

How plant traits respond to and affect vertebrate and invertebrate herbivores—are measurements comparable across herbivore types?

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Abstract

Examining how plant traits respond to and affect herbivory is a common approach to exploring plant-herbivore interactions and their impact on ecosystem processes and functioning. Despite plants being potentially exposed to both vertebrate and invertebrate herbivores simultaneously, fundamental differences in the ecology and evolution of these two herbivore guilds results in them often being studied separately. A synthesis of the literature is needed to understand the types of plant traits examined and their response to, and effect on (in terms of forage selection) vertebrate and invertebrate herbivory, and to identify associated knowledge gaps. Focusing on grassland systems and species, we found 139 articles that met our criteria: 40 invertebrate, 97 vertebrate and 2 focussed on both vertebrate and invertebrate herbivores. Invertebrate focussed research, research conducted in the Southern Hemisphere and research on non-domesticated herbivores was significantly underrepresented based on our search. Differences in study focus (trait response or trait affect), along with considerable differences in the types of traits examined, led to limited capacity for comparison between the two herbivore guilds. For both invertebrates and vertebrates however, plant traits related to growth, such as leaf nitrogen and photosynthetic capacity, were often positively associated with herbivory. Future research should prioritise understanding how invertebrates, and the combined impact of both invertebrates and vertebrates' respond to and affect plant traits. This review can be used as a guide for future research to select plant traits which are commonly measured either within one, or across both guild/s, as to help improve comparability and the broader significance of results, while also extending research breadth and knowledge.

Introduction

Plant-herbivore interactions link primary production and food webs. They are the catalyst for the transfer of energy/nutrients between trophic levels and the abiotic environment and are crucial to the shaping of community dynamics and ecosystem function. Due to their fundamental role in the web of life, plant-herbivore interactions have been the focus of many fields of research, including ecology (such as, Risch et al., 2018), evolution (such as, Johnson et al., 2015; Maron et al., 2019), entomology (such as, Roohigohar et al., 2022; Zalucki et al., 2001) and agriculture (such as, Christensen et al., 2013; Wari et al., 2019). Questions range from fundamental knowledge building (Ramsey & Wilson, 1997) and practical understanding, such as learning how to produce crops or meat more efficiently, to testing and developing ecological theory, such as understanding the role plant/herbivore interactions play in ecosystem coupling and stability (Risch et al., 2018).

Because of the complexity of plant-herbivore interactions, it is easy for knowledge silos to form within respective fields of expertise and investigation—where for example, a plant ecologist may experiment in different ways to an entomologist. A potential silo, perhaps easily conceived, is that which develops between different herbivore guilds, and specifically between vertebrate and invertebrate herbivores (Peisley et al., 2015). Due to fundamental differences in their ecology and evolution, these two broad taxonomic groups attract sometimes contrasting interests, expertise and methodologies (Andrew et al., 2022). This review aims

to systematically investigate differences between vertebrate and invertebrate focused research, specifically regarding how herbivores respond to and affect plant traits.

Plant functional traits have been used as a ‘common currency’³ to collate, compare and contrast response and effect correlations in plants within and between different ecosystems and species (Lavorel & Garnier, 2002; Suding et al., 2008). Functional traits also provide the opportunity to discover generalities which arise out of complex interactions between species within and across trophic levels (Carmona et al., 2011; Lind et al., 2013). Further, using a common currency correlated with function, lends well to exploring the influence of other abiotic or biotic variables on traits and untangling their role in modifying plant-herbivore interactions (Funk et al., 2017).

Plants employ a variety of traits to defend themselves against herbivory. These can be morphological (e.g., spine length, see Gödel et al., 2016), phenological (e.g., lifeform, see De Bello et al., 2005) and physiological (e.g., photosynthetic capacity, see Shen et al., 2019), and usually are associated with herbivore avoidance or herbivore tolerance (Núñez-Farfán et al., 2007). For example, plants might avoid herbivory by being small and short (Wakatsuki et al., 2021), expressing secondary metabolites (Jones et al., 2003) or being covered in spines (Coverdale et al., 2019). Plants which tolerate herbivory might have a fast growth rate and efficient nutrient acquisition strategies to allow them to quickly regain photosynthetic tissue after feeding (Briske et al., 1996). In general, plants with functional traits on the conservative end of the leaf economic spectrum (e.g., relatively smaller specific leaf area, lower nitrogen content, a slower assimilation rate) are more tolerant of herbivores than those on the resource acquisition end of the spectrum (e.g., relatively higher specific leaf area, higher nitrogen, fast growth rate). Herbivory, in addition to plant productivity, can moderate the abundance of species within this spectrum (Wright et al., 2004).

Plant traits can be constitutive, i.e., present throughout a plants life, or can be induced, i.e., expressed when herbivory takes place (Barton, 2016; Züst & Agrawal, 2017). An example of a constitutive trait is the presence of plant spines. Traits such as this are expressed all the time, although the degree of expression can vary with abiotic and biotic factors, including herbivory (Hulshof et al., 2013). In this way the expression of constitutive traits can also be induced. For example, spine length (Young, 1987), or the expression of secondary metabolites may increase (beyond their constitutive expression) in response to herbivore attack (Huitu et al., 2014). Expression of induced defence traits can occur immediately in response to herbivore attack, such as the release of volatile organic compounds (VOCs), or over time, such as the increased accumulation of carbon or silica within an individual’s leaves. Plant traits also can either respond to or affect their abiotic and biotic environment (Funk et al., 2017). In the context of herbivory, response traits ‘respond’ to herbivore attack through an induced response and effect traits can ‘affect’ herbivory by attracting or deterring herbivores. The capacity for plant traits to change in response to short- and long-term changes in herbivory and other perturbations creates the foundations for adaptation and speciation to occur over longer evolutionary timeframes (Ackerly et al., 2000).

Plants are most of the time exposed to different types of herbivores simultaneously, and therefore may express a suite of traits also known as a ‘defence syndrome’, to effectively defend against different types of herbivory (Agrawal, Fishbein 2006; Moles et al. 2013). Vertebrate and invertebrate herbivores for instance, vary in size, feeding strategy, behaviour and ecology. Traits of the herbivores can then significantly influence the type, duration and degree of damage experienced by the plant and consequently the plants defence syndrome (Kotanen & Rosenthal, 2000b). Thorns, for example, are relatively ineffective at reducing herbivory from small invertebrates such as aphids, but function well against large browsing animals, like ibex or deer (Crawley, 2019). Similarly, some plant secondary metabolites might deter invertebrate herbivory, but may be ineffective against most vertebrate herbivores (Marsh et al., 2020; Salminen & Karonen, 2011). The type of herbivore, as well as the research question and context, will therefore likely influence the scientific lens researchers adopt and the traits chosen to be measured when asking ‘How do plant traits respond to and affect herbivory?’.

