



1 **Title**

2 Reviews and Syntheses: Impacts of plant silica - herbivore interactions on terrestrial biogeochemical  
3 cycling

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18 **Abstract**

19 Researchers have known for decades that silicon plays a major role in biogeochemical and plant-soil  
20 processes in terrestrial systems. Meanwhile, plant biologists continue to uncover a growing list of benefits  
21 derived from silicon to combat abiotic and biotic stresses, such as defense against herbivory. Yet despite  
22 growing recognition of herbivores as important ecosystem engineers, many major gaps remain in our  
23 understanding of how silicon and herbivory interact to shape biogeochemical processes, particularly in  
24 natural systems. We review and synthesize 119 available studies directly investigating silicon and herbivory  
25 to summarize key trends and highlight research gaps and opportunities. Categorizing studies by multiple  
26 ecosystem, plant, and herbivore characteristics, we find substantial evidence for a wide variety of  
27 important interactions between plant silicon and herbivory, but highlight the need for more research  
28 particularly in non-graminoid dominated vegetation outside of the temperate biome as well as on the  
29 potential effects of herbivory on silicon cycling. Continuing to overlook silicon-herbivory dynamics in  
30 natural ecosystems limits our understanding of potentially critical animal-plant-soil feedbacks necessary  
31 to inform land management decisions and to refine global models of environmental change.



## 32 1 Introduction

33 For centuries researchers have intensively studied cycles of key nutrients influencing plant growth and  
34 diversity such as nitrogen (N) and phosphorus (P) across a diverse range of ecosystems (*e.g.*, Elser et al.,  
35 2007). Meanwhile, studies have often overlooked other nutrients such as silicon (Si), which is important  
36 for plant function and protection (Cooke et al., 2016) as well as for biogeochemical cycling (Street-Parrott  
37 and Barker, 2008). For instance, Si can reduce the impact of many abiotic and biotic pressures, including  
38 water, temperature and salinity stress, as well as nutrient deficiency, heavy metal toxicity, disease, and  
39 herbivory (Debona et al., 2017). Plants can likewise affect terrestrial silica fluxes by controlling weathering  
40 rates and activity of dissolved Si in soils and streams (Derry et al., 2005). Plants and their associated  
41 microbiota can accelerate the weathering of silicate minerals by altering the physical properties and  
42 reactivity of the soil environment (*e.g.*, pH, moisture, exposed surface area of minerals), and by taking up  
43 essential nutrients which destabilizes silicate minerals (Drever, 1994; Street-Parrott and Barker, 2008 and  
44 references therein). Since the silicate weathering process consumes carbon dioxide (CO<sub>2</sub>) through  
45 chemical weathering of calcium- and magnesium-silicate minerals in continental rocks, the effects of  
46 plants on the Si cycle may influence the global carbon (C) cycle (Street-Parrott and Barker, 2008).

47 Plants take up dissolved Si from direct weathering of mineral silicates and biogenic Si released from leaf  
48 litter to soil (Cornelis and Delvaux, 2016), and Si in plants exceeds the concentrations of many plant macro-  
49 nutrients (Epstein, 1999). Si accumulation varies among species, with some plants containing only trace  
50 amounts, whereas Si can constitute up to 10% plant dry mass in “high Si accumulators” such as many  
51 grasses (Hodson et al., 2005). In the last decade, many studies have focused on agricultural systems  
52 (Guntzer et al., 2012; see also Fig. 1), in particular looking at grass species (*e.g.*, McNaughton et al., 1985;  
53 Hartley and DeGabriel, 2016), with fewer studies examining the role or importance of plant Si in natural  
54 (*i.e.*, non-agricultural and in the field) environments even though the degree of dissolved Si passed through  
55 ecosystems as filters can vary dramatically by biome (Cooke and Leishman, 2011; Schoelynck et al., 2014;



56 Cornelis et al., 2016; see also Fig 1). In natural systems, studies have focused on graminoid-dominated  
57 vegetation types in the temperate biome, with relatively little research in tropical and boreal/subarctic  
58 forest and herbaceous vegetation types, even though plant Si uptake and storage in these systems may be  
59 significant (Cornelis et al., 2010; Katz, 2014).

