



Review

Prospects for Integrating Augmentative and Conservation Biological Control of Leaffolders and Stemborers in Rice

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Abstract: Possibilities to combine augmentative biological control using *Trichogramma* spp. egg parasitoids and conservation biological control through habitat manipulation, for the management of rice leaffolder and rice stemborer pests have received only cursory mention in the literature. We reviewed information on the use of *Trichogramma* releases and on habitat manipulation to manage leaffolders and stemborers in rice. Stemborers have become a priority for biological control since the 1990s with research focusing mainly on *Chilo suppressalis* in China and Iran, *Scirpophaga incertulas* in South and Southeast Asia, and *Chilo agamemnon* in Egypt. In most cases, 100 K wasps (*T. japonicum* or *T. chilonis*) released over 30–100 release points ha^{−1} at least once during early crop stages, resulted in good control (>50% reduction in damage). Despite positive results accumulated over decades, larger scale releases in rice have only been conducted very recently. Research on conservation biological control of stemborers has focused on manipulating rice field habitat, particularly along rice bunds (levees). Several studies reported higher *Trichogramma* densities or greater egg parasitism in rice fields with flowering plants on bunds compared to control fields (without bund vegetation and usually with insecticides). These trends have mainly been attributed to nectar as a supplementary food for the adult wasps, although evidence for this mechanism is weak. Trap plants, such as vetiver grass (*Chrysopogon zizanioides*) attract ovipositing stemborers, but suppress larval development. Repellent and banker plants have not yet been identified for rice stemborers or leaffolders. We outline the opportunities and challenges for combining augmentative and conservation biological control of leaffolders and stemborers in rice.

Keywords: agroecology; biodiversity; ecological engineering; egg parasitoids; integrated pest management; strip vegetation; striped stemborer; trap plants; tropical rice; yellow stemborer



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1. Introduction

Rice (*Oryza sativa* L. [Poaceae]) is the staple food for about half the world's population. Ensuring rice productivity is therefore essential for global food security. Furthermore, rice farming provides work and income for millions of smallholder farmers, particularly in Asia [1,2]. While in some countries high yields have been achieved through the use of modern and hybrid rice varieties with substantial amounts of fertilizers (e.g., China and Thailand: [3–5]), yields are still relatively low in other countries, such as Laos or Myanmar [4]. These low yields are largely associated with a limited adoption of intensification practices such as irrigation, nutrient management, or varietal improvement [4,6];

however, closing yield gaps in these countries will also require a reduction in damage to rice from phytophagous insects, mites and snails [7]. Despite the diversity of herbivores than can feed on rice plants, relatively few species (ca 20) are of concern to pest managers [8]. These species are important either because the damage they cause results in yield and/or profitability losses, or because farmers, concerned about potential economic losses, will apply large amounts of often broad-spectrum pesticides that are prejudicial to human and environmental health [7].

Among the most damaging rice pests are a range of stem-boring flies (Diopsidae: Diptera) and moths (Crambidae, Noctuidae: Lepidoptera) [9,10]. Cheng et al. (2010) [11] suggest that stem borers regularly cause yield losses of around 20% in Asian rice producing countries. In some regions, continuously high stemborer densities can cause losses of >70% during some seasons [10,11]. Leafrollers (Crambidae, Pyralidae: Lepidoptera) and planthoppers (Delphacidae: Hemiptera) are also important rice pests and the latter, especially, can have devastating effects on rice production in fields that overuse broad-spectrum insecticides [3,7,12] often in an attempt to control stemborers and leafrollers (i.e., secondary pest outbreaks [7,12,13]). Most of these broad-spectrum chemicals are also highly toxic to rural communities [14,15] and pesticide applicators (especially since protection gear is seldom used in tropical countries [15–17]).

While a large number of herbivores (including those that are of least economic concern) have been documented from the rice crop, there is also a remarkably rich natural enemy complex. For example, Lou et al. (2014) [18] have recently shown that at least 889 species of predatory natural enemies and 424 parasitoids of rice insect pests occur in Chinese paddy fields and that each of the key insect pests of rice has around 50 or 60 natural enemies. Despite the high diversity of pest natural enemies, generalist natural enemies—although they contribute to overall pest mortality—do not demonstrate marked responses to spatial and temporal variability in pest densities. In contrast, a relatively small number of key predators and parasitoids are thought to directly regulate pest populations through marked functional responses to pest densities [7]. In particular, a number of hymenopteran egg parasitoids have been shown to respond behaviorally and numerically to pest densities and thereby contribute to pest regulation [19–22]. There are numerous examples of insecticides that are more toxic to natural enemies than target pests, and a large number of well-documented cases have shown how field applications of insecticides can reduce pest regulation, thereby causing greater damage to rice [12,23,24]. This is exacerbated where target insects have developed resistance to applied insecticides, or, where certain insecticides stimulate pests to feed more, reproduce more, or migrate further [12,25,26].

An increasing awareness of the role of insecticides as an underlying cause of herbivore outbreaks has prompted greater research attention to the possibilities for enhancing the biological control of rice pests through augmentative [27–29] and/or conservation biological control [30–33]. For example, an increasing number of field studies from across Asia has indicated that agroecological interventions, such as planting rice bunds (levees) with flowering plants, increases the diversity and abundance of predatory mirid bugs (Miridae: Hemiptera), spiders (Araneae: Class Arachnida) and egg parasitoids (Hymenoptera; Diptera), thereby promoting regulatory ecosystem services [21,33–35]. Furthermore, large-scale attempts at augmentative biological control of rice leafrollers and stemborers have been implemented in Asia with apparently good success in terms of reducing pest damage and reducing pesticide use [27,28]. Despite reported successes in both augmentative and conservation biological control in Asian rice, to our knowledge, no study has combined both methods simultaneously. Indeed, research on conservation biological control in Asian rice has not generally included other IPM technologies or crop production practices as factors in field designs [7,36,37] (but see Zhu et al. (2022) [38]).

In this review, we explore some of the possibilities for combining augmentative—using *Trichogramma* spp. (Trichogrammatidae: Hymenoptera) egg parasitoids—and conservation biological control for Lepidoptera pests in rice. We first review available reports of attempts at augmentative biological control. A number of recent reviews have been published that

explore augmentative biological control of Lepidoptera by *Trichogramma* spp.; however, previous reviews have focused mainly on pre-release technologies, or have restricted their focus to China [29,39–42]. Similarly, there has been a recent review on ecological engineering (a form of conservation biological control) in China [38]. Unlike these previous reviews, ours mainly focuses on post-release augmentation technologies, which probably has a greater influence on the compatibility of augmentative and conservation biological control. We also include published field studies from all rice growing regions. We then review studies that report the results of conservation biological control or similar methods (i.e., using habitat manipulation) on pest Lepidoptera in rice production systems. Finally, we examine the possibilities for combining augmentative biological control and conservation biological control, and identify a series of knowledge gaps that could be addressed in future research.

2. Literature Review

We conducted separate searches for information related to augmentative biological control and conservation biological control. The first search focused on studies dealing with field releases of *Trichogramma* spp. against rice pests. Because many field reports have been published in non-ISI journals, we used Google Scholar, CAB abstracts and the China National Knowledge Infrastructure to retrieve documents published until August 2022. Search terms included '*Trichogramma*' and 'rice', or '*Trichogramma*' and '*Chilo*', '*Scirpophaga*', '*Tryporyza*', '*Sesamia*', '*Cnaphalocrocis*', 'leaffolders', or 'stemborers'. For each retrieved paper, the research methods were appraised to identify studies that monitored *Trichogramma* spp. releases under field conditions. A number of publications included in this review, in particular older ones in Chinese, had not been screened through a rigorous peer review system: while aiming to be as comprehensive as possible, we excluded studies with apparent methodological issues (e.g., no replication or with plot sizes being only a few m²) from analyses of results; but we noted all studies to assess the prevalence of research topics. For papers that included a number of different treatments in addition to biological control, we provide information only as relates to *Trichogramma* releases. However, we generally excluded papers where *Trichogramma* spp. releases were only a small component of studies that otherwise dealt mostly with insecticides. A substantial number of field reports published in Chinese are difficult to access outside China. These reports are also included here, making their main findings available to international readers for the first time. As much as possible we attempt to be specific in indicating baselines for the respective studies (i.e., whether *Trichogramma* releases were compared to untreated controls or to farmers' standard practices based on pesticides). From our search, and excluding papers for the above-mentioned reasons, we retrieved a total of 95 papers that describe field releases of *Trichogramma*. We list all these studies and annotate the main findings from some of the larger studies in Table S1.

The second search focused on *Trichogramma* spp. under natural field conditions or where agroecological interventions have been implemented and address Lepidoptera pests. The search was conducted using Google Scholar and ISI Web of Science for the period 1970–August 2022 by applying the search terms '*Trichogramma*' and 'rice', together with 'conservation', 'agroecol*', 'ecological engin*', 'flower', 'floral', 'nectar', 'honeydew', 'trap plant', 'banker plant' or 'egg parasitism'. We used the initial retrieved papers to snowball to other related articles. The search retrieved 49 peer-reviewed papers. The retrieved papers included both laboratory and fields studies. Studies were assessed on the basis of including information relevant to the abundance or damage caused by rice stemborers or leaffolders or where egg parasitism was monitored. Many of the papers reported the results of non-replicated, comparative field or field-plot studies; however, we included these non-replicated studies in the review as an indication of current interest in the technologies; nevertheless, where information is presented, we clearly indicate whether experiments were replicated or not. The final list of included papers is presented in Table S2.

