

Review

Why do plants silicify?

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Despite seminal papers that stress the significance of silicon (Si) in plant biology and ecology, most studies focus on manipulations of Si supply and mitigation of stresses. The ecological significance of Si varies with different levels of biological organization, and remains hard to capture. We show that the costs of Si accumulation are greater than is currently acknowledged, and discuss potential links between Si and fitness components (growth, survival, reproduction), environment, and ecosystem functioning. We suggest that Si is more important in trait-based ecology than is currently recognized. Si potentially plays a significant role in many aspects of plant ecology, but knowledge gaps prevent us from understanding its possible contribution to the success of some clades and the expansion of specific biomes.

Silicon in plant ecology

Biominingeralization (see [Glossary](#)) in plants has long fascinated plant physiologists and ecologists [1], and is gaining momentum in recent years through studies of Si and **silicification** [2]. Despite seminal papers that highlight the significance of Si as a beneficial element in plant biology [3,4], many aspects of Si in plant ecology remain puzzling. Why does the variation in foliar Si concentrations comprise several orders of magnitude in terrestrial plants, ranging from virtually none to very high concentrations that greatly exceed those of macronutrients (up to 10% dry weight)? Does silicification have adaptive value, and does it contribute, or has it contributed, to the success of clades and the expansion of specific biomes (e.g., grasslands [5])? What are the costs and benefits of Si, and can trade-offs with other **functional traits** be identified?

Although the compelling questions raised above remain unanswered, our understanding of Si in plant biology has progressed significantly in recent years. **Si transporters** have been identified in several taxa, and the ability of a plant to accumulate Si is thought to be both heritable and inducible, interspecific variation is well characterized, and major functions have been identified for Si in plant tissues [6–9]. In particular, when supplied to plants, Si often increases their resistance to biotic (herbivores and microbial pathogens) and abiotic stresses (metal toxicity, salt and water stress, wind and other physical forces, UV, and nutrient deficiency), augments the mechanical strength of plant organs, and, as a result, promotes plant growth and crop yields [2,7,10,11]. Several mechanisms may contribute to these benefits depending on the nature of the stress [12], although a recent model has attributed most Si-related functions to the deposition of **silica** in the apoplast through the process of silicification [2].

The well-established functions of Si have attracted interest in its role in plant ecology [7,13–15]. The role of Si in plant defense is better understood, and silicification is increasingly seen as an important functional trait that impacts on plant fitness [7,13,14,16]. However, the potential for Si to enhance fitness remains speculative, as does the importance of Si in ecological functions other than defense against herbivores and pathogens. The element is still under-appreciated by many ecologists, especially compared to macronutrients such as nitrogen (N) and phosphorus (P). In fact, significant

Highlights

The significance of silicon (Si) in plant ecology remains elusive.

Trait-based analyses show that Si accumulates most in leaves of small non-woody species and is linked to key functional traits, suggesting trade-offs and physiological constraints on the evolution of Si accumulation in plants.

Plant Si-related functions affect fitness components (growth, survival, reproduction), but a sound understanding of Si–fitness relationships is missing. In grasses, there is evidence for a Si-mediated trade-off between growth and defense.

Si accumulation is more expensive than is currently acknowledged, and cost-benefit analyses are pivotal to understand how variation is dependent on environment and on trade-offs with other traits.

Si plays a significant role in many aspects of plant ecology, but major gaps prevent us from understanding why this trait has been selected for and has contributed to the success of specific clades.

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gaps in elementary knowledge on Si – including its costs of accumulation and potential links to **fitness components** and the environment – prevent us from better understanding variations in Si concentration and discerning its significance in plant ecology. For instance, trait-based approaches have proved to be helpful to study trade-offs in ecological strategies and constraints on evolution [17–19], but Si is under-represented in trait-based ecology.

We review here the significance of Si in plant ecology at different levels of organization. We have considered Si concentration in leaves (hereafter leaf [Si], in mg.g^{-1} dry weight), because we have significantly more information for this organ. We discuss (i) leaf [Si] variation among terrestrial plant species and its inclusion in trait-based ecology, (ii) adaptive values of leaf silicification, (iii) Si effects on **ecosystem processes**, and (iv) the costs and benefits of leaf Si accumulation.

Silicification: evolution, constraints, and trade-offs

Phylogenetic approaches are useful to understand interspecific variation in leaf [Si] [8,20–22]. Poales (e.g., Poaceae, Cyperaceae, Juncaceae) accumulate more Si than plants in other orders, but substantial Si accumulation has also been demonstrated for other orders (e.g., Cucurbitales, Fabales) [8,23–25]. Interestingly, there is no single stimulus or function that explains the multiple emergences of this trait [9,22]. Phylogenetic analyses show that Si transporters in all land plants evolved from a small clade of aquaporins that do not differ substantially from the known Si transporters [21]. The potential capacity to take up and accumulate Si is probably ancestral to all land plants, and fully evolved only in the clades in which all necessary Si transporters evolved, possibly under specific evolutionary pressures [9,22,26,27].

In a pioneering work conducted in the Serengeti National Park, McNaughton *et al.* [28] showed that plants native to the more heavily grazed grasslands accumulate more Si than plants from less heavily grazed sites. This work supported the hypothesis that silicification has adaptive value in response to increased herbivore pressure when open grasslands expanded (e.g., mid-Cenozoic) (reviewed in [5]). However, silicification might also have adaptive value in habitats characterized by seasonal aridity, low atmospheric CO_2 concentrations, low nutrient availability, or strong wind exposure, and the adaptive origin of silicification may not have been in defense against mammalian grazers [29–34]. In fact, paradigms that associate grassland evolution with any single environmental factor (e.g., grazing) are not well supported by chronology – at least at the global scale [9,35] – and various environmental factors may have contributed to grassland evolution in various parts of the world [35], suggesting that silicification is more likely an **exaptation** rather than an adaptation to grazing.

In addition, environmental factors, including soil properties (e.g., degree of weathering, mineral composition), might also have impacted on soil Si availability and might explain the evolution of silicification [36], but soil Si availability is barely considered in evolutionary studies. For instance, overgrazing enhances the expression of P-mobilizing traits in the **rhizosphere** (e.g., root exudates) [37], which in turn increase chemical weathering and soil Si mobilization [38]. Implementing long-term experimental evolution studies would be particularly relevant to understand the adaptive value of Si according to different environmental parameters [39].