60 Herbivory also creates a number of important feedbacks between plants and soils (Bardgett and Wardle,  
61 2003). For example, invertebrate herbivores can supply a remarkably large amount of nutrients to tropical  
62 and subarctic systems compared to other major sources, bringing likely labile nutrients to the forest floor  
63 in the form of frass and bodies (Hartley and Jones, 2004; Metcalfe et al., 2013; Kristensen et al., 2018).  
64 Selective herbivory may also result in the dominance of plants that are nutrient poor and/or better  
65 defended, which ultimately produces more recalcitrant litter that decomposes more slowly (Bardgett and  
66 Wardle, 2003). Since plant Si is involved in plant defense (Debona et al., 2017), interactions between  
67 herbivory and plant Si (Quigley and Anderson, 2016) may have the potential to exert a powerful influence  
68 over ecosystem biogeochemistry and function.

69 There are multiple detailed reviews covering silicon terrestrial biogeochemistry (*e.g.*, Conley, 2002; Struyf  
70 and Conley, 2012) as well as Si-derived benefits to plants such as herbivore defense (*e.g.*, Frew et al., 2018;  
71 Katz, 2019). However, given the likely importance of Si in multiple terrestrial biomes and the strong  
72 evidence for a tight coupling between plant Si and herbivory, remarkably few studies have investigated Si-  
73 herbivory dynamics in the context of biogeochemical cycling. Here, we review the role of plant Si-herbivore  
74 dynamics in biogeochemical cycles in order to summarize existing knowledge and emerging patterns,  
75 identify gaps in knowledge, and describe future research priorities. Towards this effort, we surveyed  
76 available literature between 1900-2020 in the Web of Science core collection database using search terms  
77 “silic\*” and “herbivor\*” and not “in silico” (314 results). We then filtered the results until only those  
78 publications that directly studied Si and herbivory remained (119 publications), which we categorized into  
79 various ecosystem, plant, and herbivore characteristics (Fig. 1). Our purpose is to identify areas where this



80 knowledge can be currently useful, such as agricultural and land management, and assist efforts to better  
81 integrate potentially important but overlooked herbivore-plant-soil interactions into global  
82 biogeochemical models to more accurately predict ecosystem function shifts in the face of environmental  
83 change (Van der Putten et al., 2013).

## 84 **2 Silicon in terrestrial systems**

85 The biogeochemical Si cycle impacts global CO<sub>2</sub> concentrations through weathering silicate minerals and  
86 transferring CO<sub>2</sub> from the atmosphere to the lithosphere (Conley 2002). In terrestrial systems, soil is the  
87 primary source of plant Si, with global variability of soil-forming factors (*e.g.*, parent rock, climate,  
88 topography, age, biota) explaining the large variability in Si cycling rates (Cornelis et al., 2016). Many plant  
89 species accumulate Si predominantly in leaves and needles as amorphous, biogenic silica, in large discrete  
90 bodies known as phytoliths. Si then returns to soil when plant material decomposes either as dissolved Si,  
91 a quickly-available source of Si for terrestrial plants, or as phytoliths, where C incorporated by phytoliths  
92 may accumulate in soils and sediments for hundreds to thousands of years. For this reason, phytolith  
93 accumulation is considered as a key mechanism of biogeochemical C sequestration (Parr and Sullivan,  
94 2005). Plant-accumulated Si has been shown to reduce the magnitude of Si released from terrestrial to  
95 aquatic ecosystems, thereby having direct implications on Si availability in coastal waters, which could the  
96 influence diatom blooms and C uptake rates (Coney et al., 2008, Carey and Fulweiler, 2012). Ultimately,  
97 terrestrial systems supply approximately 78% of annual silica inputs to oceans (Tréguer and De La Rocha,  
98 2013) and Si-accumulating vegetation accounts for 55% of terrestrial net primary productivity (33 GtC per  
99 year), on par with the rate that marine diatoms sequester C (Conley, 2002; Carey and Fulweiler, 2012).

100 Plants may preferentially use Si for certain functions such as structure and defense instead of C (Cooke  
101 and Leishman, 2012) as Si can provide plants with structural support at a lower metabolic cost than C  
102 (Raven, 1983). In some cases, Si is negatively correlated with lignin and cellulose content, possibly  
103 contributing to plant structural support, and phenol content (Schoelynck et al., 2010; Cooke and Leishman,



104 2012). Intermediate Si fertilization additions, for example, have enhanced aboveground growth for crops  
105 and reeds, possibly due to a partial substitution of organic C compounds by Si in plant tissue (Schaller et  
106 al., 2012; Neu et al., 2017).