In this review, we aim to synthesise current evidence and understanding of how plant traits respond to and affect (in terms of forage selection) vertebrate and invertebrate herbivory. Further, we identify and

discuss any potential biases (i.e., taxonomic, geographic and climatic) and knowledge gaps. We will focus our literature search on grasslands and grassy woodlands. Grasslands cover ~30% of the Earth’s terrestrial surface (White et al., 2000) and herbivores are crucial to their functioning, diversity and evolution (Axelrod, 1985; McNaughton, 1984). Grasslands are also important to the provision of food for people, (Habel et al., 2013; Simon et al., 2009) and are important for maintaining global carbon and nutrient cycling (Scurlock & Hall, 1998). Because of the pressures of human food production, many grasslands have been extensively used and modified by humans and as a consequence the persistence of many grassland species are under threat (Cousins & Eriksson, 2008; Deák et al., 2020; Scholtz & Twidwell, 2022). To conserve plants and animals within these important and widespread ecosystems, we need to have a mechanistic understanding of the complex functional relationships between plants and herbivores. By studying the potentially disparate fields of vertebrate and invertebrate focused studies, we aim to provide a more wholistic understanding of plant trait-herbivore interactions in grasslands and highlight knowledge gaps to guide future research.

We structured our review around the following three questions:

1. Are their geographic, taxonomic or climatic trends evident within grassland plant trait-herbivore literature?
2. What plant traits are measured in vertebrate and invertebrate herbivore focussed studies?
3. How do plant traits respond to and affect (in terms of forage selection) vertebrate and invertebrate herbivory?

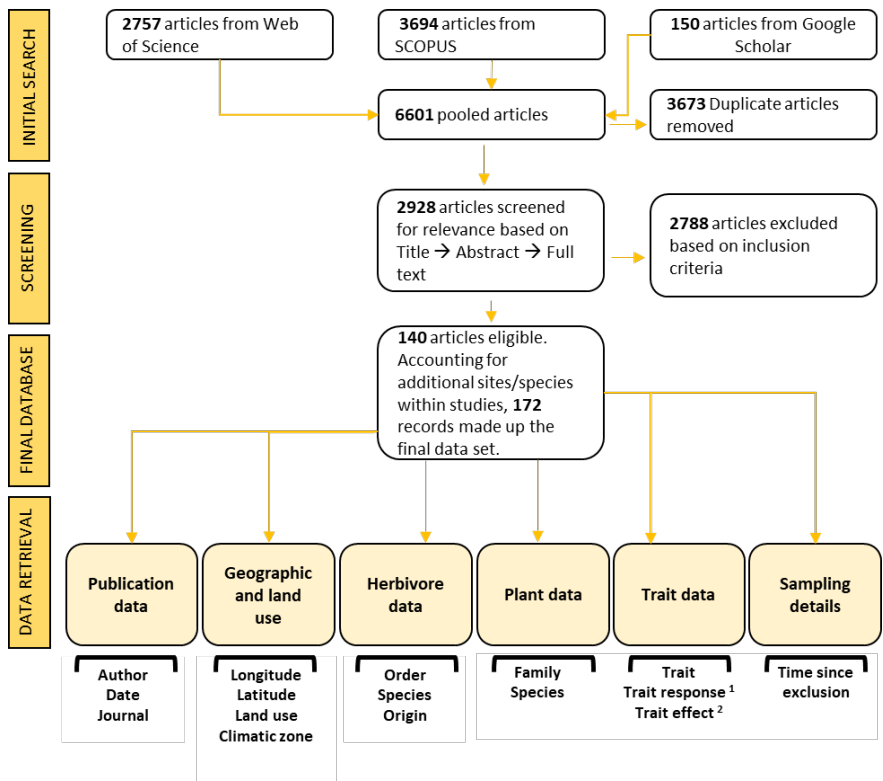


Figure 1. Procedures used in systematic literature review for articles examining herbivore effect on or response to, in regard to forage selection, plant traits in grassland ecosystems. Key data retrieved from each article is also shown within their categories, publication, geographic and land use, plant, trait and sampling details. A full list of the type of data collected is available in Appendix A and B. ¹ Plant trait response to herbivory. ² Herbivore selection response to plant traits.

2) Methods

2.1) Search Strategy

Our literature search and screening processes are shown in Figure 1. Using a specific set of keywords and criteria the following databases and internet search engines were searched for literature investigating how plant traits respond to and effect vertebrate and invertebrate herbivores in grasslands across the globe.

Databases and Internet searches

SCOPUS (<http://www.scopus.com>)

Web of Science Core Collection (<http://www.webofknowledge.com>)

Google Scholar (scholar.google.com)

Search terms and combinations

Searches were conducted in English and using the default date range for each database/ search engine (1980s to present for SCOPUS and Web of Science (WOS); 1970s onward for Google Scholar). To ensure a comprehensive search, we selected search terms related to herbivores and herbivory, plant functional traits and grasslands or other grass dominated systems (e.g., grassy woodlands) or the species that occur in these systems. The following search terms were utilised in each of the online databases and searches.

TS=((herbivor* OR graz* OR brows * OR feed* OR forag*) AND (“plant trait*” OR “functional trait*” OR “leaf trait*” OR “foliar trait*” OR secondary* OR defens* OR defenc*) AND (grass* OR grassland* OR “grassy woodland*” OR meadow * OR pasture* OR prairie* OR monocot* OR graminoid* OR pampa* OR savanna* OR savannah OR campos OR cerrado OR espinal* OR fynbos OR veldt* OR veld* OR llanos OR downs OR tundra* OR pustaz))

Using the field tag function in SCOPUS and WOS these terms were searched within the title, abstract and key words of these databases.

Search results from databases were exported to Endnote citation manager (Clarivate 20.3) and cleaned for duplicates. To check for additional results not within these databases, the first 150 papers (sorted by relevance) were exported from Google Scholar.

2.1) Search results

The initial search in WOS and SCOPUS yielded 4282 and 4082 respectively. To narrow down our search results we confined returned results to the field of ecology, plant sciences, environmental sciences, biodiversity conservation and entomology in WOS and environmental science and agricultural and biological sciences in SCOPUS. This returned 2757 in WOS and 3694 in SCOPUS, in addition to the 150 from Google Scholar. After duplicates were remove a total of 2928 papers were screened using the below screening process and criteria.

2.2) Article screening and criteria

To ensure articles were relevant and aligned with the review aims, only articles which adhered to the below criteria were included. We started with the title (to exclude obviously irrelevant articles), then the abstract, then full text. At conclusion of the screening process 139 articles remained (Appendix F) and were included for data collection

Criteria

Article type: Article documents an empirical investigation. This excludes reviews. Article is peer reviewed and in English.

Question: Article examines how vertebrate or invertebrate herbivory affects or responds (in terms of forage selection) to plant traits.

Subjects: Include one or more herbivore/s and plant trait/s and be within a grassland/grassy woodland ecosystem or on a plant species which occurs in these ecosystems.

Study design and treatments: Article included a no herbivory control treatment, either through herbivore exclusion, herbivore addition or natural herbivory gradients which included areas of no herbivory.

Excluded studies: Articles reporting on simulated grazing. Articles with only categorical traits. Articles which focussed on plant species which are crops. Articles which artificially modified plant traits and measured herbivore response (e.g., application of silica onto plants).

Rules for multiple treatments or time periods: Where articles report results from over multiple time periods, the most recent comparison was recorded. Where articles report results from multiple grazing intensities only difference between the control and highest grazing intensity were used.

