

## Opinion

## Keystone Herbivores and the Evolution of Plant Defenses

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Plants need to defend themselves against a diverse and dynamic herbivore community. Such communities may be shaped by keystone herbivores that through their feeding alter the plant phenotype as well as the likelihood of attack by other herbivores. Here, we discuss such herbivores that have a large effect on the interaction network structure with associated fitness consequences for the plant, as dominant agents of selection on plant defense traits. Merging the keystone herbivore concept with plant fitness and trait selection frameworks will provide an approach to identify which herbivores drive selection in complex multispecies interactions in natural and agricultural systems.

## The Concept of Keystone Herbivores

Understanding the organization of ecological communities and the role individual species play in influencing community structure have been central questions in ecology [1,2]. The concept of keystone species is at the core of these questions and has shaped theory in community ecology profoundly [3]. It revolves around the hypothesis that individual species through their consumptive and non-consumptive activities may have impacts on the composition and dynamics of entire communities that go beyond the effect predicted by its mere abundance [4,5]. Typically, the presence of such species affects the interactions of other species in the community and thereby the resulting state of the community or ecosystem as complex systems [6]. The keystone term has been first introduced for predators [4] to define the phenomenon that certain predators significantly affect herbivore populations and thereby strongly drive the composition of the entire plant–herbivore community [7]. Alternatively, herbivore species may themselves drive the composition of the community. Several classes of keystone herbivores can be identified. First, keystone herbivores may alter plant competitive interactions by affecting the abundance and diversity of plant species on the community and landscape level. Second, on a plant level, keystone herbivores may alter the growth form or quality of plants as food source and save haven for other organisms. Both processes may shape community organization beyond what would be predicted from the direct consumptive interaction between the plant and herbivore and may involve organisms of additional trophic levels. Moreover, while such indirect, outcome-enhancing effects are particularly well studied in plant–insect interactions they may play important roles in all types of organismal interactions and even at different organizational levels from molecules to ecosystems [6,8] (Box 1).

## Keystone Herbivores Change the Arena of Natural Selection

Organisms that have significant effects on community composition can be expected to also have effects on the genetic structure of populations within the community. For example, in the North American Asteraceae-dominated forb communities, herbivory, primarily by two Chrysomelidae beetle species, can dramatically alter plant community composition and diversity through interactions between herbivory and competition [9]. In addition, at the plant population level, herbivory selects for increased resistance specific to the dominant herbivore species, *Trirhabda virgata* [10], and decreased competitive ability in one of the dominating plant species, *Solidago*

## Trends

Keystone herbivores affect the composition of plant-associated communities through plant-mediated species interactions and thus affect the integrative effect of the herbivore community on plant fitness.

Through their role in mediating the outcomes of plant–herbivore community interactions, keystone herbivores are expected to be major agents of natural selection on constitutive and induced direct and indirect resistance although they may individually not significantly affect plant fitness. Thus, they are key to understanding evolution of plant defenses.

Identifying keystone herbivores and measuring their plant fitness effects would be equivalent to identifying the fitness effect of plant-associated interaction networks and provide a shortcut to understanding diffuse (co)-evolution.

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### Box 1. Defining Keystone Herbivores and Their Plant Fitness Effect

The concept of keystone species has recently been expanded to keystone communities or ecosystems, in which species assemblies or ecosystems have a disproportionate effect on a metacommunity as compared with other groups of species or ecosystems [59]. Moreover, on the opposite end of organization and through interactions within one trophic level, individuals may have disproportionate effects on group performance when they profoundly impact the behavior of a group. Such effects of social dominance of individuals have been circumscribed as a characteristic of keystone individuals [60]. In his seminal book chapter, Hunter [8] argued that herbivores should be considered keystone herbivores when they modify plants as a resource and thus impact plant–animal community composition and dynamics as a whole. Different classes of keystone herbivores can be defined as: (i) those that by their feeding alter community composition by affecting plant diversity and abundance, and (ii) those that alter communities associated with individual plants by their feeding induced changes in plant structure and plant chemistry. Here, we focus on the class of keystone herbivores that induces plant phenotypic changes that affect plant-associated insect communities and thereby influence selection on plant defense.

