasture supplied 2440-4860 kg dry matter already in spring and there was additional regrowth during summer. This amount of excess forage ensured that cattle selected plants based on preference rather than being pressured by shortage.

Each pasture was subdivided into three paddocks with highly comparable conditions (Pauler et al., 2020). The three paddocks of a pasture were grazed simultaneously by three groups – one of each breed. After three to four days, the three groups were transferred to the three paddocks in the second and subsequently the third, pasture. This procedure was repeated three times. Different groups and, therefore, different animals were used for each rotation to avoid pseudoreplication. Applying a Latin square design, a different breed grazed each paddock in each rotation, and therefore, each breed visited each paddock once. On each pasture, movement and foraging behaviour of every cow were observed.

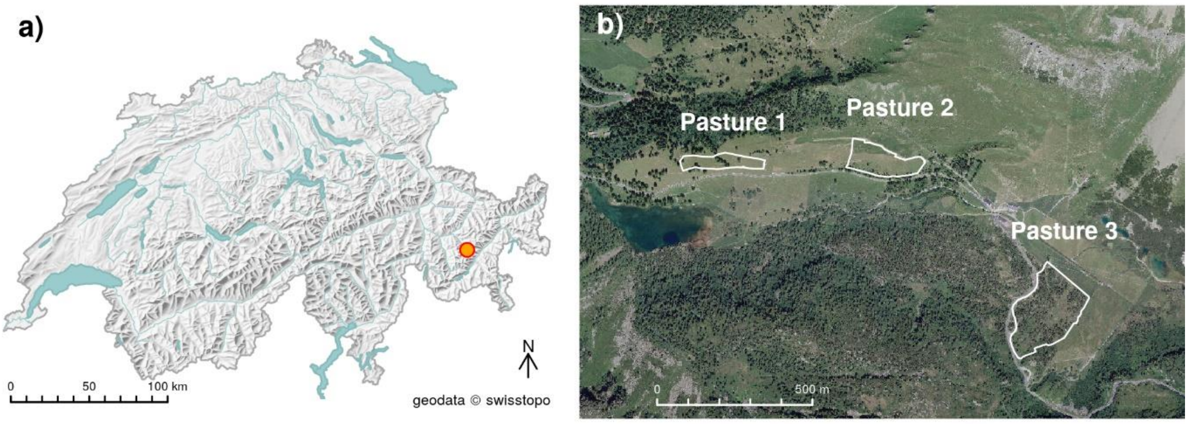


Figure 5.1 | a Overview map and **b** aerial image of the study area in Swiss Alps with the three pastures grazed by cattle in the experiment.

Table 5.1 | Characterization of the three pastures the cattle were grazed on. Table provides a short description of each pasture, its size (ha), the average, minimum and maximum slope in %, the predominant bedrock, the forage quality relative to the other pastures and as average forage indicator value (Briemle et al., 2002), the available biomass (kg dry matter) and the main vegetation type (Delarze and Gonseth, 2008).

	Pasture 1	**Pasture 2**	**Pasture 3**
Description	Nutrient-rich, flat	Heterogeneous, steep with few flat parts, nutrient-poor with few nutrient-rich parts	Steep wood pasture, flat fens, extremely nutrient-poor
Size (ha)	1.05	1.83	4.38
Bedrock material	Calcareous	Calcareous	Crystalline
Slope (%)[1]	19.2; 0.3; 56.7	48.1; 1.2; 122.6	25.1; 0.3; 146.7
Forage quality	High (5.9)[2]	Medium (4.6)[2]	Low (2.7)[2]
Available biomass (kg DM)	3380	2443	4859[3]
Vegetation type	Fertile pasture	Fertile pasture Mat-grass community Dwarf-shrub-community	Alpine fen Larch-Pine forest

[1] SwissAlti3D, Federal Office of Topography swisstopo, Wabern

[2] Average cover-weighted mean of forage quality indicator value (Briemle et al., 2002) of all vascular plant species within 18 vegetation subplots per pasture, estimated before the first grazing in spring. For details, see Pauler et al. (2020).

[3] Total standing biomass including woody structures in the herb layer (mainly dwarf shrubs).

Table 5.2 | Characterization of the vegetation types. Table provides the main vegetation types in the study area (classification according to Delarze and Gonseth (2008)), the scientific name of these plant associations, and their dominant plant species.

Vegetation type	**Association**	**Dominant plant species**
Fertile pasture	*Poion alpinae*	*Trifolium pratense* L. *Trisetum flavescens* (L.) P. BEAUV. *Phleum rhaeticum* (HUMPHRIES) RAUSCHERT *Ranunculus acris* L. *Carum carvi* L. *Alchemilla xanthochlora* ROTHM.
Mat-grass community	*Nardion*	*Festuca rubra* L. *Nardus stricta* L.
Dwarf-shrub-community	*Juniperion communis*	*Erica carnea* L. *Calluna vulgaris* (L.) HULL
Alpine fen	*Caricion fuscae*	Various mosses *Trichophorum cespitosum* (L.) HARTM. *Carex nigra* (L.) REICHARD *Carex panicea* L.
Larch-Pine forest	*Larici-Pinetum cembrae*	*Larix decidua* MILL. *Pinus cembra* L. *Vaccinium myrtillus* L. *Vaccinium gaultherioides* BIGELOW *Juniperus communis* L.

5.2.3 Assessment of anatomy: body weight and claw base

All cows were weighed at the beginning and at the end of the grazing experiment (Weighing System FX15, Texas Trading, Windach, Germany). The body weight after ten weeks of grazing alpine pastures was used for analysis. The average change in body weight during the grazing period was calculated for each cow.

Two weeks prior to the experiment, the shape and health status of the claws of all cows were examined by an approved expert and corrected if necessary. At the end of the grazing season, after ten weeks under similar conditions, the claw base of each cow was measured using the left forefoot and the left hindfoot. Adapting the method of Nuss and Paulus (2006) to living animals, we took a picture of the claw base in a scaled frame (**Figure 5.2a**) and rectified the photograph (software: Office Lens, Microsoft, Redmond, USA). Using the software “Measure pictures” (CAD-KAS Kassler Computer software, Markranstädt, Germany), we traced the outline of the claw base and calculated the area of this polygon based on the scale included in the picture (**Figure 5.2b**). Thus, we measured the medial and lateral claws of both feet. Assuming the left as proxies for the right claws (Andersson and Lundström, 1981), we doubled the values and summed them. Static pressure to the ground was calculated by dividing the body weight by the summed claw base.

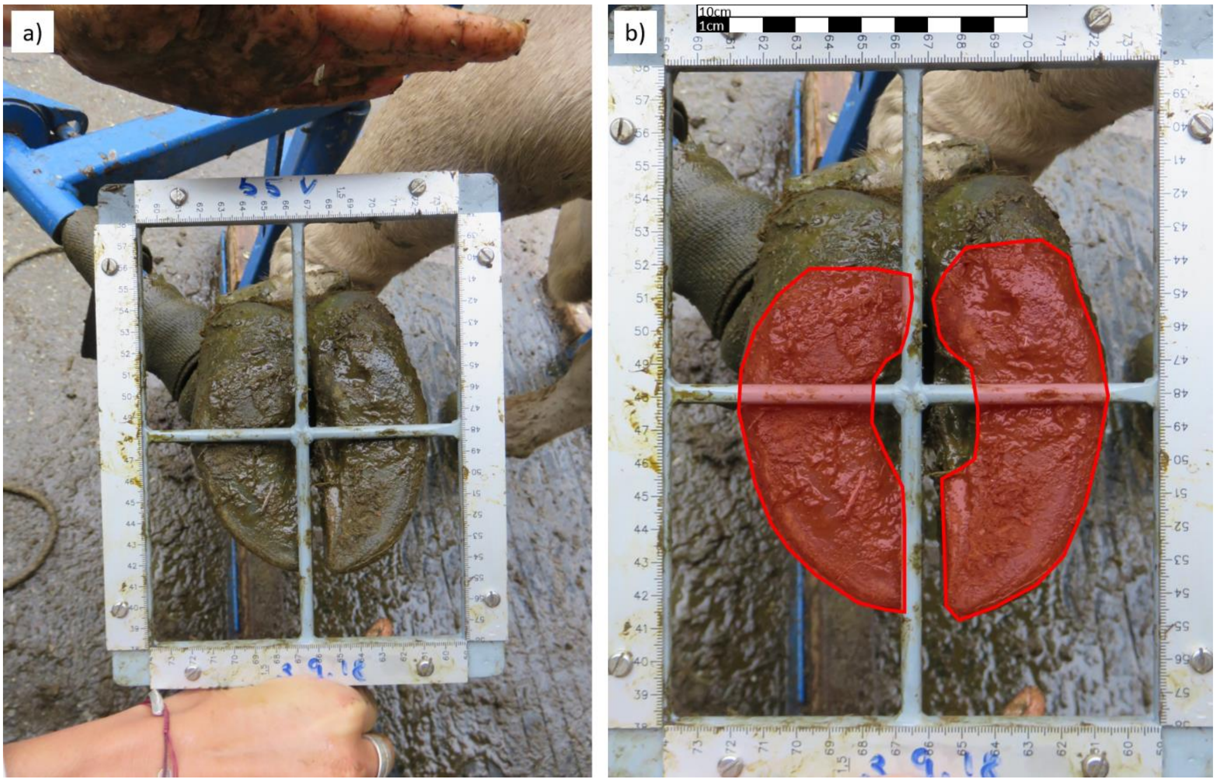


Figure 5.2 | Measurement of claw base: **a** Unedited photograph of the ground of a cow's left forefoot with scaled frame. **b** The same photograph after rectifying with scale and red polygons, drawn to measure the base of the lateral (on left here) and the medial (on right here) claw.

5.2.4 Assessment of movement behaviour: GPS logger and pedometer

Movement behaviour of cows was observed by pedometers and GPS loggers, which recorded data for the entire duration cows were on the study pastures. To quantify movement intensity, we used IceTag pedometers (IceRobotics, Edinburgh, UK). This device is a three-axis accelerometer that uses the force of movement to identify the number of times a cow lifts its leg and records these events as steps. The time that the sensor is horizontal is recorded as lying time. A pedometer was fixed at the left hindfoot of six cows per breed for a total of 18 pedometers installed. The step counts and lying time was recorded for each cow in each pasture separately, from which average steps per hour and the proportion of time spent lying (lying ratio) were calculated.

In addition, all 27 cows were equipped with collars carrying a box with a GPS logger (Qstarz BTQ1000XT, Qstarz, Taipei, Taiwan) and 3.6 V lithium batteries (Homburger et al., 2014). Positions were logged every 15 seconds, providing information about the distance covered during a certain time. We computed the average speed in m/h for each cow in each pasture. Furthermore, we were interested in how often cattle visited different portions of the entire available area of each pasture. Therefore, we calculated the evenness of space use by counting the number of GPS positions within 5 × 5 m grid cells and by calculating Camargo's index of evenness across all cells (Payne et al., 2005).

5.2.5 Assessment of foraging behaviour

We assessed the foraging behaviour of all cows by direct visual observation of the plant species consumed. On each pasture, each cow was observed foraging for 15 - 41 minutes (mean: 26 minutes). Before the experiment started, animals became accustomed to the observer. Hence, it was possible to monitor the cows from close proximity, within a distance of 0.5 - 2 m. For every second bite, the plant species with the highest share within the bite was recorded. Despite the short distance, it was not always possible to discriminate between some species with similar habitus in the short time available. We therefore combined a few plant species into groups: broad-leaved Poaceae (except *Deschampsia ceaspitosa*, which was easy to identify and has much lower forage quality than other broad-leaved Poaceae); fine-leaved Poaceae (except *Nardus stricta*, for which the same applies as for *D. caespitosa*); yellow Asteraceae; *Carex* species; *Trifolium pratense* and *T. repens*; *Potentilla aurea* and *P. erecta*. All other plants were recorded at species level.

Subsequently, we calculated the relative consumption of each plant species or species group per cow and pasture. As a proxy for palatability to cattle, we used the indicator values of forage quality by Briemle et al. (2002). The indicator values were multiplied by the relative consumption of all species to estimate the average quality of the consumed forage. For species groups, the relative abundance of the individual plant species within each group in each pasture was calculated based on 186 vegetation relevées (Pauler et al., 2020). Because we were interested in how strictly cattle select their forage, we also calculated Pielou's evenness of the selected plant species.

5.2.6 Statistical analysis: Tukey range tests and allometric line fitting

All calculations were conducted in R 3.6.1 (R Core Team, 2018). Differences between breeds were tested using Tukey range tests as implemented in package *multcomp* (Bretz et al., 2016). For movement variables and foraging behaviour of each animal in each pasture, tests were conducted on the mean value per animal over all three pastures, as well as on separate mean values for each pasture. In the text, pairwise comparisons are shown by symbol ~.

Allometric relationships were estimated by fitting standardized major axes (SMA) using the R package *smatr* (Warton et al., 2012). SMA is appropriate if there is no causal relationship between two variables x and y, and if x and y differ in variance (Warton et al., 2006). In contrast to linear regression, SMA minimizes residuals for both axes, not only the y-axis, i.e. both variables are presumed to produce errors. The allometric lines fitted for the three breeds were tested for differences in slope, shift, and elevation. In the case of differing slopes (**Figure 5.3a**), the relationship between x and y varies among the three breeds. If there is a difference in shift (**Figure 5.3b**), breeds differ consistently in the levels of x and y. In this case, breeds have similar values of x at similar values of y. If allometric lines differ in elevation (**Figure 5.3c**), the level of the relationship of x and y differs consistently among breeds. In this case, breeds have different values of x at similar values of y. For example, in order for the green breed to have a similar elevation as the blue breed, it would have had to have either larger x or smaller y values.

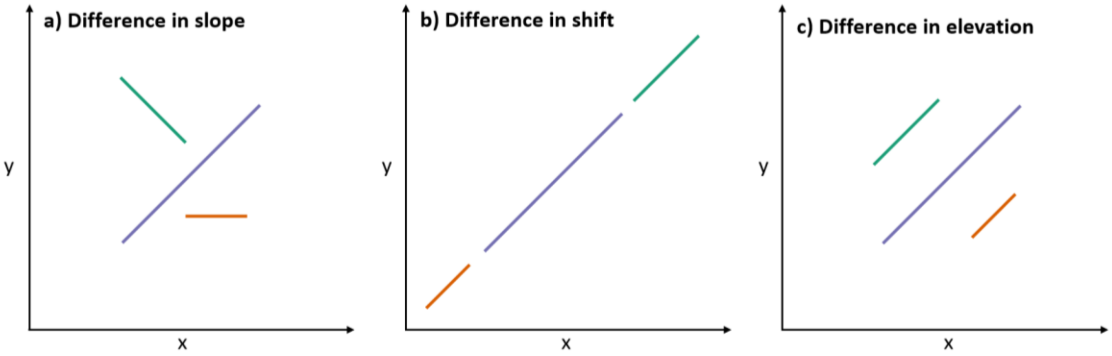


Figure 5.3 | Schematic illustration of differences among allometric lines of three exemplified breeds (adapted from Warton et al. (2006)): **a** Allometric lines differ in slope, i.e. the relationships of x and y differ among breeds. **b** Allometric lines are shifted along their common slope, i.e., the x and y vary consistently across breeds. **c** If allometric lines differ in elevation, they are shifted in parallel to each other, i.e., the values of x differ among groups at similar values of y. The length of allometric lines reflects the data range, but does not affect the allometry.

5.3 Results

5.3.1 Differences in body weight and claw base among breeds

The three breeds differed considerably in body weight and claw size (**Figures 5.4a, b**). Highland cattle were the lightest breed on the smallest claw base, followed by Original Braunvieh. Angus×Holstein cattle were the heaviest breed and had the largest claws. However, whereas the body weight differed significantly among breeds, the claw base was more similar. Hence, claw base generally scaled with body weight, but there were significant differences among breeds that went beyond individual effects: Although lighter Highland cattle also had smaller claws, their claw base was *relatively* large compared to their body weight (**Figure 5.4c**). Therefore, the static pressure of the body mass on each square centimetre of claw base was significantly lower in Highland cattle than in the other two breeds.

The cattle spent a total of ten weeks on the alpine pastures, which are relatively nutrient-poor compared to the pastures of their home farms. During this period, Angus×Holstein and Original Braunvieh cattle lost, on average, 0.6 and 0.3 kg per day, respectively (**Figure 5.4d**). With an average daily weight gain of 0.08 kg, Highland cattle differed significantly from the other two breeds ($p_{\mathrm{HC\sim OB}} = 0.002$ and $p_{\mathrm{HC\sim AH}} < 0.001$, respectively).

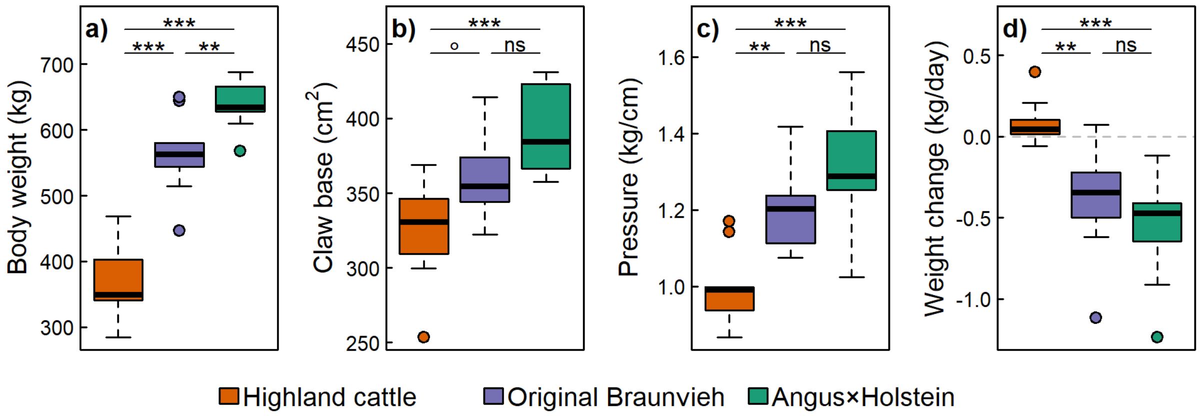


Figure 5.4 | Differences in **a** body weight, **b** claw base, **c** the pressure of body mass on the ground, and **d** the average daily body weight change during ten weeks on alpine pastures of three cattle breeds: Highland cattle, Original Braunvieh and Angus×Holstein. Nine cows were measured per breed (box: 25th to 75th quartile range (IRQ); line: median; whiskers: max. 1.5 x IQR; points: outliers; ns: $p > 0.1$; $\circ$ $p < 0.1$; $*$ $p < 0.05$; $**$ $p < 0.01$; $***$ $p < 0.001$).

5.3.2 Differences in movement behaviour among breeds as influenced by pasture conditions

The breeds differed significantly in the number of steps recorded by the pedometers, the average distance they covered in an hour, and the evenness of space use. Pasture type also influenced these indicators of movement behaviour, but the breed effect was detected consistently over all pastures.

Step count and speed were highly correlated ($R^2 = 0.90$) and showed similar patterns for the breeds and the pastures (**Figures 5a, b**): We found Original Braunvieh to be the breed that moved most, followed by Angus×Holstein, which differed marginally (steps: $p_{\mathrm{OB\sim AH}} = 0.86$, speed: $p_{\mathrm{OB\sim AH}} = 0.02$). Highland cattle took significantly fewer steps than Angus×Holstein ($p_{\mathrm{HC\sim AH}} = 0.04$) and Original Braunvieh ($p_{\mathrm{HC\sim OB}} = 0.02$), moved slower (speed: $p_{\mathrm{HC\sim AH}} = 0.09$, $p_{\mathrm{HC\sim OB}} < 0.001$, respectively), and spent more time lying than the other two breeds (**Figure 5.5c**).

All breeds were least active on the nutrient-rich pasture 1 and most active on the nutrient-poor pasture 3. Apart from this general trend, there was a consistent effect on all pastures. For instance, on pasture 3, where all breeds moved most, Highland cattle took about as many steps and covered about the same distance as the other two breeds on pasture 1, where Angus×Holstein and Original Braunvieh moved least.

The evenness of space use showed the opposite (**Figure 5.5d**): Highland cattle used the pastures most evenly, whereas the space use of Angus×Holstein was more clustered. This breed explored the available area least. There were no significant differences in evenness of space use between Angus×Holstein and Original Braunvieh ($p_{OB\sim AH} = 0.2$), but both breeds differed significantly from Highland cattle ($p_{HC\sim AH}$ and $p_{HC\sim OB} < 0.001$). In contrast to movement intensity, the evenness of space use was higher on the relatively homogeneous, flat pasture 1 than on the heterogeneous pastures 2 and 3. Again, however, on all pastures, Highland cattle used the area most evenly.