2.3) Data retrieval

To characterise each of the 139 relevant studies, we compiled information for six main categories: publication data, geographic and land-use data, herbivore data, plant data, trait data and sampling design (Figure 1, Appendix A, B). All data was compiled using information provided in the papers, except for climate information which was obtained by overlaying study locations with ESRI World Terrestrial Ecosystems, Temperature Regime data (Esri, USGS, TNC) (Sayre et al., 2020). Land use at the study area were extracted from information provided within the publications, although collated into four categories: pastoral, natural area/minimal use, protected area and research facility. These features were used as descriptive variables to quantitatively summarise plant trait-herbivore research in grasslands and to examine trends in a) the effect of vertebrate and invertebrate herbivores on plant traits and b) the response of vertebrate and invertebrate herbivore forage selection to plant traits. In scenario a) plant traits are the response, while in scenario b) plant traits are the effect and herbivore forage selection is the response. As some studies included multiple herbivory treatments or multiple sites, there were a total of 172 records from which we extracted trait and herbivore responses.

Where trait information had been collected across multiple sites or species, all trait responses are recorded. Plant traits were grouped a priori into broad categories; morphological, biochemical, physiological and phenological. A list of all traits and the broad category they fall into can be found in Appendix C. The response of plant traits to herbivory or the response of herbivore forage selection to the plant traits was extracted from each article and recorded within the ordinal scale; negative, positive and not significant. For example, a study which found leaf nitrogen to be lower in grazed plants compared to ungrazed plants, would be given a *negative* score. Alternatively, if herbivore selection increased with leaf nitrogen, this would be given a *positive* score. For traits with more than 5 responses recorded across all studies, we calculated the proportion of trait responses which were negative, positive or not significant.

As our study is focussed on reviewing and examining coarse differences between vertebrate and invertebrate focussed herbivore research, we did not to collect information on effect size. We do however present the proportion and total number of studies which found positive, negative or non-significant results. As such this study only accounts for statistically significant results and not overall practical significance.

3) Results and Discussion

3.1) Overall publication trends and biases

Our final dataset comprised 139 articles from 68 journals and spanning the year range from 1985 to 2022. Of these, 40 investigated invertebrate herbivory and 97 investigated vertebrate herbivory. Two studies investigated both vertebrate and invertebrate herbivores, however only one examined the combined effect of both herbivore guilds on plant traits. Despite diverse and abundant invertebrates' assemblages within grasslands, relatively poor representation of invertebrates within plant trait-herbivore research aligns with trends in ecological research more generally (Eisenhauer et al., 2019).

Research on vertebrate herbivores focussed more on the response of plant traits to herbivory (76% of vertebrate studies and 51% of invertebrate focussed studies). In contrast research on invertebrate herbivores focussed more on the effect of plant traits on herbivore forage selection (24% of vertebrate and 48% of invertebrate studies respectively; Table 1). These differences in focus may reflect experimental biases, such as conducting appropriately replicated selection experiments is easier with invertebrates or may reflect the perceived importance of plant traits in influencing herbivore forage selection among these two guilds of herbivores. Vertebrates are polyphagous, which suggests that they are less affected by declines in food quality in comparison to invertebrate herbivores (Oduor et al., 2010). Similarly, vertebrates can generally move more easily between food sources increasing their available food options and perhaps making initial food selection strategies less important. Vertebrates also have greater bite and chewing capacity than invertebrates, perhaps making some morphological traits such as leaf hairs or leaf toughness less relevant to their forage selection (Kotanen & Rosenthal, 2000b). Nevertheless, chemical cues and morphological traits are regularly studied for understanding vertebrate forage selection in grasslands, and this is highlighted in the 24 studies analysed in this review (Appendix C).

Table 1. Summary of the 139 articles which adhered to the criteria of this review. ‘Study focus’ details the total number of studies which examined trait response or effect. ‘Taxonomy’ details the total number of plant and herbivore orders/families/species examined across and within all studies. ‘Plant traits’ details the total unique traits examined across and within all studies.

Final data set 139 studies, 171 records¹, 1516 trait/herbivore responses

	Vertebrate focussed	Invertebrate focussed	Overall total
Study focus			
Trait response to herbivory	76	21	97 ²
Trait effect on herbivore selection	20	20	40
Taxonomy			
<i>Plants</i>			
Total families	23	11	28
Total species	90	46	132
Total plant community studies	58	11	69
<i>Herbivores</i>			
Total orders	7	8	15
Total species	20	13	30
Total herb community studies	6	8	14
Plant traits			
Total traits examined	158	9	209

¹ Accounting for additional sites/species within the 139 studies, 171 records made up the final data set.

²Two studies examined plant trait response to both vertebrate and invertebrate herbivores.

3.2) Geographic, land use, climatic or taxonomic trends and biases

Research was conducted across 35 countries, with most research confined to the Northern Hemisphere and the cool temperate ecosystems of China and Europe (Figure 2). Tropical and sub-tropical grasslands, such as the cerrados and savannas of South America, Africa and Australia were significantly underrepresented. As these ecosystems make up ~50% of grasslands across the globe (Dixon et al., 2014), there is considerable room for improvement in our understanding of plant trait-herbivore interactions in global grassland systems. Poor representation of the Southern Hemisphere is a trend common within ecological research (Carlucci et al., 2020; Weidlich et al., 2020). Several studies have also highlighted the need for greater ecological research within tropical ecosystems (Clarke et al., 2017; Wilson et al., 2016).

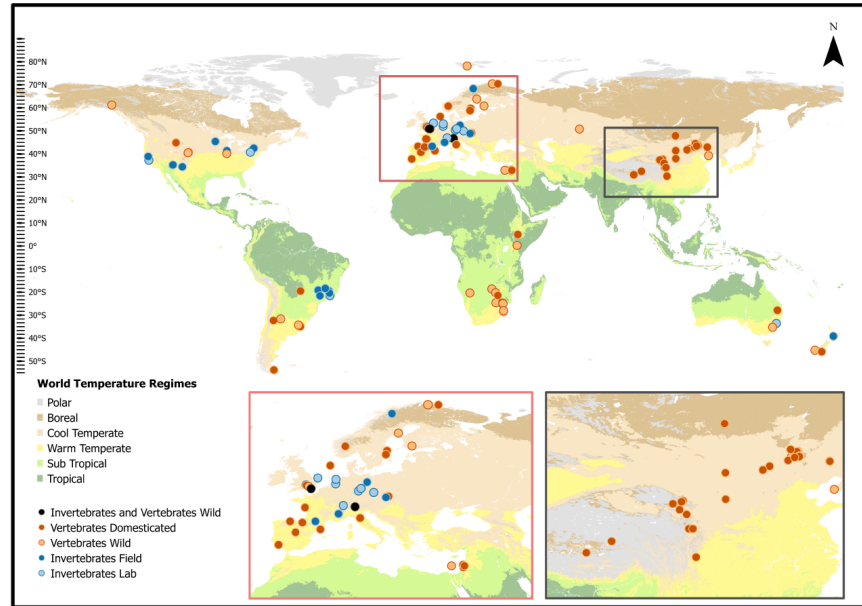


Figure 2. Map showing the location of each study within the ESRI World Terrestrial Ecosystems, Temperature Regime Map (Esri, USGS, TNC) (Sayre et al. 2020). The focal herbivore guild (vertebrate or invertebrate) and herbivore origin (Wild/Field, Domesticated/Laboratory) is also shown. 11 studies are not mapped due to multiple locations or insufficient geographic information provided.