It may be argued that many species apply to this definition of keystone herbivore when considering, for example, herbivores that with their feeding remove large proportions of a plant and thereby affect plant-associated communities. These effects are often caused by organisms with large biomass, such as many mammalian herbivores, or those with large abundance that are predicted to have strong direct effects on individual plants. Therefore, following earlier definitions of keystone species, a correction for biomass and abundance should be incorporated to define keystone herbivores as those species that exceed their effect on community composition as predicted by their biomass or abundance in that community [5,61].

By adding a fitness component, here we further expand the definition of keystone herbivores. This definition includes herbivores that through indirect trait-mediated effects (e.g., plant-induced responses to herbivory) influence herbivore community composition with associated plant fitness consequences and thus natural selection on plant traits that, in turn, mediate interactions with herbivores. Specifically, plant metabolic changes in response to herbivory qualify for such traits, because they can have dramatic effects on subsequent community interactions [32,62] and interaction network structure [17,20], even if the actual plant tissue damage is minimal and the primary food resource remains apparently plentiful.

*altissima* [11]. The altered plant community as well as the altered distribution and frequencies of defense phenotypes in a plant population, in turn, affect other organisms interacting with these plants. Thereby, keystone herbivores change the arena in which natural selection is played out. In addition to the effects that keystone herbivore species can have at the community and population level, we argue that the class of keystone herbivores that affects plant growth form or quality drives selection on plant defense traits. Here, we focus on plant-induced responses to keystone herbivores, the effect of these responses on community composition of species interacting with an individual plant, and the resulting plant fitness consequences.

In plants, interactions between their community members are profoundly driven by induced responses to attack. For example, when plants are attacked by a herbivore, they usually respond with significant changes in secondary metabolism [12]. These changes in secondary metabolite production can function to increase plant resistance to attackers directly or indirectly. At the same time attackers may manipulate plant metabolic responses to their own benefits by optimizing susceptibility, enhancing resource availability, or increasing resistance to competing herbivores [13]. For each of these scenarios, induced responses change the phenotype of the host plant that acts as a resource for other community members [12,14]. This includes enhanced resistance or susceptibility to other herbivores (above- and belowground) and altered interactions with pollinators or predators of multiple trophic levels [14–21]. Induced plant responses may persist over an entire season and thus mediate interactions among early and late herbivore colonizers [14]. Consequentially, the presence of a particular herbivore can be hypothesized to increase or decrease the strength of a subsequent herbivore on plant fitness and thus cause non-additive natural selection on plant traits [22–24]. For example, leaf feeding by Japanese beetles (*Popillia japonica*) induces accumulation of defense compounds in the reproductive tissues of evening primrose (*Oenothera biennis*), which reduces rates of colonization by seed-predating caterpillars and hence increases plant fitness [25]. Subsequent colonization of plants by other herbivores then depends on the nature of plant responses to a previous attacker. Thus, induced plant responses and indirect plant-mediated species interactions [26] can profoundly affect strength and direction of natural selection on herbivore resistance.

Here, we argue that the concept of keystone herbivores will allow us to identify which herbivores drive plant-mediated interaction networks and help us understand evolution in plant defense traits. We address (i) what characterizes herbivores as keystone species in plant-associated assemblies of insects, (ii) how the impact of keystone herbivores may be evident in plant fitness measures, and (iii) how keystone herbivore effects should be incorporated into the conceptual framework of plant defense trait selection.

### Empirical Support for Keystone Herbivore Effects

In the past decade, many years after Hunter had defined the keystone herbivore concept in 1992, several field studies have provided empirical support for insect herbivores altering the insect community on individual plants as early colonizers through altering plant quality [27–30]. Functioning as a keystone herbivore through the indirect plant-mediated mechanism is determined by key characteristics of the herbivores' interaction with plant metabolism and includes specificity and persistence of the plant-induced response.