107 Soil Si may also facilitate the acquisition and release of other essential plant nutrients. For example, a  
108 laboratory experiment demonstrated that silicon addition significantly increased P mobilization in a variety  
109 of arctic soils (Schaller et al., 2019). Researchers have found that Si can also increase plant N use efficiency  
110 while decreasing C and increasing P in grasslands (Neu et al., 2017) and affect the calcium (Ca) content of  
111 grasses (Brackhage et al., 2013). The abundance of certain plant functional groups (*e.g.*, Si-rich grasses) in  
112 plant communities can affect Si and Ca biogeochemistry as a result of differences in elemental  
113 concentrations among plant species and related effects on nutrient cycling via processes such as  
114 decomposition (Schaller et al., 2016). The potential of Si to affect plant growth and elemental  
115 stoichiometry in grasslands can, by extension, then affect biogeochemical cycles (Schaller et al., 2017).  
116 Changes in plant nutrient stoichiometry due to Si may have broad implications for other natural systems,  
117 where the (un)availability of essential nutrients can shape the productivity, composition, diversity,  
118 dynamics and interactions of plant, animal, and microbial populations (Vitousek, 2010). For example, P can  
119 be limiting in weathered tropical forest soils (Vitousek, 2010), so changes in P availability due to Si (Neu et  
120 al., 2017) can have concomitant effects on productivity. Furthermore, the recycling of Si within forests  
121 impacts continental Si cycling, especially in tropical forests which take up Si at a faster rate in terms of  
122 mass per unit ground area than other biomes, particularly in highly weathered soils (Alexandre et al., 1997;  
123 Cornelis et al., 2016; Schaller et al., 2018). Notably, unlike major plant nutrients for which foliar  
124 concentrations significantly decreased with increasing soil age, foliar Si concentrations continually  
125 increased with increasing soil age in two Australian soil chronosequences (de Tombeur et al., 2020).  
126 Returning phytoliths to topsoil can result in the slow-release of Si that sustains the terrestrial cycle during  
127 ecosystem retrogression.



128 A summary of literature shows that studies of Si-herbivore dynamics have focused on the ecology and  
129 physiology of Si in the grass family (Fig. 1), *Poaceae*, which includes many species that accumulate large  
130 amounts of Si in their tissues. Species richness can increase plant Si stocks via its positive relationship with  
131 biomass production but can have a negative effect on Si concentration in the aboveground biomass, which  
132 may influence processes such as decomposition, nutrient cycling and herbivory (Schaller et al., 2016).  
133 Some studies indicate Si content of plant litter may be positively correlated to decomposition rate (*e.g.*,  
134 Schaller et al., 2013). Because plant-stored Si releases Si into soils and sediments relatively rapidly, high Si-  
135 accumulating plants like grasses can influence Si turnover rates in ecosystems by uptake, storage, and  
136 release of Si during plant decomposition (Schaller et al., 2016 and references therein).

137 However, several non-monocot angiosperms also store significant foliar Si (Hodson et al., 2005), and  
138 variation in foliar Si can play important roles such as in plant defense and metal toxicity reduction even for  
139 low-accumulators (Katz, 2014 and references therein). Si contents vary by as much as 2-3 orders of  
140 magnitude among plant families, orders and phyla (Hodson et al., 2005), and grass-rich systems tend to  
141 be richer in Si and more productive than systems without grasses (Carey and Fulweiler, 2012). However,  
142 nutrient use strategies can vary intra-specifically across environmental gradients at least within controlled  
143 settings (Harley and DeGabriel, 2016 and references therein). Therefore, we need more field-based  
144 information about how Si content varies along large-scale environmental gradients to improve global  
145 biogeochemistry models.