Leverage trait-based approaches might be useful to better understand constraints on the evolution of Si accumulation in plants, and potential trade-offs or linkages with other traits having similar functions. The global spectrum of plant form and function (GSPFF) describes a dimensional phenotypic space made of six major traits crucial for growth, survival, and reproduction [18]. One major axis of variation reflects a plant size gradient (height, seed mass, specific stem density), whereas the other balances more conservative species with high leaf mass per area (LMA) versus

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more acquisitive fast-growing species with high leaf N concentration [18]. The association of leaf [Si] with the plant size axis of the GSPFF (Box 1) reflects the greater Si accumulation in leaves of non-woody compared to woody species (Box 1 and Figures S1 and S2 in the supplemental information online). Leaf silicification might play, or have played, a role in physical support and plant defense mechanisms mostly for non-woody plants, and possibly at the expense of C-based compounds such as cellulose and lignin (Box 2). As discussed above, the evolutionary history of grasslands is the most widespread argument to explain the higher levels of leaf Si in non-woody species, but silicification could also represent significant constraints for taller woody species.

Another major trait-based framework is the leaf economics spectrum (LES), that describes a major axis of cross-species leaf physiology comprising key traits such as LMA, leaf lifespan, N and P concentrations, and photosynthetic (A_{mass}) and respiration (R_{mass}) rates [17]. The spectrum extends from fast-growing species with rapid resource acquisition to slow-growing species with conservative strategies [17]. Evaluating whether and how Si aligns with the LES is challenging because leaf [Si] might be associated with fast growth and return on C investment given its role as a growth-promoting beneficial element [40], but prominent ecological theories predict more investment in anti-herbivore defenses for slow-growing species [19,41]. Cooke and Leishman [40] showed that species with shorter leaf lifespan generally exhibit higher leaf [Si], and concluded that Si could be a metabolically cheaper alternative to C in shorter-lived leaves, and that leaf Si might be associated with the fast end of the LES. Despite significant relationships between leaf [Si] and the LES traits (Box 1 and Figure S3 in the supplemental information online), leaf [Si] seems to be independent of the LES overall (Box 1), at least globally and at the interspecific level. It is possible that implementation of the LES in Si research is most promising at the intraspecific level, or at least in a phylogenetically controlled set of related species, to reduce the strong phylogenetic signal of Si accumulation [20]. We also suggest combining trait-based approaches with metabolomics (i.e., tens of thousands of metabolites that are the substrates and products of enzymatic reactions) in Si research which has the potential to provide a better mechanistic understanding of trade-offs and ecological strategies [42].

For non-woody species, the question remains as to how high silicification affects leaf density, which has long been postulated [4]. Species that accumulate more Si in their leaves do indeed have denser leaves (greater leaf dry mass content, LDMC) because of the higher density of silica compared to C-based compounds (Box 1). Leaf thickness decreases with increasing silicification (Box 1), and we suggest a trade-off between thick leaves and high degree of silicification as different solutions to minimize the impact of some biotic and abiotic stresses (e.g., water stress, herbivory) and improve leaf mechanical properties [43,44]. Overall, silicification seems to be a neglected driver of LDMC in non-woody species that allows leaf mechanical protection and/or water stress avoidance, especially for species with thinner leaves, and future studies on leaf physical strength (e.g., force to punch, force to tear) should integrate Si into their framework. Leaf [Si] is also positively related with leaf mass per area (LMA), albeit with a weak R^2 (Box 1). This is possibly because silicification increases LDMC, but high Si-accumulating species have thinner leaves, making the relationship to LMA unclear. Overall, we argue that phylogenetic analyses must be coupled with trait-based approaches to better identify potential trade-offs and constraints on Si evolution.

Si and plant fitness: to grow or to survive?

Positive effects of silicification on plant fitness have long been postulated [13], but convincing evidence is lacking so far. Si addition to the growth medium mitigates numerous stresses and can stimulate plant growth [2,6,10], which led to the idea that Si is a growth-promoting, beneficial

Glossary

Active Si accumulation: movement of $\text{Si}(\text{OH})_4$ into plants from a lower to a higher $\text{Si}(\text{OH})_4$ concentration catalyzed by specific transporters that are energized directly (primary active transport) or indirectly (secondary active transport) by metabolism.

Biomining: the process by which organisms form minerals.

Diatoms: single-celled photosynthesizing algae that have a silica-containing wall (frustule) and are found in almost every aquatic environment.

Direct cost: a decrease in growth and/or reproduction associated with greater stress resistance (e.g., growth rate, change in phenology) that is not mediated by interactions with other species.

Ecological cost: a decrease in growth and/or reproduction associated with greater stress resistance that manifests itself only through interactions with other organisms.

Ecosystem process: a process that impacts on the flow of energy and matter between the biotic and abiotic components of an ecosystem; it includes primary production, trophic transfer between plants and animals, and nutrient and C cycling.

Exaptation: any adaptation that performs a function different from the function that it originally held.

Fitness components: individual performance including survival, growth, and reproduction; estimating fitness components yields an estimate of fitness.

Functional trait: a morpho-physio-phenological trait that impacts on fitness indirectly via its effects on growth, reproduction, and survival.

Model species: extensively studied plant species chosen for the ease of investigating particular biological phenomena.

Monosilicic acid: the soluble form of Si in soils with the chemical formula $\text{Si}(\text{OH})_4$ that is available for plant uptake.

Passive Si accumulation: the accumulation of Si in plant tissues that is related to transpiration driven by sunlight as well as to meteorological conditions.

Rhizosphere: a narrow region of soil that is directly influenced by root secretions and associated soil microorganisms.

Si transporter: a transplasmalemma protein that catalyzes $\text{Si}(\text{OH})_4$ transport into or out of cells.

nutrient overall. This is particularly true because studies have also demonstrated positive effects of Si on growth of unstressed plants [45–47], although this remains contentious [2]. However, information on the effect of Si on plant growth is based mainly on experiments under controlled conditions in which Si is manipulated in the growth medium, and no studies have addressed leaf [Si] in relation to fitness and the three fitness components, namely growth, survival, and reproduction. This gap in the literature prevents establishment of a clear association between Si and fitness (Figure 1).

Identifying links between leaf [Si] and fitness components is challenging because of antagonistic processes (Figure 1). For instance, there are well-established trade-offs between growth and survival [48] because investment in defense or resistance traits reduces the resources that are available for growth (i.e., growth–defense trade-off) [19]. High leaf [Si] might be linked to higher survival rates because it mitigates biotic and abiotic stresses, but may also be linked to growth because of its links with plant architecture, light capture, photosynthesis, and eventually competition (Figure 1 and Box 2). The absence of clear links between leaf [Si] and the LES, as discussed above, prevents us from associating silicification with growth or survival, at least at the interspecific level. In addition, although Si supply increases grain yield in crops [45,46], no links between Si and seed production are known for natural systems (Figure 1).