First, plant responses to their attackers tend to be highly specific. Thus, herbivores attacking a plant may differentially affect other species interacting with the plant. Herbivores with similar feeding modes tend to induce responses that are mediated by relatively similar hormone pathways in plants. Leaf-chewing herbivores induce responses that are primarily regulated by jasmonic acid (JA) and ethylene (ET), whereas sap-sucking herbivores induce salicylic acid (SA) to a greater extent. Variation in herbivore-derived chemical elicitors from herbivore saliva or the feeding pattern are likely the major factors affecting plant response specificity [13,31]. The resulting induced responses can either increase resistance to the attacker or specifically induce increased susceptibility to the benefit of the attacker [14,32]. In milkweed (*Asclepias syriaca*), early season herbivory by weevils, leaf beetles, or monarch caterpillars differentially affected richness of subsequent herbivore assemblies on individual plants as compared with untreated control plants. Moreover, effects on richness of the assembly were accompanied by effects on damage to the plant and hence in specific years only two herbivore species induced indirect plant-mediated species interactions that had consequences for insect community composition and plant damage levels [27].

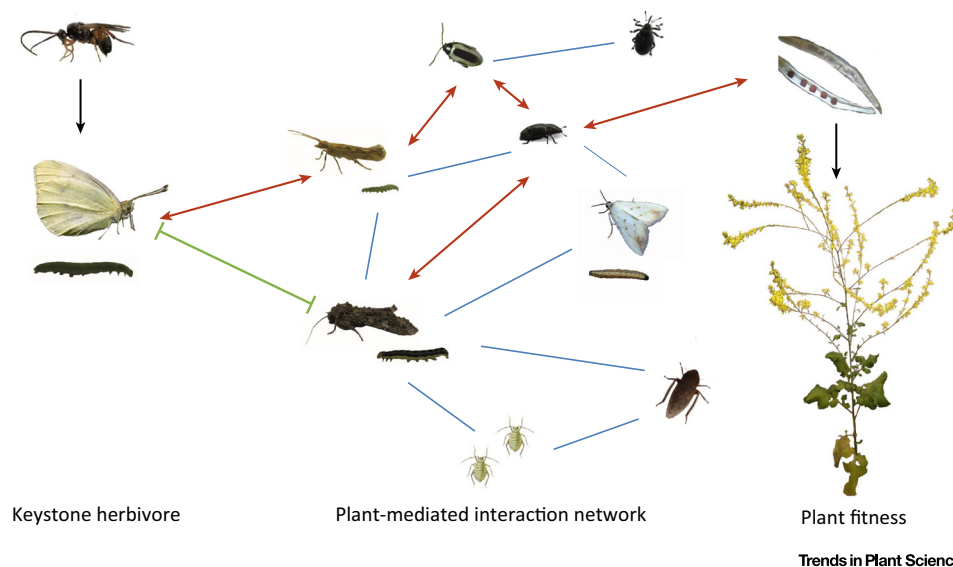
Second, herbivores differ in the persistence of their induced plant responses. Some early season herbivores canalize the responses of plants so that subsequent herbivory only contributes little to the plants phenotype [33]. Other herbivores may override effects of early season herbivory and redirect plant phenotypes [34]. Both mechanisms can characterize keystone herbivores, because their strong effect on the plant phenotype can have community wide effects even when the inducing herbivores are no longer present on the plant. Especially changes of plant secondary metabolism induced by lepidopteran caterpillar feeding are frequently found to be strong and systemic throughout the plant, which can mediate strong effects on other community members [27,29,30]. In a study on cultivated *Brassica oleracea*, early season herbivory by *Pieris rapae* caterpillars was found to more strongly affect community composition than did the genetic differences between *Brassica* accessions. This illustrates that the effect of plant phenotypic changes induced by early season herbivory on community composition may exceed the effect of constitutive phenotypes [30]. Such indirect species interactions can be stronger than direct species interactions in both aquatic and terrestrial ecosystems [35].

### How Do Keystone Herbivores Affect Plant Fitness?

Specificity and persistence of plant-induced responses are important factors affecting plant resistance and arthropod community composition on the plant, but these effects may not always translate into plant fitness consequences. Herbivores may significantly affect plant fitness through influencing plant-associated communities when their induced responses (i) affect the occurrence of other herbivores that singly or in combination with the initial attacker have

a significant fitness effect on the plant through ecological or plant physiological processes, and (ii) influence the recruitment of their own predators and parasitoids that change dynamics within the arthropod community with significant plant fitness effects.

