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The benefits of floral border crops in smallholder rice production depends on agronomic inputs and landscape context

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Abstract

1. Ecological intensification (EI) provides an important and increasingly adopted pathway for achieving more sustainable agricultural systems. However, the implementation and success of on-farm EI practices may vary depending on landscape context and local management practices.
2. We evaluated how EI interventions, including two different agricultural input regimes (high or low use of synthetic pesticides and fertilizers) and floral border crops, affected local natural enemy biodiversity, pest abundance and crop yield, and how this was influenced by the surrounding landscape context across 12 rice fields on smallholder farms in Puducherry, India.
3. Reducing agricultural inputs positively impacted the overall natural enemy assemblage; however, responses to landscape factors varied. For example, coccinellid beetles were negatively correlated with higher densities of field edges (landscape configuration). In contrast, spiders, the most abundant group surveyed, were not significantly influenced by any landscape metric. Furthermore, pest abundance was greatest in fields with reduced inputs but only at sites where floral border crops were not present.
4. Mean rice grain yield was lower across low-input sites compared with high-input sites and floral border crops had opposing effects across high- and low-input sites. At low-input sites, mean yields were 33% higher where floral border crops were present. At high-input sites, the presence of floral border crops was correlated with a lower mean yield (16%).
5. These findings show that ecological intensification practices can benefit smallholder crop systems but highlight the need to account for variations in landscape context and local management practices for developing effective sustainable management practices.

KEYWORDS
ecological intensification, ecosystem services, natural enemies, pests

INTRODUCTION

Globally, agricultural systems are dependent on ecosystem services such as pest control and pollination for continued functioning (IPBES, 2019). However, conventional intensive agricultural practices, used across smallholder and large-scale systems, threaten biodiversity and ecosystem service provision, undermining the long-term sustainability of food production (Dainese et al., 2019). Securing food supply while simultaneously minimizing or reversing land and biodiversity degradation through sustainable agriculture practices are current global priorities (e.g., targets set within the United Nations Sustainable Development Goals), with some countries supporting these changes through policy (e.g., National Mission for Sustainable Agriculture, India; https://nmsa.dac.gov.in/frmObjectives.aspx). One approach towards sustainable farming is ecological intensification where farmers manage biodiversity and the ecological processes it supports to promote crop yield and reduce synthetic inputs (Bommarco et al., 2013; Garibaldi et al., 2019). While ecological intensification is an increasingly adopted pathway towards more sustainable agricultural systems, understanding which practices are effective (i.e., will support local functional biodiversity and crop yield) and how they can be best implemented across varied smallholder agricultural contexts remains a priority for research, decision makers and farmers (Kansiime et al., 2021; Peñalver-Cruz et al., 2019).

India has a high proportion of smallholders, approximately 86% of all farmers, who primarily farm rice crops across different local contexts. Rice is a staple food crop across India (FAO, 2021), and the steady increase in the availability and use of agricultural inputs to assist in rice cultivation observed over the past 50 years is a concern (Horgan et al., 2016). This increase has been identified as a key driver of increasing pest outbreaks and reduced natural enemy populations that might otherwise regulate pests (Bakker et al., 2020). Pests such as yellow stem borer (YSB), *Scirophaga incertulas* (Walker) (Lepidoptera:Crambidae), cause serious damage in rice-growing regions across India resulting in considerable economic losses every year (Ali et al., 2019; IRRI (International Rice Research Institute), 2018). YSB are challenging to control due to their cryptic behaviour and feeding habits. Adults and eggs are exposed to the environment; however, the larvae once it bores into the rice stem to feed and pupate is more protected inside the plant (IRRI, 2018). Natural enemies play an important role in controlling YSB, including species that parasitise the eggs, larvae and pupae and predators that feed on all stages of YSB (Chandramohan & Chelliah, 1990; Hikim, 1988; Ooi & Shepard, 1994).

Although studies have shown the considerable economic value of ecosystem services, such as pest control, to smallholders (e.g., Huang et al., 2018; Myrick et al., 2014), further evidence of their effectiveness across different tropical regions is still needed to support and guide farmer uptake and the development of appropriate ecological intensification (EI) practices (Rusere et al., 2019; Westphal et al., 2015). The different biophysical and socio-economic contexts of smallholders can also affect the implementation of ecological intensification practices (Kansiime et al., 2021). Therefore, considering EI approaches that smallholders are willing and able to adopt will be a key part of successful ecological intensification.

Diversifying resources available at a field scale using uncultivated, non-crop or sown floral strips or maintaining borders adjacent to crops is important for supporting natural enemies (Albrecht et al., 2020; Amaral et al., 2013; Mateos-Fierro et al., 2021; Tschumi et al., 2015; Venzon et al., 2019). Evidence from across tropical smallholder regions has shown that florally diverse planted strips can be effective at increasing the abundance and species richness of different natural enemy groups (including spiders, parasitoids, beetles and flies) in a range of crops, potentially resulting in greater pest control services (Gurr et al., 2016; Lu et al., 2015). However, varied results have also been found, with variations attributed to differences in plant and beneficial species interactions (Amaral et al., 2013) and interactions between plant, beneficial and herbivorous species (Lavandero et al., 2006). Furthermore, the structure of rice fields in tropical regions, typically connected through a network of raised field margins called bunds, offers a natural space to host diverse floral resources (Gurr et al., 2012). However, the potential for sown bunds to act as sites for increased floral diversity, supporting natural enemies and increasing income streams from secondary crops has not been studied across many regions.

