

## Article

# Direct and Indirect Effects of Planting Density, Nitrogenous Fertilizer and Host Plant Resistance on Rice Herbivores and Their Natural Enemies

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**Abstract:** In rice ecosystems, seeding densities can be adjusted to compensate for lower nitrogen levels that reduce GHG emissions, or to increase farm profitability. However, density-induced changes to plant anatomy could affect herbivore-rice interactions, and alter arthropod community dynamics. We conducted an experiment that varied transplanting density (low or high), nitrogenous fertilizer (0, 60 or 150 kg added ha<sup>-1</sup>) and rice variety (resistant or susceptible to phloem-feeding insects) over two rice-growing seasons. Yields per plot increased with added nitrogen, but were not affected by variety or transplanting density. Planthopper and leafhopper densities were lower on resistant rice and in high-density field plots. Nitrogen was associated with higher densities of planthoppers, but lower densities of leafhoppers per plot. High planting densities and high nitrogen also increased rodent damage. The structure of arthropod herbivore communities was largely determined by season and transplanting density. Furthermore, two abundant planthoppers (*Sogatella furcifera* (Horváth) and *Nilaparvata lugens* (Stål)) segregated to low and high-density plots, respectively. The structure of decomposer communities was determined by season and fertilizer regime; total decomposer abundance increased in high-nitrogen plots during the dry season. Predator community structure was determined by season and total prey abundance (including decomposers) with several spider species dominating in plots with high prey abundance during the wet season. Our results indicate how rice plasticity and arthropod biodiversity promote stability and resilience in rice ecosystems. We recommend that conservation biological control, which includes a reduction or elimination of insecticides, could be promoted to attain sustainable rice production systems.

**Keywords:** *Bph3*; *Bph32*; density dependence; herbivory tolerance; parasitoids; pesticides; regulatory ecosystem services; rice yields; tillering; tropical rice

## 1. Introduction

Herbivore-induced yield losses to rice (*Oryza sativa* L.) are largely determined by densities of phloem-feeding and defoliating insects during vulnerable crop stages, and by the ability of rice plants to deter oviposition and feeding (resistance) or to compensate for damage (tolerance) [1]. In well-managed rice production systems, particularly in the tropics, herbivore densities are regulated by their natural enemies and damage is consequently low [1–3]. Furthermore, rice plants can often tolerate appreciable levels of herbivore damage without affecting rice yields [4–7]. Indeed, damage from herbivores can sometimes lead to overcompensation in rice and higher yields [7,8]. This is because rice has modular growth, and can compensate for herbivory by shunting resources away from damaged tillers to newly developing tillers, or to growing meristems [5,7]. Herbivory tolerance in rice is therefore associated with fast-growing plants and high tillering. Tolerance is often greatest during early crop stages, when plants are most vulnerable to herbivores [7,9].

Rice also expresses varying levels of resistance to different herbivore species during growth and development [9,10]. Resistance is the ability of the rice plant to deter oviposition and feeding by herbivores or to reduce damage. Rice plants gain resistance as they develop by accumulating lignin and cellulose and by assimilating silicon [11–13]. However, certain rice varieties also possess relatively rare resistance genes that defend early crop stages against herbivore attacks through induced or constitutive biochemical defenses [14,15]. Over the last 50 years, rice breeders have identified traditional landraces or rice species with relatively high resistance to key insect herbivores, and have used these landraces and species in breeding programs to attain resistant rice varieties [15]. In particular, and compared to other rice herbivores (e.g., leaf-chewers, stemborers, or grain-feeding bugs), the development of rice varieties with resistance to phloem-feeding planthoppers and leafhoppers (*Nilaparvata lugens* (Stål), *Sogatella furcifera* (Harváth), *Nephotettix virescens* (Distant), and *N. cincticeps* Uhler) and galling midges (*Orseolia oryzae* Wood-Mason and *O. oryziivora* Gagne) has advanced considerably [14–16]. This is partly because researchers have identified major resistance genes against these herbivores and, through marker-assisted selection, can incorporate the genes into breeding pipelines for high-yielding varieties [15].