Taxonomic trends

Herbivores

Domestic vertebrate herbivores, namely sheep, cows and goats were by far the most studied herbivores (Figure 3). This trend likely reflects funding and societal priorities to support global red meat production (Lemaire et al., 2005). Invertebrates, and other native mammalian herbivores, however, can also have huge impacts on grassland productivity and consequential livestock production (Risch et al., 2013; Saunders, 2018; Umina et al., 2021). Improving our understanding on how these herbivores impact plant defence syndromes may benefit the pastoral industry, while also providing a better overall understanding of how herbivores affect grassland plant communities. Many invertebrate species examined were also commercially important or very common species such as the cotton worm (*Spodoptera littoralis*) and cabbage moth (*Mamestra brassicae*). Ensuring future research focuses on both agriculturally and ecologically important herbivore species is important.

Most invertebrate studies were not focussed on particular invertebrate species but examined the response and effect of invertebrate communities to/on plant traits, usually by measuring total leaf damage (Effah et al., 2020) or by excluding invertebrate with the use of insecticide and/or exclosures (Carson & Root, 1999; Firn et al., 2017). These studies are useful for examining the overall influence of invertebrate herbivore on plants and can be easier than species focussed studies to conduct in the field.

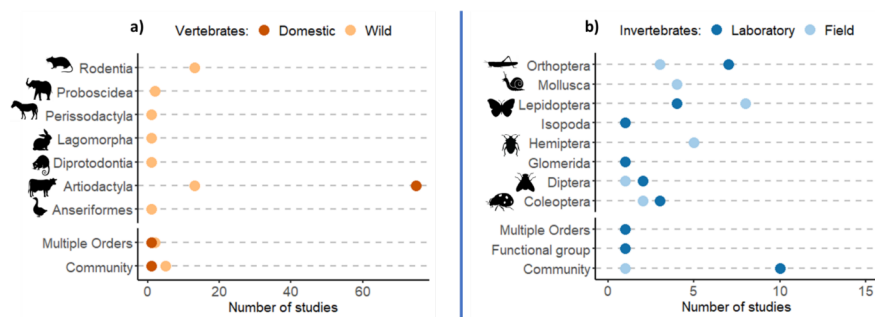


Figure 3. Number of studies per studied herbivore taxon, a) vertebrates and b) invertebrates. For vertebrates, dark orange circles denote domestic animals and light orange circles wild herbivores. For invertebrates, dark blue circles denote laboratory-based studies and light blue circles denote field-based studies.

Plants

A total of 31 plant families and 134 plant species were examined across all studies (Figure 4; Appendix B). Plant traits were mostly measured at the community level using mean traits values for dominant species (70 records total: 59 vertebrate and 11 invertebrate) or from species within the Poaceae family (grasses) (37 records total: 26 vertebrate and 11 invertebrate studies, 37 and 19 species respectively). Research involving plant functional traits are often inherently biased towards dominant species within the community due to the need to achieve adequate sampling and replication across treatments and because of the strong influence dominant species have on ecosystem function (Grime, 1998). The focus on species from the Poaceae family may also be due to the focus on domestic vertebrates who predominantly eat grass. For invertebrate focussed studies, plants from the family Asteraceae were also frequently examined, totalling eight studies and 13 species overall. This finding is again likely a matter of their dominance within grasslands, as the most commonly studied Asteraceae are disturbance tolerant and fecund, such as the common dandelion (*Taraxacum officinale*) and common milk weed (*Asclepias syriaca*). Invertebrate focussed studies also often examined the response of flowering traits (such as flower number) to herbivory. As Asteraceae species generally flower frequently and have easily observable flowers, this may be another reason for their focus, along with Fabaceae which were also commonly examined in invertebrate focussed studies.

Most plant species examined were native to their study range (Appendix B). Six studies examined plants invasive to their study range: 3 from America, 1 from Australia and 2 from New Zealand. As most studies were from the Northern Hemisphere, mainly China and the European Union, this result is unsurprising as these regions contain few non-native species. In contrast, in the southern hemisphere many non-native species are dominant due to a strong history of Eurasian plant introductions (Cook & Dias, 2006). Understanding the relationship between invasive non-native plant traits and herbivory is important for understanding factors associated with their spread and dominance and may help to predict and manage the impact of invasive plants. Future plant trait-herbivore research should work to further unravel these interactions between herbivory and plant invasion.

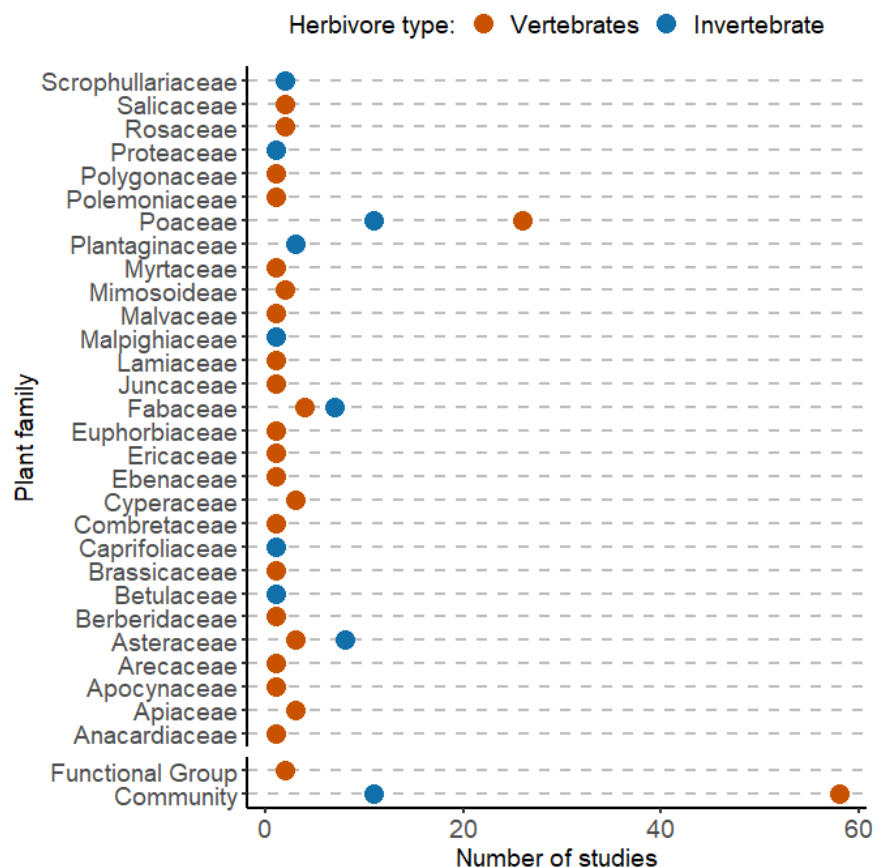


Figure 4 Number of studies per studied plant family for vertebrate (orange) and invertebrate (blue) focussed studies.

3.3) What plant traits are measured in vertebrate and invertebrate focussed studies?

Across all studies, 209 unique plant traits were measured. Of these 209, 115 were unique to vertebrate focussed studies, 50 unique to invertebrate focussed studies. Of these traits, 44 were measured commonly across vertebrate and invertebrate studies (Appendix C). Leaf traits were the most frequently measured (115), but stem (34), whole plant (24), root (16), flower/fruit (13) and seed traits (7) were also measured.