Beyond the field scale, the composition and configuration of the landscape plays an important role in shaping arthropod community structure (Karp et al., 2018; Martin et al., 2019) and can moderate the effects of local field-level practices aimed at supporting beneficial insect populations (Scheper et al., 2013). Landscapes associated with smallholder farming systems are often more heterogeneous than their large-scale counterparts, although variations ranging from locally complex to locally simple landscapes exist and depends upon the region (Steward et al., 2014). A better understanding of how landscape composition and configuration influence natural enemy communities, including their role as source habitat, in aiding colonization and as shelter habitats, at various spatial and temporal scales is still needed in many tropical agroecosystems (Raymond et al., 2015; Shackelford et al., 2013; Tscharntke et al., 2005). This, in turn, will aid in tailoring EI practices to regions where they can provide the greatest benefit (Garibaldi et al., 2019; Scheper et al., 2013).

Overall, we hypothesise that reducing agricultural inputs such as pesticides will increase the abundance of natural enemies and potentially pests in fields. We also hypothesise that, by providing necessary habitat close to crop fields, increased cover, proximity and heterogeneity of non-crop habitats will increase natural enemy abundance in crops. Finally, the additional forage and shelter provided by floral border crops will increase natural enemies, reduce pests and improve yield outcomes, although the extent of these effects are likely moderated by management and landscape context. To test these hypotheses, we explored how reduced synthetic agricultural inputs (fertilizer and pesticide) and the use of floral border crops (present, absent) within different landscape contexts (measured as compositional and configurational heterogeneity and proportion of semi-natural habitat) influenced (a) natural enemy diversity and abundance; and (b) the abundance of a pest species, yellow stem borer and how these results correlated with (c) yield outcomes in rice fields across smallholder farms in Puducherry, India.

METHODS

Study region

The study took place during the 2019–2020 samba paddy season in the state of Puducherry, India (September 2019–January 2020). There are typically three rice cropping seasons in this region, *sornavari* (short duration rice varieties, June–September), *samba* (long-duration varieties, September–Jan) and *navarrai* (short duration varieties, February–March and June–July) (Government of Puducherry, 2020). A local variety of rice, white ponni, was used in this study; this is a long-duration rice variety and is grown in the samba season. The study region is coastal and has a flat terrain characterized by a high proportion of agricultural fields (rice, sugarcane, banana, vegetables and coconut) interspersed most frequently by semi-natural vegetation. The climate is tropical with a distinct dry (January–June) and a monsoon season (October–December), and the mean annual rainfall for the Puducherry district was 1320 mm (IMD (Indian Meteorological Department), 2020).

Field study design

We used farm-level interventions combined with landscape assessments to determine the impacts of inputs and floral border crops on natural enemy communities and pest abundance. We selected 12 farms managed by individual smallholders; each farm was less than 2 ha in size (ranging in size from 0.02 ha to 1.17 ha Supporting Information Table 1). We aimed for a distance of 1 km between each of the 12 farms, and all but one pair were separated by this distance, as a minimum (sites 6 and 9 were separated by a distance of 836 m).

Farms were allocated to one of two agricultural input management approaches in this study (6 farms per management approach). The first, our 'high input' treatment involved managing crops with a high use of agricultural inputs to control pests and diseases and to provide plant nutrition. Farmers used insecticides including chlorpyriphos and cartap hydrochloride and fertilizers including mono ammonium phosphate, di ammonium phosphate, urea or balanced nitrogen:phosphorus:potassium (NPK 19:19:19) complex fertilizers. The majority of the fertilizers (75%) were applied before seedling were transplanted with the remaining amount applied as a top dressing at either tillering or flowering stage dependent on crop growth.

Our 'low input' approach was co-developed by the local research team and farmers. It aimed to reduce the application of agricultural inputs and replace these with alternatives. This included applications of organic growth stimulants such as Panchakavya (primarily a mix of urine, ghee, dung, milk and curd, ripe bananas and jaggery), which was applied as a foliar spray at 15-day intervals from the active tillering stage until the flowering stage. Dasa kavya, a fermented plant extract, and neem seed oil were both used to repel pests as alternatives to synthetic pesticide applications. Common to both high and low groups was the basal application of farmyard manure (2 t/ha) before the first ploughing, with manure sourced from their own farms.

To explore the effects of floral border crops around rice paddy fields on natural enemies, pests and yield, we selected three farms from each input type (high, low) and planted black gram, *Vigna mungo* (Linneaus) (Fabales:Fabaceae), on the bunds surrounding the chosen rice fields (floral border crop present). The other three farms for each input type had bunds that remained fallow without additional flowers planted (floral border crop absent). The pulse, black gram, was chosen for the floral border crop around rice, as it not only provides nectar and pollen resources for beneficial arthropods but can also be harvested and used as an additional source of food and income by farmers (Praharaj et al., 2021).

Pest and natural enemy surveys

Pest and natural enemy surveys were conducted three times over the course of the rice season corresponding with the early, mid and late rice-growing stages. We sampled YSB using six quadrats (75 cm^2) in each field. Quadrats were divided between the crop edge (three quadrats within 5 m of the crop edge) and the crop centre (three quadrats greater than 10 m from the crop edge) and were spaced at least 10 m apart from each other. Within each quadrat, all rice plants (leave, stem, head) were searched, and the number of YSB adults and egg clusters was recorded. We pooled the data from quadrats to obtain a single value each for adult abundance and egg abundance, per field position (edge, centre) per sampling date.