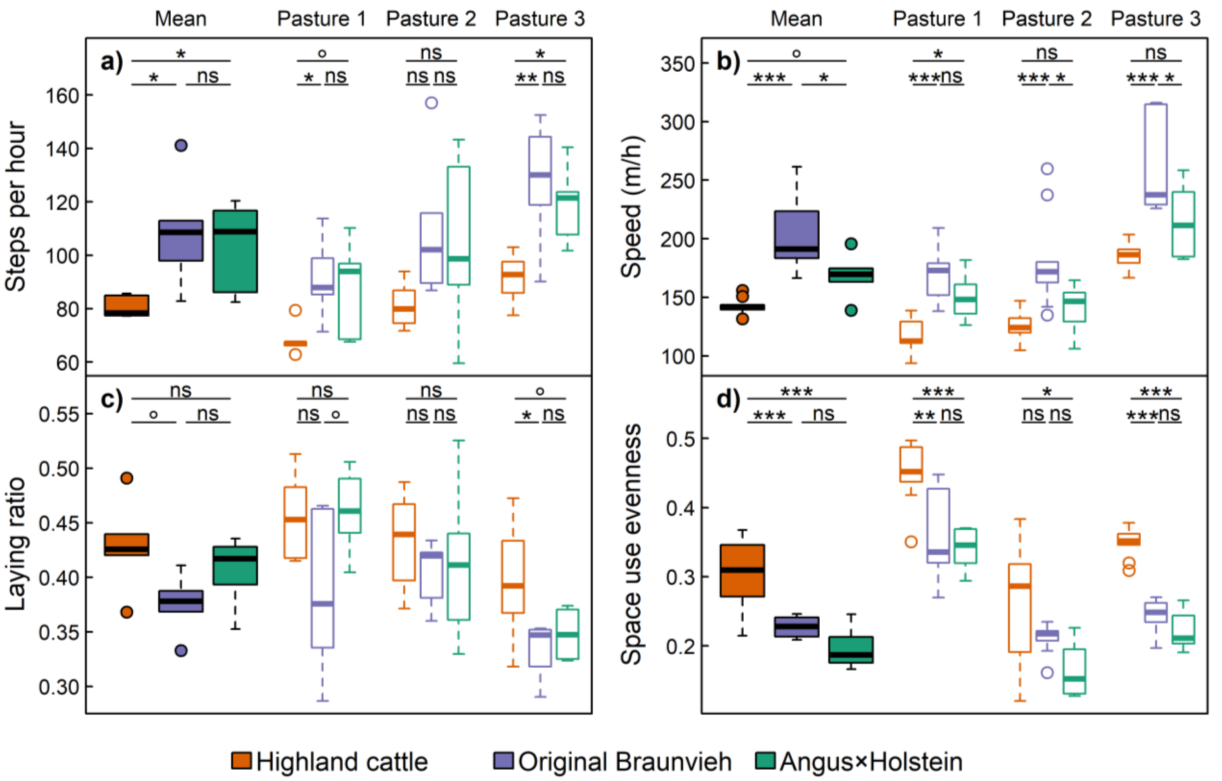


Figure 5.5 | Movement behaviour of the three breeds Angus×Holstein, Original Braunvieh and Highland cattle: **a** The average number of steps recorded per hour; **b** the average covered distance per hour (i.e. the speed); **c** the ratio of the time spent lying and **d** the evenness of space use. Steps and laying ratio were recorded for six, speed and space use evenness for all nine cows per breed. Filled boxplots represent mean values, empty boxplots differentiate by the three types of alpine pastures: (1) nutrient-rich, flat pasture, (2) heterogeneous dwarf-shrub pasture, (3) nutrient-poor fen and wood pasture (box: 25th to 75th quartile range (IRQ); line: median; whiskers: max. 1,5 x IQR; points: outliers; ns: $p > 0.1$; ∘ $p < 0.1$; ∗ $p < 0.05$; ∗∗ $p < 0.01$; ∗∗∗ $p < 0.001$).

5.3.3 Differences in foraging behaviour among breeds as influenced by pasture conditions

We found differences in the evenness of forage selection and the forage quality of selected plant species among cattle breeds, indicating that different breeds preferred different groups of plants. For all investigated indicators, Highland cattle differed from the other two breeds, whereas Angus×Holstein and Original Braunvieh behaved quite similarly. In fact, the two latter breeds did not differ significantly from each other (p = 0.29-1.0) for any of the indicators of foraging behaviour.

Highland cattle foraged more evenly than the other breeds (**Figure 5.6a**), as observed in the overall average ($p < 0.001$), as well as in pasture-wise values. Only the evenness of forage selection by Highland cattle in pasture 3 did not significantly differ from Angus×Holstein cattle. Simply put, Highland cattle ate what was available. Thereby, they selected forage with significantly lower quality than the other two breeds ($p < 0.001$; **Figure 5.6b**). This was also reflected in breed-specific preference and avoidance of certain plant groups. Broad-leaved grasses and legumes were the plants with the highest forage quality in our study area. Angus×Holstein and Original Braunvieh had a stronger preference for these plants than Highland cattle (**Figures 5.6c, d**). In contrast, thistles and shrubs had the lowest forage quality in our study area, and were foraged much less by Original Braunvieh and Angus×Holstein than by Highland cattle (**Figures 5.6e, f**). Because thistles primarily grew on pasture 2 and shrubs on pastures 2 and 3, differences were only detectable on these pastures.

In addition to breed, the pasture type also influenced foraging behaviour: Cattle selected their forage more evenly on the homogeneous, nutrient-rich pasture 1 than on the heterogeneous, nutrient-poor pasture 3. In contrast, the quality of selected forage was highest on pasture 1, where plants with the highest forage quality grew, and was lower on pasture 3, where only forage of low quality was available. Plant groups were most grazed on the pastures where they were most abundant, i.e. broad-leaved grasses and legumes on pasture 1, thistles on pasture 2 and shrubs on pasture 3.

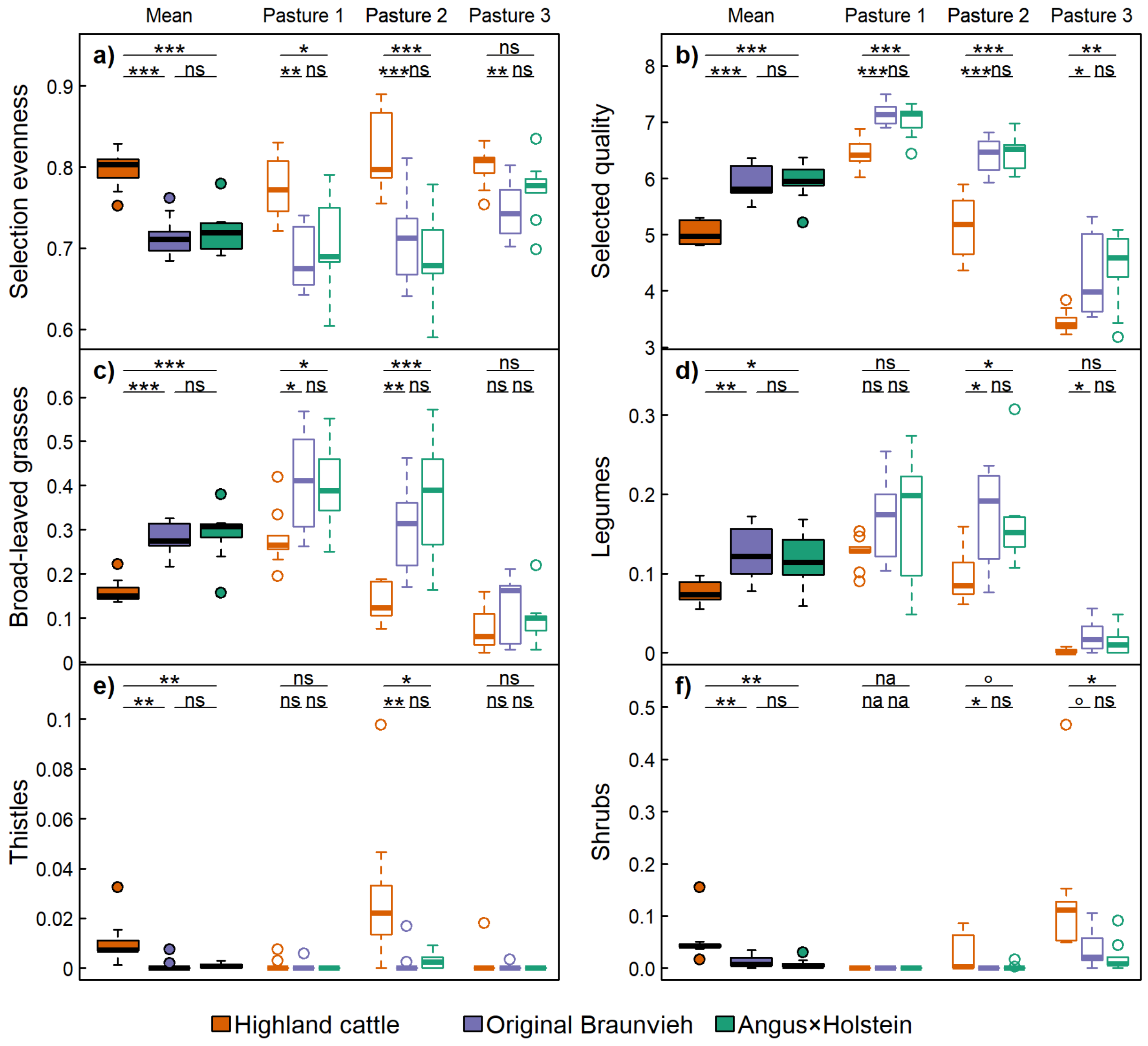


Figure 5.6 | Forage selection behaviour of three cattle breeds Angus×Holstein, Original Braunvieh and Highland cattle. For all the nine cows per breed, **a** the evenness of forage selection, **b** the average forage quality of the selected plants (Briemle et al., 2002), and the share of **c** broad-leaved grasses, **d** legumes, **e** thistles and **f** shrubs within the selected forage plants were measured. Filled boxplots represent average values, empty boxplots differentiate by the three types of alpine pastures: (1) nutrient-rich, flat pasture, (2) heterogeneous dwarf-shrub pasture, (3) nutrient-poor fen and wood pasture (box: 25th to 75th quartile range (IRQ); line: median; whiskers: max. 1,5 x IQR; points: outliers; ns: $p > 0.1$; $\circ\ p < 0.1$; $*\ p < 0.05$; $**\ p < 0.01$; $***\ p < 0.001$, na: not available).

5.3.4 Allometry of body weight, movement and foraging behaviour

There were various strong allometric relationships among the variables tested (**Figure 5.7**). Most allometries were more reasonably explained, if breed was taken into account. As described above, Highland cattle differed from Original Braunvieh and Angus×Holstein in all measured variables, as indicated by a significant shift along the allometric lines (i.e., data clouds in **Figure 5.7** are shifted along the direction of the lines). In addition to the simple positive or negative relationships, there were numerous effects of cattle breed on the specific allometries itself: We found significant differences in elevation among breeds' allometric lines (i.e., a parallel shift of the lines) for five out of nine allometries investigated.

Body weight and claw base (**Figure 5.7a**) were highly related to each other ($R^2 = 0.54$). The relationship was similar for all three breeds, as indicated by the lack of significant differences in slopes of the breeds' allometric lines. That is, heavy animals always had larger claws than light animals, independent of breed. However, breeds significantly differed in weight and claw base as indicated by a significant shift ($p < 0.001$) of Highland cattle data along the allometric lines compared to the other two breeds, which did not differ significantly from each other. In addition, not only the position of the point clouds of the breeds along the allometric lines, but also the elevation of their lines differed ($p = 0.01$). Highland cattle had significantly larger claw base in relationship to the body weight than the other two breeds.

There was an overall negative relationship between the average daily change in body weight and the quality of the selected forage for all breeds ($R^2 = 0.34$, **Figure 5.7b**): animals that selected forage of higher quality lost more weight. Taking breeds into account reveals that this is primarily a breed effect, as indicated by the highly significant differences in elevation of the allometric lines ($p < 0.001$) and that the relationship within each breed was positive, contrary to the overall negative relationship. In contrast to the other breeds, Highland cattle increased body weight despite low forage quality.

Breed also strongly affected the allometric relationship between selection evenness and lying ratio ($R^2 = 0.17$, **Figure 5.7c**). In general, animals that selected their forage more evenly, spent more time lying. Forage selection was most even for Highland cattle and they spent the most time lying (shift: $p < 0.001$), but relative to the evenness of their forage selection, the lying ratio was low (elevation $p = 0.005$).

Space use evenness showed a positive relationship with selection evenness ($R^2 = 0.52$, **Figure 5.7d**) and a negative relationship with the selected forage quality ($R^2 = 0.55$, **Figure 5.7e**), which in turn was negatively linked to selection evenness ($R^2 = 0.78$, **Figure 5.7f**). Animals that used space evenly also selected forage plants evenly, but they foraged plants of lower quality. Highland cattle used space and foraged most uniformly, but selected forage of lowest quality (shift of all allometries $p < 0.001$).

Over all breeds, the average number of steps recorded per hour was negatively related with the evenness of space use ($R^2 = 0.22$, **Figure 5.7g**). Animals that walked a lot covered less space. However, within each breed, the linkage of steps and space use evenness was less clear, pointing to a breed effect instead of a real allometric relationship (elevation: $p = 0.001$).

Finally, the number of steps recorded had a negative relationship with the evenness of selection ($R^2 = 0.55$, **Figure 5.7h**) and a positive one with the selected quality ($R^2 = 0.52$, **Figure 5.7i**). Animals that moved a lot, selected their forage plants more strictly and ingested forage of higher quality. Highland cattle, the breed that walked least, selected plant species least strictly and of lowest quality (shift of both allometries $p < 0.001$). The significant differences in elevation ($p = 0.02$) among breeds' allometric lines show that Highland cattle would have foraged more selectively or taken fewer steps, if the relationship of steps and selectivity only depended on the individual.

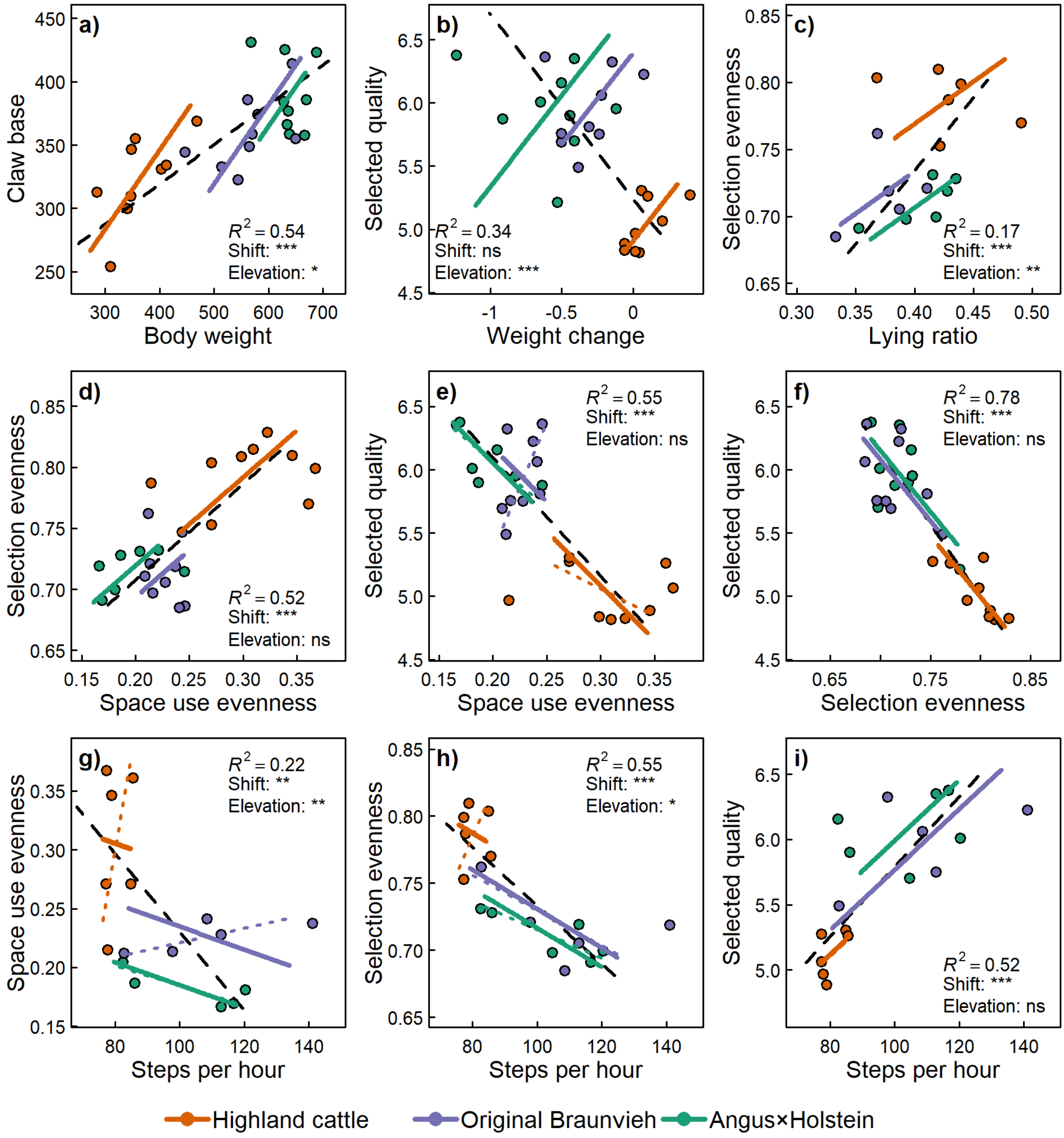


Figure 5.7 | Selected allometric relationships among variables concerning anatomy, movement and foraging behaviour of three cattle breeds: body weight (kg), claw base (cm), average daily body weight change over ten weeks on alpine pastures (kg/d), the average number of steps recorded per hour, the ratio of the time spent lying, the evenness of space use, the evenness of plant species selection and the average forage quality of the selected plants (Briemle et al., 2002). The number of recorded steps and lying ratio were available for six cows per breed and the other variables for nine cows per breed. Figures show the overall allometric line for all animals (dashed black) with their regression coefficient (R^2) as well as allometric lines for each of the three breeds. For all allometries where the slope differed significantly among breeds, the breed-specific allometric lines are provided (dashed lines) together with the forced common slope (solid lines). This was necessary for testing shift and elevation, for which significances of differences among breeds are given (ns: $p > 0.1$; $\circ$ $p < 0.1$; $*$ $p < 0.05$; $**$ $p < 0.01$; $***$ $p < 0.001$).

5.4 Discussion

5.4.1 Anatomical differences between breeds have consequences for animal health, soil and vegetation

This comparative study of three cattle breeds on alpine pastures identified several close allometric relationships between anatomy, movement, and foraging behaviour. In addition, the gradient of productivity, from low-productive Highland cattle over intermediate Original Braunvieh to high-productive Angus×Holstein, was consistently reflected in the parameters analysed.

Body weight and claw base were closely related at the individual level: The heavier a cow was, the larger was the area of its claw base. However, breed also mattered: Relatively small claws were measured for the two high-productive breeds compared to those of Highland cattle. Therefore, the static pressure of body mass on every square centimetre of claw base was relatively high for Angus×Holstein, marginally less for Original Braunvieh, and significantly lower for Highland cattle. The similar weight-claw allometry of the two productive breeds goes along with Tuohy et al. (2014), who found only small differences in weight-claw allometry between Holstein and Holstein×Jersey dairy cows. The relatively large claws of Highland cattle have been presumed (Nuss et al., 2014), but never been quantified in a comparative assessment before. For this experiment, cows where kept under similar, but not identical housing condition over winter. To increase comparability, they grazed the same grounds during ten weeks prior to the claw measurement. An explanation for the differences observed between breeds may be that the breeding process increased cattle’s body weights to a much larger extent than their claw bases – likely because nobody declared “large claws” as a breeding objective.

These differences may strongly affect the animals as well as the pastures they graze. Huge body mass on a small base has the potential to affect claw health and may be an overlooked source of claw pathologies. Comparing high-productive breeds among each other, previous studies have not found a clear impact of breed on claw health (Andersson and Lundström, 1981; Baird et al., 2009). However, testing a broader range of productivity, low-productive dairy breeds showed significantly fewer claw diseases than high-productive breeds (Mattiello et al., 2011). This may, at least partially, be explained by differences in allometry between body weight and claw base, because less weight burdens each square centimetre of claw. Correspondingly, many Highland cattle farmers have told us that they almost never observe claw diseases and rarely need claw trimming or veterinary assistance. Unfortunately, the relative frequency of claw diseases in Highland cattle has never been compared to other breeds.

Claw pressure not only influences animal welfare, but also the soil and vegetation of pastures. Generally, heavy animals on relatively small claws compress the soil more forcefully, thereby promoting erosion (Taboada et al., 2011). Herbin et al. (2011) reported an increase in soil penetration resistance and a decrease in porosity on pastures grazed by heavy animals with relatively small claw base. Accordingly, Pauler et al. (2019) found more open ground susceptible to erosion in pastures of high-productive breeds than in those of Highland cattle. If grazing intensity increases, to which trampling pressure contributes, soil organic carbon in C3-dominated grasslands decreases, with negative consequences for greenhouse gas emissions (McSherry and Ritchie, 2013). High trampling pressure comes along with structural deterioration and compaction of soil (Proffitt et al., 1993), whereas water storage capacity and pasture productivity decrease (Drewry et al., 2008). The negative effects of trampling (Bilotta et al., 2007) are particularly notable where heavy animals are present on steep slopes (Sheath and Carlson, 1998). In contrast, light Highland cattle with large claws have the potential to minimize trampling-induced erosion effects, especially on shallow alpine soils that benefit notably from light and moderate grazing (Trimble and Mendel, 1995). In addition, trampling pressure affects vegetation composition. In the long term, plant species adapted to trampling stress are promoted and outcompete trampling-susceptible plants on pastures of high-productive breeds more than on pastures of Highland cattle (Pauler et al., 2019).