Towards a siliceous growth–defense trade-off in grasses?

Despite the lack of information on fitness–leaf [Si] relationships (Figure 1), recent comparative studies show that higher leaf [Si] is associated with slower growth rates in grasses [49–52]. In particular, Massey *et al.* [50] showed that leaf [Si] is negatively correlated with relative growth rate (RGR) and N concentration among 18 grass species. Similarly, Simpson *et al.* [49] found that higher leaf [Si] is associated with lower RGR among eight cultivated species. In addition, Thorne *et al.* [51] showed a strong negative correlation between RGR and leaf [Si] among 19 rice genotypes. Although few, these studies consistently suggest (i) the existence of ignored **direct costs** associated with leaf Si accumulation, (ii) that silicification might be positively associated with survival, rather than with growth, and (iii) that there is a Si-mediated trade-off between these two fitness components. In addition to direct costs, the **ecological costs** of Si accumulation – that emerge from interactions with other organisms (e.g., plant–plant or plant–herbivore interactions) [19] – have never been considered and should also be estimated in future studies.

Silica: silicon dioxide (chemical formula SiO_2). Silica in plants is amorphous and hydrated: $\text{SiO}_2 \cdot n\text{H}_2\text{O}$. It may also contain other elements, including C.
Silicification: the process by which an organism incorporates soluble silicic acid $\text{Si}(\text{OH})_4$ in the form of polymerized insoluble hydrated silica ($\text{SiO}_2 \cdot n\text{H}_2\text{O}$).

Box 1. Si – an overlooked trait in trait-based ecology

Studying leaf [Si] in relation with other key plant ecophysiological traits is useful to elucidate constraints on evolution, and to identify trade-offs and potential links with plant strategy theories (e.g., the leaf economics spectrum, global spectrum of plant form and function, Grime's competitive ability (C), physiological tolerance to stress (S), and ruderal species adapted to disturbance (R) – CSR – strategy [17,18]). Despite of some exceptions [73,112], Si remains poorly considered in trait-based ecology. We found that leaf [Si] is well represented in the global spectrum of plant form and function [18] (Figure 1A and Table S1 in the supplemental information online for principal component analysis (PCA) results), and aligned with the first dimension of the spectrum, namely the plant size axis (plant height, stem density, and seed mass).

Cooke and Leishman [40] aimed to include leaf [Si] in the leaf economics spectrum (LES) [17]. They showed that species with shorter leaf lifespan generally exhibit higher leaf [Si], but did not identify correlations between leaf [Si] and other LES traits [40]. With more species, we found that leaf [Si] was significantly positively related to leaf [P], A_{mass} , and A_{area} , and was significantly negatively related to leaf lifespan and LMA (see Figure S3 in the supplemental information online). However, leaf [Si] was independent of the LES (Figure 1B) because of weak R^2 (see Figure S3 in the supplemental information online) compared to the LES framework [17]. A fairly good relationship with A_{mass} was identified, however ($R^2 = 0.19$; $N = 454$).

For non-woody species that have higher leaf [Si] (see Figures S1 and S2 in the supplemental information online), the question remains of how strongly silicification affects the density of leaf tissues and leaf morphological traits [4]. We found that leaf [Si] is significantly positively related to leaf dry mass content in non-woody species, reflecting the presence of silica in plant tissues (Figure 1C). The relationship coefficient increases when leaf Si is expressed on an area-basis ($R^2 = 0.18$; $N = 458$). Leaf [Si] is also negatively related to leaf thickness and positively to LMA, although the relation was less clear than for leaf dry mass content (LDMC).