Key areas of difference were between the proportion of biochemical and morphological traits examined, with the former a greater focus in invertebrate, and the later, in vertebrate studies (Figure 5). This difference in traits studied between vertebrate and invertebrate studies may be due to the scale at which these two herbivore guilds operate, explained largely by differences in body size (Kotanen & Rosenthal, 2000a). Due to their greater capacity for defoliation at larger scales, vertebrates can influence plant morphology readily (e.g., plant height or biomass) and thus plants are potentially more likely to change their morphology in response to herbivory. In contrast, invertebrate herbivory usually occurs over relatively longer time periods (e.g., a caterpillar feeds on one leaf longer than a cow), at smaller scales and targeted to specific tissues (Hulme, 1996; Oduor et al., 2010). This may allow the plant more time to distribute re-mobilise nutrients and induce a biochemical defence against herbivores, for example using VOCs (Ameje et al., 2018) or other secondary metabolites. Nevertheless, there are some instances where insects can have huge impacts on plant morphological traits, such as biomass. One example are migratory insects (e.g., grasshoppers) that can reach high densities and in regard to extent of consumption, act like vertebrate herbivores (Tschardt & Greiler,

1995). Many vertebrate studies were also conducted over several years (Appendix A) and are therefore more likely to capture changes to plant morphology than invertebrate focussed studies, which were mostly conducted within a month or less.

Physiological traits, such as photosynthetic capacity and water use efficiency were only examined in relation to vertebrate herbivory (Figure 5). This is perhaps surprising as invertebrate impact on plant physiology has been relatively well-studied for crops (Nabity et al., 2008; Peterson et al., 1998; Thomson et al., 2003; Velikova et al., 2010), and findings have shown invertebrate herbivory to be both negatively and positively associated with photosynthetic rate. Similarly, across all studies only one phenological trait, flowering onset, was examined and only in four vertebrate focussed studies. This may reflect constraints within research budgets and priorities as phenological research generally requires experiments to run over several years, for which funding is generally limited (Hughes et al., 2017; Lindenmayer et al., 2012). The lack of focus on plant phenological responses to herbivory in grasslands is concerning as phenological patterns can influence regeneration capacity (Rawal et al., 2015), community composition (Lavorel & Garnier, 2002), and adaptation across trophic levels (Bagella et al., 2013; Wray & Elle, 2015). For example, research in the alpine rocky ecosystems in Colorado found herbivory by mule deer delayed flowering phenology in a perennial herb which consequentially reduced invertebrate seed predation and overall increased plant fitness (Freeman et al., 2003). Understanding how plant phenology and herbivory interact with climate is also an important area of future research, particularly under uncertain climatic conditions (Hamann et al., 2021; Lemoine et al., 2017). With advances in remote sensing technologies, studies on plant phenological studies are now easier and cheaper to perform and we see these technologies already starting to be used to answer other phenological questions (Dronova & Taddeo, 2022).

At the individual trait level and ignoring additional responses from multiple species or sites examined within studies, the five most common traits assessed in vertebrate focussed studies were specific leaf area (SLA), plant height, leaf nitrogen, LDMC and leaf area (descending order of use; Figure 4; Table 2). For invertebrate focused studies the most common traits were VOCs, SLA, aboveground plant biomass, LDMC and leaf nitrogen (Figure 4, Table 2). Specific leaf area, LDMC and leaf nitrogen were common focal traits across both vertebrate and invertebrate studies. These traits are often referred to as ‘soft’ traits as they are relatively easy to measure and have been found to correlate with traits which are harder to measure such as relative growth rate (Hodgson et al., 1999; Perez-Harguindeguy et al., 2016). These ‘soft’ traits also represent important components of the leaf economic spectrum (Hodgson et al., 1999; Wright et al., 2004) and inform us about the plant’s individual response to abiotic and biotic factors, and in the context of herbivory can inform us about the species ability to tolerate or avoid herbivory.

The study of VOCs was a key point of difference between vertebrate and invertebrate focussed studies, with eight studies examining VOCs in relation to invertebrate herbivory and only one in relation to vertebrate herbivory (Zhang et al., 2014). Analysis of VOCs is usually done via dynamic headspace sampling (Chen et al., 2003) under laboratory-controlled conditions, which may limit its capacity for use on vertebrate herbivores. Zhang et al. 2014 however used this system to first identify and isolate the VOCs released from grass species *Artemisia fridgida* and then apply these VOCs to control plants during a selection experiment with domestic sheep. Some studies have also successfully employed the head-space sampling system in a field setting to examine VOC production from grass leaves with high and low levels of invertebrate herbivory (see Kigathi et.al. 2009). It may be possible to use a similar strategy to examine VOC production in response to vertebrate herbivory. In response to invertebrate herbivory, VOC production can act as a signal to attract vertebrate and invertebrate predators (Kessler & Baldwin, 2001; Mäntylä et al., 2008) and to communicate the potential for herbivore attack to neighbouring plants (Baldwin et al., 2002). In other studies, not reviewed here, vertebrates have been shown to use plant VOCs to find food and increase feeding efficacy (Bedoya-Pérez et al., 2014; Stutz et al., 2016). Overall, the influence of VOCs were mostly studied in relation to invertebrates and expanding this research to further examine their response to, and effect on vertebrate herbivory would be an interesting avenue for future exploration.

The huge diversity and high proportion (61%) of traits examined from a single study was in part due to

traits being generally characteristic to particular plant families or functional groups, such as rhizome length (Amiaud et al., 2007), woody density of shrubs and woody forbs within grasslands (Whitworth-Hulse et al., 2016), thorns (Woodward & Coppock, 1995) or latex (Rasmann et al., 2009). Some studies researched unique aspects of plant-herbivore interactions. For example, Ribeiro et al. (2017) examined the influence of metals and micronutrients on invertebrate herbivore selection and this study accounted for 31 (15 %) of the single study traits. They found most metals examined did not affect invertebrate selection, although aluminium, iron, magnesium, manganese, and total leaf metals were found to have a negative effect on herbivore selection. Other studies examined specific morphological attributes, such as leaf symmetry or grass blade width, or specific anatomical aspects of a plant, such as spine angle. For example, Santos et al. (2013) found herbivory by gall midge was negatively correlated with leaf symmetry in the plant *Bauhinia brevipes*. They also found less symmetric leaves had lower leaf nitrogen, which is thought to be favourable for gall development. These results reveal interesting relationships between morphological and biochemical traits and their interaction with herbivores.

Using a common list of traits across research groups exploring plant-trait herbivore interactions would help to standardise trait measurements and improve comparability across studies and this has been flagged in previous reviews on the topic (Diaz et al., 2007) but at the same time, researchers should remain open to new emerging plant traits as technologies advance and our understandings improve. Shortlists of traits that should be favoured or disfavoured by herbivory have been identified (Coley et al., 1985; Weiher et al., 1999). Although these are mostly focussed on vertebrate herbivory, used alongside results from this review, a list of potential focal plant traits which are relevant to both vertebrate and invertebrate herbivores can be determined.