5.4.2 Movement behavioural characteristics are allometrically related at the breed level

The observations of more open ground and trampling-adapted vegetation on pastures of high-productive breeds (Pauler et al., 2019) can be further explained by differences in moving behaviour. Not only the intensity of pressure affects soil and vegetation, but also the frequency of treading and its spatial distribution. It should be noted that static claw pressure, as measured in the present study, only applies when the animal is standing, equally weighting all four feet. Since pressure concentrates onto three or even two claws while moving, trampling pressure increases as the cow walks and exerts additional destructive kinetic energy (Bilotta et al., 2007). In our study, Highland cattle moved least and slowest on almost all pastures as measured by pedometer and GPS tracking. Thereby, they exert less physical pressure on vegetation and soil.

Generally, cattle do not cover available space evenly, especially on heterogeneous alpine pastures (Homburger et al., 2015; Kaufmann et al., 2013). It seems logical that animals that walk less visit fewer parts of the pasture and leave most places undiscovered. Yet, the opposite was the case. The fewer steps an animal took, the more evenly it occupied the available space. This unexpected negative allometry makes sense, if the breed effect is considered. Despite their slowness, Highland cattle discovered the most distant places on the pastures. In contrast, Original Braunvieh and Angus×Holstein took many steps, but explored a smaller share of the available area. The sparse flat and nutrient-rich parts of the pastures, where they spent the most time, provide plants of high forage quality and smooth terrain, which are both attractive qualities (Homburger et al., 2015; Kaufmann et al., 2013), especially for cattle with high nutritive demand and large body size. The data suggest that both productive breeds moved more than Highland cattle, but within a smaller space. Undemanding Highland cattle gathered less frequently on the attractive parts of the pastures, although pasture size was large enough not to force them to forage on the poorer parts of the pastures. Even space use is expected in smaller paddocks and at higher stocking density (Venter et al., 2019), but Highland cattle moved evenly voluntarily. The differences in movement behaviour among breeds go along with Spiegal et al. (2019), who found a traditional cattle breed visiting more different places than a high-productive breed, which preferred the hotspots more clearly. As Highland cattle move more evenly, they comply with farmers’ ambitions to utilize remote or unattractive parts of their land.

5.4.3 Foraging behaviour of the breeds is well explained by energy need for production

Generally, animals that used space evenly also foraged evenly, as supported by Bailey et al. (2006), and cattle that walked little also selected forage plants evenly. Independent of the breed, a cow that visited many different places, grazed many different plants and took only few steps. In other words, a highly selective cow needs to cover more distance to find the most palatable plants, while a less selective cow eats what is in close proximity of her mouth, not caring much about the quality. This corresponds with the low quality of the selected forage for those animals that took only few steps. Highland cattle moved the least, thereby foraging most evenly and selecting a diet of lowest quality compared to the other two breeds. Original Braunvieh cattle took an intermediate position, but were much more similar to Angus×Holstein than to Highland cattle.

Through modern breeding, Original Braunvieh and Angus×Holstein have been genetically designed for a higher growth rate and milk production than Highland cattle (Albertí et al., 2008). Therefore, they are in need of high-nutritive forage, such as broad-leaved grasses and legumes (Briemle et al., 2002) and move longer distances to reach these plants, whereas slow-growing Highland cattle, with low milk production, are satisfied with forage of lower quality and save steps while foraging.

In the long term, the higher selectivity of more productive breeds has important consequences for pasture vegetation (Pauler et al., 2019). If unattractive plants, such as toxic species (e.g., *Ranunculus*, *Aconitum*), plants of low forage quality (e.g., *Nardus stricta*), plants with physical defence mechanisms (e.g., thistles, *Deschampsia ceaspitosa*), or shrubs are avoided by cattle, they become more and more dominant (Augustine and McNaughton, 1998; Briske, 1996) . Thereby, they can outcompete species less-adapted to grazing, resulting in reduced plant species richness (Zehnder et al., in revision). The biodiversity of European mountainous pastures, for example, suffers from the continuous spread of shrubs and wood on formerly diverse and open grasslands (Agnoletti, 2007; Komac et al., 2013; Lasanta et al., 2009; Queiroz et al., 2014).

Interestingly, cattle that forage more evenly spend more time lying. A diet that is chosen evenly across the pasture contains more fibre-rich plants with higher leaf dry matter content and smaller specific leaf area than a strongly selected diet (Pauler et al., 2020). Fibre increases the ruminal retention time and, hence, the time required to digest the forage (Adin et al., 2009; Laca et al., 2001). Therefore, an animal that forages evenly, selects a diet of lower digestibility and, subsequently, spends longer time ruminating, normally done while lying. Highland cattle that foraged most evenly and selected plants of lowest digestibility, spent the longest time lying due to increased ruminal retention time. In addition to the overall allometric relationship of selection evenness and lying time concerning all individuals, there was a clear breed effect as indicated by the difference in elevation: If the relationship were independent of breed, Highland cattle would have lied even more, indicating that Highland cattle digested relatively quickly with respect to the quality of their forage. This suggests that Highland cattle have a more effective food conversion than higher-productive breeds, as already assumed by Bailey et al. (2002).

Highland cattle seem to make use of fibre-rich and nutrient-poor forage more efficiently and may, therefore, be better adapted to the harsh environment of alpine pastures than high-productive breeds. As a result, Highland cattle were able to gain body weight, even on the nutrient-poor pastures of our study area, where both of the production-oriented breeds lost weight. Additionally, the energy balance of Highland cattle is positively influenced by the woollier fur that provides thermal insulation and saves energy more effective than the short fur of Original Braunvieh or Angus×Holstein cattle. Finally, the positive weight gain of Highland cattle may be promoted by more efficient movement and foraging behaviour: By selecting plant species more evenly and consequently moving less and lying more, Highland cattle save legwork and kinetic energy. This unhurried behaviour balances the lower nutrient content of their diet.

In addition to more efficient ruminal food conversion, a warming fur, energy-saving movement and foraging behaviour, a higher dry matter intake of Highland cattle could explain the difference in weight gain among breeds. However, higher forage mass intake seems unlikely, as visual observation suggested rather smaller bites and bite rates for Highland cattle.

5.4.4 Implications for management, breeding and biodiversity

Cattle’s tendency to avoid plant species of low forage quality and the places where such plants are dominant counteracts pasture improvement and maintenance. To reduce the abundance of weeds and shrubs and thereby maximize pastural value, cattle should ideally forage all plants and visit all parts of a paddock evenly. Usually, alpine grasslands are so heterogeneous that cattle almost inevitably use it unevenly (Homburger et al., 2015). Highland cattle, which grazed most evenly among the investigated breeds, were able to exploit even unattractive plants and places.

The differences in space use evenness among breeds were most evident on pasture 3, which was more heterogeneous and offered poorer forage quality than the two other pastures in the experiment. This observation emphasizes the benefit of undemanding breeds, especially for grasslands that are unsuited for modern agricultural management (Eriksson, 2011).

It is indisputable that the production output of Highland cattle is low. Under intensive housing conditions, they cannot compete with the growth rate and carcass weight of other breeds (Albertí et al., 2008). Their real advantage is to cope with unfavourable conditions. This is highlighted by Highland cattle's small, but existent increase in body weight during the experiment, whereas the other breeds lost weight due to the poor nutritive supply. Though modern breeds have a higher weight gain potential, they cannot fulfil it on nutrient-poor pastures. Therefore, grazing such areas with high-productive breeds is economically inefficient due to the loss of body weight. In contrast, Highland cattle, which grow less effective and efficient in intensive farming systems, are still able to create a small output under poor conditions, resulting in a positive cost-value ratio (Mills, 2008).

Highland cattle breeders are proud of the benefits their animals provide, including high robustness, soil protection, reduction in problematic plant species, increased biodiversity, and a general efficiency even in these low-productive systems. Breeders should bear in mind that these qualities are closely related to the low productivity of this breed. Although it is tempting to modify breeding aims towards higher output, our data suggest that if Highland cattle were bred more productively, many of these benefits would be lost, as has been the case with other breeds.

In mountainous regions, pasture biodiversity is not only under general pressure of climatic and socio-economic changes (Dong et al., 2011; Liechti and Biber, 2016; MacDonald et al., 2000). The structural changes in modern agriculture have also negatively affected marginal grasslands: Pastures and meadows that are difficult to manage due to steep slope, too-wet or too-dry conditions, and poor forage quality become unattractive to farmers of high-productive cattle, because these animals cannot exploit their genetic potential under these conditions, as demonstrated by Bovolenta et al. in 1998. Therefore, the intensity of management decreases, and pastures are eventually abandoned (Gellrich and Zimmermann, 2007; Herzog and Seidl, 2018). Consequently, the rich biodiversity of these habitats vanishes under encroachment of shrubs and trees that are no longer suppressed (Tasser and Tappeiner, 2002; Zehnder et al., in revision). Although biodiversity conservation continues to receive increasing attention as an important ecosystem service of alpine pastures (Bürgi et al., 2015), not even public financial support for mountain farmers is currently able to halt the abandonment of marginal pastures (Schulz et al., 2018). An appropriate use of these habitats is grazing with undemanding livestock breeds like Highland cattle. There is no need for farmers to change their entire livestock, but some Highland cattle can often be added to existing herds without difficulty, as they are undemanding, not only in forage quality, but also in housing conditions. Incorporation of low-productive cattle breeds is, therefore, a key strategy to use low-productive, marginal grasslands efficiently and to conserve their biodiversity.

6 General discussion

6.1 Challenges in investigating breed differences and their impact on vegetation

Analysing plant-herbivore interactions poses numerous challenges and it was not able to answer all research questions in a single setup. Generally, there are two possible approaches: (1) an observational study at a large number of sites without manipulating the existing conditions or (2) a controlled grazing experiment in which the effects of different treatments, in this case breeds, are tested. To get a broad picture of breed differences and their impact on vegetation, both methods were used in this thesis.

6.1.1 Observational study: Addressing long-term effects and environmental variation

To measure the long-term impact of grazing by different breeds, an observational study comparing 50 paired pastures at 25 sites was designed (**Chapter 3.2; Figure 6.1**). At each site, one pasture of the pair was grazed by low-productive Highland cattle, the other one by a high-productive breed. Because vegetation adapts slowly, a controlled experiment would have needed years or even decades to show the long-term impacts of grazing. This may be the reason why earlier experimental studies found only weak effects after three or four years of grazing with a certain livestock breed (Dumont et al., 2007b; Jerrentrup et al., 2015; Scimone et al., 2007). In contrast, for the observational study presented here, pastures were selected which were already grazed at least five and up to 25 years by the respective cattle breed. Assessing the current vegetation composition as a result of grazing history made it possible to estimate the long-term effect without waiting for years.

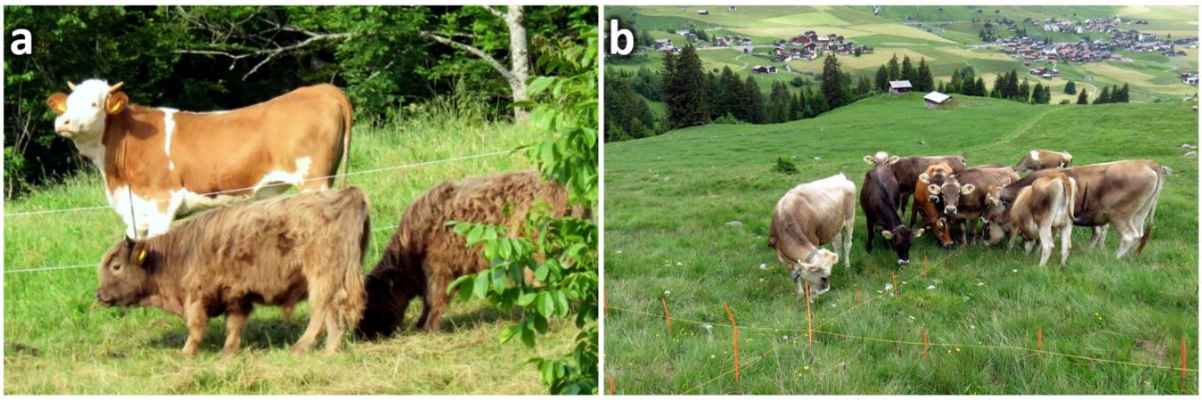


Figure 6.1 | Study design of the observational study: **a** At 25 locations, comparable and adjacent pastures of low-productive Highland cattle (foreground) and a high-productive breed (here Simmental Fleckvieh in the background) were analysed. (Side note: Despite the difference in size, the depicted animals are of about the same age.) **b** The percentage cover of every plant species was estimated in three vegetation subplots of 5 × 5 m in each of the paired pasture for a total of 150 surveys. As pastures were grazed for at least five years by the respective cattle breed, long-term effects on vegetation could be estimated.

However, the selected paired pastures necessarily needed to be highly comparable. It may be argued that Highland cattle pastures are generally less productive than pastures of more productive breeds, because farmers choose the breed based on the available land. However, a single pasture field seldom guides the choice of breeds on a farm. It was thus possible to select pairs of pastures which were quite similar in site conditions and management, even if they belonged to farms of totally different structure and intensity. For example, the most extensive pasture of an intensive farm raising a production-oriented breed and the most intensive pasture of an extensive farm raising Highland cattle may be adjacent and similar in environmental conditions. Additionally, if the vegetation differences between the paired pastures resulted from site conditions alone, they would not increase with time, as shown in **Figure 3.5**. The dependence on adaptation time suggests that differences in vegetation at least particularly trace back to the breed. Finally, the analysis showed that the two sampled pastures in each pair were indeed similar and comparable (**Chapter 3.3.1 and 3.4.1; Figure 3.2**).

A second important advantage of an observational study is to be representative for a large range of environmental conditions. If site conditions (elevation, inclination, pH value, soil nutrient contents, stocking rate) were considered in the models, there was a consistent breed effect across sites.

6.1.2 Controlled grazing experiment: Addressing herbivore movement and foraging behaviour

To quantify behavioural differences among herds and individuals, a grazing experiment was conducted on heterogeneous summer pastures in the Swiss Alps (**Figure 6.2; Chapter 4 and 5**). A controlled approach allows to observe animals simultaneously under similar conditions. Gathering data simultaneously is essential because weather, time of the day, season and forage on offer can affect the behaviour of cattle and these confounding effects can falsify the results (Hurlbert, 1984). From this point of view, it would have been best to graze all animals on the same pasture at the same time. However, cattle are herd animals. They permanently interact with each other and the behaviour of one animal can influence the behaviour of others. For estimating the behaviour of a single breed (**Chapter 5**), it was thus crucial to observe the breeds separately.

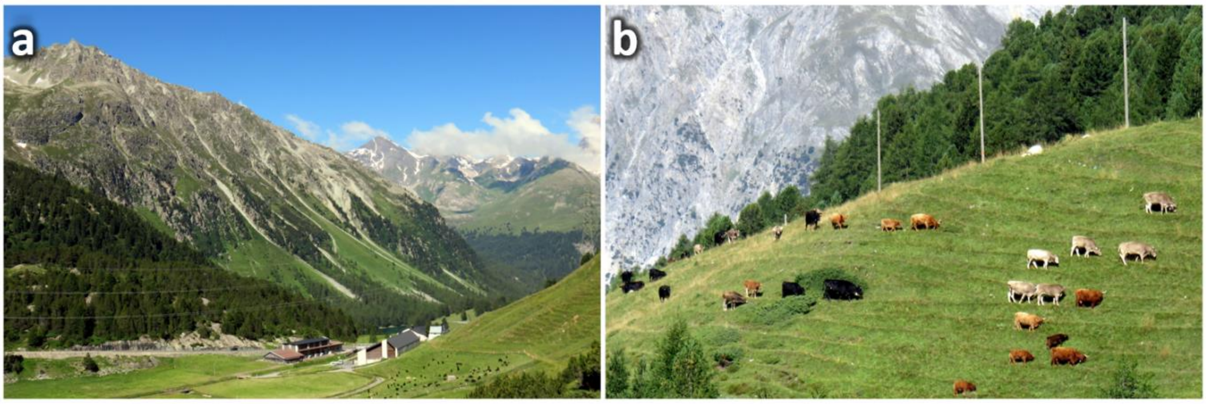


Figure 6.2 | a The grazing experiment was conducted on the alpine pastures of Alp Weissenstein, a research station of ETH Zurich/AgroVet Strickhof in the eastern Swiss Alps (2026 m asl., 46.5816° N, 9.8002° E). Picture **b** shows the cows and calves involved in the grazing experiment while changing pastures.

Observing the breeds on the same pasture one after the other would have provided similar site conditions for all breeds, but in this case, animals could not have been observed simultaneously. Additionally, the forage preference and avoidance of the breed grazing the pasture first would have altered the forage on offer for the breed grazing the pasture hereafter.

The best alternative was to keep the breeds in separate paddocks simultaneously. However, thereby the problems of comparable site conditions and their interaction with breeds reoccurred. Thus, confounding effects were avoided by finding homogeneous pastures that were subdivided into most comparable paddocks – one for each breed – and additionally applying a Latin square design in which each breed grazed each paddock once (**Chapter 4.2.3 and 4.3.1**). In order to avoid pseudoreplication of cattle individuals, different animals were used for each rotation (Hurlbert, 1984).

To estimate the effect of different vegetation types and to make the study more representative for other marginal pastures, this setup was repeated on three pastures of contrasting conditions available in the study area (Michna et al., 2013; **Chapter 4.2.1, 5.2.2 and Figure 6.3**). The nested study design allowed for independent replications of paddocks, vegetation subplots and herds. The pastures offered significantly contrasting conditions, whereas the paddocks of each pasture were highly comparable (**Chapter 4.3.1**). Thus, cattle could graze simultaneously under similar conditions and the study design fulfilled the requirements adequately.

Figure 6.3 | Three pasture types were analysed in the controlled grazing experiment: **a** A flat, fertile pasture. **b** A heterogeneous, steep and nutrient-poor pasture with a few flat, nutrient-rich parts. **c** A steep and extremely nutrient-poor wood pasture. Each pasture was subdivided into three comparable paddocks grazed simultaneously by three different breeds. Every paddock was grazed once by each breed during the summer in a Latin square design. Thereby, pseudoreplication was avoided and interactions of behaviour and site conditions could be estimated.

Two distinct assessment layouts were established within the controlled grazing experiment that focused on different aspects which could not been analysed in a single setup (**Figure 6.4**):

The first sub-study (**Chapter 4**) laid the focus on the exact composition of cattle's diet at plant species level. The huge species richness of alpine pastures (Wilson et al., 2012) is a challenge for analysing plant-herbivore interactions. Plant composition is heterogeneous and the large number of species makes it impossible to identify all of them from afar while the cattle are foraging. Former consumption studies therefore avoided permanent pastures and focused on homogeneous sown grassland with clearly defined species easy to identify (Ganskopp et al., 1997; Parsons et al., 1994) or limited their analysis to vegetation types instead of plant species (Wallis de Vries and Daleboudt, 1994). Nevertheless, it is essential to identify single plant species within the diet in order to understand the mechanisms of selection and the drivers of botanical composition in these species-rich habitats. The study presented here overcomes these limitations by comparing biomass proportions of each plant species before and after grazing on a continuous scale (**Figure 6.4a; Chapter 4.2.4 and 4.4.1**) and not only by classes of consumption as formerly done (Iussig et al., 2015; Meisser et al., 2014; Mládek et al., 2013). This approach allowed precisely estimating the impact of various plant traits on selection behaviour.

The second sub-study (**Chapter 5**) focused on behavioural differences among individuals. Unfortunately, it was not possible to gather the consumption data of the first sub-study on cattle individuum level, because due to animal welfare reasons, a number of cattle grazed the pasture together. It was thus not distinguishable which cow exactly foraged the analysed plants. Separating the cows from each other would have falsified the results by causing unnatural behaviour. Therefore, the foraging behaviour of single cows was estimated by visually observing each cow separately while foraging (e.g. Katjiua and Ward, 2006; Sanon et al., 2007; **Figure 6.4c**). Using this layout, plants could not be analysed on species level, because a number of species had to be grouped together as they are not distinguishable from afar. However, it was possible to gather information about the diet composition of individual animals. Additionally, the movement behaviour of individuals was monitored by step-counting pedometers (**Figure 6.4e**) and GPS trackers (**Figure 6.4f**), which recorded covered distance and the evenness of space use (as done for example by Homburger et al., 2015; Leso et al., 2018)

Figure 6.4 | Illustration of methods applied in the grazing experiment: **a** The biomass of every plant species was estimated in vegetation subplots of 3 × 3 m before and after grazing. A total of 186 surveys were done. **b** All cows were weighed and the area of their claw base was measured. **c** The forage selection of each cow was observed during grazing by recording consumed plant species. **d** Animal-borne sensors were applied to explore movement behaviour: **e** movement intensity was estimated by pedometers counting steps; **f** GPS loggers provided information about covered distance and evenness of space use.

6.1.3 Challenges in working with animal-borne sensors

Animal-borne sensors such as pedometers and GPS loggers allow to permanently observe cattle and provide information about movement behaviour at the individual level. However, they entailed two kinds of problems. The first was a mere technical issue: The application of sensors is time-consuming and, as battery and storing capacities are limited, they had to be put on and off several times during the grazing experiment. Additionally, under alpine outdoor conditions, some devices broke and had to be replaced. These technical problems resulted in an additional time effort.

The second problem was a rather scientific one: The reliability of the black box data provided by sensors had to be verified, since for both sensors existed concerns: (1) The pedometers were developed for Holstein cows and the validity for other breeds had not been comparatively tested before. (2) Flanking mountains are known to compromise the GPS-signal and the reliability of data. Therefore, the concordance of both sensors was carefully checked and compared with visual observations. The step count of pedometers was highly correlated with the covered distance measured by GPS loggers and both were supported by visual observation. Therefore, the sensor data were considered as reliable and they fit into a consistent overall picture of other findings.