We used sweep nets along six 10-m transects per field to survey natural enemy insects present in study fields. The six transects were divided between the crop edge (three transects within 5 m of the crop edge) and the crop centre (three transects greater than 10 m from the crop edge) and were spaced at least 10 m apart from each other. For each transect, all insects captured after 10 sweeps with a net along the transect (1 sweep per metre) were collected and stored in plastic vials with 70% ethanol until they could be sorted, identified and counted. Specimens collected through sweep netting were identified to species level where possible; those that could not be identified to species level were recorded as morpho species. Specimens collected were identified in the laboratory by a trained entomologist using morphological keys (Nishida & Torii, 1970; Wilson & Claridge, 1991). For the analysis, we included those invertebrates considered important for natural pest regulation, both generalists and specialists, and who have been recorded as parasitising and/or predating YSB (IRRI, 2018; Supporting Information, Table 2).

Landscape characterization and analysis

To understand the influence of landscape context in this study, we assessed landscape within a 500-m radius of our study fields as this represents a scale at which an individual or a collective of smallholder farmers could potentially act cooperatively to alter landscape composition, and it is also relevant for a number of different invertebrate groups that were important in this study (Karp et al., 2018; Martin et al., 2019). The landscape within this 500-m radius surrounding each site was classified into 11 different land use categories (Figure 1). We then used features including land use proportion, landscape composition and landscape configuration to investigate the influence on arthropod abundance (natural enemies and pests) and community composition (natural enemies).

To characterize the landscape, we used 1.5-m resolution SPOT7 imagery (sourced from LANDINFO World Mapping and captured on 16 October 2020) and ArcGIS (10.5.1 ESRI). We manually added polygons and assigned landscape categories and then used this to map and calculate landscape metrics. For our analysis, we were interested in the proportion of land that could potentially offer year-round habitat (with foraging, reproductive and shelter resources) to natural enemy groups and potential pest species, hereafter referred to as landscape %. This included semi-natural and remnant vegetation, crop borders, bunds and riparian vegetation. This contrasted with the proportion of land that was occupied by cultivated fields, which may be a more hostile habitat (harvesting, spraying) at times throughout the year (Supporting Information, Table 1). The proportions of these two categories were significantly negatively correlated. Therefore, we included only landscape % in our data analysis. We assumed that higher proportions of landscape % would benefit natural enemy groups and potentially pest species, as has been found in previous studies (Chaplin-Kramer et al., 2011).

Landscape composition was measured using Shannon's diversity index, covering all land use categories at the 500-m radii scale excluding roads, industrial and infrastructure sites. The equation for this is given as $H' = -\Sigma \cdot p_i \ln p_i$, where p_i is the number of land use polygons and *ln* is the natural logarithm (landscape composition increases as landscape diversity increases).

Finally, landscape configuration was measured as the density of edges available for exchange between landscape patches (Martin et al., 2019; Holzchuh et al., 2010). We calculated the total length of edges per area (metres per hectare) of each landscape category between crop fields and their surroundings. In this study, we considered crop/non-crop edges and crop/housing edges within this group as home gardens may provide resources for natural enemy and pest insects (Klein et al., 2002).

Yield measures

We worked with farmers to get a measure of yield for each study field. The farmers harvested their respective fields to get a total yield measure. The grain was harvested, bagged, threshed, cleaned, dried and weighed separately. Yield (kgs) per hectare (ha) was recorded and used to allow for comparison across sites.

Data analysis

All analyses were conducted using *R* statistical software (R Core Team, 2019) using the packages *vegan* v. 2.5–6 (Oksanen et al., 2022), *glmmTMB* (Brooks et al., 2017), *emmeans* (Lenth, 2019) and *DHARMa* for model diagnostics and checking (Hartig, 2022). All figures and graphs were produced using the package *ggplot2* (Wickham, 2016).

To understand if there were differences in natural enemy community composition across experimental treatments, we conducted a distance-based redundancy analysis (db-RDA). This was based on Bray–Curtis dissimilarity distances, which account for species