3. Results and Discussion

3.1. Augmentative Biological Control

Globally, the best known and most widely used augmentatively released biological control agents are *Trichogramma* egg parasitoids [43]. Nearly 4 million hectares of maize (*Zea mays* L. [Poaceae]) are treated annually with *Trichogramma* spp. in China alone [29,44] and these small wasps are also used on large areas in several other crops such as sugarcane (*Saccharum officinarum* L. [Poaceae]) [45]. In rice, many attempts have been made to use *Trichogramma* as biological control agents against key Lepidoptera pests over the last 50+ years with highly varying but often good results. However, in contrast to maize and sugarcane, no large-scale commercial releases of *Trichogramma* egg parasitoids were conducted in rice until about 5–10 years ago [46]. There are a number of reasons for this, some of which will be looked at in this review in more detail. Furthermore, the rice ecosystem has some peculiarities, in particular because rice is generally produced in semi-aquatic systems, meaning that field application techniques can be relatively awkward. It is noteworthy, however, that this picture has changed recently with substantial efforts to develop *Trichogramma*-based biological control methods for rice in China [29].

Among the studies of augmentative biological control that we retrieved, virtually all were conducted in irrigated or rain-fed rice and the target pests (indicated in Table S1) were mainly stemborers but, especially in China, also included leaffolders. Work on testing *Trichogramma* spp. in rice began more than 60 years ago. For example, in the early 1960s, Nickel (1964) [47] examined the potential for biological control of stemborers in rice. Based on rather limited experimental evidence at the time, he stated that mass-released *Trichogramma* spp. could potentially control stemborers, even though this would be only temporary in nature. Despite also citing critical papers, e.g., Japanese studies which considered the mass release of *T. japonicum* (Ashmead) as not very effective in rice [48], Nickel's (1964) [47] conclusion was, that given the potentially huge benefits of biological control, the subject deserved further research attention. Despite this, few studies were conducted on the biological control of rice pests using *Trichogramma* spp. during subsequent years, with those few studies almost exclusively conducted in China (Table S1). Nevertheless, interest in the topic has increased considerably during the last 20–25 years (see Table S1), with most of the research conducted in China and India; for example, out of the 95 studies that we reviewed 43% were conducted in China and 32% in India with relatively few studies from other regions. Despite a general lack of published research from other regions, augmentative biological control is, nevertheless, promoted by national agricultural research and extension systems in many other countries; for example, *Trichogramma* spp. egg cards are produced and distributed to rice farmers in parts of Indonesia [49] and the Philippines [50,51].

3.1.1. Target Herbivore Species for Augmentative Biological Control

The main pests against which *Trichogramma* spp. have been released in rice are leaffolders and stemborers [27,29]. The parasitoids will kill the eggs of several different leaffolder species or several stemborer species that occur in the paddy fields at the same time (see below) and will also attack other pest species. For example, in Iran, the impacts of releasing *T. maidis* Pinureau e Voegelé on the green rice semi-loopers (*Naranga aeneicincta* Moore [Noctuidae: Lepidoptera]), has been assessed during programs that mainly targeted the striped stemborer (*Chilo suppressalis* Walker [Crambidae: Lepidoptera]) [52]. Furthermore, a small number of studies have examined the possibilities of using *Trichogramma zehneri* Polaszek sp. n. against the rice hispa beetle, *Dicladispa armigera* (Olivier [Chrysomelidae: Coleoptera]), in Bangladesh [53,54].

Each of the Lepidoptera pest complexes of rice comprises several species. Furthermore, the composition of these complexes varies from region to region [9,31]. Despite this, few studies have examined interactions between the different species within these herbivore complexes, or examined the relative contributions by different species to overall damage [55]. *Cnaphalocrocis medinalis* (Guenée) (Crambidae: Lepidoptera) and *Marasmia patnalis* (Bradley)

(Pyralidae: Lepidoptera) are the most abundant species that make up the rice leaffolder complex [31]. In China, all studies conducted before 1986 targeted leaffolders (Table S1). After a period of no studies published at all, the striped stemborer became a more frequent target for research (see below), indicating a shift in relevance, possibly due to a change in general rice production practices and a growing awareness of the relatively minor impacts of leaffolders on rice yields [56,57]. Researchers in India and Pakistan have continued to examine the impacts of *Trichogramma* releases against leaffolders (Figure 1); however, in most of these cases, researchers have only included leaffolders together with stemborers during their field evaluations [58–60]. Currently, *Trichogramma*-based biological control against leaffolders in rice is not a prevalent research topic and, where considered, parasitism of leaffolders is often only incidental during releases that mainly target stemborers.

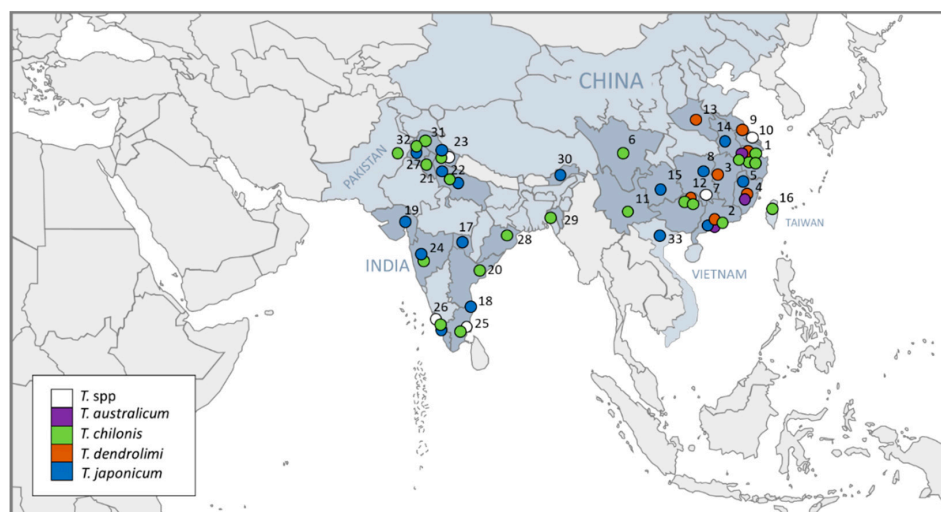


Figure 1. Locations of published case studies that used *Trichogramma* spp. as biological control agents against leaffolders in rice. Symbol colors indicate the *Trichogramma* spp. released. CHINA—1: Zhejiang [61–65]; 2: Guangdong [66–68]; 3: Jiangxi [69]; 4: Fujian [70,71]; 5: Fujian (Jiangyang) [72]; 6: Sichuan [73]; 7: Hunan (Guiyang) [74,75]; 8: Hunan (Changsha) [76]; 9: Jiangsu [77]; 10: Jiangsu (Tongzhou) [78]; 11: Yunnan [79]; 12: Guangxi [41]; 13: Henan [80–83]; 14: Anhui [84,85]; 15: Guizhou [86]; TAIWAN—16: [87]; INDIA—17: Telangana (Hyderabad) [88]; 18: Podicherry [88]; 19: Gujarat [88]; 20: Andhra Pradesh [89]; 21: Haryana [90]; 22: Uttar Pradesh [91–93]; 23: Uttarakhnad [94,95]; 24: Maharashtra [96]; 25: Tamil Nadu [97,98]; 26: Kerala [99,100]; 27: Punjab [59,60,101]; 28: Odisha [102]; 29: Tripura [103]; 30: Arunachal Pradesh [58]; 31: Himachal Pradesh [104]; PAKISTAN—32: Faisalabad [105]; VIETNAM—33: Me Linh [106].

The stemborer complex (Crambidae: Lepidoptera) in rice consists of three main pest species, *C. suppressalis* (striped stemborer–SSB), *Scirpophaga incertulas* (Walker) (yellow stemborer–YSB) and *Scirpophaga innotata* (Walker) (white stemborer–WSB) as well as a number of other species that occasionally damage rice (e.g., *Sesamia inferens* (Walker) [pink stemborer–PSB], *Chilo auricilius* Dudgeon [gold-fringed stemborer], and *Chilo polychrysus* Meyrick [dark-headed stemborer]) but mainly damage other crops [9,107,108]. SSB is among the most widespread species that damages rice (occurring from northern Japan to Western Europe); however, where it occurs, damage from YSB is often more severe, particularly in tropical rice-growing regions [9,55,109]. Studies of stemborers as targets of *Trichogramma*-based biological control have differed between regions (Figure 2). Much of the focus of biological control in China has been directed against SSB with a few, more recent studies, involving YSB, particularly in Yunnan. Studies in Japan and Iran have also targeted SSB (Figure 2). The stemborer complex in India is relatively species diverse, with five or more species attacking rice in some regions [108]. Perhaps for this reason, studies from India have tended to report results based on changes to the impacts of regional complexes of stemborers (i.e., reductions in damage, comparisons of yields). Where Indian studies

have targeted a single species, this has mainly been YSB (Figure 2). Two other species that have been the targets of biological control in rice are WSB (research from Pakistan, Indonesia and the Philippines) and the corn borer *C. agamemnon* Bleszyński (Crambidae: Lepidoptera) (research from Egypt) (Figure 2).