6.1.4 Challenges in working with cattle as experimental animals

A fundamental challenge was the fact that dealing with cattle on pastures is much more difficult, time-consuming and expensive than dealing with common experimental animals in a laboratory environment. The number of replications was inevitably lower. As the main focus of the thesis laid on specific interactions between vegetation and cattle and their ecological implications, it was not possible to replace them by another model organism. However, a large number of cattle not only amplifies cost and labour, but also complicates finding appropriate pastures with homogeneous conditions. Hence, with nine cows and nine calves of each breed, the number of individuals was set as high as manageable and affordable, but of course, it was not comparable with the number of replications in a laboratory mice experiment. Despite this limitation, the sample size proved to be large enough to point out significant breed effects in all sub-studies.

Additionally, it was not affordable to raise cattle exclusively for this study, as it is commonly done with smaller laboratory animals. The cattle observed in the grazing experiment originated from different farms and the possibility cannot be ruled out that behavioural differences are caused by former conditioning. To minimise the effect of earlier learned behaviour, care was taken to select animals from comparable farms: All animals originated from farms in the montane zone and were kept as suckler cows. They all had experience in grazing high-elevation summer pastures and had regular access to pastures in spring. Additionally, all animals grazed the pastures of the study area together two weeks before the experiment started and thereby have acclimatised to the alpine conditions.

6.2 Novel ecological findings

For the first time it was shown that differences in the vegetation of high- and low-productive cattle breeds' pastures can be consistently explained by formerly unknown differences in anatomy, movement and foraging behaviour among cattle breeds. These findings allow to answer the questions initially asked (marked by boxes).

6.2.1 Overlooked consequences of breeding

Did the changes, that intentionally formed modern cattle breeds, come along with unintended anatomical and behavioural modifications?

→ **Yes. Comparing three cattle breeds modified by breeding to different extent, demonstrated significant differences in anatomy, movement and foraging behaviour** (**Chapter 5**).

The three breeds analysed in the grazing experiment were chosen with care to represent different levels of breeding intensity:

(1) Highland cattle breeders did not focus on higher meat or milk production. Modesty, undemanding foraging and housing requirements and robustness have been the main criteria of artificial selection until today (Highland Cattle Society Switzerland, 2020).

(2) Original Braunvieh is a traditional, dual-purpose breed. Meat and milk production were moderately enhanced by modern breeding, but it has not undergone the intensive breeding transformations of Brown Swiss, formed from the same original population and modified to a high-productive dairy breed (Original Braunvieh Association Switzerland, 2020). Thus, Original Braunvieh has an intermediate position between low-productive Highland cattle hardly affected by modern breeding and the third, high-productive breed: Angus×Holstein crossbreed cattle.

(3) Angus×Holstein cattle resulted from crossbreeding Angus bulls with Holstein cows. Holstein cattle are the most productive and most common dairy breed in the world. In Switzerland an average Holstein cow produces more than 9 000 kg milk annually (Holstein Association Switzerland, 2020); in the USA, where the feeding of concentrates is less restricted, actually 12 800 kg are recorded on average (Holstein Association USA, 2020). Angus cattle are a popular, polled (i.e. genetically hornless) beef breed with large muscle content. They are particularly fast-growing and early maturing (Mutterkuh Schweiz, 2020; **Figure 3.3**).

The three breeds represent a straight gradient of productivity from (1) cattle that were bred for robustness rather than for meat or milk yield increase, (2) cattle moderately bred for milk and for meat production as a dual-purpose breed and (3) crossbreed of cattle intensively bred for milk or meat production, respectively, in two separate single-purpose breeds.

The anatomical and behavioural parameters analysed consistently reflected this gradient (see below in detail and **Chapter 6.6.2**): The less productive a breed was, the lighter it was and the larger was the claw base relative to the body weight (**Chapter 5.3.1**). In addition, the low-productive Highland cattle foraged least selective and most evenly followed by intermediate Original Braunvieh. The most intensive breed, Angus×Holstein cattle, grazed most selectively (**Chapter 5.3.3**). The same pattern was seen for movement behaviour: The less intensive a breed, the more even the animals covered the space of the pasture and the less distance they covered (**Chapter 5.3.2**). Moreover, the least productive breed was able to deal with nutrient-poor fodder best and subsequently gained weight on alpine pastures. The more productive breeds, however, lost weight – most significantly for the most productive breed (**Chapter 5.3.1**).

The underlaying mechanisms of artificial selection do not differ from natural selection: Populations adapt to drivers of selection. The more important a criterium is for the reproductive success, the more clearly the population will evolve with regards to this trait. By selecting strictly for milk or meat yield, breeders establish strong selective drivers that override many traits less focused on. Characteristics which are less important for reproductive success (i.e. breeders do not select for them), are subordinated to stronger selective drivers. Subsequently, if there is no evolutionary pressure for a certain trait, it will alter or disappear unintentionally (Darwin, 1859; Hall and Colegrave, 2008). If, for example, breeders do not select towards an efficient conversion of fibre-rich fodder, and concentrated feed is supplemented, efficiency becomes a less essential driver of reproductive success and subsequently decreases.

6.2.2 Impact on pasture vegetation

If there are anatomical and behavioural differences, do high-productive cattle breeds influence pasture compositions in different ways than low-productive breeds?

What are the long-term effects of cattle grazing on pasture vegetation?

→ Yes. Anatomical and behavioural differences among cattle breeds can explain differences in pasture vegetation and long-term effects of grazing depend, inter alia, on the grazing cattle breed.

The findings of this thesis presented a consistent picture of mechanisms of cattle impact (**Chapter 4 and 5**) and how they are reflected in vegetation (**Chapter 3**; most illustrative in the structural equation model: **Figure 3.6**). To point out in which way cattle behaviour in general and breed characteristics in particular influence pasture vegetation, it is useful to recapitulate the initially mentioned, general mechanisms of grazing impact which promote plant species with certain traits: fast-growing, short, unpalatable, trampling-resistant, nutriphilous, heliophilous and zoochoric plant species.

Vegetation is influenced by *universal* grazing mechanisms

Mechanisms: Several plant traits were not influenced by the grazing breed, because the underlaying mechanisms are universal and apply to cattle in general. Fast-growing and heliophilous plant species were not affected by breed. These plant characteristics rely on biomass removal by herbivores: Fast-growing species can rebuild destroyed organs quickly. Heliophilous species benefit from the removal of neighbouring individuals and make use of incident light efficiently. Hence, both have a competitive advantage on pastures, independent of the grazing breed. The same universality applies for plants with short habitus, which have about the same abundance on pastures of different breeds. This means that low-productive breeds forage the sward not higher or lower than high-productive breeds, and short plants cannot be reached by cattle's mouth, irrespective of the breed.

Additionally, it was shown that unpalatable plants are generally avoided by cattle (**Chapter 4.3.3**). Subsequently they are indirectly promoted on pastures (**Chapter 3.3.3**). Plant traits which make a plant tasty or unpalatable for cattle were analysed in more detail. Thereby, a number of universal preference-avoidance mechanisms were detected, consistently across different locations, seasons and breeds (**Chapter 4.4.2**):

Plants with high nitrogen and phosphorous content (Woodward and Coppock, 1995) were generally preferred. In grassland diets, especially on nutrient-poor alpine pastures, these nutrients are in short supply. As cattle essentially need these nutrients, they select plants of high nitrogen and phosphorous content. On the contrary, plants with high C:N ratio due to structural tissue were avoided, because carbon is abundantly available on alpine pastures. Foraging plant species with a high share of cellulose and lignin and with high leaf dry matter content, increases the time spent foraging and digesting. Thereby, the total intake of desired nutrients (Katjiua and Ward, 2006) and animals productivity decrease (Pakeman, 2014). Besides nutrient content, cattle's foraging behaviour was generally influenced by the physical texture of plants. Species with thin leaves (i.e. high specific leaf area; Cingolani et al., 2005; Mládek et al., 2013) are easy to crop, ingest and digest and therefore, they are preferred. In contrast, the grazing experiment demonstrated that cattle generally avoid woody plants and species with defence structures such as hairs, thorns or spines (in accordance with Fraser et al., 2009; Gong and Zhang, 2014; Laca et al., 2001).

<u>Consequences</u>: In long-term, heliophilous, fast-growing, short plants of low nutrient content and with defence mechanisms become dominant on all cattle pastures, irrespective of the grazing breed, as they outcompete plans species less adapted to grazing.

Vegetation is influenced by *breed-specific* grazing mechanisms

In addition to the above-mentioned mechanisms that count for all cattle breeds, there are differences among cattle breeds which in long-term change pasture plant species composition.

Unpalatable plant species – influenced by foraging behaviour

<u>Mechanisms</u>: Besides the universal preference of nutrient-rich fodder and avoidance of unpalatable plant species, it is noteworthy that even these general mechanisms were not independent of breed. The more productive a breed was, the stricter was the preference for tasty and the avoidance of unpalatable plants.

Highland cattle, the least productive breed, foraged least selectively and most evenly, whereas Angus×Holstein cattle, the most productive breed analysed for this thesis, foraged most selectively and least evenly. Plant species commonly assumed as high-quality fodder (e.g. broad-leaved grasses and legumes) were foraged more frequently, while plants of low forage quality (e.g. fine-leaved grasses, Cyperaceae, Juncaceae) were consumed less frequently by high-productive than by low-productive breeds. The same applied for plants with physical or chemical defence mechanisms, (e.g. thistles and toxic species). Highland cattle cared much less about these constraints and foraged them anyway (**Figure 6.5**). One Highland cow was observed willingly foraging silver thistles (*Carlina acaulis* L.) while refusing the grasses and legumes on offer. Another one ate a whole aconite – one of the most toxic plants in Europe, of which a few grams can kill a human. Highland cattle even consumed toxic ivy

(*Hedera helix* L.) or autumn crocus (*Colchicum autumnale* L.) frequently whereas more productive breeds avoided these plants consequently.

However, the impact of breeds productivity on selection was not only seen on the plant species level but also on the level of plant traits: Traits, associated with high forage quality (e.g. high nitrogen and phosphorous content, large specific leaf area) were clearer preferred by high- than by low-productive breeds, with Angus×Holstein preferring the best forage plants most clearly. On the contrary, traits associated with low forage quality (large C:N ratio, high leaf dry matter content and effective defence mechanisms) had least negative impact on the forage decision of low-productive Highland cattle.

Original Braunvieh, which are less productive than Angus×Holstein, but more productive than Highland cattle, took an intermediate position in their foraging behaviour. With regard to trait selection and consumption of plant species, they were intermediate between the two extreme breeds, but their foraging behaviour was more similar to Angus×Holstein than to Highland cattle.

It is likely that the higher selectivity of high-productive breeds is caused by an enhanced nutrient requirement. To meet their demand for genetically defined weight gain and milk production, high-productive animals have to select plant species with high nutrient density. On the contrary, breeds with lower growth rate and milk production (Albertí et al., 2008) can satisfy their needs with fodder of lower quality and thus select less strictly.

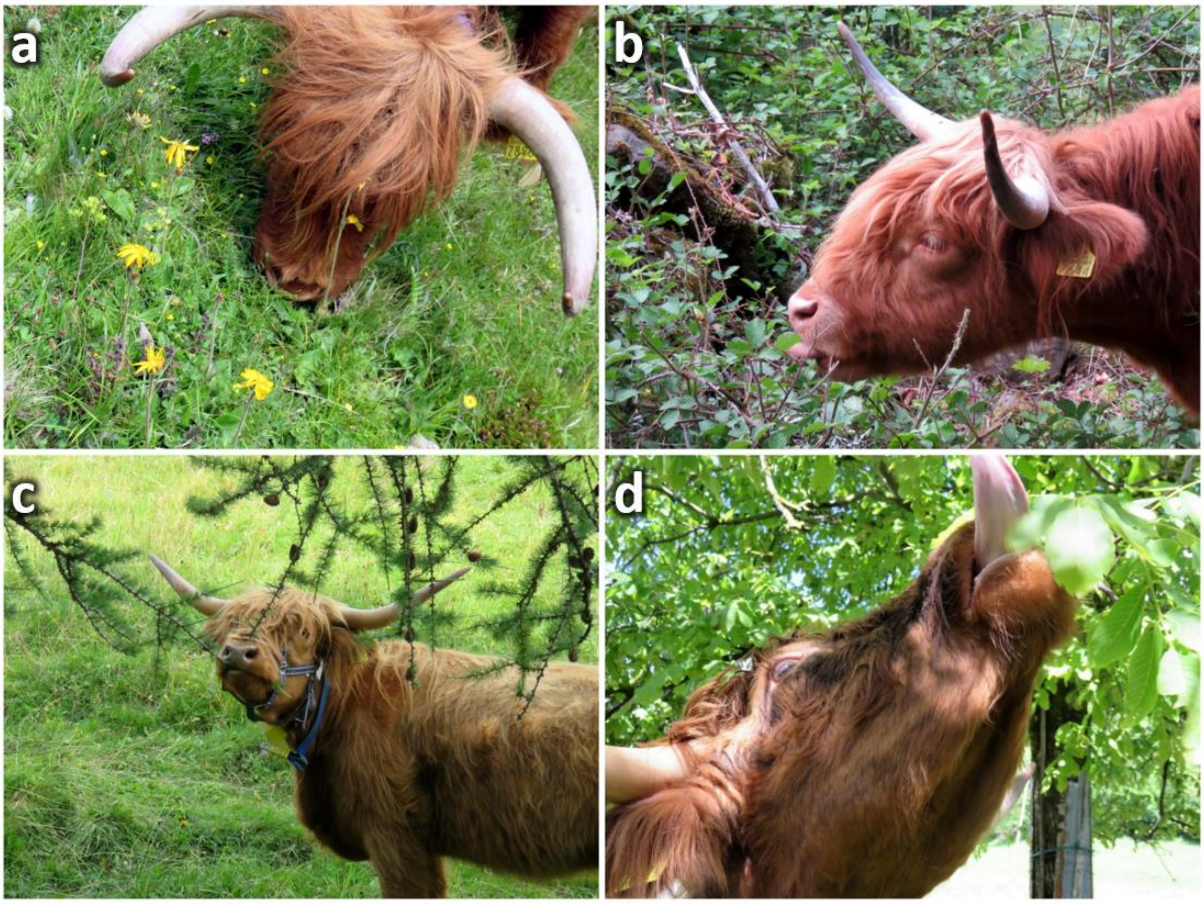


Figure 6.5 | Low-productive cattle avoid plant species protected by physical defence mechanisms or woodiness less strictly than high-productive breeds. Displayed are Highland cows foraging **a** dwarf thistle (*Cirsium acaule* SCOP), **b** blackberry (*Rubus fruticosus* agg. L.), **c** larch (*Larix decidua* MILL.) and **d** walnut (*Juglans regia* L.).

Consequences: In the long term, the enhanced selectivity of high-productive breeds strongly impacts plant species composition of pastures (**Chapter 3.3 and 3.4**). Vegetation grazed by production-oriented breeds showed more typical aspects of grazing adaptation (Adler et al., 2001; Díaz et al., 2001) than pastures of low-productive Highland cattle as for instance indicated by significant differences in grazing indicator values (Briemle et al., 2002). The stricter avoidance of species with physical defence, for example, was reflected in a four times higher cover of thistles (genera *Carduus*, *Carlina* and *Cirsium*) and a higher abundance of woody species (mainly shrubs and dwarf-shrubs, e.g. *Juniperus communis* L., *Calluna vulgaris* (L.) HULL, *Vaccinium myrtillus* L., *Pinus mugo* TURRA) on pastures of high-productive breeds than on pastures grazed by Highland cattle for a long time (**Chapter 3.3.3**).

If unattractive plant species are avoided, their distribution is indirectly promoted and they become increasingly dominant (Augustine and McNaughton, 1998; Briske, 1996). Thereby, these grazing-adapted species outcompete less specialised plants to a greater extent on pastures of high-productive cattle, resulting in a lower plant species richness on pastures of high- than of low-productive breeds (**Chapter 3.3.5 and 3.3.6**).

Trampling-adapted species – influenced by anatomy and movement behaviour

Trampling pressure occurs, of course, under every cattle claw and therefore, trampling resistant plants are generally promoted on pastures. However, there were remarkable differences in anatomy and movement behaviour between low- and high-productive breeds that modify the impact of trampling.

Mechanisms I (anatomy): The body weight differed among cattle breeds. The more productive a breed was, the heavier it was on average and the more mass burdened the vegetation. However, body mass distributes over the entire base of the claw. Therefore, the static trampling pressure is a function of both, body weight and claw base.

This thesis showed for the first time in a comparative assessment, that the ratio of body weight and claw base differs among breeds and that these differences depend on the breeding intensity (**Chapter 5.3.1**). Claw base was correlated with body weight at the individual level, but high-productive breeds had small claws in relation to their body weight. That means that the more intensive a breed was, the more mass burdened every square centimetre of claw base. In the last century, breeding societies paid close attention to increase body weight, but only little attention to the base on which this mass burdens. Thereby, body weight increased to a larger extend than claw base and subsequently, the trampling pressure enhanced unnoticed.

Consequences I: A large body mass on relatively small claws has the potential to influence animal welfare, pasture soil and vegetation composition. First, it may be an overlooked source of claw pathologies and explain the differences in claw health found earlier when comparing cattle of varying breeding intensity (Mattiello et al., 2011). Large claws of low-productive breeds may contribute to their better claw health status, reported by farmers.

Second, the negative impact of forceful trampling on the soil increases with the static pressure. Trampling pressure compresses the soil, decreases water storage capacity, reduces pasture productivity and increases structural deterioration and erosion (Bilotta et al., 2007; Drewry et al., 2008; Herbin et al., 2011; Kissling et al., 2009; Proffitt et al., 1993; Taboada et al., 2011). Accordingly, more open ground was found on pastures of high-productive breeds (**Chapter 3.3.3**) causing problematic erosion, especially on shallow alpine soils (Trimble and Mendel, 1995).

Finally, trampling is an important driver of plant species composition (Cole, 1995; Lezama and Paruelo, 2016). The observational study clearly pointed out higher trampling indicator values on pastures of high-productive cattle breeds (Briemle et al., 2002; **Chapter 3.3.3, 3.3.5 and 3.4.3**). Moreover, trampling adapted plant species like *Trifolium repens* L., *Poa annua* L. or *Plantago major* L. were more dominant there (**Chapter 3.3.6**). In the long term, high trampling pressure is negatively correlated to plant species richness (Jägerbrand and Alatalo, 2015; Pickering and Growcock, 2009), as consistently demonstrated in this study (**Chapter 3.4.3**). The differences in claw size and body weight are able to explain differences in plant species richness well: In grasslands trampled by heavy cattle on small claws trampling-susceptible species are outcompeted and plant diversity decreases, whereas these species can survive on pastures of lighter, low-productive breeds with relatively large claws.

Mechanisms II (movement): In addition to the breed-specific weight-claw ratio, there are differences among cattle breeds in the movement behaviour (**Chapter 5.3.2**) that can explain breed-specific trampling adaptation of pasture vegetation (**Chapter 3.3.3 and 3.4.3**).

Besides the amount of static weight, the frequency and shearing force of steps influences the impact of pressure on vegetation. Highland cattle were found moving least and slowest. Hereby, they reduced frequency and intensity of trampling pressure. Additionally, Highland cattle covered the space of their pastures most evenly and thereby caused least damage of plants at favoured resting places (**Figure 6.6**). The imposed destructive trampling pressure on vegetation and soil was lowest for low-productive Highland cattle, increased for intermediate Original Braunvieh and was largest for most-productive Angus×Holstein.

Moreover, the grazing experiment not only demonstrated that the movement behaviour differs among breeds, but also newly pointed out that movement is related to selective foraging: Highland cattle as a slow-growing breed had the lowest nutritive requirements. Consequently, the diet they chose had the lowest quality, because they foraged least selectively. As they just consumed what was in close proximity to their mouths, not caring much about the quality, they had to move less while foraging. In contrast, the more productive breeds had to cover longer distances to reach the best forage plants, which can be far apart from each other on heterogeneous alpine pastures. In such vegetation, a nutrient-rich diet demands a large invest in movement. Subsequently, the more productive a breed was, the more it moved and hence, the more physical pressure it inserted.

Consequences II: The differences in movement-caused trampling pressure enforce the above-mentioned differences in trampling adaptation, plant species richness and erosion of pastures grazed by high- or low-productive breeds.

Figure 6.6 | Illustration of differences in movement behaviour: **a** High-productive breeds spend more time at attractive places characterised by smooth terrain and high forage quality, **b** whereas low-productive breeds cover the available space more evenly and thereby, also explore steep slopes. Picture **c** portrays the only fertile and flat place of one of the grazing experiment pastures, whose majority is much less attractive for cattle. The vegetation of the Highland cattle paddock (foreground) is hardly untouched, whereas Angus×Holstein cattle (background) overused the attractive sward.

Nutriphilous species – influenced by movement behaviour

Mechanisms: The high-productive breeds were least willing to spend time at areas of steep slope and within plant communities of low forage quality. Subsequently, they used the space less evenly, and commonly stayed at the sparse attractive places (**Chapter 5.4.2**). Smooth terrain and high forage quality were formerly found attractive for cattle (Homburger et al., 2015; Kaufmann et al., 2013). The results of this thesis suggest that these preferences especially apply to heavy animals with high nutritive demand. Thus, high-productive breeds concentrated not only their destructive trampling pressure, but also excretion at a small share of the pasture.