146 Anthropogenic perturbations, such as agriculture, deforestation, urbanization, and climate warming, can  
147 also have profound effects on terrestrial silica biogeochemistry (Conley et al., 2008; Struyf and Conley,  
148 2012; Carey and Fulweiler, 2016; Gewirtzman et al., 2019). Deforested areas can increase soil erosion,  
149 resulting in the loss of high biogenic Si concentrations found in surface soils (Saccone et al., 2007). Urban  
150 areas have limited ability to take up dissolved Si into vegetation and agricultural lands retain less biogenic  
151 Si as it is frequently removed through harvesting and may not be replenished by vegetation-stimulated



152 silicate weathering (Struyf and Conley, 2012; Vandevenne et al., 2012). Global agricultural Si export from  
153 harvesting is estimated to be 223 kg Si yr<sup>-1</sup> (Matichenkov and Bocharnikova, 2001) compared to the 142  
154 kg Si yr<sup>-1</sup> total quantity of dissolved Si transferred from continents to oceans by rivers (Tréguer et al., 1995).  
155 In addition, soil warming due to climate change can increase the extent of internal Si recycling in temperate  
156 forests (Gewirtzman et al., 2019) and changes in precipitation intensity as expected with climate change  
157 can increase surface run-off and top-soil erosion reducing biogenic Si in surface soils (Conley et al., 2008;  
158 Struyf et al., 2010). Thus, researchers should take into account the potential impact of land-use and climate  
159 changes on terrestrial Si fluxes when modeling terrestrial Si mobilization.

### 160 **3 Effects of silicon on herbivory**

161 Si is known to defend plants against a wide range of biotic stresses, including pathogen infection and  
162 herbivory (Reynolds et al., 2009; Guntzer et al., 2012; Frew et al., 2018 and references therein). Si-  
163 mediated defenses against herbivores involve both direct and indirect physical or mechanical barriers, as  
164 well as indirect biochemical or molecular mechanisms (Fig. 2). In addition, plant communities with high Si  
165 can affect herbivore communities. Plant groups with high leaf toughness, high Si concentrations, and low  
166 leaf nitrogen concentrations, for example, can also be associated with decreased grassland herbivore  
167 species richness (Schuldt et al., 2019). Furthermore, studies have reported how grass Si content can drive  
168 herbivore populations, which may be synchronized with plant Si content cycles (Massey et al., 2008;  
169 Hartley, 2015).

170 Si-derived mechanical barriers are often thought to effectively shorten the duration of attack, both directly  
171 or indirectly, by making tissues more difficult to chew, penetrate, and digest (Hunt et al., 2008; Massey  
172 and Hartley, 2009), and increasing exposure time to predators (Massey and Hartley 2009). For example,  
173 discrete silica bodies in and on the surface of leaves can reduce herbivory (Hartley et al., 2015). Si  
174 structures may wear down herbivore mouthparts (Massey and Hartley 2009), affecting herbivore ingestion  
175 and nutrition (Frew et al., 2018; Hunt et al., 2008). These abrasive phytoliths can also lacerate herbivore



176 body parts or facilitate pathogen transmission into herbivores (Lev-Yadun and Halpern 2019). Si may also  
177 alter nutritional quality indirectly via changes to foliar C : N ratio and P concentrations (Frew et al., 2018)  
178 while plant nutrient status may influence the overall efficacy of Si-based defenses against herbivory (Mosie  
179 et al., 2019). As a consequence, some herbivores demonstrate low preference for Si-rich plants and slower  
180 growth rates when feeding on Si-rich diets (Massey and Hartley, 2006, 2009).

181 Several studies have documented effects of soil Si addition on plant chemical defenses (*e.g.*, Reynolds et  
182 al., 2009), anti-herbivore phytohormonal signaling (*e.g.*, Hall et al., 2019), and changes in plant nutritional  
183 quality (*e.g.*, Frew et al., 2018; Moise et al., 2019). For example, Si may induce indirect defense  
184 mechanisms by altering the composition of herbivore-induced plant volatiles that attract herbivore  
185 parasitoids and predators (Liu et al., 2017). Some studies also point to effects of Si on plant secondary  
186 metabolism and gene expression in plant development and defense (Markovich et al., 2017; Frew et al.,  
187 2018 and references therein). But because Si has relatively limited chemical reactivity, its role on plant  
188 chemical changes may be indirect rather than direct (Coskun et al., 2019). For example, effectors released  
189 by insects could be trapped within the extracellular Si matrix, precluding them from deregulating the plant  
190 defense response, or from recognizing the plant as a suitable host (Coskun et al., 2019).