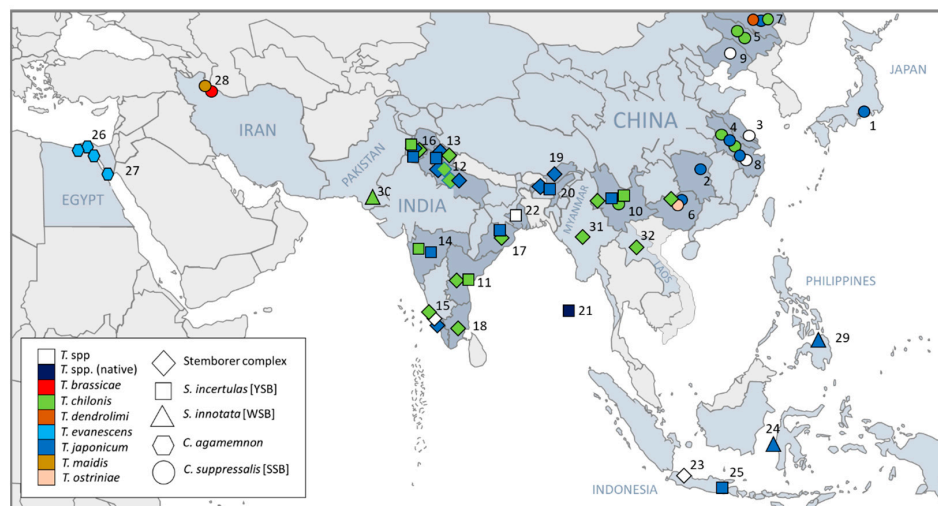


Figure 2. Locations of published case studies that used *Trichogramma* spp. as biological control agents against stem borers in rice. Symbol colors indicate *Trichogramma* spp. released; symbol shapes indicate target stem borers. JAPAN–1: Honshu [110,111]; CHINA–2: Hunan [76]; 3: Jiangsu (Tongzhou) [78]; 4: Anhui [85,112,113]; 5: Jilin [114,115]; 6: Guangxi [27,116]; 7: Heilongjiang [117–119]; 8: Zhejiang [120,121]; 9: Liaoning [122]; 10: Yunnan [27,123,124]; INDIA–11: Andra Pradesh [89]; 12: Uttar Pradesh [91–93,125–127]; 13: Uttarakhand [94]; 14: Maharashtra [96,128]; 15: Kerala [99,129]; 16: Punjab [59,60,100,101,130–135]; 17: Odisha [102,136]; 18: Tamil Nadu [98]; 19: Anunachal Pradesh [58]; 20: Assam [137,138]; 21: Andaman Islands [139]; 22: West Bengal [140]; INDONESIA–23: East Java [141]; 24: Ternate [142]; 25: West Java [49]; EGYPT–26: Nile Delta [143–146]; 27: El-Sheikh [147]; IRAN–28 [148,149]; PHILIPPINES–29: Mindanao [50]; 30: PAKISTAN Sindh [150]; MYANMAR–31: Mandalay [27,151]; LAOS–32: [27].

3.1.2. *Trichogramma* spp. Used in Augmentative Biocontrol

The main *Trichogramma* spp. used in biological control attempts against leaffolders have been *T. japonicum* and *T. chilonis* Ishii. In many early studies, particularly in China, *T. confusum* Viggiani was used. The status of *T. confusum* and its relation with *T. chilonis* has been the subject of recent research and the two species have been regarded either as one species or as cryptic species in previous studies: currently *T. confusum* is regarded as a close sister species of *T. chilonis* and is no longer applied in biological control attempts in rice [152]. Because of their morphological similarities and possible confusion during identifications in previous studies, we combine *T. confusum* and *T. chilonis* as a single group (*T. chilonis*). Early research on the biological control of rice leaffolders in China also often included *T. dendrolimi* Matsumura, but this species has not been applied during studies of biocontrol in rice since the early 1990s. *Trichogramma australicum* Girault has been included in a small number of studies from China, with results mainly reported as parasitism or reductions in damage levels after multispecies releases (generally in combination with *T. chilonis* and *T. japonicum*) (see below). Where different species of *Trichogramma* have been compared for their biological control potential against leaffolders, *T. dendrolimi* has performed relatively poorly (usually <50% parasitism) [41,63,68], with *T. japonicum* (>70%) attaining higher levels of parasitism compared to *T. chilonis* (<60%) [68].

Releases against stem borers have included at least seven *Trichogramma* species. Of these, *T. japonicum* and *T. chilonis* were the most frequently studied (Figure 2). *Trichogramma japonicum* has been used almost exclusively for the biological control of stem borers in the Philippines and Indonesia [50,142]; whereas *T. chilonis* has been used in Myanmar and

Laos [27]. In a comparative study by Wu et al. (2016) [119], *T. japonicum* (>60% parasitism) performed better than *T. chilonis* (about 30%) in parasitizing SSB eggs; *T. japonicum* also performed better than both *T. dendrolimi* and *T. chilonis* in reducing stemborer damage to rice [119]. To our knowledge, no similar comparative studies have examined the success of different *Trichogramma* spp. against YSB. An unidentified, native *Trichogramma* sp. was released in the Andaman Islands (India) for the control of YSB (Figure 2). More recent reports suggest that the species may have been *T. japonicum* [153]. The only other *Trichogramma* species used against stemborers in East Asia has been *T. ostrinae* Pang et Chen (Figure 2). In Iran, two species, *T. maidis* and *T. brassicae* Bezdenko, have been used for the biological control of SSB in rice. *T. brassicae* is usually applied as a biological control agent for pests of vegetable crops, but could be conveniently acquired and was released for the biological control of SSB in Iranian rice [148,149]. In Egypt, all published studies have reported the use of *T. evanescens* Westwood against rice stem borers [144,147]. This wasp species also causes relatively high levels of parasitism (>50%) under natural conditions in the country [154].

3.1.3. Release Methods during Augmentative Biocontrol

Few details are provided on the release methods used in many of the published field reports, or where biological control has been compared to other control methods. Where information is available, in most cases, 2–7 releases of $\sim 100,000$ wasps ha^{-1} each were made [58–60], although in some cases releases were as low as 50,000 wasps ha^{-1} [96,128,138]. Release rates of greater than 300,000 wasps ha^{-1} have also been reported, especially in China [114,119] (see Table S1). A small number of experimental field studies have reported on the efficacy of different release rates. For example, a number of studies have reported significantly higher parasitism rates or rice yields [94] or greater reductions in damage from stemborers [92,94,130] at higher release rates. Nevertheless, most evidence suggests that releasing more than 150,000 wasps ha^{-1} does not increase pest control significantly and that the cost–benefit ratios are likely to decline rapidly at higher release densities [130]. While more than one release may be necessary for season-long control of key rice pests, this cannot be easily concluded from available information on the number of necessary releases. In most studies, between three and six releases were implemented, but only a few studies tested different numbers of releases and these indicate that a larger number of releases may not always result in better pest control [103].

Usually, 100 release points were established per ha, with egg cards stapled to leaves or attached to bamboo sticks placed in the rice fields. This method is still being used regularly today [27], indicating that the *Trichogramma* release system in rice is less elaborate compared to, for example, the one established for maize [28,29,155] where applications via drones are becoming more common. In general, studies apply higher numbers of release points each with fewer wasps—usually 100 points with 1000 eggs per card as a standard. Where different numbers of release points have been compared, higher densities of points (over 30 ha^{-1}) generally improved the parasitism of leaffolder eggs [82–84]. Similar studies have not been conducted to examine the effects of release point density on the control of stemborers, but densities of 75–120 cards ha^{-1} (releasing 75–150 K wasps ha^{-1}) give good stemborer control [60,85]. In recent studies from China, the effects of placing egg cards at different canopy levels were tested; however, no clear differences were found between release heights in these studies [85,86]. While generally *Trichogramma* releases start about 30 days after transplanting (DAT), studies have also initiated *Trichogramma* releases as early as 25 DAT, 15 DAT or -more recently—even at 7 DAT [58] without compromising the success of pest control (Table S1). At least one study [123] released *Trichogramma* to rice seedbeds, with good results.

Taken together, these observations suggest that for optimal control, *Trichogramma* wasps (optimally *T. japonicum* where the species is endemic or established) can be released at 100 K–150 K ha^{-1} , with ca 50–100 release points roughly 3–4 times during the early crop stages (10–40 DAT). However, where conservation biological control is also implemented

(see below), fields should be monitored carefully and *Trichogramma* releases only conducted when populations of stemborers or leaffolders reach potentially damaging levels. Stemborers, particularly SSB, perform relatively poorly as the rice crop develops [9,55], such that releases of *Trichogramma* during reproductive crop stages in well-managed paddy fields will probably give diminishing returns.

3.1.4. Parasitism Rates during Augmentative Biological Control

Parasitism rates have been reported for a relatively small number of field studies, with most studies preferring to evaluate biocontrol through comparative damage estimates (see below). Furthermore, for studies of stemborers it is often unclear whether parasitism has been reported on a per egg mass or per egg basis. In any case, parasitism levels have been more frequently reported for studies of leaffolders.

Figure 3A presents the results of reported biological control attempts against leaffolders in China. The figure indicates a gradual decline in reported parasitism rates since studies began in the early 1970s. However, it is difficult to relate this decline to any single factor; for example, early studies (up to the 1980s) often released $>3\times$ the numbers of *Trichogramma* wasps compared to later studies [61,66,67,69,70,73]. Furthermore, many of the earlier studies released two or more species at the same time [62,66,67,70]. Earlier studies also generally included *T. dendrolimi* [63,66–68,77,80], whereas later studies (after 1985) concerned only *T. chilonis* and *T. japonicum*.