Through inducing plant responses, keystone herbivores can affect the likelihood with which a plant is being colonized by a herbivore with a large negative impact on plant fitness. Herbivores with strong direct effects on plant fitness may, for example, directly feed on reproductive tissues or strongly reduce the plants' resources to be allocated in reproduction (Figure 1). Thereby, the net plant fitness outcome of the interaction between the keystone herbivore and another herbivore can be bidirectional. First, the plant-induced response to the keystone herbivore may enhance the abundance of other herbivores that infer fitness costs to the plant. This increased susceptibility after herbivore damage has been identified to particularly occur in species assemblages that contain specialist herbivores. When plants respond to herbivory by enhancing the concentration of their taxon-specific secondary chemistry they become more apparent to specialist herbivores, but repel generalist herbivores [30]. In such cases one would expect to detect strong natural selection for resistance to the keystone herbivore in the context of the natural community, even if this herbivore in isolation may not affect plant fitness. Second, the induced response may decrease the likelihood of colonization by herbivores with strong direct effects on plant fitness. For example, in *Nicotiana attenuata*, the mirid bug, *Tupiocoris notatus* induces plant responses that reduce the colonization of plants by the more damaging chewing caterpillars *Manduca sexta*. These caterpillars typically consume large parts of a plant including its flowers and seed pods. The mirids do not cause direct fitness costs to the plant through an induced compensation mechanism [36]. However, in response to the mirids plants become more resistant to other herbivores that may inflict fitness costs. This scenario may result in strong natural selection on increased attractiveness to mirid bugs for they increase relative plant fitness when other herbivores are part of the interacting community [28]. One of the key



**Figure 1. Keystone Herbivore and Associated Interaction Network Affects Plant Fitness.** Through their feeding on a plant, keystone herbivores increase (red lines) or decrease (green lines) the likelihood of attack by some herbivores via the plant-mediated interaction network arising from induced responses. Other herbivores in the community may be neutral (blue lines) in their response to keystone herbivores. Thereby, keystone herbivores may indirectly affect plant fitness. Predators linked to keystone herbivores may cause similar plant fitness effects. Keystone herbivores may be important agents of selection on plant defenses by having strong indirect effects on plant fitness, which largely exceed the selection pressure by this herbivore as predicted by its direct effect. Positive and negative effects are indicated by arrows and lines with bars, respectively.

characteristics of this type of keystone herbivore is the ability to invoke strong selection on plant defense traits beyond that expected based on the herbivore's individual effect on plant fitness. Such effects can even be further emphasized when considering mutualist pollinators. Because pollinator attraction can also be significantly affected by plant chemistry, herbivore-induced changes in plant secondary metabolism can significantly affect pollination success and thus directly plant fitness. So far, only few studies have thoroughly studied such plant-mediated herbivore–pollinator interactions [16,37], but suggest significant fitness effects. The magnitude and direction of which are likely to vary with the primary attacking herbivore species and the interacting community.

The plant fitness consequences of induced responses after attack by a keystone herbivore may also be mediated via higher trophic levels. Predators that are trophically connected to keystone herbivores can function as selective agents on plant traits. Extra floral nectaries, structures that offer housing to predators or volatile profiles that in particular attract natural enemies of keystone herbivores may reduce the impact of the keystone herbivore [38]. Hence, this implies that these highly specific plant traits to optimize presence of natural enemies may not necessarily be selected through the most common herbivore or those with strongest direct negative impact on plant fitness. Herbivores that have the largest effect size on the community and its associated plant fitness consequences may be strong agents of selection on plant traits that enhance direct and indirect resistance to these keystone herbivores. To measure the plant fitness effect of enemies of keystone herbivores, individual natural enemy species have to be omitted from otherwise complete communities. Such experiments are challenging and this may be the reason why the link between natural enemy responses to volatiles and the plant fitness benefit of attracting natural enemies has not been established [38].

Keystone herbivores are most likely present in plant-associated insect communities that are relatively species rich. The larger the number of potential selective agents, the more likely feedback loops in communities may have a larger effect size in trait selection than direct selection that is exerted by individual species [39,40]. Thus, natural selection is predicted to optimize the information transfer with keystone herbivores so that the plant can engage the entire community in its strategy of coping with a particular fitness-affecting biotic stress [41]. This does not mean that there can be only a single species of keystone herbivore associated with a plant species. In the same or different years, different species may affect the composition and dynamics of the community on a plant [27]. Depending on the predictability of a particular keystone species colonizing a plant, this may lead to frequency-dependent selection of plant genotypes repelling or attracting specific keystone herbivores. Moreover, in a spatial context selection by several species of keystone herbivores may occur in a geographic mosaic meta-population framework [42].