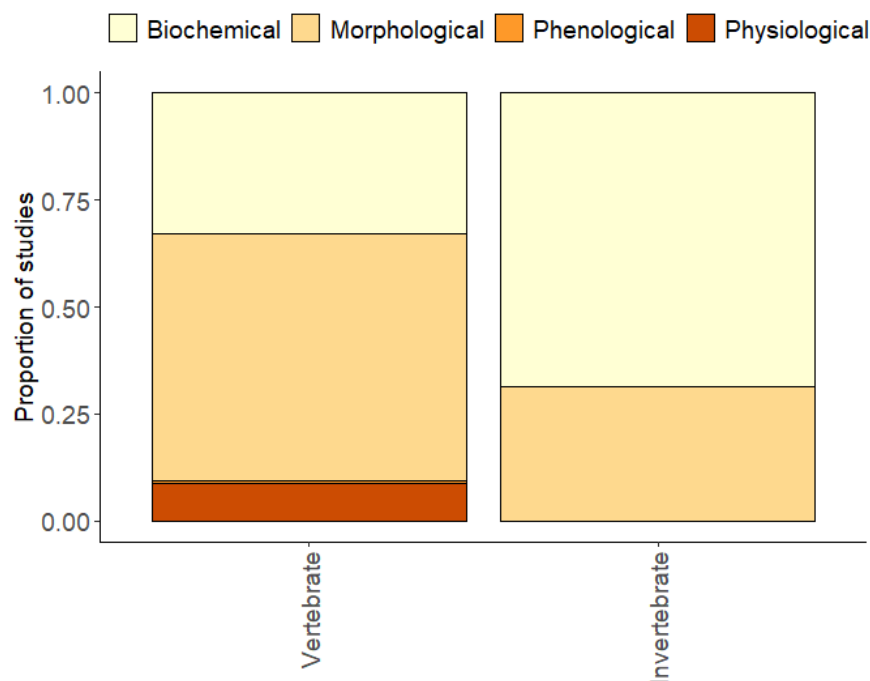


Figure 5 Proportion of biochemical, morphological, physiological and phenological traits examined in vertebrate and invertebrate focussed studies. Biochemical, morphological, phenological (only 1 trait; flowering onset) and physiological traits were examined in vertebrate focussed studies. Only biochemical and morphological traits were examined in invertebrate focussed studies.

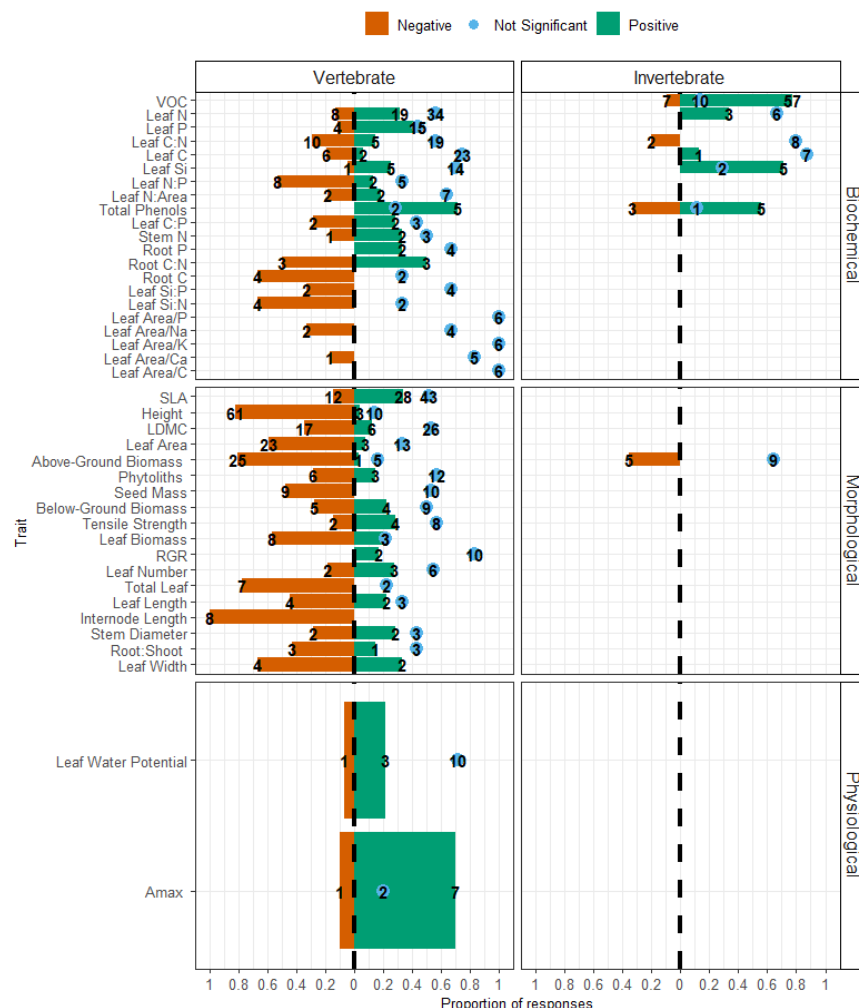


Figure 6 Response of plant traits to vertebrate (left) and invertebrate (right) herbivory, measured as a total proportion of studies which found a positive, negative, and non-significant result. Only traits with more than 5 responses recorded overall are included. Traits are grouped into broad categories biochemical, morphological, and physiological. There were less than five responses recorded for phenological traits. Numbers in black show the total number of studies. Where there was the same total number of studies recording a positive and non-significant result for a particular trait, only one number is shown.

3.4) Plant trait response and effect

Accounting for the multiple traits and site and/or species records within studies, we had a total of 1516 recorded responses (plant trait response to herbivory or plant trait effect on herbivore selection). Despite some similarities in studied plant traits between vertebrate and invertebrate focused studies overall, once responses were separated into either trait response to herbivory or trait effect on herbivore selection there was little overlap, and thus our capacity to compare responses between vertebrate and invertebrate herbivores is limited. Subsequently, interpretations below predominantly discuss trait response and effect for these two herbivore guilds separately. We also focus our discussion predominantly on the top-five traits of the most measured responses (Table 2). All trait information can be found in Appendix B and C.

Traits response to herbivory

Overall, there was a high proportion of studies which found non-significant trait responses to herbivory (Figure 6). At the study level, plant traits might not change with herbivory because the traits measured may not be indicators of specific plant-herbivore interactions studied in their focal system. It may also be that some traits which confer grazing tolerance/avoidance are also helpful, or of neutral advantage under ungrazed conditions. This is particularly relevant for vertebrate focussed studies which often compared plant traits values between grazed areas and exclusion plots, which usually had grazers excluded for between 5-10 years. The dominant plants that exist in these exclosures likely possess traits which confer grazing avoidance/tolerance, but these traits may not be a fitness disadvantage to the plant in ungrazed conditions and remain similarly expressed.

Trait response to vertebrate herbivory was most frequently recorded for SLA, LDMC, leaf nitrogen, plant height and leaf area; wherefor invertebrate herbivory it volatile organic compounds (VOCs), leaf nitrogen, aboveground biomass, total phenols and total tannins were most frequent. Vertebrate herbivory was mostly positively correlated with leaf nitrogen and SLA, and negatively with LDMC (Figure 6). As SLA and leaf nitrogen are positively correlated with high relative growth and LDMC positively correlated with leaf carbon content (Perez-Harguindeguy et al., 2016), these results suggest that many of the plant species and communities examined in these grassland studies, invest more in growth to tolerate herbivory, and less in carbon based defensive structures to avoid herbivory. This also aligns with the response of photosynthetic capacity and leaf phosphorous content, which mostly responded positively to vertebrate herbivory (Figure 6). Indirect influences from grazing such as nitrogen deposition through urine and faeces, may also increase the availability of nutrients in grazed environments and facilitate growth (de Mazancourt et al., 1998). Tolerating herbivory through rapid growth, is a common strategy for species from the Poaceae family, which dominate grasslands. This is particularly true for grass species growing in productive environments (Briske, 1996; Briske, 1999; Diaz et al., 2007; Díaz et al., 2001), where their dominance is often mediated via herbivory (Lunt et al., 2007). When grazers are removed in these environments, dominant grasses can sometimes reach a point of maximum growth, where restrictions space and/or nutrients limits further growth, and their growth rates may decline. In this scenario, grasses may invest more carbon in their stems and less in their leaves as structural support to grow tall under competitive light conditions (Irving, 2015).