Despite their utility, anti-herbivore resistance and herbivory tolerance in rice may diminish under certain environmental conditions, and particularly under the influence of certain crop production practices; for example, a number of studies have shown that nitrogenous fertilizer increases rice susceptibility to a range of herbivores, even in varieties with major resistance genes [4,17–21]. Furthermore, certain insecticides are antagonistic to anti-herbivore resistance in rice and can lead to outbreaks of key pests such as planthoppers [1,22]. Although a large number of studies have focused on the impacts of varieties, fertilizers, or insecticides on insect herbivory, the roles of seed and seedling quality, establishment methods, flooding regimes, planting densities, and other practices on the nature of herbivore-rice interactions, remain understudied [21,23–31] and anti-herbivore resistance has not generally been included in existing studies of herbivore responses to agronomy [1]. Additionally, very few studies have examined the role of crop production practices (other than fertilizers and insecticides) on natural enemies in rice fields [17,26,32,33], despite evidence that natural enemies are effective regulators of herbivore populations in tropical rice ecosystems.

In this study, we examine the effects of rice variety (susceptible or resistant) and planting density (low and high) on rice arthropod communities and crop health under a gradient of nitrogenous fertilizer. We focused particularly on planting density because density determines levels of intraspecific competition by limiting resources (soil, water, nutrients, light) to individual rice plants [34–37]. Rice sustainability programs in Southeast Asia have promoted reductions in seeding densities to improve farm profitability [38]. In contrast, a large number of recent studies have proposed that planting rice at high densities can reduce nitrogen requirements while maintaining yields (i.e., rice at high densities has greater nitrogen use efficiency) [35,39–42]. However, high planting density is

predicted to reduce herbivory tolerance because competition limits the individual plant's capacity to grow and to produce tillers; this might increase herbivore damage and prevent compensation [22,23,43]. In contrast, slower growth rates at high planting densities might reduce rice susceptibility to herbivores (i.e., maintaining resistance) under increasing levels of soil nitrogen, particularly if plant maturation is accelerated in response to resource limitations [4,7,22]. Apart from these indirect, plant-mediated effects on herbivory, planting density will also have direct effects on herbivores and on their natural enemies. For example, plants grown under high densities might provide more suitable microclimates (temperatures, humidity, shade) for certain arthropods [42], or might provide greater structural complexity to the rice habitat, thereby providing refuges for natural enemies or their herbivore prey [44,45].

To examine these possibilities, we conducted a field experiment in the Philippines during two rice-growing seasons. Rice plants grown at high densities produce fewer tillers, have slower growth, and mature faster than plants at low densities; but yields are often similar between high- and low-density plots because of spatial constraints on tillering. Therefore, we predicted that planthopper and leafhopper densities would be lower in rice grown at high densities, particularly on the resistant variety, because smaller and slow-growing plant modules would be less attractive to ovipositing females [7,29,43]. We further predicted that natural enemies would respond numerically to changes in the abundance of their arthropod prey as a result of varying inputs (plant density, host resistance, and nitrogen) to stabilize herbivore populations. Predators are often most abundant during early crop stages, where, in the absence of established herbivore communities, they mainly feed on decomposers [46,47]. Therefore, we concentrated our sampling on the early crop and assessed the richness and abundance of herbivores, decomposers, and their natural enemies. We expected herbivore and decomposer abundance to increase in response to nitrogen inputs, and that natural enemy numbers would similarly respond to this increased availability of potential prey. We also expected higher natural enemy abundance in plots with the susceptible rice variety because of higher prey densities. We discuss our results in the context of developing sustainable rice production systems that promote the natural regulation of rice herbivores.