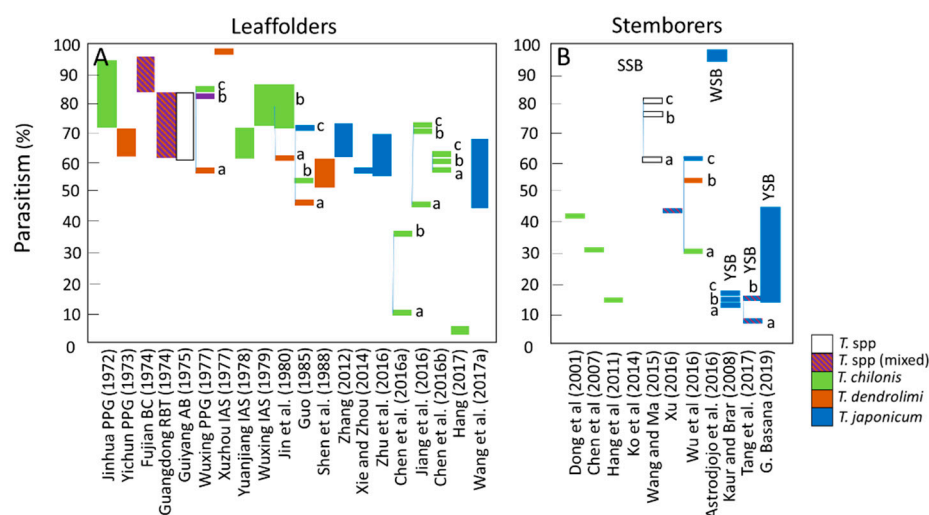


Figure 3. Parasitism rates reported from field studies using *Trichogramma* spp. as biological control agents against rice leaffolders in China (A) and against rice stemborers in China, Indonesia and India (B). Results have been reported as ranges in some studies (tall bars) and means in other (short bars). Bar colors indicate *Trichogramma* species as shown in the legend. Note that some studies compared *Trichogramma* species (indicated by lowercase letters associated with different species in the same study) or compared different release methods (indicated by lowercase letters associated with the same species in one study, i.e., Chen et al. (2016) [82], a = 90 K, b = 144 K released; Jiang et al. (2016) [83], a = 300 K, b = 450 K, c = 600 K; Chen et al. (2016) [81], a = 150 K, b = 450 K, c = 750 K; Wang and Ma (2015) [122], a = 1 \times , b = 2 \times and c = 3 \times releases; Kaur and Brar (2008) [130], a = 100 K, b = 125 K, c = 150 K; Tang et al. (2017) [124], a = 50 K, b = 100 K). Stemborers included WSB (Astrodojo et al. (2016) [142], YSB (Kaur and Brar (2008) [130], Tang et al. (2017) [124] and G. Basana et al. (2019) [136]), and SSB (all other studies in (B)) (See Table S1 for further details).

Where baseline studies have been included, augmentative biological control with *Trichogramma* spp. against leaffolders has generally compared well to control fields (without chemical-based management), or fields where insecticides have been used. For example, comparative baselines reported by Yichun Plant Protection Group (1973) [69], Fujian Bio-control Group (1974) [70] and Shen et al. (1988) [80] were below 30% parasitism; baselines

reported by Guiyang Agricultural Bureau (1975) [74], Yuanjiang Institute of Agricultural Sciences (1975) [79] and Zhang (2012) [72] were below 20%; and baselines reported by Jinhua Plant Protection Group (1972) [61], Wuxing Institute of Agricultural Sciences (1979) [63], Xie and Zhou (2014) [75], and Chen et al. (2016) [82] were below 10%. These compared to >60% in most cases where parasitoids were released. In a study by Hang (2017) [85], parasitism by *T. chilonis* was below 10% in both release and control areas. Where studies compared parasitism of leaffolder eggs in sprayed fields against non-sprayed and non-biocontrol fields, rates were generally lower in the sprayed fields than in control fields [72,82] (Table S1).

Few studies have reported parasitism rates of stemborer eggs after *Trichogramma* releases (Figure 3B). Furthermore, where rates have been reported, parasitism levels varied greatly between studies. For example, Astrodjojo et al. (2016) [142] have reported levels above 90% for *T. japonicum* on WSB eggs. Meanwhile, Hang et al. (2011) [112] and Tang et al. (2017) [124] reported parasitism levels below 20% for *T. chilonis* on SSB and *T. japonicum* on YSB, respectively. Although not conclusive, a comparison across studies suggests that *Trichogramma* spp. may be more successful as control agents against leaffolders (comparing Figure 3A,B; but see below). Parasitism against YSB, may be limited due to the nature of the YSB egg masses that are coated with a layer of protective hairs and because the eggs are more densely packed inside YSB egg masses compared to SSB egg masses [55].

3.1.5. Damage Reductions Associated with Augmentative Biological Control

In a majority of studies, damage by leaffolders was reduced by 50–80% in *Trichogramma* spp. release fields/plots, compared to untreated controls (Figure 4). Earlier studies (i.e., pre-1980), with the notable exception of Jinhua Plant Protection Group (1972) [61], tended to report consistently large reductions in leaffolder damage (i.e., always above 50%). Many of the more recent studies have reported reductions of less than 50% [41,58,85,88,89,103]. Across reports, there are no consistent trends in terms of which *Trichogramma* spp. performed best in reducing damage from leaffolders (see for example Wuxing Plant Protection Group (1977) [62], Mishra and Kumar (2009) [92] and Sangha et al. (2018) [60] (Figure 4).

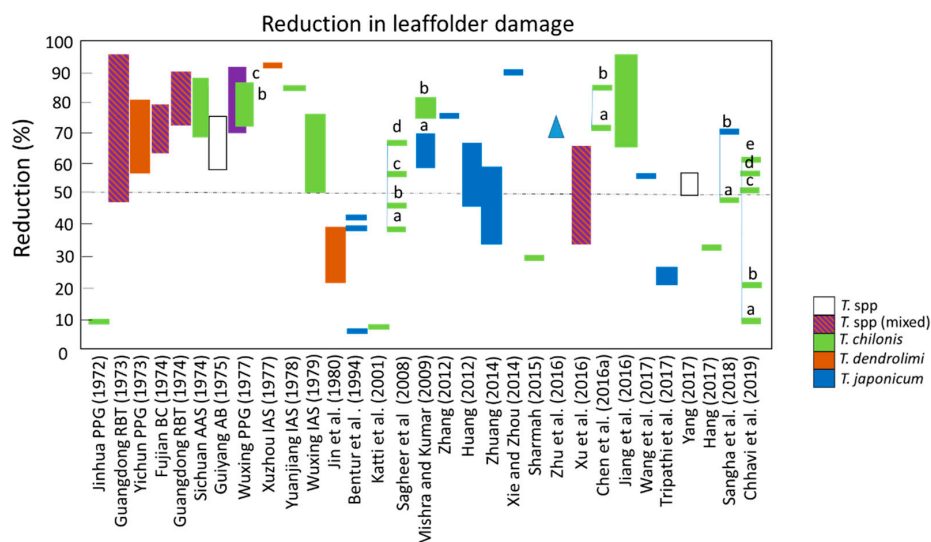


Figure 4. Reductions in rice damage from leaffolders due to *Trichogramma*-based biological control releases as reported for a range of field studies. Bar colors indicate *Trichogramma* species as indicated in the legend. The triangle indicates ‘equal to or greater than’. Note that some studies compared *Trichogramma* species (indicated by lowercase letters associated with different species in the same study) or compared different release densities (indicated by lowercase letters associated with the same species in one study; i.e., Sagheer et al. (2008b) [105], a = 50 K, b = 75 K, c = 100 K, d = 125 K released; Chen et al. (2016) [82], a = 90 K, b = 144 K; Chhavi et al. (2019) [104], a = 50 K, b = 75 K, c = 100 K, d = 125 K, e = 150 K). Damage reductions indicated for Bentur et al. (1994) [88] correspond to 1991 results for Hyderabad (42%), Nawagam (38.5%) and Pondicherry (8%) (See Table S1 for further details).

Despite often lower levels of parasitism reported for *Trichogramma* on stemborer eggs (Table S1, Figure 3B), reported reductions in stemborer damage to rice were often similar to those reported for leaffolders (compare Figures 4 and 5). Furthermore, reductions in the percentage of dead hearts (i.e., death of a non-reproductive rice tiller: DH) or whiteheads (i.e., death of a reproductive rice tiller that results in a sterile panicle: WH) were generally similar in those studies that reported both (Figure 5) (but see Metwally et al. (2009) [143] and Lyla et al. (2010) [131] where reductions in the percentage of WH were higher than reductions in the percentage of DH). These results suggest that higher parasitism rates are required to reduce leaffolder damage by the same amount as stemborer damage. This is possibly related to spatial restrictions on stemborers and intense antagonistic intraspecific and interspecific interactions (e.g., competition, cannibalism and repellence [55]) between stemborer larvae, compared to leaffolder larvae that can have multiple individuals on a single tiller.

