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Can herbivores sharing the same host plant be mutualists?

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Resource partitioning is considered to be a prerequisite for coexisting species to evolve from competition to mutualism. This is uniquely different for two major pest insects of rice. These herbivores preferentially opt to coinfest the same host plants, and through plant-mediated mechanisms, cooperatively utilize these plants in a mutualistic manner.

Interspecies interactions: from competition to mutualism

It is increasingly evident that **mutualisms** (see Glossary) are key modulators of biodiversity and play important roles in **coexistence** processes. Mutualistic interactions rarely occur within the same trophic level [1], and conventional interspecific competition theory stipulates that coexisting species sharing the same resources commonly engage in fitness-reducing **competition**. This has been widely recognized for a diverse range of taxonomic groups [2]. Accordingly, **niche differentiation** theory predicts that in order for an interaction between coexisting species to evolve from competition to mutualism, there needs to be a transition from overlapping to partitioning resources. In most cases of mutualism, the participants utilize distinct food resources; for example, in the classic types of cooperative interactions between aphids and ants, and between microbes and higher organisms [3,4]. Yet, interactions between species that simultaneously exploit the same resource are not always negative and there can be considerable variation ranging from competition to mutualism [3,5]. Positive interspecific interactions have been mainly reported for plants and sessile animals, and have been rarely found in mobile animal communities [3]. We argue here that mutually beneficial interactions between insect herbivores occupying the same host plant can also occur.

Mutualism between herbivorous insects sharing the same host plants

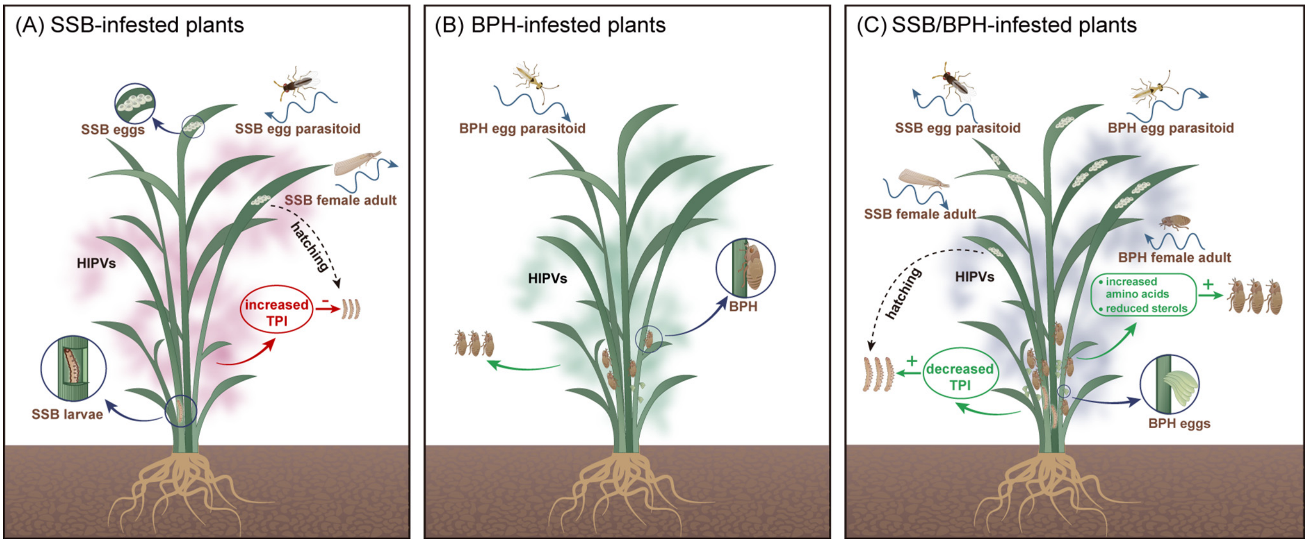
It is evident that many conspecific herbivores benefit from aggregating to jointly attack a plant; for instance to overwhelm the defense mechanisms of a plant [6,7]. In exceptional cases, such cooperative intraspecific interactions can also occur between different developmental stages, as in the flea beetle *Bikasha collaris*; its root-feeding larvae induce the Chinese tallow tree *Triadica sebifera* to emit shoot volatiles that attract their adults above ground. Leaf herbivory by these adults increases root nutrients and decreases root defenses, thus enhancing larval performance [7]. Recent studies suggest that there are similar mutualistic interactions between different species of insect herbivores. A unique example is the plant-mediated cooperative interaction between two of the most destructive rice pests in Asia, the brown planthopper (BPH), *Nilaparvata lugens*, and the rice striped stem borer (SSB), *Chilo suppressalis*. Sole infestation by SSB induces direct and indirect defensive responses of rice plants, resulting in poorer development of SSB caterpillars and increased attraction of egg parasitic wasps (Figure 1A) [8,9]. Similarly, infestation by only BPH results in plant defensive responses that are detrimental to the hoppers (Figure 1B). However, coinfestation by the two insects significantly suppresses defensive responses in rice plants, benefiting both species. BPH is attracted to SSB-infested rice plants and obtains direct fitness benefits from feeding on these plants due to increased amino acid contents, and reduced levels of toxic sterols (Figure 1C) [10]. In addition, SSB-infested plants provide 'enemy-free' space for the offspring of BPH because of changes in volatile emissions that make the plants less attractive to parasitoids [8] (Figure 1C). In return, simultaneous infestation of rice plants by BPH suppresses the production of defensive proteinase inhibitors. The changes in plant volatile emissions due to the double infestation also makes rice plants less attractive to egg parasitoids of SSB, thus significantly enhancing its fitness [9] (Figure 1C). The two pests optimally take advantage from these reciprocal benefits by actively seeking and preferentially laying eggs on plants that are already occupied by the other herbivore [8–10]. Hence, SSB and BPH apparently have evolved a highly effective strategy of **facultative mutualism** that allows them to maximize the benefits that they derive from the other's presence.