## 2. Materials and Methods

### 2.1. Field Plot Design

The field experiment was conducted during the 2013 dry (DS) and wet (WS) seasons at the Ecological Function Experimental Platform (EcoFun) of the International Rice Research Institute (IRRI) Experimental Field Station in Los Baños, Philippines. The Platform has been described in a related paper [48]. At the time of the experiment, the platform consisted of six rice fields divided into 18 plots of 33 × 12.5 m (L × W). Separate sub-irrigation channels were installed around each plot. These connected to the main field canals for irrigation and drainage, but prevented leakage of nutrients between adjacent fields and between the plots within each field. The field plots were treated with one of three nitrogen levels each season. These were: zero added nitrogen (0 Kg N ha<sup>-1</sup>), 60 Kg N added ha<sup>-1</sup> and 150 Kg N added ha<sup>-1</sup>. Nitrogen (ammonium sulfate) was applied as four top dressings each season. Solophos, muriate of potash, and zinc were applied basally with the ammonium sulfate.

We used two rice varieties in the experiment: IR62 is a 'modern' variety with relatively high resistance to planthoppers (*N. lugens* and *S. furcifera*) and leafhoppers (*N. virescens*) [49,50]. The source of IR62 resistance against *S. furcifera* has not been identified and is largely absent in seedlings, becoming stronger in older (>25 days) plants [50]. The variety's resistance to *N. lugens* is derived from the Indian landrace PTB33 and is likely associated with the *Bph3* locus, which contains the *Bph3* and/or *Bph32* resistance genes [51]. The apparent durability of IR62 has been attributed to a limited planting of the variety since its release in 1984 together with relatively strong resistance associated with the *Bph3* locus [49]. The second variety, IR64, was used as a susceptible control in the experiment. IR64 is regarded

as a mega-variety in South and Southeast Asia. The variety's popularity is largely due to its high-quality grain. Although IR64 contains the *Bph1* gene for brown planthopper (*N. lugens*) resistance [52], widespread exposure of the gene over several decades throughout Asia has selected for planthopper virulence against *Bph1* such that the variety is now susceptible to the planthopper in the Philippines [49]. Seed of both varieties was acquired through the germplasm bank at IRRI. Seed was initially sown to dry seedbeds in a screenhouse and the 'seedlings' (early-tillering stage) were transplanted at 28 days, as one plant per hill, to the puddled field plots.

Rice was transplanted at two densities. The transplanting densities were selected to represent standard densities used in much of Southeast Asia ( $25 \times 25$  cm) and higher densities ( $10 \times 10$  cm) to represent typical densities based on crop establishment methods that use mechanical 'plug' transplanting [21,24,29,37]. To include the variety and seedling density treatments, each of the 18 plots was divided into four subplots of  $8.25 \times 12.5$  m. The subplots were planted as follows: (a) IR62 seedlings spaced at  $10 \times 10$  cm; (b) IR62 planted at  $25 \times 25$  cm; (c) IR64 planted at  $10 \times 10$  cm; and (d) IR64 planted at  $25 \times 25$  cm. The varieties were assigned randomly to half-plots, with each half-plot further subdivided and randomly assigned low- and high-density planting treatments.

No pesticides were used in the fields at any time and only light weeding was conducted by hand at the beginning of each cropping season followed by occasional spot weeding throughout each season. During evaluations, sampling was conducted at the maximum possible distances from bund vegetation.

## 2.2. Rice Crop Development and Yields

We assessed plant development at two crop stages to coincide with plant health evaluations and yield estimates (see below). The first sample was collected at 30 days after transplanting (DAT) and the second prior to harvest. During sampling, three rice hills were pulled from each subplot and placed in plastic sheaths. Sampled hills were examined in the laboratory by first recording the number of tillers and then separating each plant into different parts (roots, shoots, and panicles). The different plant parts were then placed in paper bags and dried at  $60^\circ\text{C}$  for  $\geq 7$  days in a drying oven. After drying, root, shoot, and panicle weights were recorded using a precision balance. The dried panicles were threshed and separated into rachis, filled grain, and unfilled grain, each of which was weighed separately. The dried grain (filled and unfilled) associated with each plant was then counted. We also estimated 100-grain weights for each subplot by separating-out 100 grains and weighing the dried grain on a precision balance.