Identifying keystone herbivores and measuring their plant fitness effects would be equivalent to identifying the fitness effect of plant-associated interaction networks and provide a shortcut to understanding diffuse (co)-evolution.

### Plant Trait Evolution Mediated by Keystone Herbivores

Through non-additive effects on the herbivore community and in consequence on plant fitness, keystone herbivores can affect plant trait evolution in three basic ways.

First, when the colonization of plants by keystone herbivores is frequent, predictable, and consistent in time, keystone herbivores may directly select on inducibility of plant responses [12]. Inducibility may be selected against when induced plant phenotypes attract community members with a large negative effect on plant fitness, or promoted when they deter such herbivores.

Second, keystone herbivores may affect the strength of selection on plant traits involved in resistance to other herbivores that through plant-mediated interactions are affected in their likelihood of colonizing the plant attacked by the keystone herbivore. For example, leaf-feeding herbivores may alter the likelihood of colonization by seed-feeding herbivores and thereby alter selection regimes on seed traits [25]. Moreover, the connectivity between agents that select on different plant traits may result in linkage in heritability of traits involved in resistance to each agent of selection. This may, for example, result in defense syndromes in which induced responses to leaf-chewing herbivores that promote the presence of flower feeders are linked with enhanced flower resistance in anticipation of flower attack.

Third, when the keystone herbivore and other herbivores that are affected by its plant-induced responses select on the same plant trait this may result in diffuse evolution of plant traits [43–47]. Importantly, diffuse evolution comes about when the non-additive effect of the keystone herbivore and responding herbivores on plant fitness results in selection on at least a single shared plant trait [48–52]. For example, when exposed to each of their herbivores squirrels, crossbills, and moth in isolation, pine cone morphology of the species *Pinus contorta latifolia* is adapted to resistance against the specific herbivore. However, cone morphology is different from each of the cones selected in isolation when interacting with more than one herbivore [53]. Diffuse selection on plant traits by interaction networks of herbivores may at the same time also result in selection on herbivore traits (diffuse co-evolution). Bill morphology of the crossbills may be altered by the suit of herbivores commonly feeding on the cones. Recent work [54] has shown that indeed keystone herbivores may affect co-evolution between herbivores and their food plant mediated by herbivore-induced plant responses. Caterpillar feeding on *Salix eriocarpa* induced regrowth of young leaf tissue on which the leaf beetles prefer to feed. The feeding preference of beetles exposed to plant populations that express regrowth show strong adaptive preference to previously damaged plants.

### Concluding Remarks and Future Outlook

The challenges in understanding evolutionary processes such as trait selection in organisms that interact with a diverse community of potential selective agents are (i) to identify the role of indirect interaction webs for structuring such communities, (ii) to identify which species act as dependent or independent agents of selection, and (iii) to identify how temporal and spatial fluctuations in community composition are reflected in trait selection [40]. In all three challenges, keystone herbivores are the major effectors by which the community is organized and hence selection is driven.

Although evidence is growing that indirect interaction webs play a profound role in structuring assemblies of insects on plants [6], we know very little about the predictability of these interactions or the fitness consequences for plants. For individual plant populations, we should identify the predictability of the insect community in terms of the order and likelihood of single plants being colonized by different insect species [55,56]. From such datasets we may extract whether some herbivores strongly affect the presence of other herbivores and which species respond to initial herbivory, hence to identify keystone herbivores and the subset of interactions that may select on plant defenses [57]. The keystone herbivore concept as discussed here can provide some major hypotheses for the understanding of the evolution of plant defenses in complex interaction networks (see Figure 1 in Box 2) [58]. Experimentally inducing plants with keystone herbivores or non-keystone herbivores and exposing them to natural communities of insects will identify whether their community wide effects do translate into plant fitness effects. A causal relationship of keystone herbivores on the selection of genes involved in induced responses may be identified in experiments where such traits have been silenced and plants have been exposed to arthropod communities in which important responding insects are present or absent. This approach can be used to identify whether plant trait selection can

### Outstanding Questions

What is the contribution of indirect interaction webs in structuring plant-associated communities?