Is the mutualism between SSB and BPH attributable to niche differentiation?

Current coexistence theory suggests that ecological niche differentiation is the basis

Glossary

Coevolution: reciprocal genetic changes in two or more species in response to each other.
Coexistence: the state of two or more species being found in the same place at the same time.
Competition: direct or indirect interaction between organisms that leads to a reduction in fitness when the organisms share the same resource.
Facultative mutualism: a type of mutualism in which the interacting species derive benefit from each other, but they are not fully dependent on each other for survival.
Mutualism: a cooperative interaction between individuals of different species that benefits both participants.
Niche: the environmental conditions and resources a species requires for growth, development, and reproduction.
Niche differentiation: the process by which competing species use the surrounding resources differently in a way that helps them to coexist.
Nutritional niche: the blend and ratio of nutrients that maximize fitness of species.



Trends in Ecology & Evolution

Figure 1. Rice-plant-mediated interactions between SSB, BPH, and their egg parasitoids, *Trichogramma japonicum* and *Anagrus nilaparvatae,* respectively. (A) Rice plants infested solely by SSB caterpillars increase the production of TPIs that provide resistance to SSB caterpillars and they also release certain volatiles that repel SSB females and attract *T. japonicum* wasps. (B) Rice plants infested solely by BPH emit specific blends of volatiles that are attractive to *A. nilaparvatae* wasps. (C) Rice plants coinfested by SSB and BPH, *Nilaparvata lugens*, have reduced levels of TPIs and sterols but contain higher amounts of amino acids, benefitting the development of SSB caterpillars and BPH nymphs. The double infested plants also released volatiles that attract both SSB and BPH females for oviposition, but repel the respective egg parasitoids of SSB and BPH. BPH, brown planthopper; HIPV, herbivore-induced plant volatile; SSB, striped stem borer; TPI, trypsin protease inhibitor.

for stable coexistence of species [5,11]. SSB and BPH share the same host plants, feed on the same plant parts, and have a similar spatial and temporal distribution throughout many Asian rice paddies [12]. This prompts the question: what are the mechanisms that ensure niche differentiation and thus enabling the two species to cooperatively utilize the same food resource? We argue that although the two insects occur side by side on rice plants, SSB as a stemborer, ingests plant protein and carbohydrates by feeding on tissues inside the rice plants without significantly interfering with the vascular feeder BPH (Figure 1). Hence, there is usually no direct physical interaction between the two species and their nutritional acquisition is essentially separated, implying that each of the two species occupies its own unique **nutritional niche** [13]. Such nonconflictual resource partitioning is usually thought impossible for species that use essentially the same resources, and therefore herbivores feeding on the same plants are commonly regarded as competitors [13]. Yet, coexistence of generalist herbivores that share the same plant can be achieved through nutritional niche partitioning by utilizing specific plant-derived nutrients (e.g., protein and carbohydrate) in distinct absolute amounts and ratios [5,13]. The unique example of SSB and BPH suggests that species can indeed achieve niche partitioning by differentially utilizing a food resource. Moreover, these rice pests benefit from each other by triggering opposing plant defense mechanisms, which has led to a mutualistic interaction and cooperation.

The dilemma of a clash between natural and artificial selection in cropping systems

Coevolutionary theory suggests reciprocal adaptations in herbivores and host plants; when one side evolves a new trait to adapt to a defense from the other, the other side develops or adapts a strategy in response, as part of a so-called arms race [14]. In the context of **coevolution** between rice and its herbivores, it appears that, in the wild, rice plants must have evolved an effective inducible defense against a sole attacker, but they appear unable to respond effectively to coinfestation by SSB and BPH. This can be expected if the two rarely co-occur in natural habitats. Because cultivated rice is under artificial selection to meet human requirements, the focus has been on the traits that favor nutritional value and yield. This may lead to a weakening or loss of defensive traits, and eliminates the possibility for the plants to evolve new defense mechanisms to cope with novel herbivory scenarios such as coinfestation by two insects [15]. In contrast, insects like SSB and BPH can evolve traits to cooperatively overcome plant defenses through natural selection, especially under conditions where the two insect species frequently share the same host plants, as is the case in vast rice monocultures. It would be interesting to investigate whether the failure in defense against the two herbivores cooperative infestation also occurs in natural communities with the wild progenitors of rice plants. In follow-up studies, we also expect to find that insects from regions where only one of the two pests occurs, when they are given a choice, will not exhibit the adaptive preference for plants already infested by the other species.

Nutritional niche differentiation in combination with differential defense induction allows herbivores to be mutualists on the same host plants

Ecologists interested in mechanisms of coexistence among species have focused their investigations on the spatial and temporal isolation of species and on differences in food sources exploited by species in large-scale ecosystems. This resource-partitioning framework seems not applicable to coexisting species that utilize the same resource, such as herbivorous insects feeding on the same plant in close proximity. The unique example of the cooperative interaction between SSB and BPH shows that coexisting herbivore species can evolve behaviors and exploit specific plant traits to use the same food source in a mutually beneficial manner. This nutritional niche differentiation concept in combination with suppressive cross-talk between plant defense pathways introduces a new mechanism of intraguild coexistence, even cooperation, at the microhabitat scale. Moreover, it provides a theoretical foundation for the development of ecology-based strategies to control agricultural pests.

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Declaration of interests

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