191 While researchers continue to debate the biological roles of Si and uncover the mechanisms behind them  
192 (Frew et al., 2018; Coskun et al., 2019), we conclude that, at a minimum, Si mitigates the negative impacts  
193 of various stressors, such as herbivory, which then enable plants to improve growth potential (Johnson et  
194 al., 2019).

#### 195 **4 Effects of herbivory on plant silicon**

196 Of the 119 reviewed studies, the majority of Si-herbivory publications have focused on insects that damage  
197 shoots (68), while other animals including mammals (35), and insects from other feeding guilds (14), are  
198 less frequently represented (Fig. 1). While many studies in the literature review investigate the effects of



199 Si on herbivory (114), few studies focus on the effects of herbivory on Si (5). Though few, these studies  
200 show that herbivores can also induce Si uptake and accumulation by plants in response to herbivore attack  
201 (Massey et al., 2007; Hartley and Gabriel, 2016). Although how much Si uptake is induced may depend on  
202 plant species, herbivore type, and environmental conditions, the degree of induction can be positively  
203 correlated with herbivory duration or frequency (Soininen et al., 2013). In one study, the Si content of two  
204 species of grasses that experienced repeated damage by voles and locusts was 2-4 times more than  
205 individuals of the same species that experienced only one damage event (Massey et al., 2007). Some grass  
206 species have been shown to have as much as twice the Si contents in more heavily grazed localities  
207 (Brizuela et al., 1986). However, one study investigating grazing effects on Si yielded different results. In a  
208 saltmarsh, Si export rates at sheep-grazed sites were actually lower than at ungrazed sites (Müller et al.,  
209 2013). Variable responses between different grasslands underscore the need for wider sampling to study  
210 Si-herbivory dynamics in different ecosystems with their unique characteristics.

#### 211 **4.1 Potential effects of herbivory on terrestrial silicon cycling**

212 While multiple reviews synthesize terrestrial Si biogeochemical cycling (*e.g.*, Conley, 2002; Struyf and  
213 Conley, 2012) and effects of Si on herbivory (*e.g.*, Debona et al., 2017; Frew et al., 2018), few studies have  
214 explored the potential effects of herbivory on Si cycling. Variation in Si accumulation and deposition  
215 associated with herbivory, Si availability, and environmental variables could have important implications  
216 for Si cycling (Cooke and DeGabriel, 2016 and references therein). Herbivores can distribute large  
217 quantities of resources across the landscape, having important effects on nutrient cycling and ecosystem  
218 productivity (Metcalf et al., 2014; Bakker et al., 2016). Schoelynck et al. (2019), for example, found that  
219 hippos contribute 32% to the biogenic Si flux and more than 76% to the total Si flux in a savannah-river  
220 system. We estimate that Si fluxes via the herbivory pathway can meet or exceed other major sources of  
221 Si, although flux information on some major habitat types is missing (Table 1). Herbivores may also  
222 influence Si pathways by making more labile forms of Si available. For example, Vandevenne et al. (2013),



223 found that grazing by cattle can increase reactivity and dissolvability of biogenic Si after digestion, leading  
224 to higher Si turnover rates and mobilization potential (2 versus 20 kg Si ha<sup>-1</sup> y<sup>-1</sup>). It is, however, unclear  
225 whether the more mobilized Si is then absorbed by vegetation, taken up by microbes, or exported from  
226 the system (Fig. 3). Future research could follow the fate of more mobilized Si derived from herbivores,  
227 which may depend on local biotic and abiotic conditions such as soil properties or plant/microbial  
228 composition. In a wetland study, litter decomposition by heterotrophic microbes was significantly  
229 influenced by the Si availability during plant growth, whereby litter decomposition rates were positively  
230 correlated with higher Si content (Schaller et al., 2013). In other words, potentially greater export and  
231 plant uptake of biogenic Si due to herbivory may impact decomposition and nutrient cycling in some  
232 systems. Grasslands demonstrate a high capacity to store biogenic Si as well as transport Si from relatively  
233 inert mineral silicate soil layers to biologically active soil layers (Blecker et al., 2006). If grazing can change  
234 the distribution and reactivity of Si in grasslands, herbivory may alter Si turnover and export at rates  
235 important to estimate for Si cycling in other agricultural and natural systems as well. Understanding the  
236 role of herbivores in mobilizing Si may have important implications for land management.