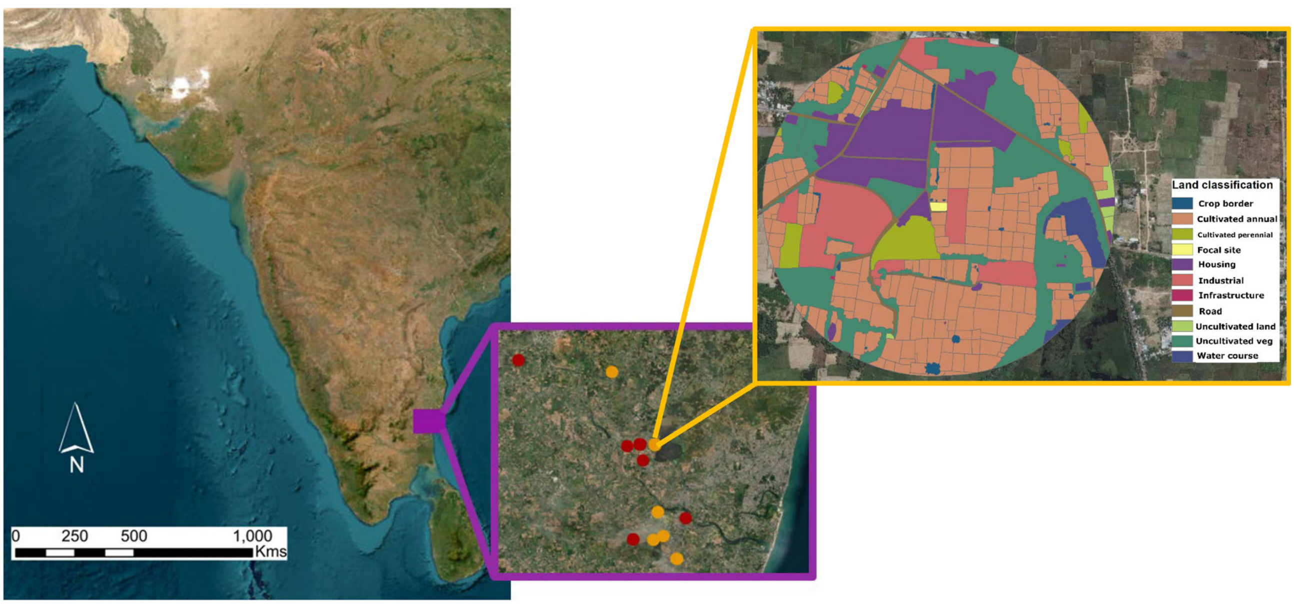

FIGURE 1 Site (plus 500 m landscape buffer) positions across Puducherry, India—all except two sites were greater than 1 km apart—low input (orange) and high input (red).

composition and abundance and excludes joint absences (Anderson et al., 2011; Legendre & Anderson, 1999). We included inputs (high, low), floral border crop (present, absent), field position (centre, edge), landscape composition, landscape configuration and landscape % surrounding each site as explanatory factors in the analysis. We tested the significance of the model, each of the constrained axes and all terms by permutation. The resulting community matrix was visualized in two dimensions with 95% confidence ellipses for input type projected onto the resulting plot to illustrate the difference in natural enemy community composition.

To understand if species abundances were different across experimental treatments (all natural enemies, spiders and coccinellids) and if landscape or spatial variables were influential, we specified three separate Poisson generalized linear mixed models (GLMMs), using the R package *glmmTMB* (Brooks et al., 2017). Each of the full models included input (high, low), floral border crop (present, absent), field position (centre, edge), landscape composition, landscape configuration, landscape percentage and the interaction between input, floral border crop and field position as fixed effects. At some sites, fewer observation rounds were conducted due to circumstances at the time (e.g., coronavirus disease [COVID] pandemic restrictions). Therefore, to account for sampling effort variation between fixed effects, an offset term (log [sampling effort]) was included in each of the above models. Site ID and date surveyed were included as random effects in all models to account for site and date level variations in the data. We arrived at minimum adequate models by first running the full model including all landscape and spatial variables and then removing these terms one by one based on significance and Akaike information criterion (AIC) values, until the model's AIC value no longer decreased (Zuur et al., 2009). For all models, we retained the manipulated experimental fixed effects input, floral border crop and their interaction. Final model residuals and diagnostics were checked, including spatial autocorrelation of residuals (Kühn & Dormann, 2012), using the *DHARMa* package (Hartig, 2022). No significant spatial autocorrelation among model residuals was detected in the analyses. Post hoc pairwise comparisons were conducted for the fixed effect interactions between floral border crop (present, absent) within input (high, low), using the *emmeans* package in R (Lenth, 2019), to understand the difference between variable levels.

Pest egg abundance was analysed using the method described above. The abundance of adult pests was not analysed, due to only very small numbers (<20 specimens across all sites) being recorded across the entire study period.

For crop yield, we evaluated the impact of the two interventions—input (high/low) and floral border crop (absence/presence). As our study did not include any direct experimental manipulation of the impact of natural enemies or pests on yield (e.g., exclusion experiments), we chose to only include those variables which were directly manipulated, as such, landscape factors we expected to influence natural enemy and pest abundance were not included here. We used GLMMs with a Gaussian distribution to assess yield. The model included input (high, low), floral border crop (present, absent) and their interaction as predictor variables. Site ID was included as a random effect in the model to account for site level variations in the data. Final model residuals and diagnostics were checked using the *DHARMa* package (Hartig, 2022).

RESULTS

Natural enemies

A total of 670 natural enemy specimens were collected in sweep nets. Spiders and coccinellid beetles were the most abundant natural enemy groups collected. The natural enemy groups observed included spiders (43% of specimens), coccinellid beetles (28%), dragonflies (20%), wasps (4%), ants (3%) and other beetles (2%).

Community composition of the natural enemy assemblage was not influenced by any of the experimental or landscape factors included in this study (Figure 2). This included inputs ($F_{(1,46)} = 0.49$, p-value $= 0.98$), floral border crop ($F_{(1,46)} = 1.07$, p-value $= 0.36$), their interaction ($F_{(1,46)} = 0.69$, p-value $= 0.81$), landscape configuration ($F_{(1,46)} = 0.65$, p-value $= 0.87$), landscape composition ($F_{(1,46)} = 1.39$, p-value $= 0.14$) or landscape % ($F_{(1,46)} = 1$, p-value $= 0.42$).