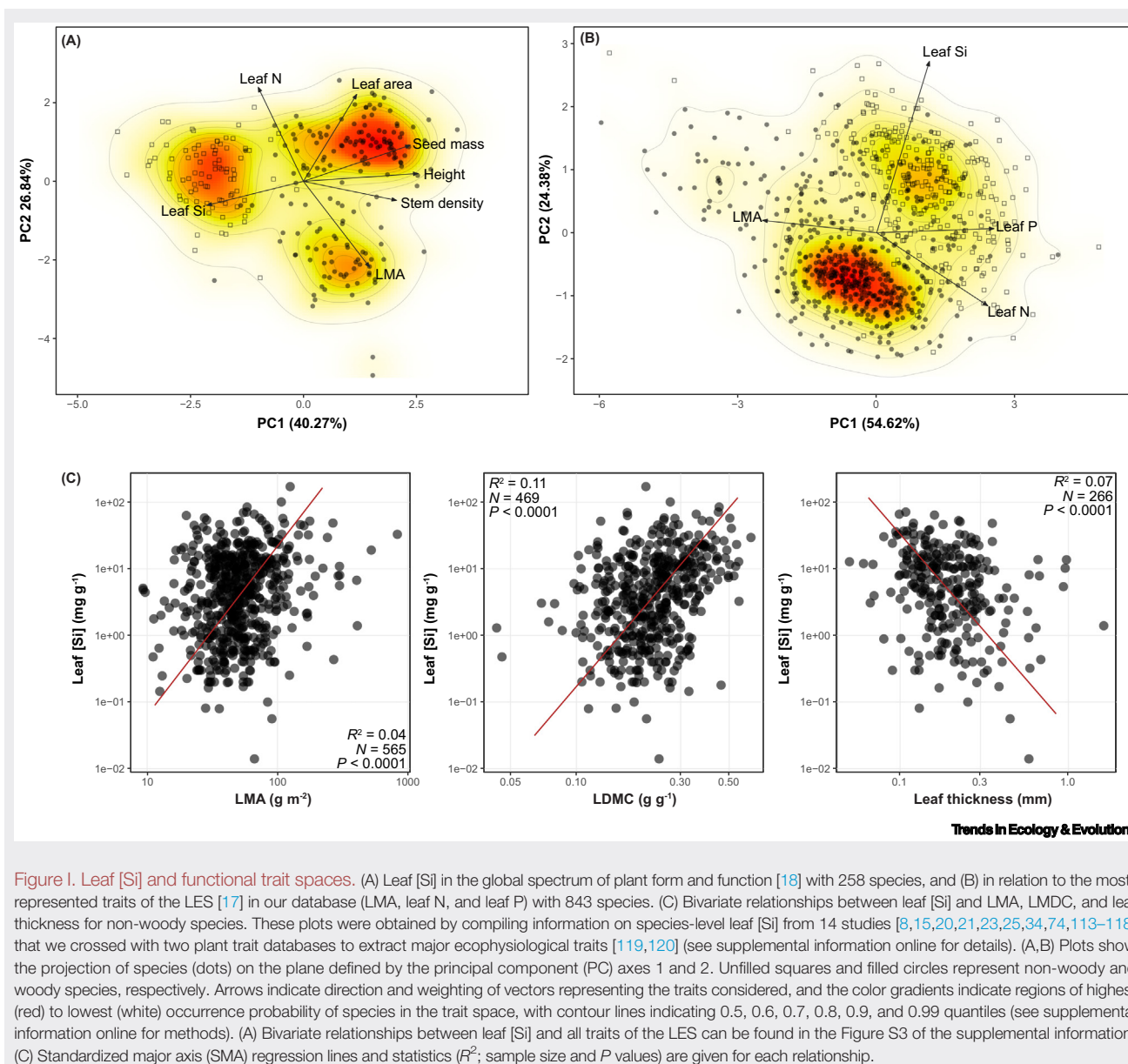


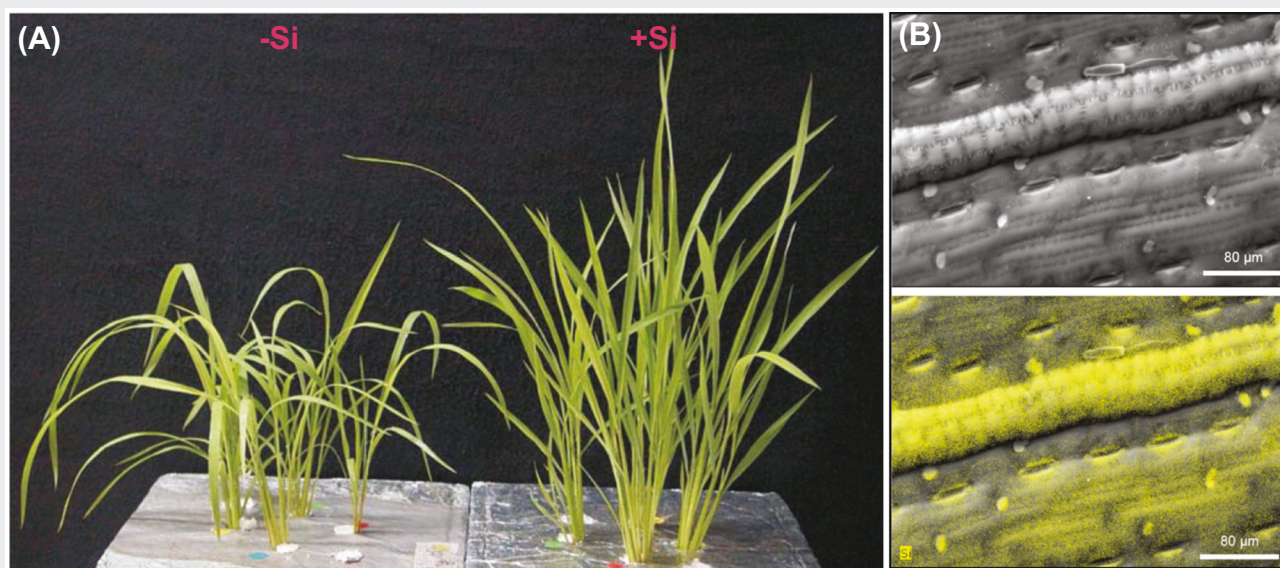
Figure 1. Leaf [Si] and functional trait spaces. (A) Leaf [Si] in the global spectrum of plant form and function [18] with 258 species, and (B) in relation to the most-represented traits of the LES [17] in our database (LMA, leaf N, and leaf P) with 843 species. (C) Bivariate relationships between leaf [Si] and LMA, LDMC, and leaf thickness for non-woody species. These plots were obtained by compiling information on species-level leaf [Si] from 14 studies [8,15,20,21,23,25,34,74,113–118] that we crossed with two plant trait databases to extract major ecophysiological traits [119,120] (see supplemental information online for details). (A,B) Plots show the projection of species (dots) on the plane defined by the principal component (PC) axes 1 and 2. Unfilled squares and filled circles represent non-woody and woody species, respectively. Arrows indicate direction and weighting of vectors representing the traits considered, and the color gradients indicate regions of highest (red) to lowest (white) occurrence probability of species in the trait space, with contour lines indicating 0.5, 0.6, 0.7, 0.8, 0.9, and 0.99 quantiles (see supplemental information online for methods). (A) Bivariate relationships between leaf [Si] and all traits of the LES can be found in the Figure S3 of the supplemental information. (C) Standardized major axis (SMA) regression lines and statistics (R^2 ; sample size and P values) are given for each relationship.

Potential relationships between fitness and leaf [Si] could be tested through comparative studies involving species and/or genotypes that have inherently different [Si], or by using mutants with contrasting expression of Si transporters [53,54]. Different methods for estimating fitness have been suggested, ranging from time-consuming quantitative common-garden experiments to easier but less rigorous population-level monitoring [48]. The use of Si-accumulating **model species** (e.g., *Brachypodium distachyon*, *Setaria viridis*) might be valuable here, although Si functions have also been reported for non-accumulating model species such as *Arabidopsis thaliana* [55] and thus should be also studied. More generally, Si-related functions are not restricted to Si-accumulating species [24,56], and future fitness–Si studies should embrace different plant families and orders.

Box 2. The overlooked influence of silicification on plant architecture, resistance to physical forces, and competition for light

In grasses, Si has been linked to different plant architectural traits such as decreased leaf insertion angle, increased leaf straightness [44,121–123] and increased plant height [46,67,123,124], as shown in Figure 1A. This has been attributed to the hardness of silica, which strengthens plant tissues, especially through silica deposits in cell walls [125,126]. In grasses, veins located on the abaxial epidermis made of fully silicified cells may also play a role in leaf erectness, as exemplified in sugarcane (Figure 1B) [76]. Negative relationships between leaf [Si] and concentrations of C-based compounds have also been reported (e.g., lignin, cellulose), which has reinforced the contention of a mechanical role of silicification, and has led to suggest 'trade-offs' between Si and C components in leaves [4,44,100,127]. We found a significant negative relationship between leaf concentrations of Si and C of 838 species that was driven by plant woodiness ($R^2 = 0.24$; see Figure S3 in the supplemental information online), suggesting that non-woody species invest relatively more in Si than in C for leaf construction/defense compounds compared to woody species. After correcting leaf [C] for silica content, the relationship is weaker but still highly significant ($R^2 = 0.10$; $P < 0.0001$), suggesting that dilution is not the only factor explaining the relationship between Si and C [30]. Nevertheless, the hypothesis of a Si–C trade-off requires more work at the cell and organ levels to better understand Si roles compared to C roles [100]. Future studies on Si and C-based components should pay specific attention to the mechanisms underpinning this apparent trade-off [100].