237 Researchers have found that even small shifts in terrestrial biogenic Si reactivity could alter the balance  
238 between Si storage and export from ecosystems (Struyf and Conley, 2012). Herbivory may increase  
239 dissolved Si mobility (Vandevenne et al., 2013), and, if absorbed by plants, thereby decrease C uptake  
240 (Cooke and Leishman, 2012), increase N use efficiency, and increase P uptake of plants (Neu et al., 2017;  
241 also see Fig. 3). Grassland herbivores may also preferentially consume plants with less Si (Massey and  
242 Hartley, 2006), potentially influencing ecosystem Si cycling and plant community dynamics (Garbuzov et  
243 al., 2011). Combined with Si-mediated changes in plant nutrient stoichiometry and efficiency (Neu et al.,  
244 2017), these findings highlight the need for more field research on how herbivory-Si interactions impact  
245 community- and ecosystem-level processes.

## 246 **5 Conclusions**



247 We have begun to understand the magnitude of impact of plant Si on herbivore populations and the  
248 potential impact of herbivores on Si fluxes, which may have important agricultural and land management  
249 implications. In an effort to improve land management decisions and projections of biogeochemical cycling  
250 to future climate and land-use changes, however, we need to expand our understanding of Si-herbivore  
251 dynamics. Long-standing research makes it clear that Si plays an important role in both biogeochemistry  
252 cycling and herbivory but major knowledge gaps remain. Based upon our review we highlight the following  
253 future research priorities:

- 254 • Fate of more mobilized Si as a result of herbivory in agricultural settings.
- 255 • How Si-herbivory dynamics operate beyond crops in controlled or agricultural settings.
- 256 • Si-herbivore dynamics in herbivore feeding guilds other than shoot feeders.
- 257 • Impact of herbivory on biogeochemical cycling in natural settings, which remain understudied but  
258 where evidence indicates that Si can cycle at a high rate and herbivory is an important ecosystem  
259 process.
- 260 • Field-based studies on Si-herbivory dynamics along key environmental gradients by different  
261 herbivore feeding guilds.

262 Given the demonstrated importance of Si and herbivores, and the relative paucity of information on their  
263 interaction particularly in natural, non-graminoid dominated systems, we believe this information is  
264 critical to generating more accurate model representations of animal-plant-soil feedbacks, and their  
265 impacts upon ecosystem processes in different terrestrial systems.

#### 266 **Data Availability**

267 The list of publications reviewed and classified for this article can be found at doi:  
268 10.6084/m9.figshare.12026997.

#### 269 **Authors' Contributions**



270 BH and DM conceived the ideas and designed methodology; BH collected and synthesized the data; With  
271 input from DM, BH led the writing of the manuscript. Both authors contributed critically to the drafts and  
272 gave final approval for publication.