The final model for total abundance of natural enemies included landscape composition and configuration in addition to input, floral border crop and their interaction (Table 1). The reduction in agricultural inputs led to a significantly greater abundance of natural enemies in these sites compared with high input sites, yet post hoc analysis showed that floral borders did not significantly influence the abundance across high (absent/present z-ratio $= -1.35$, p-value $= 0.18$) or low input sites (z-ratio $= 0.79$, p-value $= 0.43$) (Table 1; Figure 3a). Higher landscape configuration (>field edges) significantly negatively influenced natural enemy abundance in this region, while increased landscape composition also had a marginally significant negative influence on abundance (Table 1). The two largest observed groups of natural enemy taxa showed varying results. Landscape variables were not included in the final model for spider abundance (Table 1). Post hoc analysis showed that floral borders did not significantly influence spider abundance across high (z-ratio $= -0.91$, p-value $= 0.36$) or low input sites (z-ratio $= 0.34$, p-value $= 0.73$) (Figure 3b). The model for coccinellid abundance included landscape configuration. Landscape configuration appeared to act as a barrier to movement for coccinellid beetles in this region with a significant negative influence, whereas neither input nor floral border crop presence significantly influenced abundance (Table 1). Post hoc analysis showed that floral borders did not significantly influence coccinellid abundance across high (z-ratio $= -1.62$, p-value $= 0.10$) or low input sites (z-ratio $= -0.26$, p-value $= 0.79$) (Figure 3c).

Pest abundance

The final model for abundance of YSB eggs did not include any landscape or spatial variables (Table 1). Similarly, to natural enemies, pests

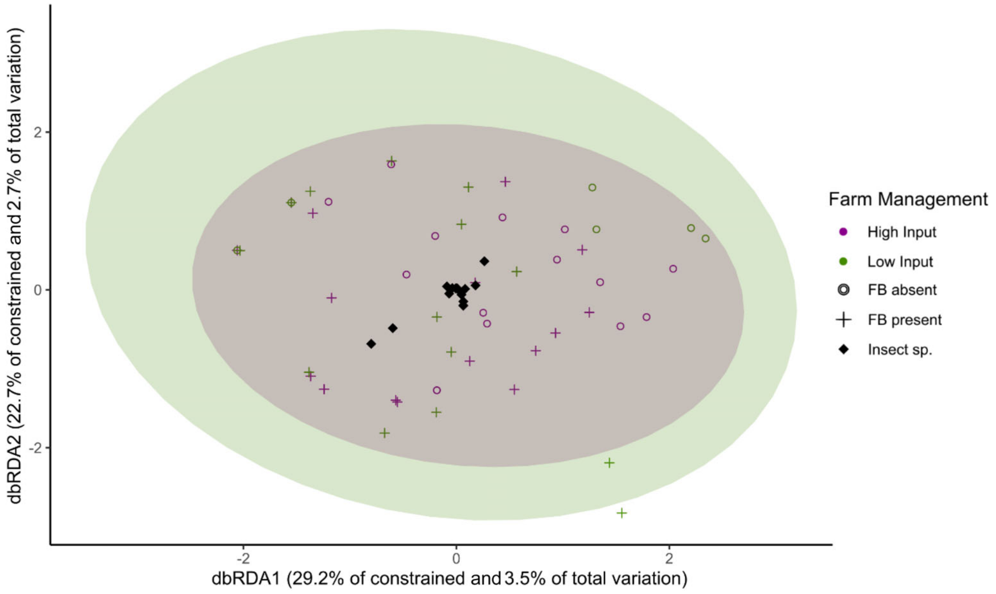

FIGURE 2 Biplot of the distance-based redundancy analysis (db-RDA) showing relationships between surveyed natural enemies of a given insect species (black diamonds) within rice crops across Puducherry [variance explained by either axis was not significant db-RDA1 (F(1, 45) = 1.8, p-value = 0.84) and db-RDA2 (F(1, 45) = 1.4, p-value = 0.96)]. Natural enemy communities are displayed across farm input constraints high input (magenta) and low input (green), and symbols reflect floral border crops (FB absent/present in legend). Each point represents one survey per field position per day. Ellipses represent the 95% confidence interval around group (farm input) centroids. The axes explain variation while being constrained to account for explanatory factor differences.

also appeared to benefit from reduced agricultural inputs with egg abundance significantly greater in low-input sites compared with high-input sites (Table 1). The interaction between input type and floral border crops was influential, although floral border crops themselves were not (Table 1). Post hoc analysis of this interaction revealed that egg abundance was significantly greater in low-input sites without a floral border crop compared with low-input sites with a floral border crop (z-ratio = 2.37, p-value = 0.02), but there was no influence of the presence of floral border crop found across high-input sites (z-ratio = −0.14, p-value = 0.89) (Figure 4).

Rice yield

Yield across the 12 sites ranged from 900 to 1725 kg/ha. Overall, yields from low-input sites were significantly lower than yields from high-input sites (Table 1). Although the interaction between input and floral border was significant in the final model, post hoc analysis revealed floral border crops influenced yield differently between high- and low-input sites; however, neither result was significant. In high-input sites, mean yield was 16% lower where floral border crops were planted (1300 ± 367; mean kg/ha ± SD) compared with sites without floral border crops (1550 ± 156) (absent/present: t-ratio$_{(6)}$ = 1.36, p-value = 0.22; Figure 5). In contrast, mean yield in low-input sites was 33% higher with a floral border crop (1300 ± 370) compared with sites without a floral border crop (975 ± 75) (t-ratio$_{(6)}$ = −1.77, p-value = 0.13; Figure 5).