Consequences: In the long term, high-productive breeds create overused and eutrophicated (resting) places (**Figure 6.6a)**. In these areas, plant species richness decreases because a few, highly specialised species are better able to cope with trampling pressure and can make use of the high nutritive supply more efficiently than others. Thereby, they outcompete the majority of other plants. These species-poor plant societies are dominated, for example, by *Plantago major* L., *Rumex alpinus* L. or *Urtica dioica* L. In contrast, undemanding Highland cattle regularly discovered unattractive and distant places of the pasture and thereby distributed the trampling impact more evenly (**Chapter 5.3.3 and 5.4.2**). Consequently, overused and species-poor places were less distinct on their pastures (**Chapter 3.4.2**).

Epizoochoric species – influenced by anatomy

Mechanisms: Herbivores serve as a dispersal vector for zoochoric plants by (1) the consumption and excretion of seeds and other diaspores of endozoochoric and (2) by external adhesion of epizoochoric plant species’ diaspores. No breed differences were found in the consumption and abundance of endozoochoric species (data not shown), but actually for the dispersal of epizoochoric plants. The longer and the woollier cattle’s fur is, the more effective diaspores can be attached and transported, and the more likely they colonise new ground and proliferate.

Consequences: Highland cattle, the overarching model for low-productive cattle in this thesis, has especially long fur. Therefore, on pastures grazed by Highland cattle, epizoochoric plant species were significantly more abundant than on pastures grazed by other cattle (**Chapter 3.3.3 and 3.3.6**). This highlights the ecological advantage, which Highland cattle provide for epizoochoric plant species. Many of these are endangered since the area of extensively managed pastureland declines (Ozinga et al., 2008; Poschlod et al., 1998). By transporting diaspores in their fur, Highland cattle contribute to biotope cross-linking and sustaining plant species richness.

However, the length and woolliness of fur is not a direct consequence of breeding intensity, but a special characteristic of this particular breed. Nevertheless, most woolly or long-haired cattle are low-productive breeds formed under rough climatic conditions (e.g. Highland cattle, Galloway, Sacha Ynaga cattle, Monchina cattle), whereas high-productive breeds are commonly smooth- and short-haired, because their reproductive success does not depend on adaptation to cold winters. However, there are exceptions on either side as for example short-haired, low-productive Hinterwälder and woolly, high-productive Salers. Long hair, especially in the winter coat, seems to be a primary, natural trait as indicated by the fur characteristics of ancient wild aurochs (*Bos primigenius*) as well as recent related species within the genus *Bos*, like bison (*Bos bison bison*), wisent (*Bos bison bonasus*) and yak (*Bos mutus*; Lampert, 2019).

6.2.3 Maintenance and efficient use of species-rich grasslands

Are there cattle breeds whose low requirements allow for an efficient use of nutrient-poor, marginal grasslands in order to sustain their species richness?

→ Yes. Due to only little modifications by breeding, low-productive cattle breeds are still appropriate for grazing and maintaining endangered, marginal grasslands. In contrast to modern, high-productive cattle, they gain weight even under challenging environmental conditions because of their high efficiency.

Maintenance of nutrient-poor, marginal grasslands

As initially shown species-rich, semi-natural grasslands are faced with a double challenge these days: Intensive management endangers species richness at productive, fertile sites as well as abandonment at nutrient-poor, marginal sites (Poschlod, 2017). Both developments were enforced by the increasing productivity of modern cattle breeds, which came along with elevated requirements. If modern cattle are grazed on pastures (what is practiced less and less in intensive farming systems), smooth terrain and high nutritive forage supply are mandatory. Thus, for the most-productive breeds only the nutrient-richest pastures easy to cultivate are appropriate.

The superior productivity of modern cattle breeds under intensive housing and feeding conditions is undoubted (Albertí et al., 2008). However, under less intensive but sustainable management they rapidly lose performance (Berry et al., 2002; **Chapter 5.3.1 and 5.4.3**), because the nutrient content of marginal pastures is too low to cover their genetically enhanced demand. As a consequence, there is little use for nutrient-poor pastures and the hay produced by marginal meadows often can be used as bedding material at best.

Subsequently, marginal grasslands are underused or even abandoned (Gellrich and Zimmermann, 2007; Herzog and Seidl, 2018). If the continuing grazing impact of herbivores decreases, the original plant communities successively come back (Tasser and Tappeiner, 2002). Below the natural tree line, shrubs encroach and they are finally replaced by forest. On Swiss summer pastures, wood-covered area increases by 2 400 ha each year (Lauber et al., 2013). Although the return of natural vegetation is generally appreciated, it is seen most critical in this case. Encroaching shrub and forest communities are scenically less attractive, less appropriate for livestock production and – most important from an ecological point of view – less biodiverse (Agnoletti, 2007; Kesting et al., 2015; Komac et al., 2013; Lasanta et al., 2009; Pornaro et al., 2013; Queiroz et al., 2014).

Thus, there is a political will, to sustain species-rich pastures (Schulz et al., 2018). For this, continuous grazing is mandatory (Schreiber et al., 2009), but high-productive breeds are not entirely able to fulfil this task. Grazing with low-productive, undemanding breeds is key to maintain the aesthetic, cultural, productive and ecological ecosystem services of marginal grassland, since these breeds are able to cope with challenging conditions.

Efficiency of low-productive breeds

The circumstances that keep farmers from grazing marginal pastures with their high-productive cattle do not apply to low-productive breeds:

First, steep terrain is less problematic for lighter cattle as indicated by the more even movement on pastures of different degrees of steepness (see above and **Chapter 5.3.2**).

Second, undemanding breeds are satisfied with the low forage quality of marginal pastures. When the cattle were transferred from a fertile to a nutrient-poor pasture in the grazing experiment, the high-productive cows roared under protest for half an hour, whereas Highland cattle just started foraging the poor fodder.

Third, low-productive breeds consume a higher share of woody and other unpalatable plant species than high-productive breeds (**Chapter 4.4.3 and 5.3.3**). Thereby, they reduce shrub encroachment and prevent species-poor weed communities (**Chapter 3.4.2 and 3.4.4**).

Finally, in contrast to production-oriented breeds, grazing with low-productive cattle is efficient on marginal pastures: The weighing data clearly demonstrated that Highland cattle gained weight during the grazing experiment on the nutrient-poor pastures while the other breeds lost weight (**Chapter 5.3.1 and 5.4.3**). The more intensive the breed was, the more weight the cows lost. The reason can be, on the one hand, a lower energy use of Highland cattle. Moving least, they saved kinetic energy. Moreover, the isolating woolly fur presumably saved thermal energy. On the other hand, a higher energy input could explain the weight gain. However, the grazing experiment clearly demonstrated that the nutritive quality of Highland cattle diet was lowest and visual observation suggest a rather smaller dry matter intake than for more productive breeds. One explanation remains: it is likely, that low-productive breeds convert nutrient-poor and fibre-rich fodder more efficiently than high-productive breeds, optimized for digesting concentrated feed.

On alpine and other marginal grasslands, the terms of "high- and low-productive" cattle are reversed. Under harsh conditions, "low-productive" cattle become more productive than so-called "high-productive" breeds. Actually, the latter are high-productive only under high input. They are commonly fed on land and by feedstuff that could also serve for human nutrition (FAO, 2006). In contrast, low-productive breeds are able to convert low-quality fodder useless for human consumption and growing on areas unsuitable for arable farming into high-quality beef or dairy products. As a positive side effect of such sustainable farming, extensively managed, low-productive cattle maintain the species richness of the pastures they graze.

6.3 Back to the farmer: practical implications

6.3.1 Implications for farm management

Although this thesis demonstrated the widely overlooked benefits of traditional breeds, it is neither desirable nor possible to replace all high-productive cattle by low-productive ones. Low-productive breeds only show their superiority where high-productive breeds reach their limits.

However, especially in mountainous regions, most cattle farmers have to manage at least some pastures and meadows of low forage quality, which they cannot efficiently use with high-productive, but also high-demanding animals. Agricultural consultants commonly advise farmers to implement a site-adapted management. This includes to adapt the intensity of use to the agronomical quality of the land. But what if in a farmer's stable are no cattle that can efficiently use the fodder produced on marginal grasslands? It is worth thinking about extending the concept of site-adapted management to the livestock level. A few low-productive cattle could be easily added to existing herds of more productive animals. They could efficiently use the entire spectrum of grasslands, incidentally sustain their diversity and promote a network of stepping stone pastures of high ecological value within the intensive agricultural landscape.

6.3.2 Implications for breeding decisions

This thesis questions the dogma of unlimited increase of productivity and the fixation on only a few traits in cattle breeding. Overlooked co-evolved traits were shown to have more far-reaching consequences for pasture vegetation composition and species richness than previously assumed. However, breeding decisions are complex and there is no single biodiversity or sustainability criteria, which simply could be added to the breeding portfolio. Breeders have already started to take claw health into account (Baird et al., 2009), because it is an important economic factor in intensive farming systems. A next step could be to increase claw base by breeding in order to reduce the negative impact of trampling on vegetation, which is technically easy to implement.

The breeders of low-productive cattle have proved their modesty in artificial selection over centuries. While the productivity of other breeds has rapidly increased, they kept their animals small, undemanding and robust. Thereby, they avoided the negative consequences of increased productivity for animal welfare (Oltenacu and Broom, 2010). Additionally, they maintained their positive contribution to grassland conservation as demonstrated in this thesis. However, there are ongoing discussions within breeding societies to enhance productivity – especially since the demand for high-priced, sustainably produced slow-food has increased. This thesis showed that the ecological value of low-productive breeds is related to their low productivity. Therefore, breeders of low-productive cattle should bear in mind that they risk losing the sustainable benefit of their animals by forming just another production-oriented cattle breed.

6.4 Open research questions

The novel findings provoke a series of related research questions which remain unanswered by this thesis. For example, it remains open whether movement and foraging behaviour are entirely genetically determined or additionally acquired by conditioning. It would be an interesting project to exchange calves of low- and high-productive cows and to check their adult behaviour. Thereby, it could be estimated if they forage rather like their nurse or like their biological mother. Quantifying behaviour-related genetic variance among individuals could be worthwhile, because if the behaviour is determined by genetics and if there is variance among individuals of a breed, new breeding aims could be defined.

Another related question yet to answer is whether there is a compromise between agricultural production and nature conservation in breeding: Is it possible to create higher-productive breeds that forage efficiently and sustainable like low-productive cattle?

The more efficient food conversion of low-productive breeds was only assumed but not proved by the field studies of this thesis. A laboratory assessment with respiratory chambers would be necessary to provide certainty about this issue.

There is also a lack of data about differences in the (claw) health status among breeds. The assumptions made in this thesis are therefore based on reports of farmers and veterinaries. Reliable conclusions would require a comparative assessment in which different breeds are housed under similar conditions for a longer period. An alternative observational study covering many different farms would have to deal with the confounding of less intensive feeding conditions on farms of low-productive breeds.

Finally, this thesis is an ecological one and does not discuss economic conditions and consequences of grazing different breeds. However, the profitability is crucial. Low-productive breeds may be ecologically most advisable, but if farmers cannot live off raising such animals, they will return to more intensive, less sustainable agriculture. Hence, if low-intensive farming is remunerated, low-productive breeds can maintain ecosystem services and species richness of marginal grasslands.

7 Picture credits

Unless otherwise stated, pictures were taken by Caren Pauler.

8 Ethical approval

The animal study was reviewed and approved by the veterinary office of Grisons (authorization GR2018_12).

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10 Output

10.1 Conferences

Poster presentations

19th Symposium of the European Grassland Federation, 7-10 May 2017, Alghero/Sardinia, Italy

Annual Meeting of the Swiss Association of Animal Science, 16 April 2019, Lindau (ZH), Switzerland

Oral presentations

Agroscope Colloquium, 1 November 2018, Zurich, Switzerland

1st European Symposium on Livestock Farming in Mountain Areas, 20-22 June 2018, Bolzano, Italy

20th Meeting of the FAO-CIHEAM Mountain Pastures Subnetwork, 9-12 September 2018, Lofoten Island, Norway

Annual Meeting of the British Ecological Society, 16-19 December 2018, Birmingham, Great Britain

1st AgroVet-Strickhof Meeting, 1 July 2019, Lindau (ZH), Switzerland

63rd Annual Meeting of AGGF (Arbeitsgemeinschaft Grünland und Futterbau), 29-31 August 2019, Raitenhaslach, Germany

3rd Meeting Parkforschung Schweiz, 29 October 2019, Bern, Switzerland

10.2 Peer-reviewed articles

Journal articles

Pauler, C.M., Isselstein, J., Braunbeck, T., Schneider, M.K., 2019. Influence of Highland and production-oriented cattle breeds on pasture vegetation: a pairwise assessment across broad environmental gradients. Agriculture, Ecosystems & Environment 284, 1–11. https://doi.org/10.1016/j.agee.2019.106585

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Pauler, C.M., Isselstein, J., Berard, J., Braunbeck, T., Schneider, M.K., in revision. Grazing allometry: anatomy, movement and foraging behaviour of three cattle breeds of different productivity. Frontiers in Veterinary Science, Ruminant grazing behavior: a tool to improve product quality and ecosystem services.

Proceedings articles

Pauler, C.M., Schneider, M.K., Tonn, B., Braunbeck, T., Isselstein, J., 2017. Influence of robust and production-oriented cattle breeds on pasture vegetation. Grassland Science in Europe 22, 209–211.

Pauler, C.M., Isselstein, J., Braunbeck, T., Schneider, M.K., 2019. Einfluss unterschiedlicher Rinderrassen auf die Weidevegetation. Beiträge zur 63. Jahrestagung der Arbeitsgemeinschaft Grünland und Futterbau (AGGF), 53–56.

10.3 Supervised bachelor theses

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Villhauer, H., 2019, Hochlandrinder und produktionsorientierte Rinderrassen: Unterschiede in Körpergewicht, Klauen und Bewegungsverhalten, University of Heidelberg.

10.4 Dissemination to the public

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Appendix

S3 Supporting information for Chapter 3: Influence on pasture vegetation

Table S3.1 | Location variables of all subplots (L=lowly, M=moderately, H=highly frequented zone) grazed by Highland cattle (HC) and production-oriented breeds (PO). Three subplots belong to one pasture, 2x3 subplots belong to one pair. For every subplot following information is given: GPS coordinates (X and Y), Elevation in m asl. (Z), Inclination in degree (slope), soil pH value (pH), plant available phosphorus (P) and potassium (K) in mg kg^{-1}, stocking rate in LU ha^{-1} a^{-1} and the plant species with the highest percentage cover in the subplot. In addition, mean, median and standard deviation of site properties are given.

	Pair	**Bree**	**Subplot**	**X**	**Y**	**Z**	**slope**	**pH**	**P**	**K**	**Stocking**	**Most frequented plant species**
Mean						1062.07	15.63	5.24	30.36	182.44	0.64	
Median						1046	15.2	5.12	16.90	120.77	0.36	
SD						520.17	7.45	0.89	42.84	177.92	0.72	
	A	HC	L	33.73726	57.39938	738	22.3	4.95	15.17	87.15	0.79	Leucanthemum vulgare, Trifolium pratense, Festuca pratensis
	A	HC	H	33.73721	57.39965	744	22.5	5.89	36.62	830.00	0.79	Lolium perenne, Dactylis glomerata, Poa supina
	A	HC	M	33.73745	57.39965	749	23.1	4.87	15.39	151.89	0.79	Trifolium pratense, Cynosurus cristatus, Lolium perenne
	A	PO	L	33.73973	57.39836	649	26.2	5.38	11.29	92.13	1.44	Prunella vulgaris, Cynosurus cristatus, Ajuga reptans
	A	PO	H	33.74050	57.39841	648	25.5	5.80	23.72	322.04	1.44	Cynosurus cristatus, Lolium perenne, Phleum pratense
	A	PO	M	33.74003	57.39865	657	26.5	4.84	12.47	97.11	1.44	Prunella vulgaris, Cynosurus cristatus, Festuca rubra
	B	HC	L	33.71796	57.28497	1538	15.4	3.76	9.03	83.83	0.12	Nardus stricta, Potentilla erecta, Hieracium murorum
	B	HC	H	33.71934	57.28605	1575	14.4	5.64	12.08	200.03	0.12	Trifolium repens, Festuca pratensis, Agrostis gigantea
	B	HC	M	33.71969	57.28538	1559	16.4	4.60	6.50	107.07	0.12	Nardus stricta, Agrostis capillaris, Briza media
	B	PO	L	33.71791	57.28579	1563	14.2	3.86	7.94	57.10	0.05	Vaccinium myrtillus, Oxalis acetosella, Dryopteris dilatata
	B	PO	H	33.71897	57.28617	1574	13.3	6.02	7.54	155.21	0.05	Geranium sylvaticum, Ranunculus acris, Dactylis glomerata
	B	PO	M	33.72036	57.28658	1596	15.1	4.52	7.63	128.65	0.05	Nardus stricta, Potentilla erecta, Carlina acaulis
	C	HC	L	33.72960	57.28293	1709	31.0	5.40	8.20	146.91	0.07	Carex sylvatica, Dactylis glomerata, Festuca rubra
	C	HC	H	33.72962	57.28249	1691	25.5	5.39	7.98	385.95	0.07	Dactylis glomerata, Carex sylvatica, Festuca pratensis
	C	HC	M	33.72923	57.28284	1691	28.8	5.28	4.19	64.49	0.07	Dactylis glomerata, Carex sylvatica, Festuca rubra
	C	PO	L	33.73121	57.28009	1631	28.0	4.74	7.54	142.76	0.14	Leontodon hispidus, Plantago lanceolata, Carex sylvatica
	C	PO	H	33.73153	57.28022	1652	34.0	5.24	20.40	353.58	0.14	Festuca pratensis, Geranium sylvaticum, Heracleum sphondylium
	C	PO	M	33.73208	57.27994	1645	31.3	5.37	9.29	88.81	0.14	Leontodon hispidus, Helianthemum nummularium, Plantago
	D	HC	L	33.75969	57.27553	1923	7.8	4.02	7.11	50.38	0.03	Nardus stricta, Festuca rubra, Leontodon helveticus
	D	HC	H	33.75949	57.27529	1922	0.9	4.82	22.02	102.09	0.03	Alchemilla vulgaris, Phleum rhaeticum, Poa alpina
	D	HC	M	33.76027	57.27512	1925	1.1	3.86	9.68	33.95	0.03	Nardus stricta, Potentilla erecta, Carex pallescens