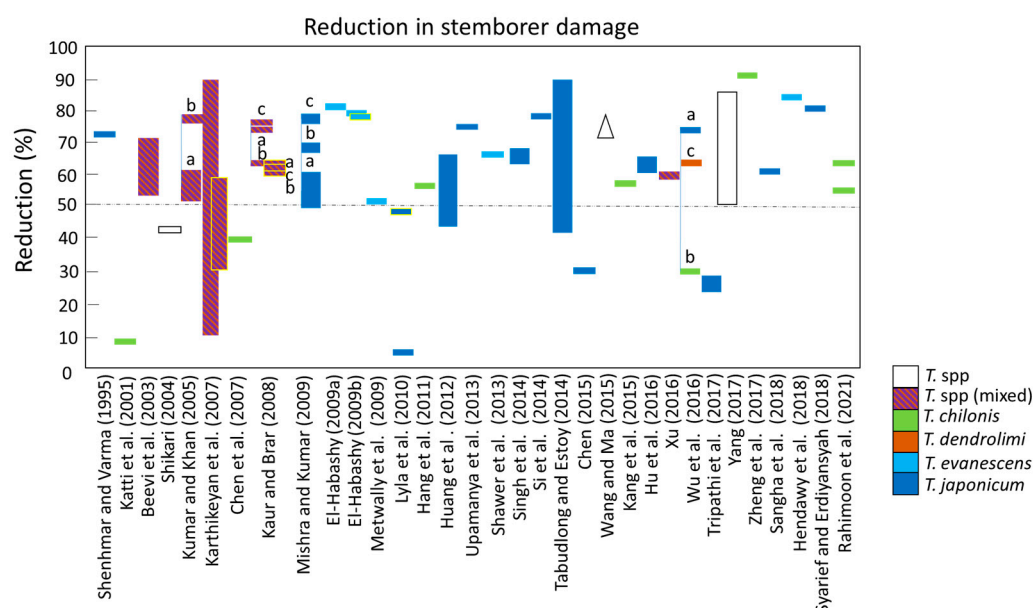


Figure 5. Reductions in rice damage from stemborers due to *Trichogramma*-based biological control releases as reported for a range of field studies. Bars outlined in yellow indicate reductions in WH damage, otherwise reductions in stem damage or DH are indicated. Bar colors indicate *Trichogramma* species as shown in the legend. The triangle indicates ‘equal to or greater than’. Note that one study compared *Trichogramma* species (indicated by lowercase letters associated with different species in the same study) and studies also compared different release densities (indicated by lowercase letters associated with the same species in a single study, i.e., Kumar and Khan (2005) [94], a = 50 K, b = 100 K; Kaur and Brar (2008) [130], a = 100 K, b = 125 K, c = 150 K; Mishra and Kumar (2009) [92], a = 50 K, b = 75 K, c = 100 K) (See Table S1 for further details).

3.1.6. Comparisons between Augmentative Biocontrol and Chemical Controls

When compared to standard farmers’ practices involving insecticide applications, generally only minor or no differences were found between *Trichogramma* releases and chemical controls (Table S1). This includes studies that compared leaffolder damage [41,85,99,100,103], and studies that compared stemborer damage [112,117,120,121,123,130,138,147] between fields using *Trichogramma*-based biological control and chemical controls. In general, where comparisons have been made, authors reported slightly lower damage in *Trichogramma* fields (i.e., Kang et al. (2015) [123], damage = 1.6% with biological control, 3.8% with chemical control and Upamaya et al. (2013) [138], damage = 2.4% with biological control, 2.9–7.6% with chemical controls); although a few studies reported chemical treatments as more effective (i.e., Hang et al. (2011) [112], Si et al. (2014) [117], Chen (2015) [120], damage = 3–3.3% with biological control, 0.3–1.7% with chemical controls). In most cases, even where pesticides reduced damage to a greater extent than biological control, damage

rates were probably so small as to have negligible effects on rice yields, particularly since rice can generally compensate well for stemborer damage [9,10].

Cost–benefit analyses (often based on Indian studies), have generally revealed similar or higher returns for *Trichogramma* release fields compared to fields involving chemical controls [89,100,101] (but see Singh et al. (2008) [93]). In a study by Kumar et al. (2007) [95], even though yields were highest in IPM plots (that included chemical applications), the highest net returns were obtained in *Trichogramma* spp. release plots. Furthermore, several publications have reported more natural enemies (e.g., ladybeetles [Coccinellidae: Coleoptera] and spiders) in *Trichogramma* release fields compared to farmers' practice fields that included insecticide applications [91,116,131]. Such information is more commonly provided in recent studies, reflecting an increasing awareness over time of the importance of other natural enemies in pest regulation.

3.2. Conservation Biological Control

Conservation biological control (CBC) aims at promoting the abundance, diversity and efficacy of the natural enemies of crop pests by providing optimal conditions for their survival, reproduction and pest-regulating behaviors [156,157]. Although CBC includes the conservation of natural enemies at regional and landscape scales by maintaining non-crop habitats as refuges for predators [158], in rice landscapes, CBC is often limited by the topography of rice-producing regions (which often consist of flat, irrigated, lowland areas that are intensively managed). For this reason, CBC for rice pest management has mainly consisted of within-field habitat manipulations such that natural enemies are conserved within or close-by the main crop [32,33,35]. Furthermore, some of the most effective natural enemies of rice pests are specialists in rice habitat and are rarely encountered in non-rice habitat that is distant from the rice fields [158,159]. As such, CBC for rice mainly focuses on the rice paddies themselves—on management of the main crop (e.g., avoiding pesticides, incorporating fallows) and on manipulating vegetation on associated bunds.

Increased interest in the CBC of rice pests during recent decades has partly been due to campaigns around 'ecological engineering for rice pest management' that began in 2008 and focused on building knowledge and capacity, initially in China, Thailand and Vietnam [33,34,38,160,161], to manipulate rice habitat such that natural enemies are protected. Because knowledge of the links between rice pests, their natural enemies and non-crop vegetation were poorly understood at the time, ecological engineering largely referred to the establishment of flowering plants on rice bunds as potential habitat for the natural enemies of rice pests [34,162]. This bund vegetation would provide nectar to support the free-living stages of hymenopteran parasitoids, as well as providing supplementary foods (alternative prey) for predators such as spiders and mirid bugs [163–166]. Laboratory and field studies began to search for the most suitable bund plants—that is, plants that promote the regulatory efficiency of natural enemies without providing any benefits for rice pests. For example, laboratory studies by Zhu et al. (2015) [163] showed that access to sesame (*Sesamum indicum* L. [Pedaliaceae]) flowers increased the longevity, fecundity and efficacy of *T. chilonis*, but had no similar effects on the longevity or fecundity of SSB or PSB. In fields with sesame planted on the bunds, egg parasitism was consequently higher than in control fields [35].

Sesame features prominently among floral strips that are deliberately planted on rice bunds to promote natural biological control [30,34,35,38,163–167]. However, a recent study by Horgan et al. (2022) [34] has indicated that Vietnamese rice farmers that incorporate vegetation strips into their rice paddies for pest management will plant a wide range of different species, including ornamental flowers, vegetables, and woody shrubs. Farmers that planted flower strips (including flowering vegetable plants) tended to use less insecticides than their conventional farming neighbors and reported higher rice yields. Many farmers that planted vegetable crops on their bunds also increased their farm profits by selling the vegetable produce. However, these same farmers were more likely to apply pesticides to their bund vegetables, which runs counter to the principals and objectives of establishing vegetation strips for CBC [34]. In a similar study, Sattler et al. (2021) [167]

found that Cambodian farmers would prefer to grow vegetables on their rice bunds and that the cost–benefit returns from ecological engineering using flowering plants on bunds were greater than conventional farming methods where insecticides were applied. By withholding insecticides, rice fields maintained a higher abundance of natural enemies compared to insecticide-treated fields, but yields were not different [167]. Prior to calls for using flower strips as a pest management strategy in rice, farmers often utilized the space on rice bunds to produce supplementary crops, particularly beans [21,168,169], so that, for many farmers a shift to ecological engineering using flower strips can be relatively simple.

As knowledge of ecological engineering in rice has accumulated, there have been recommendations to include a range of plants with different functions [38]. For example, although not widely researched in rice ecosystems outside China, trap plants that specifically target stemborers can be incorporated into vegetation strips [170,171]. Much of the initial research into trap plants was conducted in Africa to control *Chilo partellus* Swinhoe (Crambidae) in maize: These plants, mainly consist of tropical grasses such as Sudan grass (*Sorghum vulgare* Pers. [Poaceae]), Napier grass (*Cenchrus purpureus* (Schumacher) Morrone [Poaceae]), or vetiver grass (*Chrysopogon zizanioides* (L.) Roberty [Poaceae]) [172,173]. Adult stemborers are highly attracted to these grasses and lay more eggs on the grasses than on the main crop (usually maize); however, the developing larvae have low survival [170,171,174]. Other functional plants that can be included on rice bunds include species that repel herbivores or other nuisance insects. For example, several plants that produce methyl eugenol, such as basil (*Ocimum basilicum* L. [Lamiaceae]) and mint (*Mentha* spp. [Lamiaceae]), can repel rice herbivores, such as the brown planthopper (*Nilaparvata lugens* Stål [Delphacidae: Hemiptera]). As an extract, methyl eugenol has insecticidal effects on rice leaffolders [175], but the effects of growing plants that produce methyl eugenol on these moths under field conditions are still unknown. Several other flowering plants and grasses, including marigolds (*Tagetes* spp. [Asteraceae]) and lemon-grass (*Cymbopogon* spp. [Poaceae]), have been noted to repel herbivores [176–180] or attract their natural enemies [181,182]; some of these plants have been used for decades by rice farmers to repel insects, but their effects in rice systems require further research. Marigold is frequently used by farmers in Vietnam as a functional plant in ecological engineering [34] and there is some evidence that it attracts some of the natural enemies of rice pests [182].