DISCUSSION

Here, we evaluate the impact of reduced farm management inputs, the inclusion of floral border crops and the influence of local landscape context, including compositional and configurational heterogeneity, on the abundance and composition of natural enemy communities and the abundance of a key pest species, yellow stem borer, across Puducherry, India. Our findings indicate that reducing agricultural inputs, such as pesticides, can provide benefits to local natural enemy biodiversity in smallholder farms. However, YSB also benefitted from low-input approaches, although this was offset by the presence of floral border crops. Therefore, careful tailoring of EI practices within a region-specific context is required to ensure these benefits are maximized and potential negative impacts are mitigated.

Natural enemy communities and the abundance of species providing biological control services often respond positively to low-input farming approaches due to reduced exposure to harmful agricultural inputs (Garratt et al., 2011; Gurr et al., 2016). In line with this, a low-input regime resulted in a greater overall abundance of natural enemies compared with high-input regimes in our study. However, although low-input regimes benefited natural enemy abundance, other field (floral border crops) and landscape metrics, such as landscape composition and configuration, did not influence abundance as expected. This contrasts with previous studies, which have found greater numbers of natural enemies present in fields with reduced inputs and bordered by floral plantings (e.g. Zhu et al., 2014). Other factors, along with reduced input regimes, may have been driving natural enemy abundances in our study, in particular, prey abundance.

TABLE 1 Summary of GLMM analysis for total natural enemies, spider, coccinellid and pest abundance and rice yield.

	Estimate	SE	*z*-value	*p*-value
Natural enemies (total)				
(Intercept)	0.25	0.52	0.47	0.64
Input (low)	1.35	0.5	2.73	**0.006****
Floral border (present)	0.41	0.3	1.35	0.18
Landscape composition	−0.61	0.37	−1.65	0.1†
Landscape configuration	−0.006	0.002	−3.02	**0.003****
Input (low): floral border (present)	−0.77	0.53	−1.45	0.15
Spiders				
(Intercept)	−2.75	0.49	−5.66	**<0.001*****
Input (low)	1.14	0.9	1.26	0.21
Floral border (present)	0.58	0.64	0.91	0.36
Input (low): floral border (present)	−0.88	1.08	−0.82	0.41
Coccinellids				
(Intercept)	−3.56	1.23	−2.92	**0.004****
Input (low)	1.81	2	0.91	0.36
Floral border (present)	1.9	1.18	1.62	0.10
Landscape configuration	−0.01	0.004	−3.17	**0.002****
Input (low): floral border (present)	−1.39	2.06	−0.68	0.5
Pest (YSB egg clusters)				
(Intercept)	−5.76	1.05	−5.48	**<0.001*****
Input (low)	2.91	1.12	2.59	**0.009****
Floral border (present)	0.16	1.18	0.14	0.89
Input (low): floral border (present)	−2.94	1.73	−1.7	0.09†
Rice yield				
(Intercept)	1550	129.9	11.93	**<0.001*****
Input (low)	−575	183.7	−3.13	**0.002****
Floral border (present)	−250	183.7	−1.36	0.17
Input (low): floral border (present)	575	259.8	2.21	**0.03***

Note: Significant *p*-values are given in bold.
Abbreviations: GLMM, generalized linear mixed model; YSB, yellow stem borer.
****p* < 0.001; ***p* < 0.01; **p* < 0.05; †*p* < 0.1.

Previous studies in rice crops have found predator abundance to be solely driven by pest numbers (Dominik et al., 2018), without any influence of surrounding landscape features. Natural enemy abundance in our study appeared to follow pest abundance, suggesting this may be a more important driver in this region, although longer term studies are needed to confirm this. The influence of multiple local and landscape factors, and potential variations between regions, suggests a need for EI management plans to be diverse and regionally focused to support the broadest set of beneficial insects.

The taxa that compose natural enemy communities in different regions may also shape EI management plans based on specific habitat requirements (Rosas-Ramos et al., 2020; Sunderland & Samu, 2000). In addition to reducing pesticide use, ecologically intensive on-farm practices, such as planting floral border crops, can improve habitat characteristics by providing additional nectar sources, hosting alternative prey species, as well as increasing the structural complexity and ground cover present, which can increase or help conserve populations of beneficial insects (Amaral et al., 2016; Langellotto & Denno, 2004; Rosas-Ramos et al., 2020). Although not well captured in our study (most likely due to survey methodology, which was biased towards intercepting less mobile species), parasitic wasps and some flies, two important natural enemy groups of YSB (IRRI, 2018), also demonstrably benefit from additional floral resources, particularly from the nectar and pollen resources they provide (Pollier et al., 2019; Tschumi et al., 2016) as well as other local habitat features such as open fields (Harterreiten-Souza et al., 2021).