### 273 **Competing Interests**

274 The authors declare that they have no conflict of interest.

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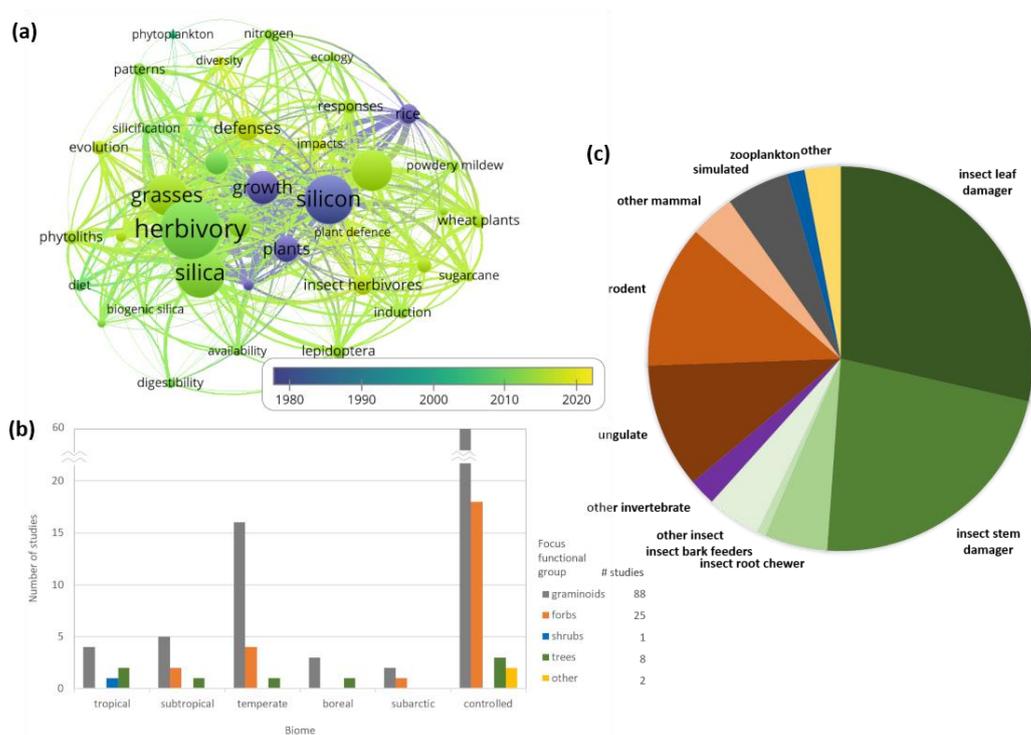
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492 **Tables and Figures**

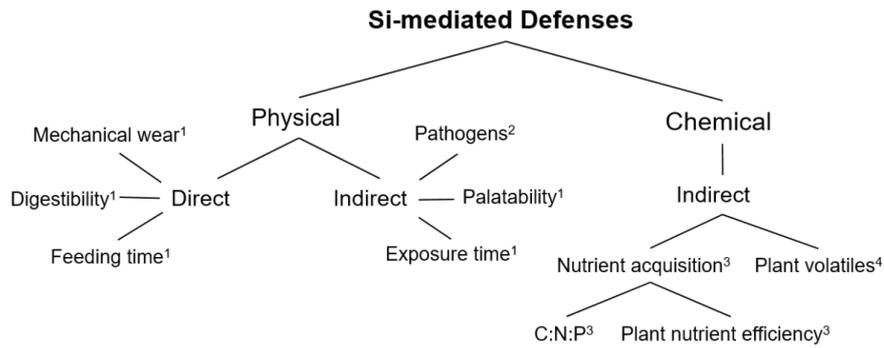


493

494 **Figure 1** Summary of literature review. **(a)** Network map of keywords from publications between 1900-  
 495 2020 in the Web of Science core collection database generated using search terms “silic\*” and “herbivor\*”  
 496 and not “in silico” (314 results). Bubble and word size is scaled to the total occurrence of the keywords in  
 497 all publications (only > 10 occurrences displayed), more proximate bubbles/keywords co-occur more often  
 498 in the publications surveyed. The year indicates the average publication year of the documents in which a  
 499 keyword occurs. The map was created with VOSviewer software (van Eck and Waltman 2018). **(b)** Number  
 500 of publications investigating each plant functional type and biome using the three search terms. We  
 501 filtered the 314 results until only those publications that directly studied Si and herbivory remained (119  
 502 publications). **(c)** Percentage distribution of herbivore types for all 119 studies that directly investigated



503 silicon and herbivory. The list of data sources and classifications for Fig. 1 are archived at doi:  
504 10.6084/m9.figshare.12026997.



505

506 **Figure 2** Direct and indirect physical and chemical plant Si-mediated defenses to herbivory <sup>1</sup>Massey et al.,