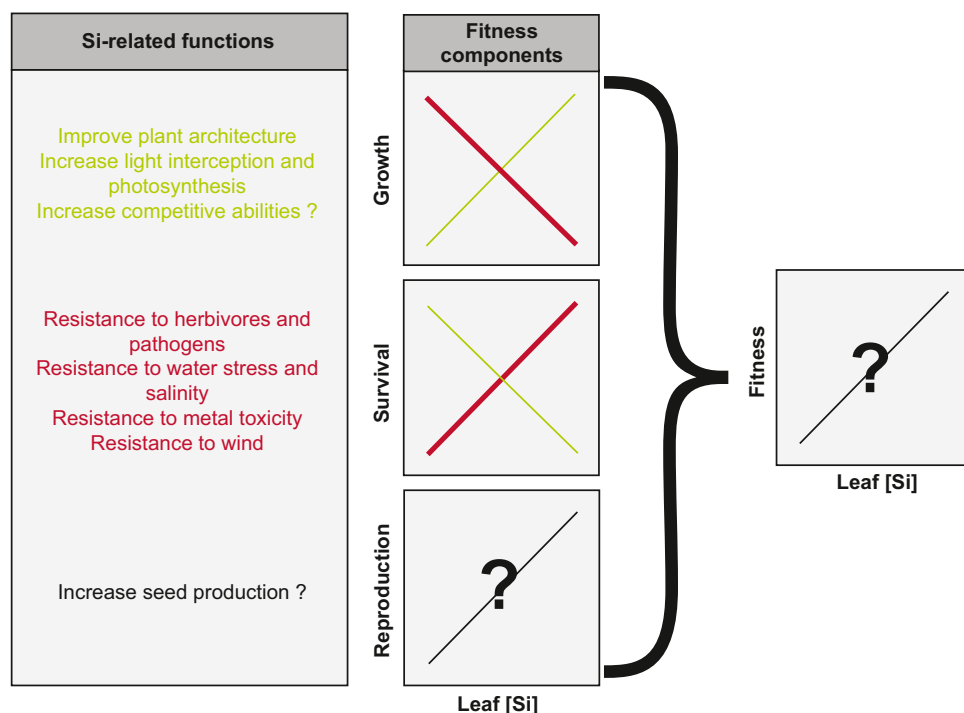
An effect of Si on plant strength may contribute to avoiding plant lodging and protection against strong winds in grasses [128], and eventually to greater photosynthetic rates due to greater light interception (see Figure S3 in the supplemental information online). In fact, some authors have suggested that high silicification could have adaptive significance against physical forces, including wind and waves, rather than the more frequently discussed herbivore pressure [15,34]. In addition, Si-induced modifications of plant architecture may play a significant role in light capture and competition for this resource [67]. Plant height is often associated with strong competitive abilities [129], and leaf insertion angle and erectness may also affect competition for light [121]. The role of silicification on plant architecture may affect plant–plant interactions and explain the selection of this trait, but this requires further investigation [9,15,67].



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Figure 1. Influence of Si on plant architecture and light capture. (A) Influence of Si fertilization on rice architecture (modified, with permission, from Zanão Júnior *et al.* [123]), and (B) silica deposits (white structures above, yellow signal below) on sugarcane abaxial surface leaf (adapted, with permission, from de Tombeur *et al.* [76]). (B) Silica deposits along veins with a width of ~20–70 μm formed by two to three rows of fully silicified short broad epidermal cells that could play an important role in leaf straightness.

In addition to its potential link with fitness, the capacity of a plant to accumulate Si in leaves is assumed to be heritable, given the evidence for genetic control of transporters [8], but remains highly plastic in response to environment. In particular, leaf [Si] shows plasticity in response to soil water availability [57], herbivory [7,58–60], N and P limitation [31,61], CO₂ concentrations, temperature [52,62,63]. However, the mechanisms underlying Si plasticity in the face of environmental changes are mostly unclear, especially regarding the relative contributions of **passive Si accumulation** versus **active Si accumulation** [58,64]. In fact, it is very likely that multiple abiotic and biotic factors that are thought to directly increase plant Si accumulation also affect soil Si availability, transpiration, and growth rates which will, in turn, affect [Si] in plant tissues. For instance, CO₂ and temperature might affect transpiration or soil water content, which would in



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Figure 1. Theoretical relationships between the functions conferred to Si, fitness components, and fitness. Silicification is thought to impact fitness positively [9,13], but experimental evidence is lacking, especially because fitness components are usually considered separately. Both growth (and perhaps competitive ability [67]) and resistance functions have been ascribed to Si accumulation. Si accumulation could be linked to increased survival rates but slower growth rates (red scenario), or the opposite (green scenario). As discussed here, the red scenario is more likely (thicker lines in the plot), at least for grasses. The relationship between Si concentration and reproduction might be positive because Si addition can increase crop grain yields, but field studies on Si and seed production for non-crop species are lacking. Overall, these gaps prevent us from establishing whether Si accumulation is linked to population growth rates and the success of this trait. Adapted from Laughlin *et al.* [48].

turn affect the passive mode of Si uptake [57,62,63]. Similarly, increased Si concentrations with N or P limitation might be physiologically controlled through activation of Si transporters [65], but could also occur with the same Si uptake in less plant biomass (i.e., dilution/concentration effect [66,67]). We suggest that future studies on the plasticity of [Si] should pay specific attention to the underlying mechanisms whenever possible. In particular, determining changes in stomatal conductance and other physiological parameters would help to estimate the contribution of passive versus active Si uptake, and information about total dry matter production and total Si content would help to understand potential dilution/concentration effects [66].