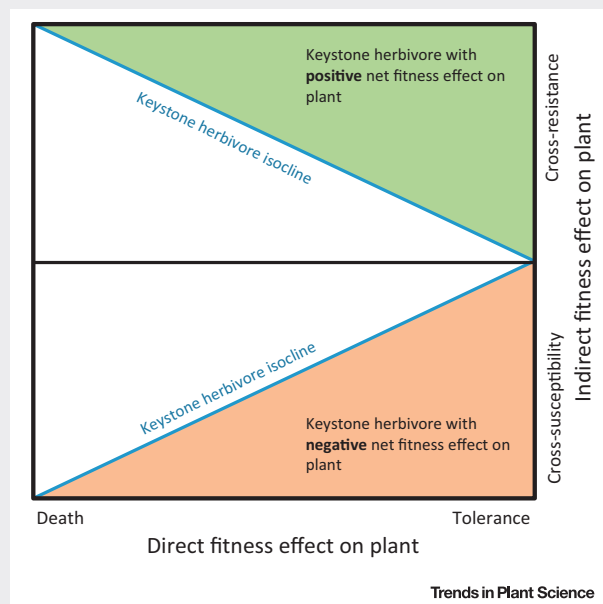
Which species in a plant-associated community act as dependent or independent agents of selection on plant traits?

How are temporal and spatial fluctuations in community composition reflected in trait selection?



### Box 2. Keystone Herbivores and the Evolution of Plant-Induced Responses to Herbivory

Keystone species (e.g., keystone herbivores) are defined to have impacts on the composition and dynamics of entire communities that go beyond the effect predicted by its mere abundance, mediated indirectly through their consumptive and non-consumptive activities [4–6]. By this definition a keystone herbivore's impact on plant fitness is predominantly through indirect mechanisms (e.g., induced change in plant metabolism and resulting cross-resistance and cross-susceptibility) relative to direct mechanisms (e.g., consumption of leaf tissue that results in reduced fitness or death) (Figure 1). It then follows that plants will be under increasing natural selection to mediate indirect effects the larger the relative importance of a keystone herbivore becomes within the community interacting with the plant. For the evolution of basic plant defense mechanisms (e.g., constitutive, induced resistance) and in light of the keystone herbivore concept, plants are expected to be under natural selection for increased inducibility of plant responses specifically to the keystone herbivore. This is assuming that the keystone herbivore functions through the induction of plant responses that mediate cross-resistance to other herbivores [28]. If the plant metabolic changes induced by the keystone herbivore increase plant susceptibility to others, thus has negative net fitness effects, plants are expected to be under natural selection to limit responses to the keystone herbivore. Within this framework the keystone herbivore concept provides hypotheses for the evolution of plant defenses.



**Figure 1. Plant Fitness Effects of Keystone Herbivores.** By primarily functioning through altering community interaction, keystone herbivores are expected to affect plant fitness indirectly (colored panels). Depending on how the activity of the keystone herbivore is affecting the presence of antagonistic species (e.g., herbivores, pathogens, competitors), net fitness effects for the plant can be positive (green panel) or negative (orange panel). The 'keystone herbivore isoclines' depict the ratio between direct and indirect effects of a herbivore on plant fitness, whereby a relatively larger impact of indirect effects relative to direct effects (e.g., an effect larger than expected from a herbivore species' size and abundance, and potentially mediated through the interactions with the community) defines the keystone herbivore. Direction (e.g., positive or negative) and shape (e.g., linear or other) of these isoclines are functions of the plants' relative tolerance and resistance to a herbivore. Thus, this figure provides a direct predictive framework for the experimental identification of a keystone herbivore as well as the key factors likely affecting the herbivore's function as keystone species.

be reduced to pairwise interactions or a core network of several agents of natural selection. The interaction network may accommodate keystone species with low direct negative fitness consequences but they may be drivers of strong indirect interactions that shape trait evolution in plants. For another class of keystone herbivores that shape plant communities, it should be explored how they change the genetic architecture of individual plant populations and if those effects interact with keystone herbivores that alter plant quality, as discussed here (see Outstanding Questions).

Using a keystone herbivore concept to include indirect interactions into standing frameworks of selection may provide new insight into trait selection in plant–insect interactions.

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