	Pair	Bree	Subplot	X	Y	Z	slope	pH	P	K	Stocking	Most frequented plant species
	D	PO	L	33.76360	57.27409	1926	13.3	4.84	9.68	53.78	0.07	Rhododendron ferrugineum, Nardus stricta, Leontodon helveticus
	D	PO	H	33.76235	57.27536	1911	3.1	4.60	44.47	187.58	0.07	Alchemilla vulgaris, Phleum rhaeticum, Deschampsia cespitosa
	D	PO	M	33.76320	57.27483	1919	10.4	3.79	19.53	50.38	0.07	Nardus stricta, Deschampsia flexuosa, Gentiana purpurea
	E	HC	L	34.80842	57.11360	1594	22.3	4.83	6.80	25.32	0.21	Briza media, Festuca rubra, Nardus stricta
	E	HC	H	34.80903	57.11350	1594	22.3	4.69	16.00	99.60	0.21	Festuca pratensis, Leontodon hispidus, Festuca rubra
	E	HC	M	34.80903	57.11400	1542	29.1	5.12	11.16	73.12	0.21	Leontodon hispidus, Briza media, Cynosurus cristatus
	E	PO	L	34.80788	57.11323	1611	21.1	4.77	6.80	32.12	0.40	Nardus stricta, Calluna vulgaris, Briza media
	E	PO	H	34.80793	57.11335	1620	21.2	4.77	22.63	86.32	0.40	Nardus stricta, Deschampsia cespitosa, Festuca pratensis
	E	PO	M	34.80615	57.11299	1633	21.2	4.36	9.50	54.20	0.40	Nardus stricta, Hieracium lactucella, Briza media
	F	HC	L	35.04699	56.97489	1558	11.1	5.45	6.37	18.84	0.20	Leontodon hispidus, Sesleria caerulea, Festuca rubra
	F	HC	H	35.04778	56.97454	1548	10.2	5.12	10.94	28.30	0.20	Alchemilla vulgaris, Festuca rubra, Sanguisorba officinalis
	F	HC	M	35.04658	56.97517	1569	14.3	5.09	9.46	47.56	0.20	Agrostis capillaris, Nardus stricta, Brachypodium pinnatum
	F	PO	L	35.04811	56.97605	1570	15.7	5.33	7.63	29.38	0.18	Bromus erectus, Nardus stricta, Agrostis capillaris
	F	PO	H	35.04705	56.97592	1577	15.1	5.15	15.39	234.89	0.18	Nardus stricta, Trisetum flavescens, Taraxacum officinale
	F	PO	M	35.04711	56.97580	1577	15.1	5.33	8.85	45.48	0.18	Nardus stricta, Rosa canina, Centaurea scabiosa
	G	HC	L	34.27496	57.07963	1542	26.9	4.23	36.06	229.41	0.07	Deschampsia flexuosa, Phleum rhaeticum, Festuca rubra
	G	HC	H	34.27335	57.08025	1491	21.1	4.11	19.49	92.13	0.07	Phleum rhaeticum, Festuca rubra, Nardus stricta
	G	HC	M	34.27375	57.07965	1518	23.3	4.19	19.10	72.21	0.07	Nardus stricta, Festuca rubra, Anthriscus sylvestris
	G	PO	L	34.27681	57.07980	1542	23.5	3.96	15.83	136.87	0.41	Vaccinium myrtillus, Nardus stricta, Deschampsia flexuosa
	G	PO	H	34.27770	57.08091	1504	25.0	4.21	34.62	221.61	0.41	Dactylis glomerata, Rumex obtusifolius, Poa supina
	G	PO	M	34.28135	57.08199	1475	15.0	3.94	18.70	100.43	0.41	Phleum rhaeticum, Nardus stricta, Anthoxanthum alpinum
	H	HC	L	32.78947	57.50019	865	15.6	4.70	12.82	124.50	1.22	Festuca rubra, Leucanthemum vulgare, Holcus lanatus
	H	HC	H	32.78843	57.50001	862	20.1	5.37	22.89	117.03	1.22	Alopecurus pratensis, Holcus lanatus, Ranunculus acris
	H	HC	M	32.78791	57.49992	863	21.9	5.74	11.03	102.92	1.22	Filipendula ulmaria, Polygonum bistorta, Geum rivale
	H	PO	L	32.77772	57.49635	938	14.1	4.54	11.51	68.48	2.00	Cynosurus cristatus, Anthoxanthum alpinum, Juncus effusus
	H	PO	H	32.78003	57.49669	911	15.6	4.68	38.76	122.01	2.00	Alopecurus pratensis, Agrostis gigantea, Anthoxanthum odoratum
	H	PO	M	32.77920	57.49615	933	14.5	4.83	23.94	130.31	2.00	Juncus effusus, Anthoxanthum odoratum, Ranunculus repens
	I	HC	L	32.78593	57.50605	903	25.2	4.68	15.00	85.49	1.39	Festuca rubra, Festuca pratensis, Agrostis capillaris
	I	HC	H	32.78639	57.50587	892	25.1	4.67	41.64	169.32	1.39	Holcus lanatus, Festuca pratensis, Lolium perenne
	I	HC	M	32.78413	57.50536	902	24.5	5.71	11.38	49.39	1.39	Anthoxanthum odoratum, Festuca pratensis, Cynosurus cristatus
	I	PO	L	32.78280	57.50473	881	20.0	5.66	27.47	168.49	3.29	Festuca pratensis, Poa pratensis, Lolium perenne
	I	PO	H	32.78289	57.50434	862	16.6	4.90	45.78	444.05	3.29	Lolium perenne, Agrostis gigantea, Festuca pratensis
	I	PO	M	32.78255	57.50414	861	14.2	4.58	26.25	217.46	3.29	Cynosurus cristatus, Festuca rubra, Lolium perenne
	J	HC	L	32.68775	57.43519	1315	19.3	5.15	7.54	108.73	0.15	Nardus stricta, Agrostis capillaris, Carex flacca
	J	HC	H	32.68711	57.43559	1304	14.1	6.02	17.31	364.37	0.15	Anthoxanthum odoratum, Poa trivialis, Festuca pratensis
	J	HC	M	32.68568	57.43584	1277	16.2	6.54	13.04	80.43	0.15	Carex panicea, Nardus stricta, Carex davalliana
	J	PO	L	32.68325	57.43716	1274	14.3	4.27	7.59	135.29	0.09	Carex panicea, Nardus stricta, Carex flacca
	J	PO	H	32.68322	57.43815	1298	12.2	4.28	22.41	119.52	0.09	Juncus effusus, Carex pallescens, Lolium perenne

	Pair	Bree	Subplot	X	Y	Z	slope	pH	P	K	Stocking	Most frequented plant species
	J	PO	M	32.68468	57.43869	1314	14.7	4.33	15.13	102.92	0.09	Juncus effusus, Carex panicea, Luzula multiflora
	K	HC	L	35.72736	56.76738	1911	23.2	5.79	24.02	163.51	0.07	Carex nigra, Agrostis canina, Juncus articulatus
	K	HC	H	35.72672	56.76898	1939	23.0	4.58	61.48	683.92	0.07	Phleum rhaeticum, Festuca rubra, Lolium perenne
	K	HC	M	35.72511	56.76874	1994	23.1	4.14	45.34	327.85	0.07	Nardus stricta, Festuca rubra, Phleum rhaeticum
	K	PO	L	35.72818	56.76939	1893	10.8	5.42	11.16	100.43	0.22	Deschampsia cespitosa, Agrostis capillaris, Carex pallescens
	K	PO	H	35.73370	56.76691	1823	24.3	5.27	63.22	725.42	0.22	Poa alpina, Trifolium hybridum, Trifolium repens
	K	PO	M	35.73297	56.76720	1844	26.5	5.38	28.17	230.74	0.22	Nardus stricta, Hieracium pilosella, Agrostis capillaris
	L	HC	L	34.86349	56.90882	1755	28.8	5.10	13.30	106.24	0.11	Carex ferruginea, Festuca rubra, Deschampsia cespitosa
	L	HC	H	34.86112	56.90927	1716	6.0	5.24	24.46	190.90	0.11	Carex ferruginea, Festuca rubra, Poa alpina
	L	HC	M	34.86294	56.90844	1762	29.8	4.96	10.81	71.05	0.11	Carex ferruginea, Festuca rubra, Carex ornithopoda
	L	PO	L	34.86110	56.90481	1792	17.4	4.94	5.62	56.86	0.12	Calluna vulgaris, Deschampsia cespitosa, Alnus glutinosa
	L	PO	H	34.86084	56.90496	1785	15.5	5.41	19.01	197.54	0.12	Festuca pratensis, Dactylis glomerata, Poa alpina
	L	PO	M	34.86255	56.90567	1803	24.6	5.51	7.41	44.57	0.12	Deschampsia cespitosa, Plantago lanceolata, Cirsium acaule
	M	HC	L	34.76024	57.00751	1101	18.5	6.42	7.59	57.69	0.85	Deschampsia cespitosa, Brachypodium sylvaticum, Glechoma
	M	HC	H	34.75953	57.00752	1100	16.9	6.57	15.26	186.75	0.85	Taraxacum officinale, Deschampsia cespitosa, Festuca rubra
	M	HC	M	34.75964	57.00719	1090	14.3	6.24	12.38	44.57	0.85	Bromus erectus, Festuca ovina, Carex caryophyllea
	M	PO	L	34.75428	57.00628	1149	17.1	6.38	15.87	115.37	0.12	Ranunculus repens, Poa trivialis, Rubus idaeus
	M	PO	H	34.75505	57.00671	1138	17.4	5.04	23.81	185.09	0.12	Poa trivialis, Helictotrichon pubescens, Chenopodium bonus-
	M	PO	M	34.75525	57.00654	1137	17.3	4.51	20.14	98.77	0.12	Phleum pratense, Festuca ovina, Poa pratensis
	N	HC	L	34.91295	57.61479	1167	22.4	4.81	13.21	112.05	0.31	Brachypodium pinnatum, Hieracium murorum, Thymus
	N	HC	H	34.91403	57.61372	1187	10.2	5.47	17.88	130.31	0.31	Agrostis gigantea, Taraxacum officinale, Lolium perenne
	N	HC	M	34.91365	57.61435	1189	14.3	4.90	16.35	130.31	0.31	Lolium perenne, Anthoxanthum odoratum, Festuca rubra
	N	PO	L	34.92337	57.62155	1154	26.4	5.89	11.42	54.95	0.52	Festuca rubra, Poa annua, Taraxacum officinale
	N	PO	H	34.92191	57.62050	1143	7.3	5.31	56.68	237.38	0.52	Rumex obtusifolius, Bellis perennis, Poa pratensis
	N	PO	M	34.92264	57.62082	1147	18.5	5.03	29.43	71.71	0.52	Anthoxanthum odoratum, Ranunculus ficaria, Lolium perenne
	O	HC	L	36.78308	59.12008	429	9.1	4.58	20.93	52.79	0.52	Festuca rubra, Anthoxanthum odoratum, Festuca pratensis
	O	HC	H	36.78382	59.11996	434	11.9	5.56	40.37	364.37	0.52	Alopecurus pratensis, Festuca pratensis, Holcus lanatus
	O	HC	M	36.78374	59.12010	430	11.5	5.01	16.70	60.18	0.52	Festuca rubra, Arrhenatherum elatius, Holcus lanatus
	O	PO	L	36.79248	59.11762	421	14.4	5.06	13.43	73.79	0.55	Festuca rubra, Crepis biennis, Centaurea jacea
	O	PO	H	36.79126	59.11816	430	15.2	5.71	77.17	518.75	0.55	Festuca pratensis, Urtica dioica, Rumex crispus
	O	PO	M	36.79316	59.11831	403	12.4	5.15	28.86	131.14	0.55	Arrhenatherum elatius, Alopecurus pratensis, Holcus lanatus
	P	HC	L	36.88811	58.90675	505	2.6	4.75	30.17	151.06	1.52	Lolium multiflorum, Taraxacum officinale, Alopecurus pratensis
	P	HC	H	36.88705	58.90665	504	1.7	5.70	78.92	534.52	1.52	Lolium multiflorum, Rumex obtusifolius, Taraxacum officinale
	P	HC	M	36.88756	58.90648	506	2.4	4.69	22.72	123.67	1.52	Festuca rubra, Taraxacum officinale, Arrhenatherum elatius
	P	PO	L	36.81733	58.89576	518	7.9	7.14	27.69	218.29	0.95	Lolium perenne, Agropyron repens, Phleum pratense
	P	PO	H	36.81678	58.89550	513	6.5	6.04	76.74	768.58	0.95	Lolium perenne, Agropyron repens, Agrostis gigantea
	P	PO	M	36.81624	58.89531	512	6.4	5.16	17.09	190.90	0.95	Taraxacum officinale, Lolium perenne, Rumex acetosa
	Q	HC	L	36.14609	59.61067	276	4.4	4.26	9.11	26.73	0.17	Agrostis gigantea, Festuca rubra, Anemone nemorosa

	Pair	Bree	Subplot	X	Y	Z	slope	pH	P	K	Stocking	Most frequented plant species
	Q	HC	H	36.14892	59.61049	284	6.5	4.32	12.03	78.93	0.17	Agrostis gigantea, Lolium perenne, Anemone nemorosa
	Q	HC	M	36.14655	59.61078	279	3.7	3.92	16.31	72.96	0.17	Agrostis gigantea, Festuca rubra, Lolium perenne
	Q	PO	L	36.19236	59.61865	423	10.6	4.10	38.98	54.20	0.53	Festuca rubra, Holcus lanatus, Luzula multiflora
	Q	PO	H	36.19215	59.61910	415	5.2	4.41	15.22	50.80	0.53	Festuca rubra, Anemone nemorosa, Colchicum autumnale
	Q	PO	M	36.19350	59.61875	429	8.0	4.35	35.32	132.80	0.53	Arrhenatherum elatius, Festuca rubra, Rubus fruticosus
	R	HC	L	36.30969	58.50338	761	9.6	7.33	22.80	97.94	0.79	Bromus erectus, Salvia pratensis, Ranunculus bulbosus
	R	HC	H	36.30911	58.50349	758	10.4	7.18	77.61	728.74	0.79	Poa pratensis, Taraxacum officinale, Lolium perenne
	R	HC	M	36.30996	58.50308	756	9.9	7.26	18.92	189.24	0.79	Bellis perennis, Lolium perenne, Poa trivialis
	R	PO	L	36.29097	58.51150	754	4.6	6.46	88.51	92.13	0.92	Lolium perenne, Taraxacum officinale, Ranunculus acris
	R	PO	H	36.29123	58.51139	755	3.6	7.29	98.97	299.63	0.92	Lolium perenne, Trifolium repens, Plantago lanceolata
	R	PO	M	36.28952	58.51159	753	6.4	6.64	102.02	108.73	0.92	Lolium perenne, Festuca rubra, Ranunculus acris
	S	HC	L	36.82893	58.94527	353	22.3	5.82	15.65	116.20	0.25	Holcus lanatus, Festuca rubra, Agropyron repens
	S	HC	H	36.83097	58.94535	325	18.4	5.69	81.10	235.72	0.25	Poa trivialis, Rumex obtusifolius, Lamium purpureum
	S	HC	M	36.83149	58.94573	332	22.3	5.49	26.86	98.77	0.25	Holcus lanatus, Poa trivialis, Agrostis gigantea
	S	PO	L	36.82201	58.94499	356	20.6	5.07	10.51	55.69	0.55	Lolium perenne, Bellis perennis, Plantago lanceolata
	S	PO	H	36.82014	58.94455	347	13.8	6.98	61.48	445.71	0.55	Lolium perenne, Rumex obtusifolius, Taraxacum officinale
	S	PO	M	36.82102	58.94468	349	17.3	5.94	16.31	185.92	0.55	Lolium perenne, Alopecurus pratensis, Taraxacum officinale
	T	HC	L	36.91587	59.36830	365	3.8	5.25	73.25	237.38	1.16	Alopecurus pratensis, Dactylis glomerata, Lamium purpureum
	T	HC	H	36.91629	59.36790	362	3.7	5.35	26.99	424.96	1.16	Rumex obtusifolius, Lamium purpureum, Poa annua
	T	HC	M	36.91578	59.36790	361	4.4	5.80	184.86	788.50	1.16	Alopecurus pratensis, Poa trivialis, Bromus hordeaceus
	T	PO	L	36.91693	59.36802	363	2.4	4.89	80.66	511.28	1.77	Alopecurus pratensis, Agrostis gigantea, Dactylis glomerata
	T	PO	H	36.91686	59.36774	362	2.6	5.31	62.78	573.53	1.77	Agropyron repens, Alopecurus pratensis, Agrostis gigantea
	T	PO	M	36.91736	59.36801	364	2.4	4.88	49.27	326.19	1.77	Urtica dioica, Bromus hordeaceus, Holcus lanatus
	U	HC	L	34.58107	58.17295	676	17.6	7.29	15.48	107.90	1.32	Dactylis glomerata, Plantago lanceolata, Galium album
	U	HC	H	34.58061	58.17369	654	9.7	7.17	98.54	574.36	1.32	Lolium perenne, Festuca pratensis, Taraxacum officinale
	U	HC	M	34.58014	58.17345	658	12.3	7.25	33.31	214.97	1.32	Festuca pratensis, Plantago lanceolata, Trifolium pratense
	U	PO	L	34.59510	58.17926	650	13.8	7.24	35.93	230.74	3.14	Lolium perenne, Plantago media, Trifolium repens
	U	PO	H	34.59695	58.17877	628	13.2	7.03	405.92	871.50	3.14	Rumex obtusifolius, Lolium perenne, Festuca pratensis
	U	PO	M	34.59701	58.17850	631	13.2	7.09	81.53	192.56	3.14	Lolium perenne, Trifolium repens, Ranunculus repens
	V	HC	L	34.19801	57.51911	707	19.4	4.71	10.55	63.91	0.15	Festuca pratensis, Holcus lanatus, Bromus erectus
	V	HC	H	34.19755	57.51912	699	18.6	4.77	20.06	94.62	0.15	Holcus lanatus, Alopecurus pratensis, Anthoxanthum odoratum
	V	HC	M	34.19774	57.51890	702	19.0	5.49	9.16	44.65	0.15	Holcus lanatus, Festuca pratensis, Festuca rubra
	V	PO	L	34.19670	57.52049	642	19.1	4.75	19.01	66.32	0.40	Festuca pratensis, Lolium perenne, Festuca rubra
	V	PO	H	34.19657	57.52094	625	15.4	4.66	25.85	117.86	0.40	Holcus lanatus, Trifolium dubium, Anthoxanthum odoratum
	V	PO	M	34.19626	57.52063	636	18.2	5.13	37.32	243.19	0.40	Holcus mollis, Pteridium aquilinum, Poa pratensis
	W	HC	L	33.42020	57.43704	1405	13.4	4.31	11.73	72.96	0.70	Briza media, Nardus stricta, Calluna vulgaris
	W	HC	H	33.41980	57.43670	1404	13.7	5.76	13.73	123.67	0.70	Carex flacca, Anthoxanthum odoratum, Carex elata
	W	HC	M	33.41916	57.43675	1404	12.7	4.14	10.68	93.79	0.70	Nardus stricta, Briza media, Calluna vulgaris

	Pair	**Bree**	**Subplot**	**X**	**Y**	**Z**	**slope**	**pH**	**P**	**K**	**Stocking**	**Most frequented plant species**
	W	PO	L	33.44328	57.44487	1442	21.3	4.21	11.68	146.91	0.22	Festuca rubra, Hieracium pilosella, Anthoxanthum odoratum
	W	PO	H	33.44307	57.44475	1432	19.4	4.54	15.57	130.31	0.22	Lolium perenne, Festuca rubra, Nardus stricta
	W	PO	M	33.44359	57.44464	1432	20.2	4.04	11.03	170.98	0.22	Nardus stricta, Hieracium lactucella, Anthoxanthum odoratum
	X	HC	L	37.25544	58.98901	465	9.2	6.21	33.27	128.65	0.19	Bromus erectus, Ranunculus bulbosus, Bromus hordeaceus
	X	HC	H	37.25624	58.98889	464	8.3	5.50	69.76	309.59	0.19	Alopecurus pratensis, Arrhenatherum elatius, Brachypodium
	X	HC	M	37.25634	58.98908	468	7.3	5.61	36.36	144.42	0.19	Alopecurus pratensis, Agrostis capillaris, Vicia hirsuta
	X	PO	L	37.25431	58.98893	455	9.0	6.31	16.44	97.94	0.86	Ranunculus bulbosus, Cynosurus cristatus, Alopecurus pratensis
	X	PO	H	37.25477	58.98892	460	9.9	6.76	41.25	151.06	0.86	Alopecurus pratensis, Dactylis glomerata, Agrostis gigantea
	X	PO	M	37.25484	58.98915	464	9.3	6.96	212.33	619.18	0.86	Bromus erectus, Alopecurus pratensis, Ranunculus bulbosus
	Y	HC	L	34.65236	57.52061	1044	18.4	4.65	9.03	118.69	0.19	Festuca rubra, Ajuga reptans, Dactylis glomerata
	Y	HC	H	34.65240	57.52016	1025	21.8	4.85	10.51	143.59	0.19	Cynosurus cristatus, Holcus lanatus, Anthoxanthum odoratum
	Y	HC	M	34.65180	57.52032	1026	21.1	5.20	19.53	48.31	0.19	Anthoxanthum odoratum, Poa trivialis, Festuca rubra
	Y	PO	L	34.65231	57.52105	1060	18.1	4.42	8.94	55.61	0.33	Pteridium aquilinum, Stachys officinalis, Anthoxanthum odoratum
	Y	PO	H	34.65132	57.52107	1048	13.1	6.37	8.15	167.66	0.33	Agrostis gigantea, Festuca rubra, Dactylis glomerata
	Y	PO	M	34.65153	57.52120	1055	13.5	4.34	9.37	63.33	0.33	Holcus lanatus, Festuca rubra, Leontodon hispidus

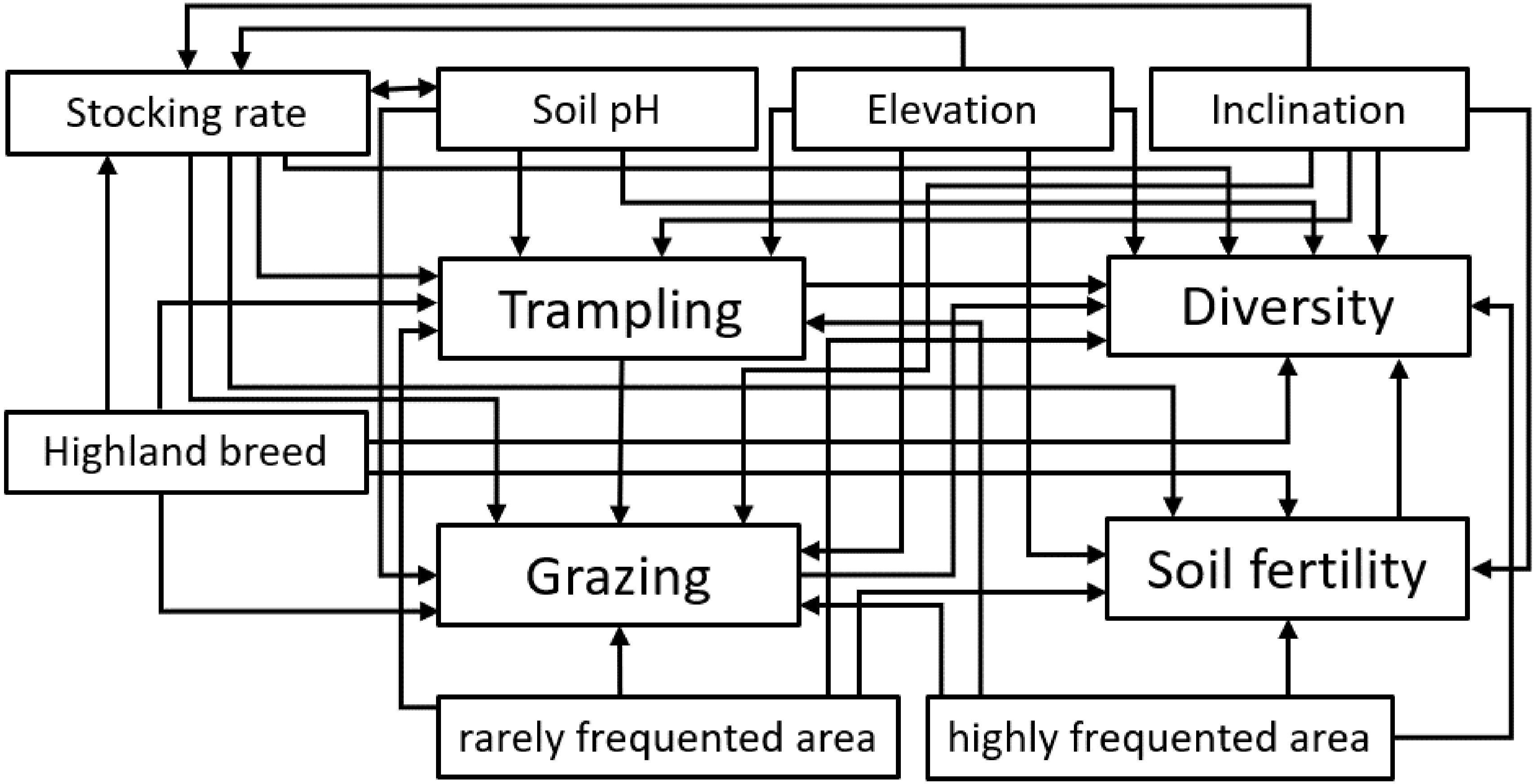

Figure S3.1: Conception of the structural equation model. All links of the model are shown between the five response variables stocking rate (= LU ha^{-1} yr^{-1}), trampling (= cumulated weighted mean of trampling indicator value), grazing (= cumulated weighted mean of grazing indicator value), diversity (= number of plant species) as well as soil fertility (= plant available phosphorus) and predictors (Highland breed, soil pH, elevation, inclination and the two study design dependent predictors of rarely and highly frequented subplots).