Si, environmental factors, and ecosystem functioning

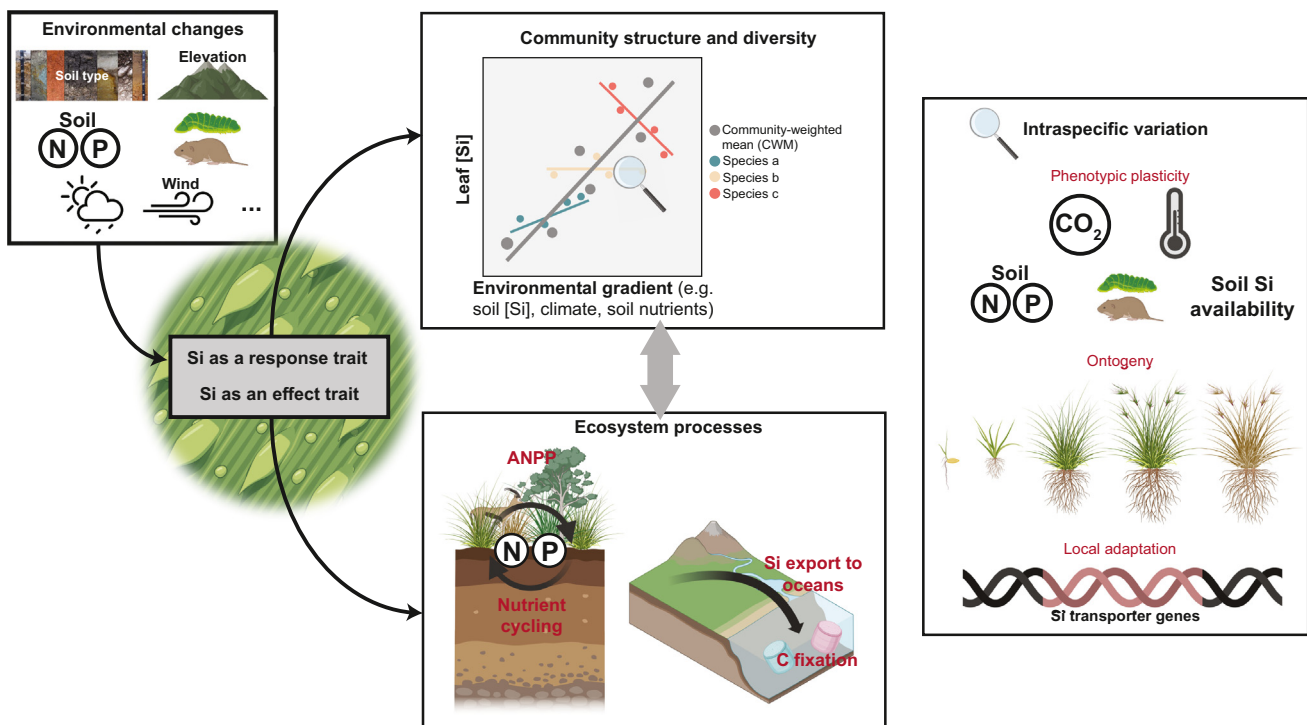
Response–effect trait frameworks are commonly used in trait-based ecology to clarify the mechanistic links between environmental factors, species traits, and ecosystem functioning [68]. Metrics that consider the relative abundance of species in a community, such as the community-weighted mean (CWM), are effective and widely used to scale-up from species to higher organizational levels [69–71]. Assigning more importance to dominant species and their traits is useful for better capturing the responses to environmental gradients and for understanding which effects can be expected on ecosystem processes, and with what magnitude [69,72]. This approach is starting to be used for Si [23,25,73–75] but still only rarely, although it might be particularly relevant because leaf [Si] is

both a response and effect trait in that it responds to environmental gradients and has an effect on ecosystem functioning [68] (Figure 2).

Si as a response trait

In natural ecosystems, leaf [Si] is significantly affected by soil Si and water availability [32,76,77], herbivory [7,78–81], wind [34], nutrient limitation [23,30], and elevation [25] (Figure 2). Although some community-level trends as a function of the environment are clear (e.g., Nakamura *et al.* [25] with elevation, and de Tombreur *et al.* [23] with soil nutrients), responses of [Si] to environmental conditions are mostly studied at the intraspecific level and mainly in grasses. Therefore, more interspecific studies along environmental gradients will be necessary to understand how [Si] is expressed in different ecosystems and plant communities.

Another challenge for community-level studies is to take into account intraspecific variation (Figure 2) [82]. So far, studies have reported both convergence and divergence between intraspecific and community-level [Si] responses to the environment [23,25]. In addition to plasticity, as discussed above, intraspecific variation can also be driven by ontogeny [83] and local adaptation



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Figure 2. Silicon as both a response and an effect trait. Leaf [Si] varies across environments (with wind [34], herbivory [28], soil type and properties such as N, P, and Si availability [23,32], elevation [25], and precipitation [30]), but the relative contributions of intra- and interspecific variation are still unclear. Intraspecific [Si] responses to environment can be contrasted among species (species a, b, and c), thereby following or not community-level trends [community-weighted mean (CWM)] [23,25]. [Si] affects several ecosystem processes (annual net primary productivity, litter decomposition, nutrient cycling, and the global C cycle at different timescales), the magnitude of which depends on the CWM [Si] not only in leaves but also in stems, wood, and roots. Intraspecific [Si] variation can be driven by phenotypic plasticity, ontogeny, and/or local adaptation. Leaf [Si] shows plasticity in response to herbivory [7,58–60], N and P limitations [31,61], CO₂ concentration, and temperature [52,62,63], but the underlying mechanisms remain unclear. Potential changes of leaf [Si] with ontogeny have been largely ignored, but leaf [Si] increases with increasing leaf age because Si continually accumulates and is not remobilized [85], and Si can be diluted/concentrated in more or less plant biomass (i.e., the dilution/concentration effect [66]). Finally, local acclimation and adaptation through changes in the expression of Si transporters (e.g., Lsi1, Lsi2, Lsi3, and Lsi6 [110,111]) can also be postulated. Created using BioRender (www.biorender.com).

[84] (Figure 2). Although few studies are available on [Si] variation with ontogeny, we know that leaf [Si] increases with leaf age because Si continually accumulates and it is not remobilized [85], and Si can be diluted/concentrated in more or less plant biomass similarly to N [83]. Examples of local adaptation with a determined genetic basis are not available.

Si as an effect trait

First, there is evidence that leaf [Si] can play a significant role in nutrient cycling [86,87] (Figure 2). For instance, silicified trichomes can slow down leaf decomposition of tropical trees by soil meso- and macrofauna [86], and Si accumulation can affect leaf nutrient stoichiometry and concentrations of C-based defense compounds in grasses (e.g., cellulose, phenols, lignin) [88,89]. Second, leaf silicification can be induced in response to increased herbivore density [80], thereby influencing herbivore growth rates, reproduction, and richness in grasslands [7,75]. Changes in wild herbivore populations affect several ecosystem processes such as nutrient cycling, C storage, and primary productivity [90]. Third, the positive effect of Si fertilization on crop productivity suggests that community-level [Si] might be linked to annual net primary productivity (ANPP). Long-term field Si fertilization showing increased aboveground biomass of grasses provides support for this [91]. We also note that more than half of terrestrial ANPP can be attributed to actively Si-accumulating vegetation (33 Gton C yr⁻¹) [92]. Finally, Si cycling in terrestrial ecosystems affects the global Si and C cycles [92–95]. On geological timescales, plant-induced weathering of silicates consumes atmospheric CO₂, thereby affecting Earth's climate [96]. On biological timescales, Si recycling by vegetation strongly impacts on soil–plant Si cycling [95,97] and affects Si transfer from land to oceans, where it is used by siliceous marine **diatoms** that contribute up to half of marine ANPP [93].