Natural enemy assemblages can also benefit from landscape-level features such as areas of semi-natural and non-cropped habitat (Amaral et al., 2016; Chaplin-Kramer et al., 2011), and more recently, the complexity and heterogeneity of landscapes have been identified as key factors in determining natural enemy biodiversity and abundance (Martin et al., 2019). Responses to landscape variables is often

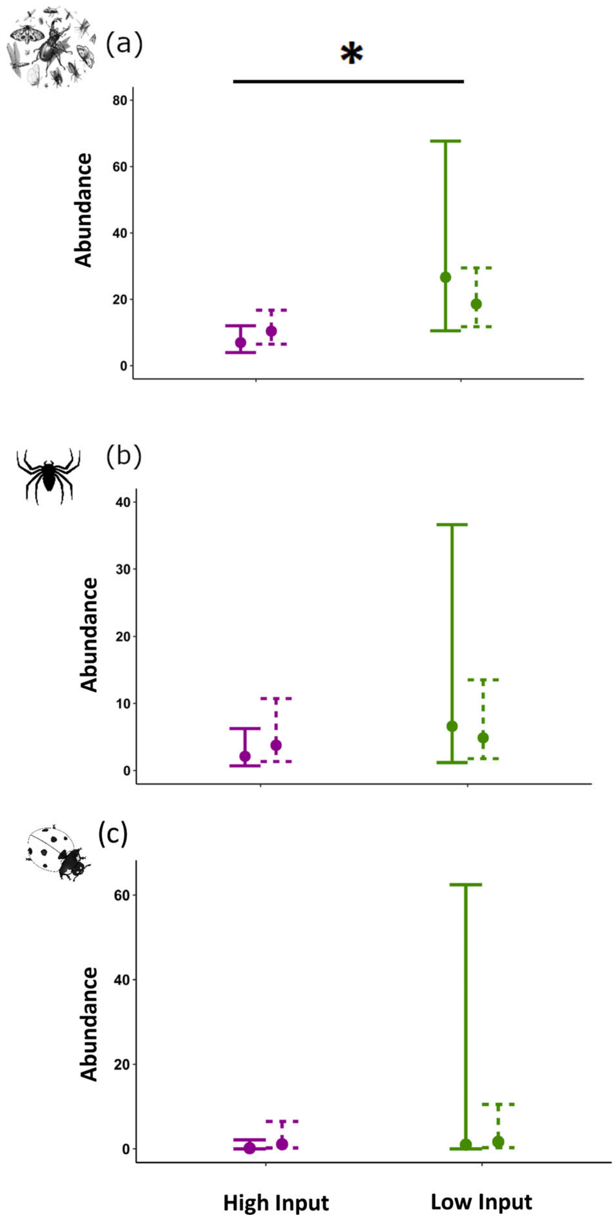

FIGURE 3 Model estimated means are shown with 95% confidence intervals for natural enemies in Puducherry, including (a) total abundance and (b) spiders and (c) coccinellids across farm management input, high (purple) and low (green) and floral border crop, absent (solid lines) and present (dotted lines). Asterisks indicate significant differences between groups at 95% level.

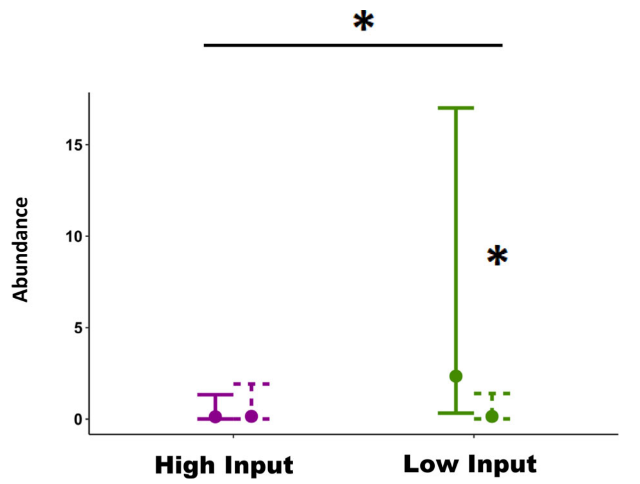

FIGURE 4 Model estimated means are shown with 95% confidence intervals for yellow stem borer (YSB) egg cluster abundance in Puducherry across farm input, high (purple) and low (green), and floral border crop, absent (solid lines) and present (dotted lines). Asterisks indicate significant differences between groups at 95% level.

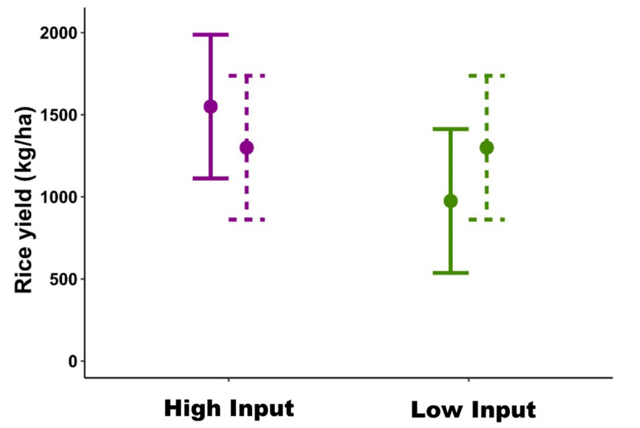

FIGURE 5 Model estimated means are shown with 95% confidence intervals for rice grain yields between high input (purple) and low input (green) with floral border crop treatment shown as absent (solid line) and present (dotted line). Asterisks indicate significant differences at 95% level.