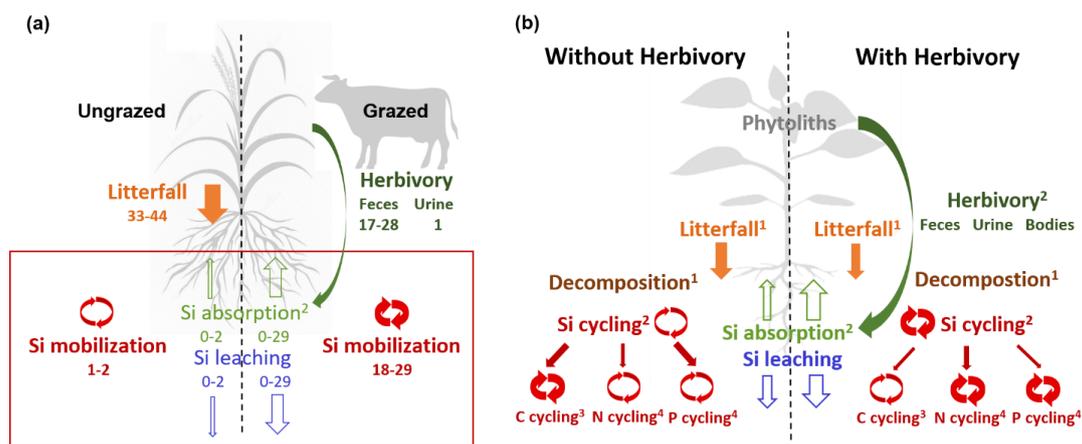
507 2009 and references therein; <sup>2</sup>Lev-Yadun and Halpern, 2019; <sup>3</sup>Neu et al., 2017; <sup>4</sup>Liu et al., 2017.



508 **Table 1** Estimated Si fluxes by atmosphere, mineral weathering and herbivory by major terrestrial habitat  
 509 type. ANPP is aboveground net primary productivity. <sup>1</sup>Cebrian 2004; <sup>2</sup>Hodson et al., 2005; <sup>3</sup>as calculated  
 510 by Carey and Fulweiler 2012; <sup>4</sup>Street-Parrott and Barker 2008 and references therein; <sup>5</sup>modeled by  
 511 Ribeiro et al., 2019; <sup>6</sup>Ariyanto et al., 2019.

512

Habitat type <sup>1</sup>	Herbivory <sup>1</sup> (% ANPP)	ANPP <sup>1</sup> (g C m <sup>-2</sup> y <sup>-1</sup> )	% Si by dry weight <sup>2,3</sup>	Si:C <sup>3</sup>	Herbivory (g Si m <sup>-2</sup> y <sup>-1</sup> )	Atmospheric <sup>4</sup> (g Si m <sup>-2</sup> y <sup>-1</sup> )	Weathering <sup>4</sup> (g Si m <sup>-2</sup> y <sup>-1</sup> )
Tundra shrublands and grasslands	1.8 ± 0.6	95.3 ± 31.0	1.07	0.02	0.04	-	-
Temperate/tropical shrublands and forests	7.9 ± 1.5	334.6 ± 24.9	0.26	0.01	0.15	0.004 - 0.2	0.3-3.2
Temperate/tropical grasslands	34.1 ± 5.3	239.4 ± 34.0	1.33	0.03	2.31	0.2	0.4-2.5
Freshwater and marine marshes	16.8 ± 5.0	958.9 ± 179.0	0.62	0.01	2.13	-	-
Mangroves	3.5 ± 0.5	500 <sup>5</sup>	0.43 <sup>6</sup>	0.01	1.60	-	-



513

514 **Figure 3 (a)** Schematic of Si fluxes ( $\text{kg ha}^{-1} \text{yr}^{-1}$ ) in hypothetical ungrazed and grazed grassland, dominated  
 515 by cows, adapted from Vandevenne et al., 2013. Annual net primary production is assumed to be the same  
 516 for both systems ( $11,000 \text{ kg ha}^{-1} \text{yr}^{-1}$ ) and all biomass is converted to litter or consumed by grazers in the  
 517 grazed system. A biomass conversion ratio of 1 : 4 for grass versus feces is suggested for all herbivores.  
 518 Mobilization percentages for faeces are based on ranges (minimum - maximum values) obtained in a  
 519 dissolution experiment by Vandevenne et al., 2013 after 24 h in rain water; for urine, a conservative  
 520 estimation of 3% mobilization was used. **(b)** Schematic of potential nutrient cycle differences in the plant-  
 521 soil system with and without herbivory. Size of arrows denotes the size of the flux relative to the  
 522 alternative scenario. <sup>1</sup>Schaller et al., 2016 <sup>2</sup>Brizuela et al., 1986; <sup>3</sup>Street-Perrott and Barker 2008; <sup>4</sup>Neu et  
 523 al., 2017; Schaller et al., 2017.