Beyond a 'Si–C trade-off': rethinking the energy costs of Si

Understanding the costs and benefits of trait values is at the very foundation of plant ecology [98]. It is paramount to understand trait variation as being dependent on environment, on trade-offs between traits, and more generally on plant ecological strategies [99]. Since Raven's paper [4], plant trading of 'expensive carbon (C)' for 'cheap Si' has become a pervasive idea in the recent literature [23,40,61,100], assuming apparent trade-offs between Si- and C-based components (Box 2), and that the accumulation of Si incurs lower energy costs than synthesizing C-based defense compounds [4]. However, the validity of this hypothesis requires work at the cell and organ levels to better understand Si roles compared to C roles [100], as well as more accurate quantification of the costs of Si accumulation. If Si is effective and less costly than C-based compounds, why do not all plants invest in it, rather than in C-based compounds? Clearly, identifying the costs of plant silicification is imperative to explain the wide variation with phylogeny and environment, and why trade-offs with other traits exist. We aim here to update the costs of Si accumulation by separating costs that are independent of soil Si availability, such as movement from the root cytosol to the xylem, from costs that increase with decreasing soil Si availability [101] (Box 3).

The costs related to Si movement from the root symplasm are estimated to be 2 mol ATP, well below the costs of synthesis of lignin and carbohydrates (around 13- and sevenfold higher for lignin and carbohydrates, respectively) (Box 3). However, this estimate is derived for *Oryza sativa*, and costs can differ according to the species and the distribution of the Si transporters Lsi1 and Lsi2 (Box 3). Moreover, significant gaps and controversies remain in our understanding of Si(OH)₄ transport in plants [102,103]. For instance, the structure of the Lsi2 putative Si(OH)₄:H⁺ antiporter is still not well characterized [104].

The costs related to soil Si mobilization before plant uptake have been ignored so far, and doing so may challenge current thinking of Si as a cheap resource [38] (Box 3). We suggest that

Box 3. The costs of silicification in plants

Costs independent of soil Si availability

Transport of Si(OH)_4 into vascular plants has been categorized as active, passive, and rejective [130]. Passive transport involves Si(OH)_4 uptake via the transpiration stream in the same $\text{Si(OH)}_4:\text{H}_2\text{O}$ ratio as occurs in the root medium. Active uptake involves a higher ratio, and rejective uptake a lower ratio. In *Oryza sativa*, active and passive Si uptake coexist, and their relative contributions depend on external Si(OH)_4 concentrations [130]. Active Si(OH)_4 uptake must occur at membrane(s) between medium and xylem sap because Si(OH)_4 concentrations in xylem exudates are >30-fold higher than in the root medium [131].

The known transplasmalemma proteins involved in Si(OH)_4 transport from the root medium to the xylem catalyze influx (Lsi1) and efflux (Lsi2). The polar locations of both Lsi1 (centrifugal) and Lsi2 (centripetal) in *Oryza sativa* exodermis and endodermis suggest that the pathway of **monosilicic acid** transport from exodermis to endodermis is apoplastic [104,132]. In some other plants, Lsi1 catalyzes influx into epidermal and cortical cells, and Lsi2 catalyzes efflux from endodermal cells into the xylem [104,132]. Lsi1 catalyzes Si(OH)_4 passive influx and Lsi2 H^+ antiport efflux with a 1 mol H^+ :1 mol Si(OH)_4 stoichiometry. With 1 mol H^+ pumped per mol ATP by the plasmalemma H^+ pump [133], 1 mol ATP is needed per mol Si(OH)_4 leaving a cell, and 2 mol ATP are therefore required per mol Si(OH)_4 transferred from the root medium to the xylem sap of *Oryza sativa*. For plants with Lsi2 only in the endodermis, 1 mol ATP is necessary to move 1 mol Si(OH)_4 from the root medium to the xylem. Transport of Si(OH)_4 by Lsi1 occurs down a Si(OH)_4 concentration gradient from apoplasm to cytosol, and requires no other energy supply, in agreement with the molecular structure of Lsi1 [134–136]. However, there is evidence of accumulation of Si(OH)_4 in the symplasm of root tips of *Oryza sativa* in both the wild type and an Lsi1 mutant [137], consistent with energized Si(OH)_4 transport at the plasma membrane that does not involve Lsi1. No evidence has been sought for the electrogenicity predicted for H^+ antiport of Lsi2 by expression in *Xenopus* oocytes. For 2 mol ATP per mol Si(OH)_4 moved from the root medium to the xylem, the energy costs of producing 1 mol of the monomers of cell wall structural compounds, lignin and polysaccharide, are 13- and sevenfold higher, respectively, than that for the inorganic substitute, SiO_2 [4]. This equivalence assumes that there is no energy cost of unloading Si(OH)_4 from xylem, or of organic compounds associated with SiO_2 deposits, and that SiO_2 /lignin or polysaccharide monomers are structurally equivalent.

Costs dependent on soil Si availability

Previous calculations [4] have assumed an inexhaustible supply of Si(OH)_4 , which is not the case in many soils worldwide [105]. Si mobilization from poorly available forms and plant Si uptake are significantly increased by release of root exudates (e.g., carboxylates) and arbuscular mycorrhizal associations [38,109,138]. These nutrient-acquisition strategies are costly [101], and, Si accumulation involving rhizosphere processes would therefore be significantly more expensive than is currently acknowledged [38], as is the case for P and Fe [101,139]. We argue that the costs of Si accumulation would largely depend on soil Si availability (Figure I). However, whether plants increase carboxylate secretion or their association with fungi – and therefore spend energy – in responses to Si deficiency itself is unknown. The possibility of changes in root morphology, mycorrhizal symbionts, and root and mycorrhizal secretions related to deficiency of Si, rather than of P or some other element, deserves further investigation [38,101]. Moreover, the costs of carboxylates and other Si-mobilizing root exudates may be negligible if they have already been covered by other processes (e.g., to mobilize soil P) or if they result from a C surplus under conditions of growth being limited by resources other than C supplied via photosynthesis [140,141] (Figure I). We call for more research at the rhizosphere level to answer these compelling questions.