Table S3.2 | Regression coefficients from the structural equation model for five response variables stocking rate (= LU ha^{-1} yr^{-1}), trampling (= cumulated weighted mean of trampling indicator value), grazing (= cumulated weighted mean of grazing indicator value), diversity (= number of plant species) and soil fertility (= plant available phosphorus). Values of phosphorus, stocking rate and number of plant species were log-transformed. Standardized coefficients (scaled by standard deviations) of significant values ($p < 0.05$) are bolded.

Response	**Predictor**	**Estimate**	**Standard Error**	**DF**	**p-value**	**Standardised coefficients**
Stocking rate	Highland breed	-0.30	0.06	122.00	**<0.0001**	-0.15
Stocking rate	Elevation	-0.68	0.14	122.00	**<0.0001**	-0.68
Stocking rate	Inclination	-0.07	0.06	122.00	0.28	-0.07
Trampling	Highland breed	-0.35	0.17	23.00	**0.049**	-0.21
Trampling	rarely frequented area	-0.15	0.11	95.00	0.18	-0.08
Trampling	highly frequented area	0.31	0.11	95.00	**0.008**	0.17
Trampling	Elevation	-0.03	0.13	95.00	0.79	-0.04
Trampling	Soil pH	0.16	0.08	95.00	**0.035**	0.19
Trampling	Inclination	0.05	0.08	95.00	0.51	0.06
Trampling	Stocking rate	0.19	0.12	23.00	0.14	0.22
Grazing	Highland breed	-0.24	0.08	23.00	**0.006**	-0.15
Grazing	rarely frequented area	0.02	0.09	94.00	0.79	0.01
Grazing	highly frequented area	0.20	0.10	94.00	**0.042**	0.11
Grazing	Trampling	0.65	0.06	94.00	**<0.0001**	0.67
Grazing	Elevation	0.01	0.08	94.00	0.93	0.01
Grazing	Soil pH	0.00	0.05	94.00	0.96	0.00
Grazing	Inclination	-0.06	0.06	94.00	0.30	-0.07
Grazing	Stocking rate	0.08	0.07	23.00	0.28	0.09
Soil fertility	Highland breed	-0.20	0.12	23.00	0.12	-0.10
Soil fertility	rarely frequented area	-0.32	0.11	96.00	**0.006**	-0.15
Soil fertility	highly frequented area	0.55	0.12	96.00	**<0.0001**	0.26
Soil fertility	Elevation	-0.31	0.14	96.00	**0.036**	-0.31
Soil fertility	Inclination	-0.08	0.09	96.00	0.37	-0.08
Soil fertility	Stocking rate	0.17	0.12	23.00	0.18	0.17
Diversity	Highland breed	0.12	0.04	23.00	**0.005**	0.18
Diversity	rarely frequented area	0.00	0.04	92.00	0.99	0.00
Diversity	highly frequented area	-0.02	0.05	92.00	0.60	-0.04
Diversity	Trampling	0.12	0.04	92.00	**0.002**	0.31
Diversity	Grazing	-0.15	0.04	92.00	**0.0003**	-0.36
Diversity	Elevation	0.09	0.04	92.00	**0.020**	0.27
Diversity	Soil pH	0.03	0.03	92.00	0.20	0.10
Diversity	Inclination	0.07	0.03	92.00	**0.013**	0.20
Diversity	Soil fertility	-0.08	0.03	92.00	**0.006**	-0.23
Diversity	Stocking rate	-0.03	0.03	23.00	0.36	-0.10
Soil pH ~ Stocking rate		-0.05	NA	150.00	0.27	-0.05

Table S3.3: Details on the specification of the structural equation model are shown together with marginal and conditional coefficients of determination of response variables.

Response	**family**	**link**	**Marginal R²**	**Conditional R²**
Stocking rate	gaussian	Identity	0.47	0.86
Trampling	gaussian	identity	0.24	0.60
Grazing	gaussian	identity	0.62	0.69
Soil fertility	gaussian	identity	0.37	0.68
Diversity	gaussian	identity	0.50	0.61

S4 Supporting information for Chapter 4: Influence of plant traits

S4.1 Information on animals used in the experiment

Animals in the experiment were of the three breeds Highland cattle, Original Braunvieh and Angus×Holstein crossbreed. The three breeds naturally differed in body weight and productivity. Because they originated from different farms, they also differed in the age of cows and calves. However, all cows were used to graze mountain grassland and had previous experience of alpine pastures.

Table S4.1-1 | Age and weight of animals involved in the study: Presented is the mean, range and standard deviation of the age (in month) and the weight (in kg) of the cows and calves as well as the alpine experience (number of summers spend on alpine pastures) of cows for the three breeds Highland cattle, Original Braunvieh and Angus×Holstein crossbreed.

	Cows			**Calves**	
	Age (month)	**Weight (kg)**	**Experience (seasons)**	**Age (month)**	**Weight (kg)**
Highland cattle					
mean	80	358	6	1	68
range	53-124	278-473	3-10	1-2	52-86
SD	27	57.4	2	0	26
Original Braunvieh					
mean	46	582	2	7	319
range	34-75	462-676	1-3	4-9	199-404
SD	13	59.3	1	2	77
Angus×Holstein					
mean	92	679	7	5	232
range	60-110	602-750	4-8	4-5	186-290
SD	18	40.4	2	0	31

S4.2 Information on areas and paddocks grazed in the experiment

The grazing experiment was carried out in a Latin square design across three areas, each subdivided into three paddocks. Breeds were rotated in a way that each breed (subgroups of three cows with their calves) grazed each paddock once, but individual animals were different for every rotation. **Table S4.2-1** provides information on animals, forage demand and availability for every paddock and rotation.

Forage demand was estimated by a linear regression of biomass dry matter consumption in alpine regions as a function of body weight, based on data of Berry et al. (2002), Estermann et al. (2003), and Wettstein et al. (2010).

In the first rotation, the actual biomass was measured by cutting and drying all plant material in 12 quadrats (0.4×0.4 m) per paddock, followed by drying for 48 hours at 60 °C and weighing. For the second and third rotation, the biomass was estimated by a linear regression of the height of the raising plate meter which was measured before all grazing events, and the dry matter.

Note that there was sufficient forage after each grazing event so that animals were not forced to consume the leftover (**Table S4.2-1**). Cattle were able to select plant species according to their preference until the last day.

Table S4.2-1 | Information about paddock size, animal weight, forage demand, swards height and biomass of each grazing event: Given are the dates of each grazing event, area and paddock unit ID (see also **Figure 4.1** in the main document), the breed (HC: Highland cattle, OB: Original Braunvieh, AH: Angus×Holstein) grazing the unit in a specific event, the size of the paddock (ha) of each grazing event, the average weight of cows and calves in kg, the average forage demand in dry matter per day (kg d^{-1}) for three cows with calves, sward height (mm) measured by a raising plate meter before each grazing event, the available biomass (kg ha^{-1}) at the onset of the grazing event, and the remaining biomass (calculated as the 'average dry matter per ha multiplied by the actual paddock size' minus 'the forage demand of the 3 cows + 3 calves grazing a unit over the given duration'). NA values were caused by device failure.

Rotation	**Area**	**Paddock**	**Breed**	**Paddock size (ha)**	**Av. weight cows + calves (kg)**	**Forage demand (kg DM d^{-1})**	**Sward height (mm)**	**Available biomass (kg DM ha^{-1})**	**Remaining biomass (kg DM)**
26/06-29/06	1	A	HC	0.26	370 + 063	33	131	3086	714
24/07-27/07	1	A	OB	0.39	602 + 288	79	96	2241	646
24/08-27/08	1	A	AH	0.39	697 + 222	82	100	2332	672
26/06-29/06	1	B	OB	0.42	577 + 334	81	163	4064	1452
24/07-27/07	1	B	AH	0.40	661 + 244	80	114	2652	820
24/08-27/08	1	B	HC	0.29	343 + 065	30	115	2677	678
26/06-29/06	1	C	AH	0.37	679 + 229	80	122	2508	691
24/07-27/07	1	C	HC	0.26	362 + 075	33	99	2314	499
24/08-27/08	1	C	OB	0.37	568 + 335	80	85	1990	500
29/06-02/07	2	A	HC	0.47	370 + 063	33	68	1028	381
27/07-30/07	2	A	OB	0.71	602 + 288	79	77	1250	568
27/08-30/08	2	A	AH	0.71	697 + 222	82	59	774	220
29/06-02/07	2	B	OB	0.65	577 + 334	81	NA	NA	NA
27/07-30/07	2	B	AH	0.69	661 + 244	80	95	1709	863
27/08-30/08	2	B	HC	0.41	343 + 065	30	81	1348	428
29/06-02/07	2	C	AH	0.71	679 + 229	80	97	1642	920
27/07-30/07	2	C	HC	0.42	362 + 075	33	124	2491	919
27/08-30/08	2	C	OB	0.71	568 + 335	80	94	1689	875
02/07-06/07	3	A	HC	1.16	370 + 063	33	50	949	1001
30/07-02/08	3	A	OB	1.91	602 + 288	79	50	731	1080
30/08-03/09	3	A	AH	1.91	697 + 222	82	52	787	1176
02/07-06/07	3	B	OB	1.57	577 + 334	81	60	903	1174
30/07-02/08	3	B	AH	1.43	661 + 244	80	48	649	610
30/08-03/09	3	B	HC	0.82	343 + 065	30	59	1027	720
02/07-06/07	3	C	AH	1.65	679 + 229	80	72	1476	2195
30/07-02/08	3	C	HC	1.04	362 + 075	33	63	1169	1077
30/08-03/09	3	C	OB	1.65	568 + 335	80	65	1238	1723

S4.3 Validation of visually estimated biomass proportions

Method: Estimated biomass proportions were validated against measured dry matter of plant species. First, we estimated the biomass proportion of all species in three quadrats of 0.4 m × 0.4 m and cut the sward at 7 cm height. That we assumed as the height cattle forage. Afterwards, we assorted all plant individuals according to species, dried them for 48 hours at 60 °C and weighed them. We compared the log-transformed and untransformed percent dry matter with estimated percent standing biomass by linear models for each sample.

Results: The values of percentage biomass estimated for each plant species were highly correlated to the percentage measured biomass in dry matter (**Figure S4.3-1**). There was a slight tendency to overestimate species with a small share and to underestimate dominant species. Nonetheless, the visually estimated biomass proportion were reliably related to the measured dry mass, irrespective of modelling on the linear or log-transformed scale (for all samples $p<0.0001$), and the variation in the data were well explained by the linear models (R^2 from 0.74 to 0.93). This goes along with Suter & Edwards (2013), who reported a similar accuracy by applying the same method.

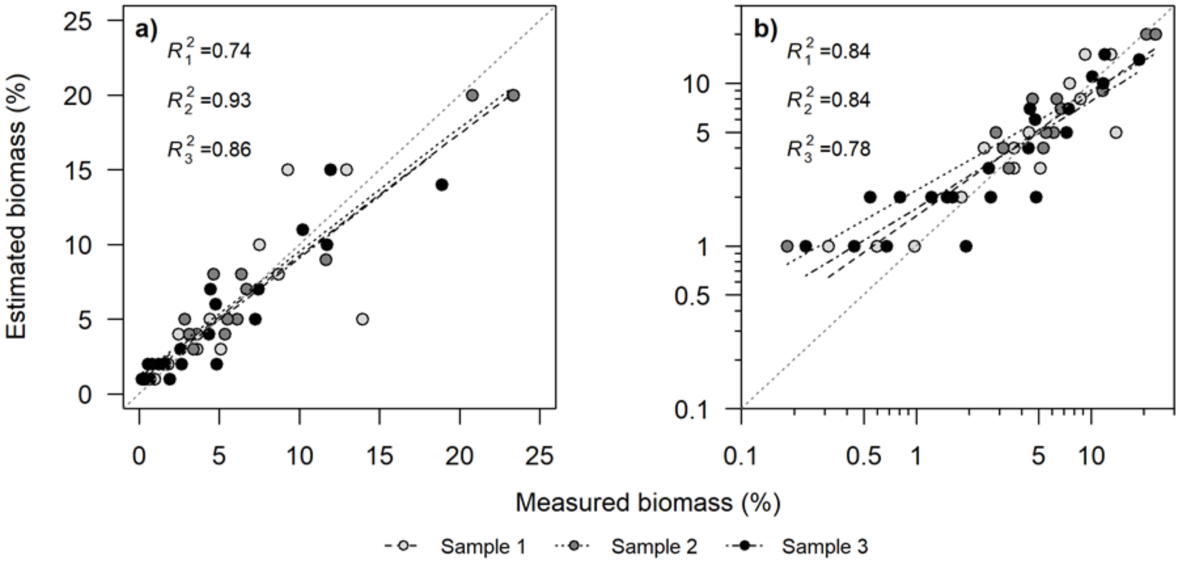

Figure S4.3-1 | Validation of estimated biomass proportions: Linear models of proportions of estimated and measured biomass of 50 plant species in three samples for validation, presented **a** on the linear and **b** log-transformed scale with adjusted coefficients of determination (R^2) for each sample.

S4.4 Detailed description of statistical analyses

Calculation of centred logratio coefficients

Observed in the field were proportions p_i of each plant species in standing biomass of a vegetation subplot before and after grazing (**Figure 4.2a**). The observations were compositional since the proportions of all n plant species in each survey of a subplot summed to one, i.e. $p = \{p_1, \dots, p_n \,/\, \sum p_{1 \dots n} = 1\}$. For further calculations, the estimated values in each survey s were therefore transformed into centred logratio coefficients (Filzmoser et al., 2018b) using package compositions (van den Boogaart et al., 2018) as

$$y_s = clr(p_s) = y_i, \dots, y_{n_s} = ln \frac{p_1}{\sqrt[n_s]{\prod_{i=1}^{n_s} p_i}}, \dots, \frac{p_{n_s}}{\sqrt[n_s]{\prod_{i=1}^{n_s} p_i}} \qquad (1)$$

Selection was inferred from the difference in biomass proportions before ($t=1$) and after grazing ($t=2$ as $d_i = y_i^{t=2} - y_i^{t=1}$. Species selected by the animals above average decreased their proportion and had $d_i<0$. Deselected species were left over and had $d_i>0$ (**Figure 4.2b**).

In R code, the calculation of d_i on two matrices p1 and p2 (survey x species) of biomass proportions before and after grazing is achieved by

```
library(compositions)
y <- lapply(1:nrow(p1), function(i){
  pre <- as.numeric(clr(p1[i,]))
  pre[is.na(p1[i,])] <- NA
  post <- as.numeric(clr(p2[i,]))
  post[is.na(p2[i,])] <- NA
  return(post-pre)
})
```

The `clr()` function returns 0 for unobserved species, and values need to be replaced by NA.

Local model of selection depending on trait values

The *local model* described the dependence of d_i on the trait values tr_i of the plant species identified in each observation i, taking into account treatments and sampling structure. The identity of the species is ignored as if a cow only cared about plants within reach of her mouth. In detail, the model used fixed and random effects to describe the expected mean μ_i of differences in biomass proportion d_i as

$$\mu_i = \beta_0 + \beta_1 tr_i + \beta_2 b_i + \beta_3 r_i + \beta_4 a_i + \beta_5 b_i tr_i + \beta_6 r_i tr_i + \beta_7 a_i tr_i + \alpha_{0i}^{S,V,P} + \alpha_{1i}^{S,V,P} tr_i \qquad (2)$$

where β_0 was an intercept and $\beta_1 tr_i$ a linear effect of a trait. Coefficients β_2 to β_7 estimate linear effects of the covariates breed b, rotation r and area a and their interaction with trait; hence, trait effects were allowed to differ among breeds, rotations and areas, respectively.

$\alpha_{0i}^{S,V,P}$ and $\alpha_{1i}^{S,V,P} tr_i$ were random intercepts and slopes for the observations in each survey S (all the plant species that form a community), nested within vegetation subplots V within paddocks P, where $\begin{bmatrix}\alpha_0\\ \alpha_1\end{bmatrix} \sim N\left(\begin{bmatrix}0\\ 0\end{bmatrix}, \Sigma\right)$ and Σ were general positive-definite variance-covariance matrices $\Sigma = \begin{bmatrix}\sigma_{\alpha 0}^2 & \sigma_{\alpha 0 \alpha 1}^2\\ \sigma_{\alpha 0 \alpha 1}^2 & \sigma_{\alpha 1}^2\end{bmatrix}$. For some traits and nesting levels, variances for random intercepts or slopes were so small that covariances could not be estimated. In this case, diagonal positive-definite matrices were used, i.e. $\sigma_{\alpha 0 \alpha 1}^2 = 0$.

To account for the multiple observations within each survey, a compound symmetry correlation structure was imposed on the residuals. The local model was fitted by restricted maximum likelihood using package nlme 3.1-137 (Pinheiro, Bates, DebRoy, & Sarkar, 2018; for details see supplementary code on https://github.com/mkschneider/trait-selection).

In R code, the modelling is as follows. First, we needed to stack the data, to add information on each survey, and to scale tr_i and d_i.

```
  y2 <- data.frame(do.call("rbind", lapply(1:nrow(y), function(i) na.exclude(cbind(i,
      y[i,], tr)))))
colnames(y2) <- c("Survey", "y_unsc", "tr_unsc")
y2 <- cbind(y2, surveyInfo[as.numeric(y2$Survey),])
y2$tr <- scale(y2$tr_unsc)
y2$y <- scale(y2$y_unsc)
```

Second, we fitted the linear mixed model in equation (2) using the following specifications:

```
library(lme)
M <- lme(y ~ tr + tr*Breed + tr*Rotation + tr*Area,
         random = list(Paddock = pdLogChol(~tr),
                        Plot = pdLogChol(~tr),
                        Survey =pdLogChol(~tr)),
         corr = corCompSymm(form=~1),
         contrasts = list(Rotation="contr.sum", Area="contr.sum"),
         data = y2[y2$consumption>0,],
         control = list(maxIter=1e100, msMaxIter=1000000, niterEM=50,
                         tolerance=1e-100, msTol = 1e-100, opt="optim")
         )
```

In case the covariance of random intercepts and slopes could not be fitted, `pdLogChol(~tr)` was replaced by `pdDiag(~tr)`.

Global model of selection depending on trait values

The *global model* took into account the multivariate structure of the species dataset in a hierarchical manner, with all the *j*=152 species observed multiple times and in different subplots. Since the differences were continuous and centred around 0, we described them as normally distributed as

$$d_i \sim N(\mu_i, \sigma_1) \quad (3)$$

The expected mean μ_{ijk} for observation *i* of plant species *j* grazed by breed *k* was modelled as a species and breed-specific selection coefficient β_{jk} plus random effects u_{ij} for vegetation subplot *V*, paddock *P*, area *A* and rotation *R*:

$$\mu_{ijk} = \beta_{jk} + u_{ij}^{V} + u_{ij}^{P} + u_{ij}^{A} + u_{ij}^{R} \qquad (4)$$

Vague normal and uniform priors were used for means and standard deviations, respectively. In the Bugs language (see code supplement) this was represented as

```
 for(j in 1:J) {
   for (i in 1:N){
     y[i, j] ~ dnorm(mu[i, j], tau)
     mu[i, j] <- beta[j, breed[i]] +
               inprod(lam.v[j, 1:num.lv], z.v[v[i],]) +
               inprod(lam.p[j, 1:num.lv], z.p[p[i],]) +
               inprod(lam.a[j, 1:num.lv], z.a[a[i],])  +
               inprod(lam.r[j, 1:num.lv], z.r[r[i],])
   }}
 tau <- 1/ (sd * sd)
 sd ~ dunif(0, 100)
```

Selection coefficients β_{jk} were distributed normally around an expected mean b_{jk}, which is a breed-specific linear effect of trait values for each species *j*, targeted to estimate the dependence of selection on the trait.

$$\beta_{jk} \sim N\left(b_{jk}, \sigma_2\right) \qquad (5)$$

$$b_{jk} = \alpha_{0k} + \alpha_{1k} * tr_j \quad (6)$$

In Bugs language, this was written as

```
for (k in 1:3){
   for (j in 1:J){
     beta[j, k] ~ dnorm(mu.beta[j,k], tau.beta[k])
     mu.beta[j, k] <- alpha0[k] + alpha1[k] * tr[j]
   }
 alpha0[k] ~ dnorm(0, .0001)
 alpha1[k] ~ dnorm(0, .0001)
 tau.beta[k] <- 1/(sd.beta[k]*sd.beta[k])
 sd.beta[k] ~ dunif(0, 100)
}
```

The random effects u_{ij} in equation (4) could be modelled as variance-covariance matrix of dimensions $m \times m$. However, given a dataset of $m=152$ plant species this was computationally infeasible. We therefore chose the latent variable approach presented by Warton et al. (2015). For each structural level *V*, *P*, *A* and *R*, the correlation between species was reduced to a linear function of a limited number of latent variables z_i, which describe some unmeasured environmental descriptors, e.g. nutrient availability.

$$u_{ij}^{V,P,A,R} = z'^{V,P,A,R}_{i} \lambda_j \quad (7)$$

The factor loadings λ_j represented the response of species *j* to that unmeasured descriptor and approximate the correlation across plant species (Ovaskainen et al., 2016).