In contrast, some studies found negative relationships between vertebrate herbivory and leaf area and plant height (Figure 6), which are typical mechanisms of grazing avoidance, documented in many other studies (Landsberg et al., 1999; McNaughton & Sabuni, 1988; Noy-Meir et al., 1989; Sala et al., 1986). A negative relationship between herbivory, leaf area and plant height may also be due to increased light availability in grazed areas, potentially reducing the need for plants to grow tall to access the light (Borer et al., 2014).

VOCs were mostly examined in relation to invertebrate herbivory and responded mostly positively, with only a handful of studies reporting a negative relationship with herbivory (Figure 6). This suggests that VOCs are mostly expressed or up regulated in response to herbivory. VOCs may also increase in response to a variety of other stimuli (Vivaldo et al., 2017) and play an important role in plant-plant and cross-trophic signalling (Baldwin et al., 2002; Mäntylä et al., 2008). Kigathi et al. (2009) who found the expression of some VOCs to decrease with invertebrate herbivory in the field, suggest that under field conditions the plant is responding to multiple stimuli at once and this may also affect the type and abundance of VOC emissions. They also highlight that reduced VOC production in response to herbivory may be due to the allocation of carbon and nitrogen being prioritised for growth or for production of others defensive compounds over VOCs.

Where a significant response was found, leaf nitrogen was usually positively correlated with invertebrate herbivory, while leaf carbon to nitrogen ratio was usually negatively correlated (Figure 6). Similar to the response to vertebrate herbivory this result suggests that for these plant species, herbivory potentially results in a greater investment in growth over carbon-based defence as indicated by higher leaf nitrogen for every part carbon. Because many invertebrate focussed studies compared leaf traits from leaves with and without visual evidence of herbivory, greater nitrogen in grazed leaves may reflect herbivore preference for leaves with higher nitrogen, rather than the leaf increasing nitrogen in response to herbivory (Loranger et al., 2012).

Aboveground biomass (measured for individual species) responded mostly negatively, but also showed little

evidence of a change with invertebrate herbivory. The non-significant responses mostly came from one paper however (Ladygina et al., 2010) which looked at the effect of belowground herbivores (nematodes and wire worms) on aboveground biomass. Because aboveground biomass was not being directly removed via herbivory the effect of herbivory may be more nuanced. Aboveground biomass was also mostly negatively associated with vertebrate herbivory. One study was the exception, finding perennial forb biomass was higher in deer grazed pastures in comparison to ungrazed exclosures, likely due to reduced competition from grass species (Paige, 1992). In fact, in some grasslands the abundance and richness of forbs is thought to dependent on niche construction by large herbivores, due to the legacy of large and mostly extinct vertebrates, such as mammoths (Bråthen et al., 2021). This points to an important distinction between direct herbivore effects and indirect herbivore effects on plant traits.

Phenols are often attributed to herbivore defence and are usually hypothesised to increase in response to herbivory (Salminen & Karonen, 2011). Phenols are an extremely diverse group of compounds, however, and play several other roles in plant metabolism (Salminen & Karonen, 2011). The production of phenols is also reliant on adequate photosynthetic capacity to allow for the accumulation of carbon molecules (Frier et al., 2012). Total phenols responded mostly positively to vertebrate and invertebrate herbivory, although one study found phenols to decline in response to herbivory across multiple sites (Knappová et al., 2018) (Figure 6). Reported high rates of folivory in this study may have compromised the photosynthetic capacity of plants and limited phenol production (Knappová et al., 2018).

Leaf silica was relatively frequently measured (31 measures) in response to both vertebrate and invertebrate herbivory and where a significant effect was found was mostly positively associated with herbivory (Figure 6). Most studies examining the response of silica were on grass species, which are known for their relatively high silica content in comparison to forbs and their ability to accumulate silica in response to herbivory, but also in response to increases in soil silica content (Hall et al., 2019). Within the studies from this review, silica responded positively to herbivory in eight different grass species (Appendix B). One study from the tundra grasslands in Norway, found that for some grass species, silica content declined with summer reindeer herbivory (Petit Bon et al., 2022). Here they suggest that silica accumulates with age in these grass species, and perhaps herbivory is keeping the phenological age of the leaves young and thus maintaining lower leaf silica levels than un-grazed plants (Bañuelos & Obeso, 2000). Understanding how plant defence traits change with stages in plant phenology is an interesting area of future research and may help to untangle variable responses of plant traits to herbivory.

Trait effect on herbivore selection

In contrast to response traits which capture changes to plant traits with herbivory, effect traits potentially inform us more about the plants constitutive mechanisms to avoid or tolerate herbivory. Trait effect on vertebrate herbivore selection was most frequently recorded for leaf nitrogen, leaf fibre, total phenols, tannins, and SLA (Table 2). In contrast, trait effect on invertebrate herbivore selection was most frequently recorded for leaf hairs, LDMC, SLA, leaf nitrogen and leaf lignin (Table 2).

Like the trait response results, there was a high proportion of studies which found a non-significant effect of plant traits on herbivore selection (Figure 7). Where there was a significant effect, leaf nitrogen and SLA was mostly positively associated with both vertebrate and invertebrate herbivore selection. For invertebrates' leaf LDMC and leaf lignin was commonly negatively associated with selection. These results are in line with the dominant ecological paradigms which highlight leaf nitrogen and leaf tenderness (high SLA, low LDM, low leaf lignin) as important influencers of herbivore selection for plants that are more nutritious and palatability (Coley et al., 1985; Perez-Harguindeguy et al., 2016).

Leaf fibre and total phenols are often postulated to be negatively associated with palatability, as fibre can make the leaf tough and hard to digest and phenols can be toxic to both vertebrates and invertebrates (Salminen & Karonen, 2011). We found support for this within the reviewed vertebrate focussed studies (Figure 7) ; however, two studies also recorded a positive effect of these traits on herbivore selection (Egea et al., 2014; Hjalten et al., 1996). As these studies allude to, and as we have discussed earlier, phenols are a

diverse group of compounds which are not just involved in defence but contribute to several other metabolic processes. Without identifying the exact compounds, it is difficult to attribute their role to defence. Further, as found in the study by Egea et al. (2014), some species, such as goats, are capable of eating tannin-rich plants due to their ability to neutralise the negative effects of tannins, a type of phenolic compound (Allegretti et al., 2012). Some studies did look at specific phenol groups and in particular total tannins, where the dominant effect on vertebrate herbivore selection was negative. Tannins are a large group of water-soluble phenols which when ingested can bind to and precipitate proteins and micronutrients and reduce nutritional gain. Herbivores have been recorded selecting tannins rich forage to self-medicate against gastrointestinal parasites (Villalba et al., 2010), although this observation was not recorded in this review.