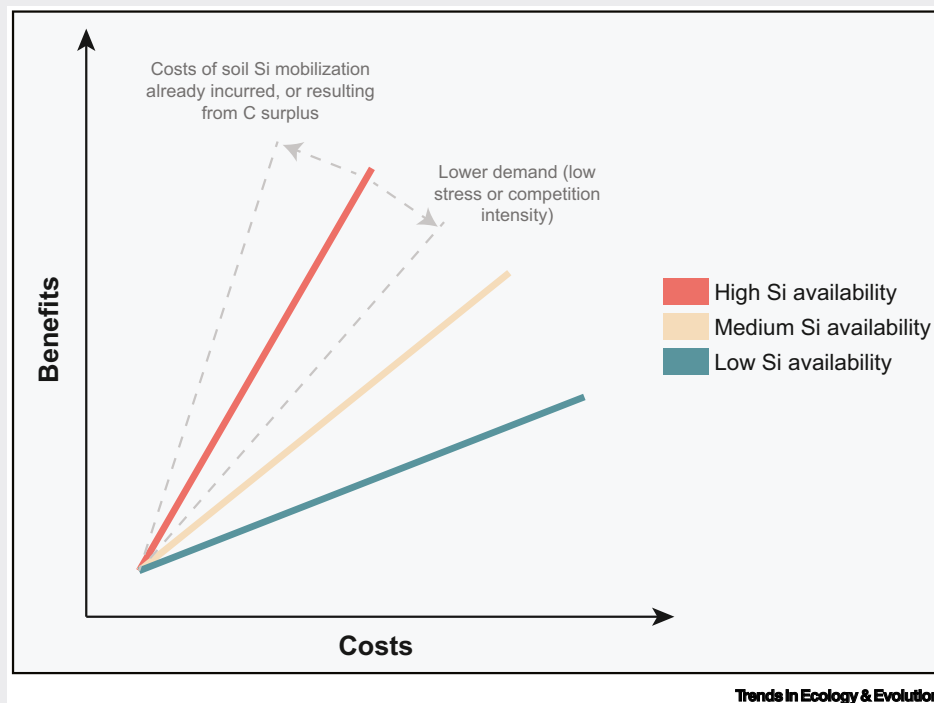


Figure I. Schematic representation of the costs and benefits of active Si accumulation in plant organs as a function of soil Si availability. For a given soil and associated soil Si availability, a lower demand for Si, for instance in less stressful and/or competitive environments, would decrease the benefits relative to the costs. Similarly, if the costs of Si-mobilizing root exudates (e.g., carboxylates, phytosiderophores) have already been incurred to mobilize other nutrients (e.g., P or Fe) [38,101,139], or result from 'free' surplus C [140,141], the benefits would increase relative to the costs.

silicification is costlier than is currently acknowledged, and that this depends primarily on soil Si availability that is limiting in many soils [105] (Box 3). Better estimating of these costs would require more research at the rhizosphere level to fill the gap between Si forms that are poorly available for plants (i.e., poorly reactive minerals) and Si transporters – root exudates, mycorrhizal associations, and silicate-solubilizing bacteria – to better estimate Si costs.

Overall, we suggest that active Si accumulation should be considered through the lens of cost–benefit analyses that incorporate soil Si availability and Si demand for plant functions (see Figure 1 in Box 3). As discussed above, Si demand might increase in stressful conditions or more competitive environments. Therefore, for a given soil and Si availability, a lower demand for Si would decrease the benefits relative to the costs. Eventually, greater silicification for defense or leaf construction might become less advantageous than C-based compounds, and cost–benefit analyses are mandatory to go beyond a simple economic Si–C trade-off. Beyond that, potential disadvantages of Si have been postulated (e.g., toxicity, high density of Si, poorer biomechanical properties compared with C-based compounds, less effective defense against some types of herbivores) to explain why Si is not universally used by plants [4,13,40,106]. We specifically provide evidence that higher leaf density is associated with silicification in non-woody species (Box 1), but other potential drawbacks mentioned above are not yet understood.

Concluding remarks

Despite a tremendous increase in Si research in plant biology in recent years, many aspects of siliceous ecology remain puzzling. We have reviewed the significance of Si in plant ecology at different levels of organization and raised several questions and perspectives for future research (see Outstanding questions). We show that silicification varies between and within species, as well as with environmental variation and other functional traits, and most likely influences plant fitness, interactions with other organisms, and ecosystem processes. Si quantification in plant organs has become increasingly fast and easy in the past decade (e.g., [107,108]), thus paving the way towards a full integration of Si at different organizational levels of terrestrial ecology. We also provide a datafile with Si concentration in leaves of about 1800 species in the online version of this article to encourage future studies to incorporate Si into their framework. A better comprehension of Si-related ecological processes could ultimately help us to develop more sustainable and diversified agroecosystems in which Si might have a more central role than is currently appreciated [109].

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Declaration of interests

No interests are declared.

Supplemental information

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Outstanding questions

Can the large variation of [Si] in land plants be explained by evolutionary constraints, and what are the trade-offs with other functional traits? For instance, does Si play a role in physical support and defense mostly in small non-woody species, but not in tall woody species because of physiological constraints? Can silicification be limited by the increase in leaf density? Elucidating these questions would require a combination of phylogenetic and trait-based approaches in future research, and should consider Si in relation to plant strategy theories (e.g., the LES, and Grime's CSR strategy).

Has Si contributed to the success of some clades and expansion of specific biomes such as grasslands? In particular, what are the links between [Si] and fitness components (growth, survival, reproduction) and population growth rates? Species and/or cultivars with inherently different [Si] should be studied to consider whether Si accumulation comes with costs (either direct or ecological) and whether and how Si is linked to fitness. In particular, the Si-mediated growth–defense trade-off in grasses should receive more attention, but future work should also embrace different plant families and orders.

How does [Si] vary in diverse plant communities and ecosystems when indices are weighted by species abundance (e.g., community-weighted mean), and how does it affect ecosystem processes such as nutrient cycling, herbivore populations, primary productivity, and C cycling?

What are the costs and benefits of Si accumulation compared to the costs of C-based compounds that could play similar functions (e.g., phenols, lignin), and do they depend primarily upon soil Si availability and Si demand? Cost–benefit analyses in different environments and for different species will be necessary to understand the impact of soil Si availability and stress and competition intensity on the costs of Si accumulation in relation to C-based compounds.

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