3.2.1. Impact of Surrounding Landscapes on Lepidoptera Pests and *Trichogramma*

Rice is grown in a variety of production systems that range from deep-water to upland, rain-fed systems, and from traditional montane terraces to lowland, intensified plains [183,184]. These production systems are embedded in landscapes that sometimes determine predominant practices (e.g., flooding regimes, irrigation infrastructure, cropping patterns), but are also influenced by climate, topography and anthropological impacts at regional scales [185]. For example, traditional terraced systems are usually part of heterogeneous landscapes where rice patches are often highly fragmented. Meanwhile, intensified production systems occur in relatively homogenous habitats and are less fragmented [183]. Furthermore, traditional production systems, including deep-water and traditional rice, tend to have lower inputs (fertilizers, pesticides) [185,186]. Research into the impact of surrounding landscapes on the structure of rice arthropod communities, including the structures of herbivore and parasitoid assemblages, has gained traction in recent years. This has been facilitated by the availability of satellite imagery, mapping technologies and advanced statistical methods [187]. These recent studies have generally examined whole arthropod communities and have not been specific to stemborers, leaffolders or their egg parasitoids (but see Zou et al. (2020) [188]). Furthermore, the effects of surrounding landscapes on the predation of rice herbivores by birds, bats and other vertebrate natural enemies has received only limited attention; however, for bats in particular, the availability of roosting sites in the landscape [189–191] probably has a marked effect on their role in suppressing herbivore populations, particularly nocturnal rice pests such as stemborers and leaffolders.

Studies of landscape effects on rice arthropods have begun to reveal associations between the abundance or diversity of arthropods and landscape features. Furthermore, different arthropod guilds appear to respond to distinct features of the surrounding landscape [187]: For example, the fragmentation of rice habitat (i.e., smaller rice fields) can have a positive effect on spiders and medium-sized predators whereas larger predators are favored by more simple, less fragmented habitat [187]. In general, spiders seem to be favored by fallow lands near rice fields, but not by natural vegetation in the proximity of the fields; however, this may differ between spider guilds—for example, Baba et al. (2018) [192] found that large ground dwelling and web-weaving spiders in Japanese paddy fields responded positively to proximate forested areas, but the abundance of smaller ground-dwelling spiders declined. Parasitoids appear to be largely favored by relatively expansive rice habitat that is not fragmented (i.e., larger rice fields), by the diversity of habitat proximate to rice [187], and where structural connectivity between rice bunds is high [193]. Indeed, Dominik et al. (2018) [193] suggested that parasitoids are affected more by such configurational landscape heterogeneity than by herbivore abundance; however, it should be noted that their study did not estimate the densities of herbivore eggs at their field sites. In a study that compared natural biological control with chemical control from sites across a gradient of landscapes in China, Zou et al. (2020) [188] suggested that pest damage and biocontrol are largely independent of landscape context; however, the authors also indicated several reasons why their results might be specific to the region they studied (i.e., landscapes were generally diverse to begin with, many of the key pests are migratory, and pesticide use tended to be low). The results of these studies therefore support a focus on manipulating bund habitat to conserve natural enemies, and parasitoids in particular.

3.2.2. Impact of Vegetation Strips on Lepidoptera Pests and *Trichogramma*

Already several reports on the outcomes of replicated field- or field-plot-studies that compared ecologically engineered and conventional (with or without pesticides) rice have been published. These include studies from China [33,35,38], Thailand [33], Vietnam [33,34], The Philippines [21,165,194–196], Cambodia [167], India [197–200], Bangladesh [30] and Papua New Guinea [182] (Table S2). A number of further reports from non-replicated experiments, including from farmer-participatory plots have also been published (i.e., Malaysia [201], Indonesia [202,203], India [204,205], and Brasil [206,207]) (Table S2). Although most studies have focused on planthoppers and their natural enemies, there are indications that bund vegetation is associated with a greater abundance of the free-living stages of *Trichogramma* wasps (i.e., [167]; and [206] non-replicated) and other parasitoids of Lepidoptera eggs [182]. A few studies have also shown that bund vegetation is associated with increased parasitism of stemborer or leaffolder eggs by *Trichogramma* spp. and other parasitoids (e.g., *Telenomus* spp. [Platygastridae: Hymenoptera]) [30,35,165,195]. However, bund vegetation has also been associated with higher densities of stemborers and leaffolders (but similar levels of damage to rice) in studies from the Philippines, possibly due to the height and density of the bund vegetation that provided perching sites and favorable microclimates for adult moths [165,195]. Similarly, in a study of alley cropping (a form of ecological engineering) for upland rice, MacLean et al. (2002) [208] found that alley crops (*Gliricidia sepium* (Jacq.) Steud. and *Senna spectabilis* (DC.) Irwin & Barneby [Fabaceae]) actually increased damage to rice from PSB. In two cases that reported Lepidoptera pests, bund vegetation had no effect on the densities of stemborers or leaffolders ([21]; and [202] non-replicated); however, Ali et al. (2019) [30] found lower densities of YSB in fields with bund vegetation (compared to non-sprayed fields) and less stemborer damage to rice in the same fields. Damage was highest where fields were treated with pesticides ([30]; see also Horgan et al. (2017) [21]). Yele et al. (2021) [199], also found lower damage to rice from stemborers and leaffolders where small field plots were surrounded by vegetation strips, and Iamba and Teksep (2021) [182] found marginally lower numbers of armyworm (*Spodoptera litura* (Fabricius) [Noctuidae: Lepidoptera]) in rice plots surrounded by marigold plants. In non-replicated trials by both Punzal et al. (2017) [209] and Nalini and Porpavai (2019) [205],

stemborer numbers were also lower in rice fields close to vegetation strips compared to control rice plots.

Taken together, these studies indicate that the planting of vegetation on rice bunds can be associated with increased parasitism of stemborer eggs (by *Trichogramma* and other parasitoids) and lower levels of damage from stemborers and leaffolders [21,30,33,35,165,167,194,195]. However, there are worrisome indications that some bund vegetation could be associated with higher incidences of pest Lepidoptera in the main rice crop if bund plants are not carefully selected or managed [21,165,195,196,208]. Many of these studies also found that insecticides (applied according to standard farmer practices) were associated with higher levels of damage to rice from Lepidoptera pests compared to non-treated fields, with and without ecological engineering [30,35,165]. Therefore, whereas further research is necessary to better select plants that promote *Trichogramma* and other natural enemies but offer no benefits to the rice pests, evidence suggests that CBC will probably give better control of pests than insecticide-based control programs.

Research is also required to better determine the effects on rice pests and their natural enemies of the plants species that are commonly planted on rice bunds as part of ecological engineering approaches to pest management. For example, apart from sesame and a few other plants [163], the role of nectar as a supplementary food for the parasitoids of Lepidoptera pests is largely unsubstantiated. Furthermore, although repellent plants such as lemongrass are frequently grown on bunds, possibly to deter mosquitoes [179], there is no conclusive evidence to justify their use during habitat manipulation for the management of stemborers. In a study by Liang et al. (2016) [210], intercropping rice with water spinach (*Ipomoea aquatic* Forssk. [Convolvulaceae]) was found to reduce stemborer damage to adjacent rice and result in higher rice yields. The mechanisms by which water spinach reduces damage to rice have not yet been elucidated, but may be associated with higher silicon contents in intercropped rice compared to rice in monocultures [211,212]. A range of other possible intercrops (i.e., sesame, mung bean–*Vigna radiate* (L.) R. Wilczek [Fabaceae] and jute–*Corchorus* spp. [Malvaceae]) have also been reported to reduce YSB damage to rice while also increasing farm profits [213]. Plants may also function as bankers that support non-pest Lepidoptera, the eggs of which are consumed by *Trichogramma* or other parasitoids and predators. Plants (e.g., *Leersia hexandra* Sw. [Poaceae] and *Zizania latifolia* (Griseb.) Hance ex F. Muell. [Poaceae]) that maintain non-pest planthoppers have been identified as bankers for the egg parasitoids of planthoppers and leafhoppers [38,214] and *Paspalum scrobiculatum* L. (Poaceae) maintains parasitoids of the African gall midge, *Orseolia oryzivora* Harris & Gagné (Cecidomyiidae: Diptera) [215], successfully reducing damage to rice by these pests. However, to our knowledge, banker plants that support *Trichogramma* egg parasitoids associated with rice pests have not yet been identified.

In contrast to some other functional plant types, there is relatively good evidence that planting trap plants on bunds can reduce the numbers of stemborers associated with the main rice crop. Trap plants such as Sudan grass and vetiver grass are highly attractive to rice stemborers (SSB [174]), and are more attractive than rice to these pests. However, stemborer larvae cannot complete development on these plants (SSB and PSB [170,171,216]). Evidence suggests that vetiver grass has a lower nutritional quality than rice, and has antifeeding or anti-digestion properties that inhibit stemborer development and reduce the activity of digestive enzymes [170,217,218]. The grass also contains unidentified substances that are toxic to developing stemborer larvae [218]. In China, Lu et al. (2019) [171] have studied the impact of planting vetiver grass on rice bunds: Compared to rice fields without the trap plant, overwintering densities of SSB were lower and, consequently, damage to rice tillers was reduced. In the same study, egg parasitoids were more abundant in fields with vetiver grass on the bunds. A number of authors give specific guidelines for the use of trap plants in temperate rice systems [38,121,219]. They suggest that trap plants are best established on bunds in clusters covering 3–5 m of bund (at 50 m intervals), 4–8 weeks before rice planting.