In Bugs language, matrices $z_i \times \lambda_j$ were constructed for every structural level as given for the level of vegetation subplots V. Following Warton et al. (2015), line 1 sets priors for the latent variable. Line 2 constrains the upper diagonal of the matrix $z_i \times \lambda_j$ to zero. Line 3 sets sign constraints on diagonal elements and line 4 and 5 sets random values to all other elements

```
for(i in 1:V){ for(lv in 1:num.lv){z.v[i,lv] ~dnorm(0,1)}}
for(i in 1:(num.lv-1)) {for(lv in (i+1):num.lv) { lam.vpl[i,lv] <- 0}}
```

```
for(i in 1:num.lv) {lam.v[i,i] ~ dunif(0,20) }
for(i in 2:num.lv) {for(lv in 1:(i-1)) { lam.v[i,lv] ~ dnorm(0,0.05)}}
for(i in (num.lv+1):J) {for(lv in 1:num.lv) {lam.v[i,lv] ~ dnorm(0,0.05)}}
```

The advantage of using latent variables was the reduction in dimensionality which made the computations feasible. Warton et al. (2015) showed that already a small number of correlations provides a good approximation to the correlation matrix. We evaluated the use of up to five latent variables in the random structure. Because there was little effect on the results (**Figure S4.4-1**), we finally worked with two latent variables per level only in order to save computation time. We further assumed that the random effects were independent of each other (Ovaskainen et al., 2016).

In addition, missing trait values for some species were sampled from a uniform distribution across the range of available trait values.

```
for(j in 1:J){  tr[j] ~ dunif(tr.min,tr.max) }
```

Parameters of the global model were estimated in a Bayesian framework using Markov Chain Monte Carlo via the software Jags 4.3.0 (Plummer, 2003). Despite the many parameters, the model converged relatively fast. After discarding the first 20000 iterations as burn-in, a single chain with 100000 iterations was run, of which every 20th was saved. In parallel to the p-values for the local model, we used the posterior samples to calculate the probabilities that α_{1k} exceeded zero or differed between breeds (see code supplement).

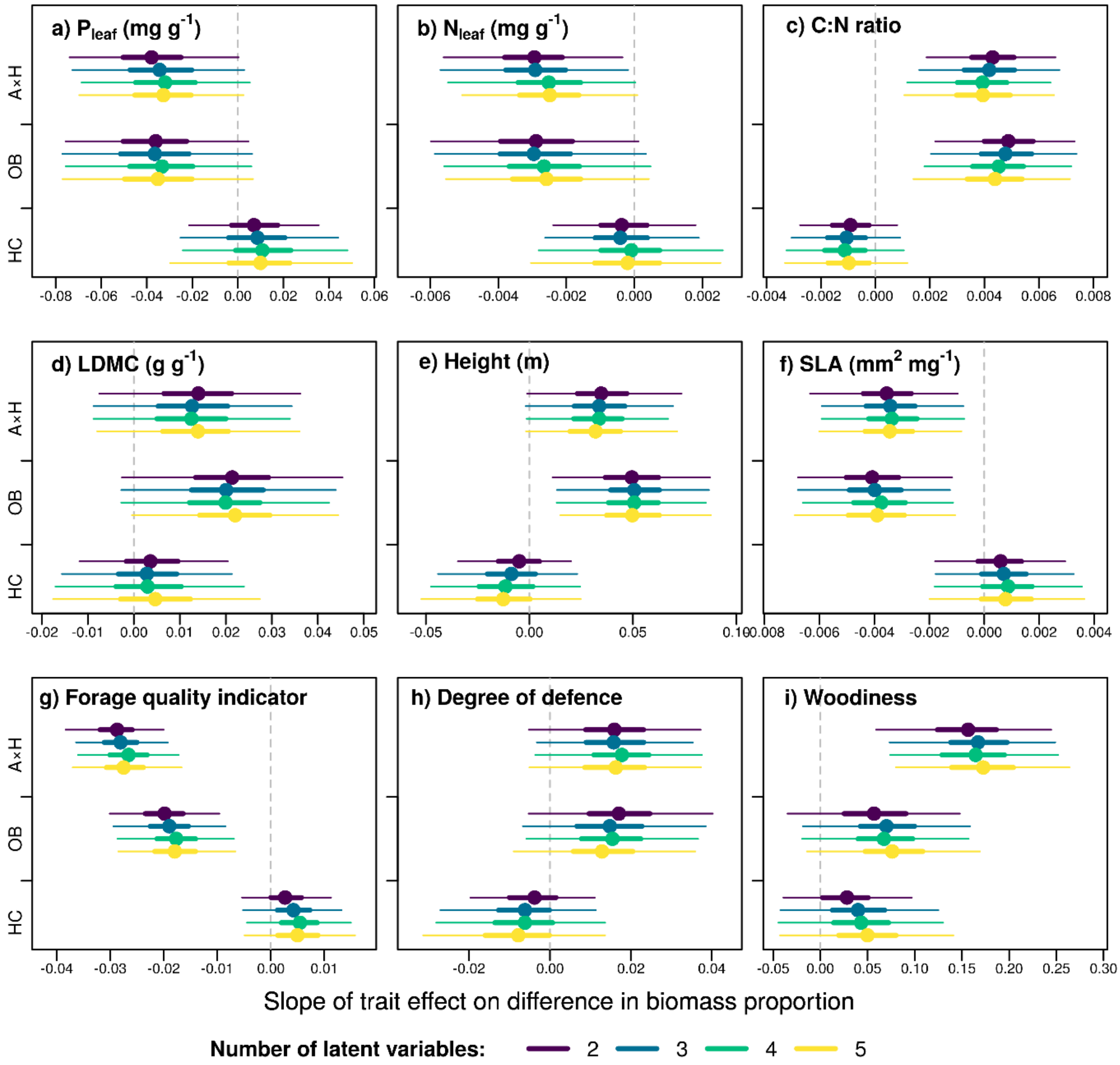

Figure S4.4-1 | Influence of different numbers of latent variables on trait responses: Shown are estimated effects of nine traits as affected by the number of latent variables included in the random structure of the global model. Lines indicate the 50% and 95% credibility interval.

S4.5 Correlation between traits

The traits of observed plant species were not independent, but there were only few strong correlations between them (**Figure S4.5-1**). The strongest correlations were found between C:N ratio, LDMC and woodiness. Woodiness further showed a negative relationship to N_{leaf} and a positive one to plant height. There were positive correlations between traits associated with nutrient-rich plants, namely between P_{leaf} and N_{leaf}, SLA and forage quality. No significant correlations were found for the defence mechanisms. Taken together, trait values were weakly correlated and only a fifth of the correlation coefficients showed values above 0.5.

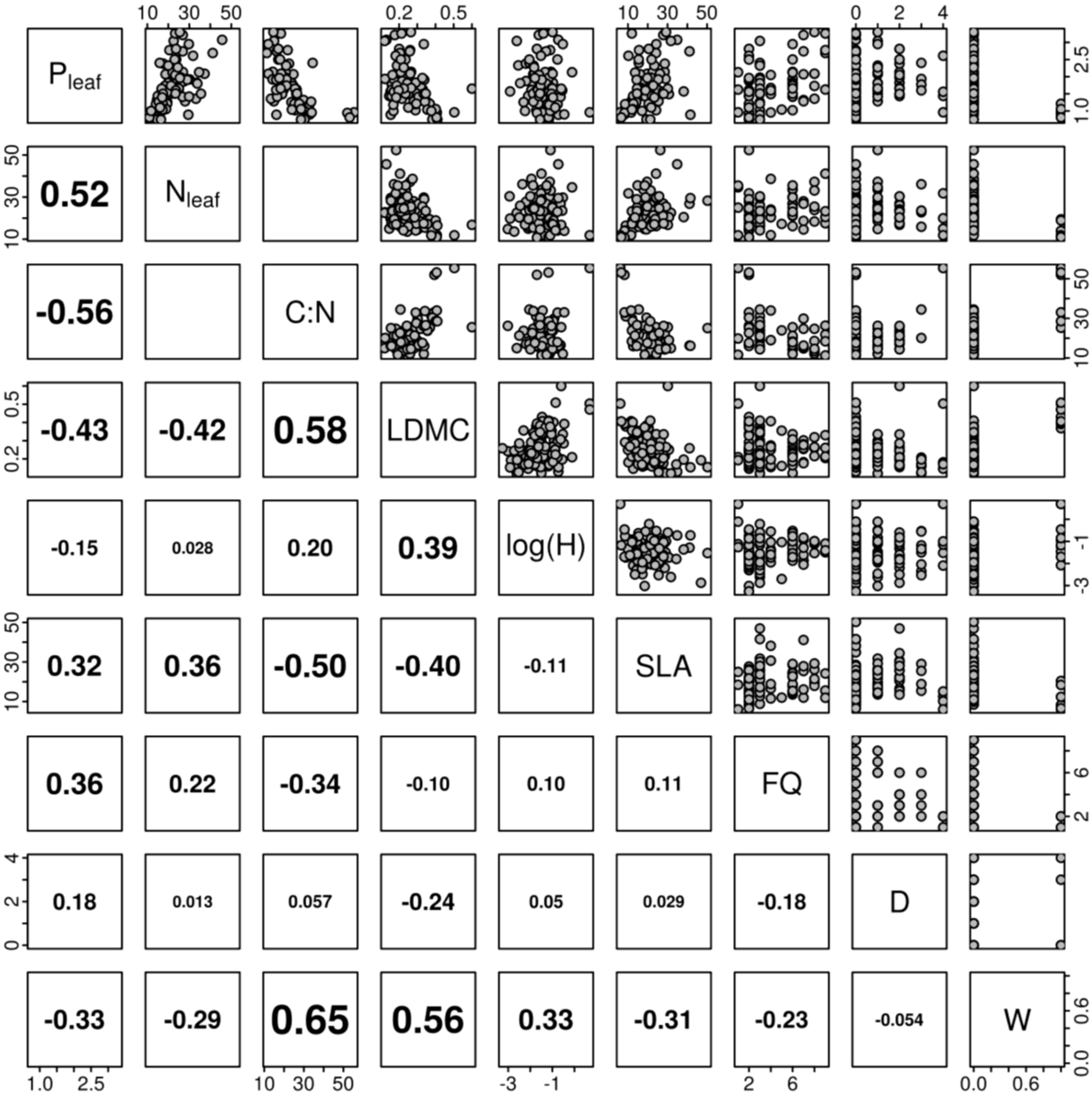

Figure S4.5-1 | Correlation coefficients of traits: Pearson correlation coefficients (lower triangle) and scatterplots (upper triangle) for the traits P_{leaf}, N_{leaf}, C:N ratio, leaf dry matter content (LDMC), plant height (H), specific leaf area (SLA), forage quality indicator value (FQ), degree of physical defence (D) and woodiness (W) of the plants growing on the study pastures. The correlation between C:N and N is not shown because it reflects a spurious relationship.

S4.6 Overview of plant species

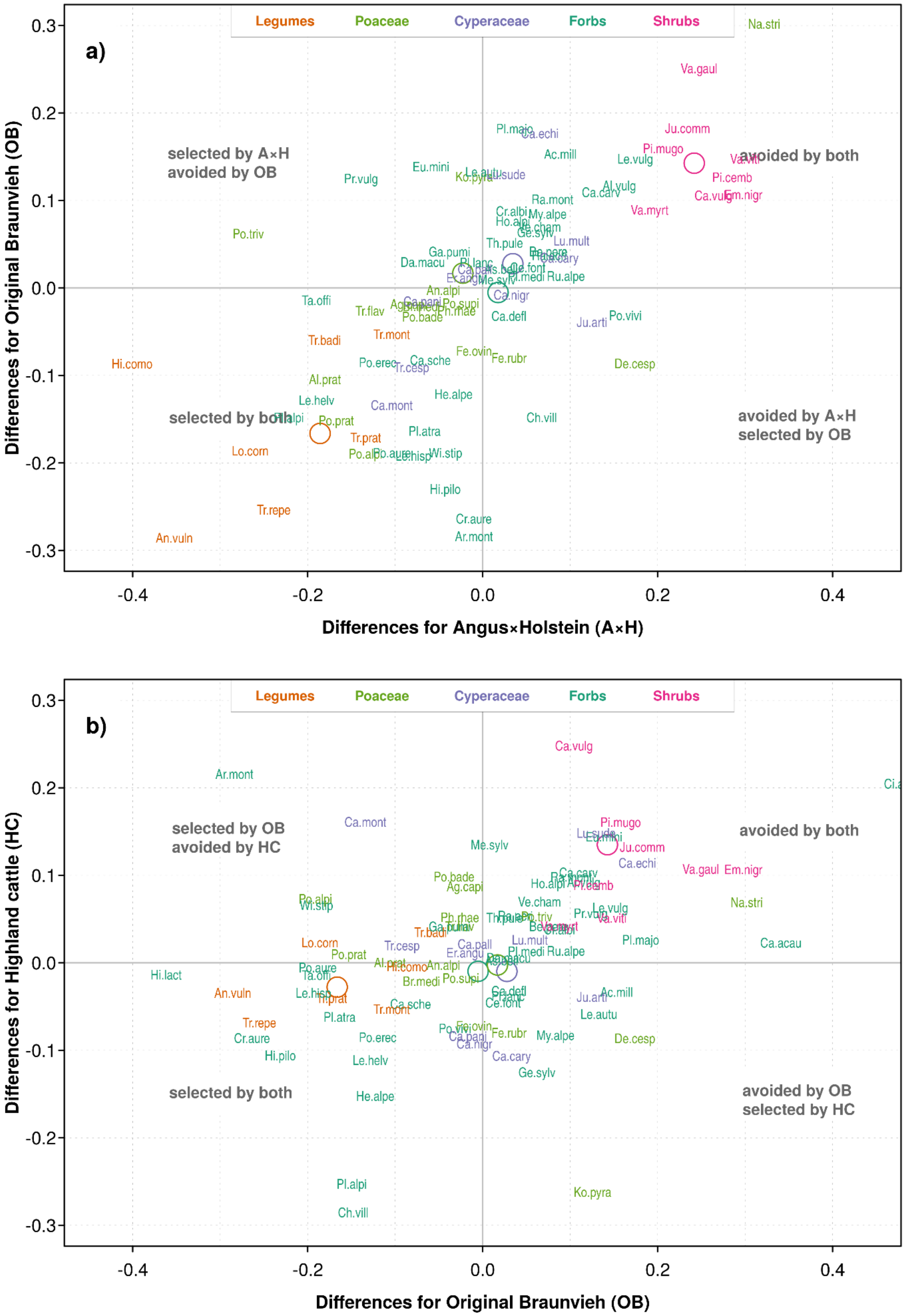

Figure S4.6-1 | Selection and avoidance of plant species by two cattle breeds: Observed differences in biomass proportions before and after grazing by **a** Angus×Holstein (A×H; x-axis) and Original

Braunvieh (OB; y-axis) and **b** Highland cattle (HC; x-axis) and Original Braunvieh (OB; 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 ten times are presented and coloured according to five functional groups. Circles indicate the mean values for each group across the entire dataset.

Table S4.6-2 | Plant species mapped in Figure 4.5: Given are the full and abbreviated names as well as the number of observation and the number of available traits for each plant species observed more than ten times.

Species	**Abbr.**	**No Obs**	**No Traits**
Achillea millefolium L.	Ac.mill	93	9
Agrostis capillaris L.	Ag.capi	91	9
Alchemilla xanthochlora ROTHM.	Al.vulg	123	8
Alopecurus pratensis L.	Al.prat	33	9
Anthoxanthum alpinum Á. & D. LÖVE	An.alpi	84	9
Anthyllis vulneraria L.	An.vuln	28	7
Arnica montana L.	Ar.mont	28	8
Aster bellidiastrum (L.) SCOP.	As.bell	12	4
Bartsia alpina L.	Be.pere	48	9
Briza media L.	Br.medi	47	9
Calluna vulgaris (L.) HULL	Ca.vulg	36	9
Campanula scheuchzeri VILL.	Ca.sche	51	5
Carduus defloratus L.	Ca.defl	15	8
Carex caryophyllea LATOURR.	Ca.cary	15	9
Carex echinata MURRAY	Ca.echi	19	5
Carex montana L.	Ca.mont	20	5
Carex nigra (L.) REICHARD	Ca.nigr	30	9
Carex pallescens L.	Ca.pall	35	9
Carex panicea L.	Ca.pani	24	9
Carlina acaulis L.	Ca.acau	23	8
Carum carvi L.	Ca.carv	79	9
Cerastium fontanum BAUMG.	Ce.font	57	3
Chaerophyllum villarsii W. D. J. KOCH	Ch.vill	15	4
Cirsium acaule SCOP.	Ci.acau	33	8
Crepis aurea (L.) CASS.	Cr.aure	35	4
Crocus albiflorus KIT.	Cr.albi	55	4
Dactylorhiza maculata (L.) SOÓ	Da.macu	45	9
Deschampsia cespitosa L.	*De.cesp*	*62*	*9*
Empetrum nigrum L.	Em.nigr	11	9
Eriophorum angustifolium HonCK.	Er.angu	15	9
Euphrasia minima SCHLEICH.	Eu.mini	33	2
Festuca ovina L.	Fe.ovin	15	9
Festuca rubra L.	Fe.rubr	147	9
Galium pumilum MURRAY	Ga.pumi	31	8
Geranium sylvaticum L.	Ge.sylv	16	9
Helianthemum alpestre (JACQ.) DC.	He.alpe	28	2
Hieracium lactucella WALLR.	Hi.lact	23	5
Hieracium pilosella L.	Hi.pilo	29	9
Hippocrepis comosa L.	Hi.como	23	8
Homogyne alpina (L.) CASS.	Ho.alpi	35	7
Juncus articulatus L.	Ju.arti	11	5
Juniperus communis L.	Ju.comm	29	9
Koeleria pyramidata (LAM.) P. BEAUV.	Ko.pyra	15	8
Leontodon autumnalis L. AGGR.	Le.autu	14	9
Leontodon helveticus MÉRAT	Le.helv	47	4
Leontodon hispidus L.	Le.hisp	52	9
Leucanthemum vulgare LAM.	Le.vulg	38	9

Species	Abbr.	No Obs	No Traits
Lotus corniculatus L.	Lo.corn	26	9
Luzula multiflora (EHRH.) LEJ.	Lu.mult	61	8
Luzula sudetica (WILLD.) SCHULT.	Lu.sude	17	4
Melampyrum sylvaticum L.	Me.sylv	21	7
Myosotis alpestris F. W. SCHMIDT	My.alpe	11	4
Nardus stricta L.	Na.stri	94	9
Phleum rhaeticum (HUMPHRIES) RAUSCHERT	Ph.rhae	131	8
Pinus cembra L.	Pi.cemb	21	3
Pinus mugo uncinata TURRA	Pi.mugo	20	3
Plantago alpina L.	Pl.alpi	69	6
Plantago atrata HOPPE	Pl.atra	45	6
Plantago lanceolata L.	Pl.lanc	42	9
Plantago major L.	Pl.majo	17	9
Plantago media L.	Pl.medi	16	9
Poa alpina L.	Po.alpi	65	7
Poa badensis WILLD.	Po.bade	26	3
Poa pratensis L.	Po.prat	59	9
Poa supina SCHRAD.	Po.supi	45	3
Poa trivialis L.	Po.triv	15	9
Polygonum viviparum L.	Po.vivi	51	9
Potentilla aurea L.	Po.aure	49	8
Potentilla erecta (L.) RAEUSCH.	Po.erec	92	9
Prunella vulgaris L.	Pr.vulg	16	9
Ranunculus acris L.	Ra.acri	110	9
Ranunculus montanus WILLD.	Ra.mont	34	6
Rumex alpestris JACQ.	Ru.alpe	72	7
Taraxacum officinale WEBER S. L.	Ta.offi	90	9
Thymus pulegioides L.	Th.pule	32	8
Trichophorum cespitosum (L.) HARTM.	Tr.cesp	20	4
Trifolium badium SCHREB.	Tr.badi	25	4
Trifolium montanum L.	Tr.mont	36	8
Trifolium pratense L.	Tr.prat	118	9
Trifolium repens L.	Tr.repe	64	9
Trisetum flavescens (L.) P. BEAUV.	Tr.flav	85	9
Vaccinium gaultherioides BIGELOW	Va.gaul	30	8
Vaccinium myrtillus L.	Va.myrt	40	9
Vaccinium vitis-idaea L.	Va.viti	34	9
Veronica chamaedrys L.	Ve.cham	33	9
Willemetia stipitata (JACQ.) DALLA TORRE	Wi.stip	12	3

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