Leaf hairs were only investigated in relation to invertebrate herbivory and only in the context of herbivore selection. Where a significant response was recorded, most studies found leaf hairs to be negatively associated with invertebrate selection (Figure 7). One study, however, found leaf hairs positively influenced selection by a specialist herbivore, but negatively influenced selection by generalist herbivores (Lau et al., 2008). This highlights the importance of accounting for species co-evolution when assessing plant trait-herbivore interactions. Although not found within the reviewed studies, evidence from other studies suggest leaf hairs can also be induced by herbivory (Björkman et al., 2008; Tian et al., 2012). It may be that leaf hairs are also be an important inducible response in grassland species.

Table 2. The most common (top 5) and frequently measured (top 5) traits across and within all vertebrate and invertebrate studies. The study level reflects the most common traits examined, irrespective of frequency the trait was measured across and within all studies (e.g., ignoring site and species replicates). The response level reflects the most frequently measured traits, considering within study site and species replicates.

Study level	Study level	Response level	Response level
Most common traits	Most common traits	Most frequently measured traits overall	Most frequently measured traits overall
Vertebrate	Invertebrate	Vertebrate	Invertebrate
SLA	VOCs	SLA	VOCs
Plant height	SLA	Plant Height	Leaf nitrogen
Leaf nitrogen	Above-ground biomass	Leaf nitrogen	Above-ground biomass
LDMC	LDMC	LDMC	Leaf C: N
Leaf area	Leaf nitrogen	Leaf area	LDMC

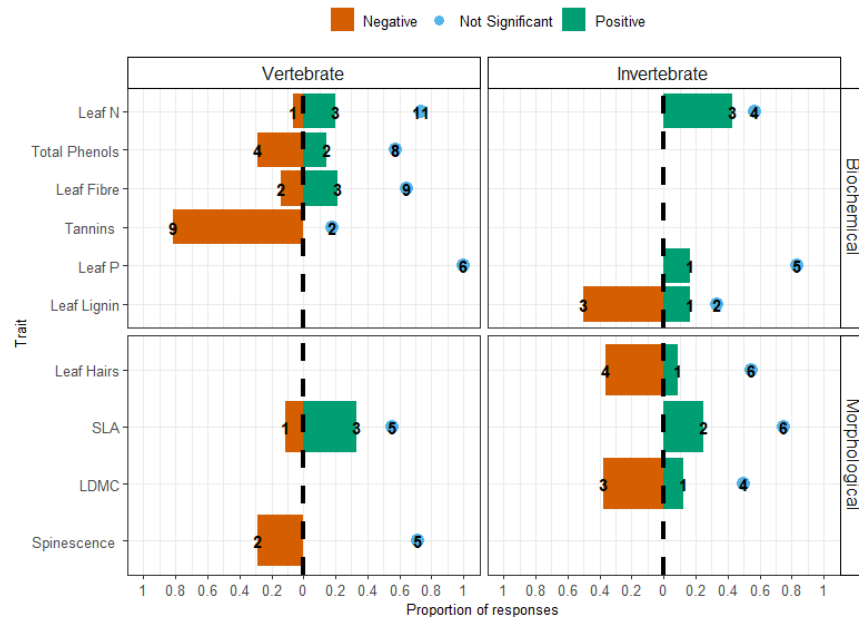


Figure 7 Effect of plant traits on vertebrate (left) and invertebrate (right) herbivore selection, measured as a total proportion of studies which found a positive, negative, and non-significant result. Only traits with more than 5 responses recorded overall are included. Traits are grouped into broad categories biochemical and morphological. There were less than five responses recorded for phenological and physiological traits. Numbers in black show the total number of studies. Where there was the same total number of studies recording a positive and non-significant result for a particular trait, only one number is shown.

3.5) Perspectives and limitations

We have presented an overview of the literature on plant trait-herbivore interactions in grasslands across the globe. Specifically, we highlight how vertebrate and invertebrate focussed studies differ in the types of traits examined, and their response to, and effect on herbivory. It is clear from the results of this review, that there is a particularly limited understanding on the impacts of invertebrates or the combined impacts of invertebrates and vertebrates on plant species in grasslands. Given the importance of grasslands for diversity, carbon cycling and human food production this is concerning. Considering that insect populations are declining across the globe (Eggleton, 2020), this highlights a particularly important area of future research to appropriately predict changes to ecosystem functioning.

Another important finding from this review is the significant bias towards domestic livestock and researching their response to, and effect on plant traits. Due to the dominant use of grassy ecosystems across the globe for livestock production, livestock potentially have a proportionally greater effect on plant traits and consequential ecosystem functioning than wild native vertebrate herbivores. Native herbivores usually exist within these pastoral landscapes however, and understanding how these species interact with domestic livestock to affect plant traits will provide a more wholistic understanding of herbivore impacts on grassland species. Further, due to differences in evolutionary history, plants likely respond differently to native compared to non-native herbivores, and this may be reflected in their trait response (Diaz et al., 2007).

As with most functional trait research, results from this review are biased toward the dominant plant species within grassland communities. This bias may be challenging to avoid, as rare species likely do not offer adequate replication, but fundamentally limits our understanding of plant-herbivore interactions. For instance, dominant plants within grazed grassland communities are likely to be selected for their traits which confer grazing tolerance or avoidance. In contrast, species which occur at low frequencies (one definition

of ‘rare’) may do so because they are highly palatability and have been selectively grazed. Alternatively, they may be inherently ‘rare’, due to low fecundity and dispersal. Subordinate and rare species can have significant influence on ecosystem functioning (Baer et al., 2002; De Vries et al., 2011; Grime, 1998) and understanding their interactions with herbivory is an important area of future research.

Although there were some similarities between vertebrate and invertebrate focussed studies in terms of the plant traits examined, there is still considerable disparity, which reduced the capacity for comparisons. Differences in the potential scale, intensity and specificity of herbivory inflicted by these two groups is important to understand the differences in the types of plant traits being chosen to be researched. In saying this there is considerable capacity to expand plant trait-herbivore research to increase comparability of results between vertebrate and invertebrate herbivores. For instance, investigating the relationship between VOCs and vertebrate herbivory or examining how invertebrates influence plant morphology using longer-term experiments would be an interesting area for future research. Overall, we suggest there is also scope to shortlist the types of traits being examined to improve comparability of results, but still remaining adaptable to change as more is learned.

Despite considerable effort to ensure all relevant studies were included in this systematic review, we recognise the search terms used may not have been sufficient to find species-focussed studies that did not specify that their focal species occurred in grasslands. For instance, for some laboratory or glasshouse studies the fact that their focal plant species naturally occurs in grasslands may have been irrelevant to their study question. Overall, we found perhaps surprisingly few studies which adhered to the criteria of this systematic review. Many potentially relevant studies were excluded because they examined how plant traits responded to various intensities of herbivory but failed to include a no herbivory control. Other key reasons for exclusion were the use of categorical traits and the use of cropping species.

Overall, there is exciting opportunity for future research to explore interactions between vertebrate and invertebrate herbivores and grassland plant traits. This will add to a growing body of literature aimed at better understanding the complex relationships between plants and herbivores. As the primary pathway for nutrient cycling and movement across trophic levels, these relationships are crucial for the functioning of agricultural and ecological systems alike. By improving our understanding of these relationships, we contribute to the development of theories around plant herbivore interactions and in doing so help to guide the development of better research questions and the building of knowledge.

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