Recently, Rajesh et al. (2021) [220] have studied water chestnut (*Eleocharis dulcis* (Burm.f.) Trin. Ex Hensch. [Cyperaceae]) as a possible trap plant for WSB in India. The water chestnut, which grows naturally in rice paddies, was more attractive than rice to ovipositing WSB adults; however, in laboratory trials, no larvae survived on the plants. Furthermore, no parasitoids were observed where WSB eggs occurred on water chestnut, but egg parasitism did occur (albeit at low levels) in the same fields where egg masses occurred on rice. Water chestnut produces tubers that are a delicacy in some countries [221]; the plants could potentially be grown in drainage channels or ponds close to rice fields, but are not suitable to be grown on rice bunds.

3.2.3. Effects of Rice Field Management on Lepidoptera Pests and *Trichogramma*

Several aspects of rice crop management affect leaffolder and stemborer abundance and consequent yield losses. Because the focus of this review is on interactions between the pests and *Trichogramma* spp., we will only discuss cases where management likely affects these interactions.

Among the principal determinants of Lepidoptera-related damage is nutrient management. Stemborers and leaffolders are attracted to rice grown in high nitrogen soils [9,55,222]. Although this reduces the host plant's resistance to the pests, it may also increase tolerance to damage [9]. Field studies from the Philippines failed to indicate any response by naturally occurring *Trichogramma* to increased densities of leaffolders in high nitrogen plots [222]. Similarly, in a study that combined vegetation strips on bunds, with rice plots under a gradient of nitrogen treatments, Horgan et al. (2019) [165], found no effect of fertilizer levels on parasitism of YSB eggs by *T. japonicum* or other parasitoids. Other soil amendments, including biochar and high silicon materials have been shown to reduce the fitness of leaffolders and stemborers [223–226]; however, silicon-based rice resistance to pests can be inhibited by high soil nitrogen [227]. In a study by Liu et al. (2017) [228], soil silicon was associated with changes to the composition of volatiles emitted from rice plants that were attacked by leaffolders. When grown in silicon amended soil, the leaffolders were more vulnerable to parasitoids that were drawn-in by the volatiles [228]. Hendawy et al. (2018) [146] combined silica applications with *T. evanescens* to control *C. agamemnon* in Egypt, however the interactions between silicon and *Trichogramma* were not investigated.

Rice varieties vary in their resistance and tolerance to pest Lepidoptera. Horgan et al. (2021) [9] have also demonstrated that rice vulnerability (largely determined by crop duration) is a key determinant of stemborer damage. Resistance is mainly related to the number and size of the rice tillers and their relative growth rates. Varieties with fast-growing and thick tillers are more attractive to stemborers (i.e., less resistant), whereas varieties with a large number of tillers are more tolerant of damage [9,55]. Stemborer larvae that develop on susceptible varieties are larger than those from resistant varieties and resulting adults produce larger egg masses [55]. Studies have shown that egg parasitism is higher on such large egg masses [20], thereby possibly countering host susceptibility as well as nitrogen-induced enhancement of stemborer fitness. The interactions between rice resistance and egg parasitism have not been reported; however, reducing crop susceptibility and/or vulnerability, and increasing crop tolerance by carefully selecting rice varieties is compatible with both augmentative and conservation biological control. Furthermore, several studies have suggested that synchronous planting of rice by farmers over large areas can reduce stemborer damage [7], but the effects on parasitism have not been reported, except for a single study of WSB by Litsinger et al. (2006) [20], where egg parasitism was marginally lower (60% versus 70%) in synchronously planted rice crops.

The main management factor determining the abundance of Lepidoptera pests and their natural enemies is the use of insecticides [229]. Although stemborers and leaffolders are frequent targets of insecticide applications, there is growing evidence that certain chemicals, particularly pyrethroids, can lead to outbreaks of these pests [21,230–232]. The phenomenon has not received the same research attention as pesticide-induced outbreaks of planthoppers [12] and the mechanisms are still largely unknown. One possible mechanism

is that pesticides reduce the efficacy of natural enemies. There is considerable published information to indicate that egg parasitoids, including *Trichogramma* species, are highly susceptible to a large range of commonly used insecticides and are more susceptible than target pests [229,233,234]. Natural enemies, including *Trichogramma* can also develop resistance to commonly used pesticides either naturally or through artificial selection in laboratory colonies [235,236]. The deliberate selection of pesticide-resistant *Trichogramma* strains for possible field applications reveals a poor understanding of the complexity of regulatory ecosystem services that must function against several herbivore species at the same time. Therefore, the use of insecticides is not generally compatible with *Trichogramma*-based biological control. Insecticides also reduce the effectiveness of habitat manipulations associated with ecological engineering [35].

Where *Trichogramma* releases are used as part of an IPM approach to Lepidoptera management, that also includes insecticides, then the insecticides should be avoided while the *Trichogramma* are active in the rice field [27,28]. Even when waiting for some time after parasitoid releases, this approach will, however, prevent *Trichogramma* from building-up numbers in the rice fields. The use of biopesticides, including microbial biological control organisms together with *Trichogramma* spp. could potentially improve pest management. For example, *T. japonicum* can be used as a vector for *Beauveria bassiana* (Bals.-Criv.) Vuill. [Cordycipitaceae] that kills SSB in rice [237]. Studies suggest that such synergistic systems result in greater mortality of the target pest than either biocontrol agent alone [238,239]. The system could be expanded to include other microbial agents and other parasitoids [240]; however, it relies on a careful selection of microbial strains to not reduce *Trichogramma* efficacy [236]. To our knowledge, the effects on other beneficial organisms (e.g., other parasitoids or predators) of vectoring microbial agents using *Trichogramma* spp. have not been studied.

3.3. Possibilities for Combining Augmentative and Conservation Biological Control

Based on the result presented in this review, both augmentative biological control and CBC can reduce the damage caused to rice by leaffolders and stemborers. Although the numbers of studies and progress in both augmentative biocontrol and CBC in rice are somewhat limited compared to other crop-pest systems, our review indicates the emergence of several guidelines as well as possible pitfalls for implementation. For example, research has indicated potential standards for *Trichogramma* releases, including the most effective species, effective release rates and optimal release times [29,42]. Similarly, research into ecological engineering has indicated that flowering plants such as sesame can enhance *Trichogramma* efficacy, and that trap plants such as vetiver grass will reduce the survival and densities of stemborers in rice paddies [163,216]. However, tall vegetation and inappropriate vegetation (e.g., tall-growing *G. sepium* and *S. spectabilis* hedgerows) can result in higher densities of adult stemborers or potentially greater damage to rice plants [21,208].

The ultimate objectives of augmentative biological control and CBC as related to the management of stemborers and leaffolders are similar: Augmentative biological control aims to increase egg mortality among target Lepidoptera pests using large numbers of released parasitoids [27,29]. CBC also aims to increase egg mortality by optimizing the rice environment such that parasitoid diversity, abundance and efficacy are enhanced, including for potentially released *Trichogramma* wasps [32,33]. However, CBC for rice pests, as it is currently emerging, also aims to directly reduce pest densities using trap or repellent plants, and takes a holistic approach to pest management such that rice vulnerability to all pests and diseases is systematically reduced [32,33,38,194].

There are five possible outcomes of combining both methods: (1) Combining released *Trichogramma* and naturally occurring predators and parasitoids could have an additive effect on egg mortality; (2) Combining the methods could have a synergistic effect that increases egg mortality beyond the combined levels of each method alone; (3) Combining methods could increase egg mortality above that achieved by either method alone, but without attaining levels greater than the sum of the methods (i.e., lower than cases 1 or 2); (4) Combining the methods might not increase mortality above that of either method alone

(i.e., redundancy of one of the methods); and (5) Combining the methods may result in lower levels of egg mortality than either method alone. Cases 1 and 2 are desirable, whereas the remaining cases imply diminishing cost–benefit returns (case 3); profitability losses (case 4) or antagonism (case 5). Where both methods are applied together, augmentative biological control is perhaps best regarded as a curative control method, whereas CBC is preventative. Therefore, to combine the methods, inundative releases should best be made after monitoring (using pheromone traps or other methods) indicates potentially damaging Lepidoptera densities. In this way, timely and informed releases will be stabilizing because they represent direct responses to Lepidoptera densities. Meanwhile, misdirected releases during times when Lepidoptera pests are at low densities—as well as representing a loss of investment—could augment attacks on the eggs of other, possibly beneficial organisms, thereby slowing the build-up of natural enemy populations.

Where rice fields are part of a diversified landscape, stemborer and leaffolder populations may benefit from alternative plant hosts (most species are at least oligophagous) to maintain populations during periods where rice plants are absent in the landscape or during times when the fields are at relatively resistant crop stages [9,55]. Rice fields are normally invaded by leaffolders and stemborers soon after planting or transplanting, and some species are migratory arriving from 1000s of kilometers distance [241]. Maintaining parasitoids that attack other arthropod eggs during periods where leaffolders and stemborers are least abundant in rice, or where rice is absent from the landscape, could provide resilience to the system against invading migratory populations. For example, Chang (1978) [242], suggested that a declining abundance of *Sepedon* spp. (Sciomyzidae: Diptera) in Korea due to habitat change and pesticide use, contributed to reduced rates of stemborer egg parasitism by *T. japonicum* between the 1950s and 1970s. Providing good connectivity of bund vegetation in particular will increase parasitoid abundance [187,193]. However, evidence suggests that favorable landscapes alone are not sufficient to avoid yield losses from stemborers [188]. Therefore, without habitat manipulation close to the rice fields, the need for augmentative releases of *Trichogramma* should be assessed each cropping season.