taxa specific and work to disentangle their effects, as well as their interaction with on-farm features, is most appropriately considered at regional levels (Brown et al., 2003; Karp et al., 2018; Shackelford et al., 2013). For example, in our study, neither spiders nor coccinellid beetles were influenced by the proportion of uncultivated, semi-natural land (landscape %) surrounding the field sites. Although this type of land is often considered a source habitat from which natural enemy taxa can migrate into surrounding crops (Alignier et al., 2014; Thies & Tscharntke, 1999), its influence has been found to vary depending on factors at different spatial and temporal scales, the taxa considered and the habitat quality (Alignier et al., 2014; Frizzo et al., 2020). Other features such as higher edge densities potentially allow for greater movement of taxa between habitats within the landscape (Martin et al., 2019), yet they may also act as barriers for particular taxa (Klaus et al., 2015). Therefore, understanding the requirements of key taxa in agroecosystems and the adoption of practices that offer the necessary resources and promote permeability will be important for stronger long-term strategies to support local beneficial taxa and their functioning.

Although natural enemy communities have been shown to effectively control pest populations in some contexts (Thies & Tscharntke, 1999), a general assumption that increased natural enemy biodiversity and abundance will lead to an increase in pest regulation services is not always appropriate at the time scales studied (Buchanan et al., 2018). For example, in our study, a reduction in agricultural inputs correlated with a significant increase in both pest and natural enemy numbers, likely because of reduced pesticide inputs (Garratt et al., 2011). Yet, floral border crops had differing effects on natural enemies and pests. For example, where they were planted, pest numbers were significantly reduced, but the natural enemy numbers surveyed did not respond to plantings. Multiple mechanisms may be responsible for this including floral border crops supporting natural enemies that helped to regulate pest numbers but that were not captured in our survey or potentially the floral plantings drew pests out of the crop. Although further research is needed to disentangle these results, it does highlight the potential of floral border crops as an EI tool when used in combination with low-input approaches in these farming systems.

The expected benefits from ecologically intensive farming approaches to natural enemy biodiversity and the pest control services they provide are clear yet evaluating crop yield responses is equally important from a farmer perspective. Our results show that mean yields for the cropping season studied were greater in high-input sites. Given the short-term yield benefits delivered by synthetic fertilizers (Garratt et al., 2018), this result is not unexpected, and previous studies conducted over longer periods have found that yields can eventually be comparable between input approaches after the initial period of change (Gupta et al., 2021) or potentially even greater in ecologically managed crops (Gurr et al., 2016). Although not directly measured in this study, natural enemy communities can contribute to crop yield increases through increased pest control (Östman et al., 2003), and pest control services are further enhanced by flower strips (Albrecht et al., 2020). Despite only being a single season of data, our results indicate that floral border crops can offset, to some degree, the initial yield losses experienced with a reduction in synthetic inputs. Furthermore, in fields where floral border crops are planted, farmers can collect additional yield (Horgan et al., 2017). Understanding the full benefits, including increased crop sales from border crops and co-benefits (e.g., soil quality from nitrogen-fixing legumes crops) and balancing these against additional costs due to increased labour or yield reductions, remains an important aspect for understanding and incentivizing sustainable management approaches (Garibaldi et al., 2019; Kleijn et al., 2019). Considerable ecological and agronomic contrasts exist between regions in India, and there are also likely differing socio-economic factors that need to be quantified to determine if, and when, EI is appropriate and how farmers can be supported to adopt ecologically intensive practices (Kansiime et al., 2021).

CONCLUSION

Smallholder farmers are among the most vulnerable to climate change and environmental threats, which affect both their food security and their capacity to farm sustainably (Masson–Delmotte et al., 2019). Adopting management strategies, such as ecological intensification, that simultaneously support biodiversity, ecosystem service provisioning and crop production is important for mitigating any further environmental damage and securing their livelihoods. With only a single season of data, due to COVID interruptions, we show here that reducing agricultural inputs (using non-synthetic alternatives to replace these) in rice crops can support a greater number of local natural enemy groups, and with the addition of a floral border crop, costs that may arise within some smallholder contexts such as increased pest numbers or reduced yields can potentially be alleviated. Furthermore, we demonstrate the critical importance of local and landscape context, and this must be co-managed when developing on-farm EI approaches. Further investigations over multiple seasons would provide information on the long-term resilience of natural enemy communities, the pest regulation services they provide and yield outcomes and crucially, evidence and data that can be used to support farmers adopting ecologically intensive practices.

AUTHOR CONTRIBUTIONS

Bryony K. Willcox: Conceptualization; data curation; formal analysis; methodology; writing – original draft. **Michael P. D. Garratt:** Conceptualization; funding acquisition; methodology; writing – review and editing. **Tom D. Breeze:** Methodology; writing – review and editing. **Natarajan Mathimaran:** Methodology; writing – review and editing. **Simon G. Potts:** Methodology; writing – review and editing. **Girija Prasad:** Data curation; methodology; writing – review and editing. **Rengalakshmi Raj:** Conceptualization; data curation; funding acquisition; methodology; writing – review and editing. **Deepa Senapathi:** Conceptualization; funding acquisition; methodology; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table 1. Study site characteristics and experimental set up across twelve rice fields in Puducherry, India.

Table 2. Natural enemy species observed in rice fields across Puducherry. Information provided by the International Rice Research Institute (IRRI, 2018) on stem borers and their natural enemies was used to determine if surveyed species were included in our natural enemy list.

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