As indicated in Figure 6, compared to landscape effects, directed ecological engineering interventions can have more predictable impacts on Lepidoptera pests and their natural enemies. Trap plants show the greatest potential to reduce stemborer populations and damage [216]. Trap plants may also overcome potential issues related to tall bund vegetation providing a suitable microclimate for the pests. If released *Trichogramma* wasps also parasitize the eggs of Lepidoptera on the trap plants, then inundative releases in the presence of trap plants may be redundant or at best give diminished economic returns. However, trap plants may also be synergistic with biocontrol releases by providing a banker system where *Trichogramma* wasps can build-up numbers that possibly result in higher parasitism rates of Lepidoptera in the main rice crop during subsequent generations. Furthermore, if *Trichogramma* wasp do not parasitize egg masses on trap plants, then the effects of combining trap plants with inundative releases will probably be additive (i.e., cases 1–3) (e.g., see Rajesh et al. (2021) [220]). There is little possibility of trap plants being antagonistic to inundative releases (case 5).

Repellent plants have not yet been used against leaffolders and stemborers in ecologically engineered rice fields. In any case, the possibilities for combining repellence with inundative releases are perhaps limited, unless the repellent plants are intercropped with rice. For example, planting repellent plants on rice bunds might push Lepidoptera pests away from the bunds and towards the rice, especially since parasitoids and rice herbivores are both favored by large areas of non-fragmented rice habitat [193]. In the search for possible repellent plants, which might function well against other rice pests, care should also be taken to screen the plants for their repellence of *Trichogramma* parasitoids. Similarly, suitable banker plants have not been identified for the parasitoids of rice leaffolders or stemborers (but see previous paragraph). It is possible that banker systems might be developed using other approaches if *Trichogramma* and other egg parasitoids are to be enhanced. If for example, *Trichogramma* wasps also parasitize fly eggs (e.g., such as *Sepidon* spp.), then

providing fly eggs in decomposing materials might enhance *Trichogramma* numbers. To our knowledge, such a system has not been assessed in rice.

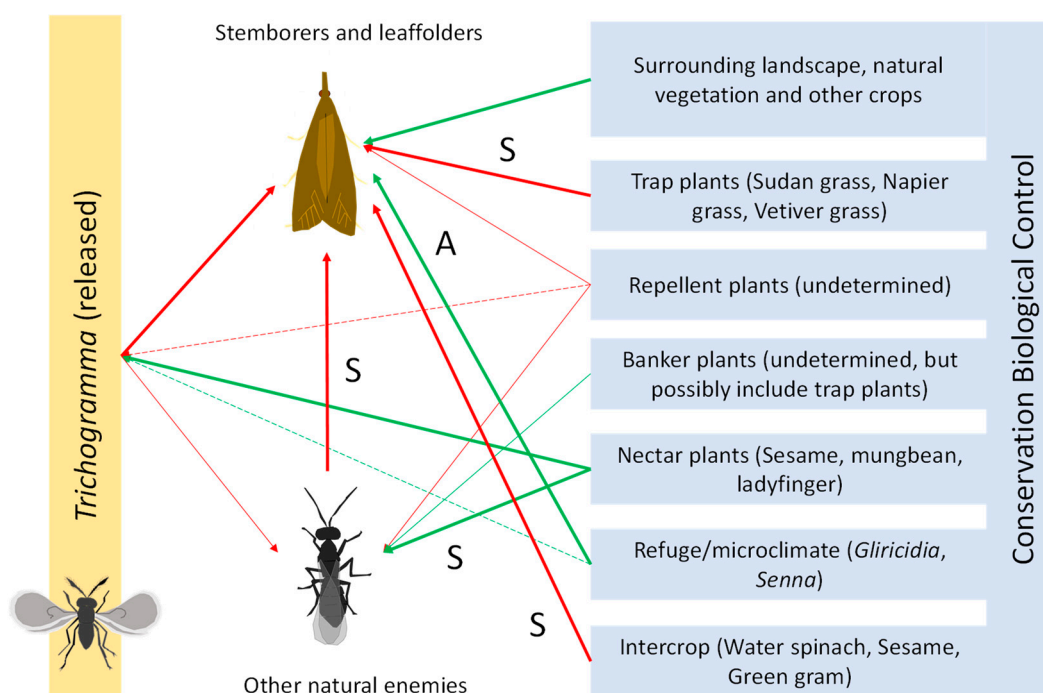


Figure 6. Summary of available technologies to support the integration of augmentative and conservation biological control of leaffolders and stemborers in rice. Green arrows indicate positive effects on Lepidoptera pests or their natural enemies of various habitat manipulations based on published reports. Red arrows indicate potential negative effects. The thickness of arrows relates to available evidence in published studies; thick = good evidence, dotted = suggestive only. ‘S’ indicates a probable synergy between the inundative release of parasitoids and conservation biological control; ‘A’ indicates possible antagonistic effects. Results suggest that trap plants, certain nectar plants, and certain intercrops are compatible with augmentative biological control. Naturally occurring predators and parasitoids may also function synergistically with laboratory-reared *Trichogramma* by, for example, attacking life-stages of the pests, other than eggs. They may also compete for available eggs, or predators may kill developing *Trichogramma* larvae during egg predation; however, such negative interactions will probably reduce the profitability (i.e., redundancy, but not antagonism) of releasing *Trichogramma*, but will not reduce overall biocontrol services.

Combining nectar plants with inundative releases makes intuitive sense because flowering plants will prolong the longevity of ovipositing *Trichogramma* females and increase their fecundity [243]. Furthermore, Vu et al. (2018) [195] found higher parasitism of YSB eggs by *T. japonicum* in ecologically engineered fields compared to conventional fields; however, in the same study the parasitism rates were generally low (<15%). Augmenting the numbers of parasitoid wasps in the fields using release cards could potentially increase the final parasitism rates in such situations, representing a possible synergy between the two biocontrol approaches. Evidence so far suggests that vegetation strips, apart from benefitting rice ecosystems generally (e.g., promoting the natural regulation of a range of rice pests including planthoppers), will provide extra resources that enhance the efficacy of *Trichogramma* spp. used in augmentation biocontrol [38,160,195].

There are also some possible antagonistic effects of combining *Trichogramma* releases and CBC that should be addressed in future research. For example, Horgan et al. (2017) [21] found that stemborer egg mortality was density-dependent in rice fields without pesticides (with and without vegetation strips). Although the source of mortality was not identified, it is probable that crickets or other arthropod predators consumed many of the eggs

(see also de Kraker et al. (1999) [244]). Such contemporaneous mortality of Lepidoptera eggs (and intraguild predation) is likely to be higher in fields where natural enemies are conserved. Whether such added mortality could result in a redundancy of inundative releases is unknown. If leaffolders and stemborers are sufficiently managed through CBC, then augmentative releases will at least result in profitability losses for farmers, and could also reduce rates of parasitism from other naturally occurring egg parasitoids such as *Telenomus* spp. that may be better adapted to the specific rice landscape.

Although several species of parasitoid will naturally parasitize leaffolder and stem-borer eggs in rice fields [21,165], little is known about their coexistence mechanisms. A number of studies have reported several different parasitoids occurring in the same stem-borer egg masses [21,165,195]. To our knowledge, possible competitive interactions or the possible exclusion of native parasitoids by released biocontrol agents have not been documented. Possible negative effects on non-target Lepidoptera or other arthropod species of conservation interest has also received little research attention. Romeis et al. (2005) [243] suggest that a range of mechanisms by which *Trichogramma* adults locate host eggs will limit their impacts on non-target species, particularly if these occur on plants that are taxonomically distinct from crop species, or where plants are protected by trichomes or other leaf-surface defenses. Further research on this topic is certainly warranted.

4. Conclusions

Based on our review of the literature, *Trichogramma*-based biological control of leaf-folders and stemborers has shown considerable potential in rice systems in Asia and North Africa. Nevertheless, biological control using *Trichogramma* wasps has not been applied at large scales until recently in China. Furthermore, CBC, particularly where this includes manipulations of rice habitat, has been associated with reductions in damage to rice from stemborers and an increase in the profitability of rice farming. Both methods have demonstrated advantages over insecticide-based controls, including more cost-effective pest management. Our appraisal of the methods suggests that trap plants, nectar plants and intercropping (Figure 6) in particular offer the clearest possibilities for combining inundative releases and CBC and thereby enhancing pest management. However, it is difficult to predict the possible outcomes of combining the methods due to a series of knowledge gaps related to both methods. In particular, there is little knowledge of the potential ecological interactions between artificially reared *Trichogramma* and naturally occurring predators and parasitoids in diversified rice systems. Furthermore, as technologies develop and improve, possibilities for redundancies or diminishing returns from combining both methods will likely increase—particularly if both methods are applied as preventative controls. However, using inundative releases as a curative measure, based on clear guidelines related to risks of damage, will avoid possible redundancies where the methods are combined.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/agronomy12122958/s1>, Table S1: Annotated list of reviewed articles related to augmentative biological control of rice leaffolders and stemborers; Table S2: List of reviewed articles related to rice habitat manipulation for rice stemborer management.

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