Grain yields per unit area for each subplot were estimated by the crop-cut method. Estimates for each season were based on two  $1\text{ m}^2$  quadrats for each subplot. Quadrat positions were arbitrarily selected, but avoided subplot edges ( $<1$  m). Plants inside the quadrats were harvested by cutting the panicles. The panicles were then threshed and unfilled grain or rachis materials were removed. The grain was oven dried at  $60^\circ\text{C}$  for  $\geq 7$  days and weighed.

## 2.3. Arthropod Fauna

Arthropods were sampled at 30 DAT (mid-tillering stage) in all subplots each season. Sampling was conducted at 30 DAT because parasitoids and predators are thought to play a major role in countering pest populations at early crop stages [1,2,47]. Samples were collected using blow-vac suction samplers [53]. To enable blow-vac sampling, a transparent acetate frame ( $100 \times 60 \times 60$  cm, H  $\times$  L  $\times$  W) was first quickly placed over the rice hills to be sampled and then covered with a fine mesh cloth that prevented any flying insects from escaping. All arthropods inside the frame were then sucked through the blow-vac into glass vials. Blow-vac sampling allowed us to standardize our samples for different plant densities within the acetate cages and thereby estimate arthropod loads (i.e., numbers per gram of plant—based on estimates of plant biomass taken at the same time). Samples were stored in 90% ethanol and all arthropods were separated into morphospecies and

counted. Where possible, morphospecies were identified to genus or species levels using an extensive voucher collection available at IRRI and referring to an identification key prepared for the region [54].

#### 2.4. Damage Assessments

Rat damage was assessed along sampling transects during the rice reproductive stage ( $\approx 70$  DAT). Each transect had five sampling points at 1 m intervals that were perpendicular to the bund. Rat damage is apparent as cut tillers (cut at a  $\geq 45^\circ$  angle to the tiller axis). The numbers of cut and healthy (not cut) tillers were counted per rice hill at each sampling point. If the hill had  $< 20$  tillers, adjacent rice hills were assessed until 20 tillers had been examined. At the same time as we estimated rodent damage, we also assessed plants as showing signs of 'yellowing' (i.e., Standard Evaluation System (SES) =  $\geq 3$  damage rating [55]). Yellowing can occur for many reasons including poor plant nutrition, drought, and pest or disease damage. We assessed yellowed plants for tungro virus by sampling plant leaves and analyzed the plants for Rice Tungro Spherical Virus (RTSV) and Rice Tungro Bacilliform Virus (RTBV) particles using an ELISA-based test [56]; at the same time, we noted the incidence of rice blast disease (*Magnaporthe grisea* (T.T. Herbert) M.E. Barr) as the number of tillers with lesions.

During the 2013 WS, a tropical storm caused extensive lodging of rice plants in some of the subplots. We assessed lodging by photographing (Nikon D90, 12.3 megapixels) each subplot from the rice bunds and analyzing the images using Image-J version 1.48 (National Institute of Health, Bethesda, MD, USA) to record areas of plants within subplots that were not in an upright position.

#### 2.5. Data Analyses

Rice growth parameters (tiller number, biomass, grain, and yields) were analyzed using univariate general linear models (GLM) for the split-split plot design. We analyzed growth parameters for 30 DAT and prior to harvest, and for the two seasons separately. Models included nitrogen level (main plot), transplanting density, variety, and their interactions as factors. We examined nitrogen for polynomial contrasts. Rice yields based on quadrat samples were analyzed in the same way. Data for tiller numbers, root, shoot, and total plant biomass, grain weights, and the numbers of filled grain were  $\log(x + 1)$  transformed, and root: shoot ratios, and the proportion of grain unfilled were arcsine-transformed before analyses. Following all analyses, residuals were plotted to ensure that they were normal and homogenous.

Rodent damage to plots was considered non-independent because rodents could move between plots using access bunds. Therefore, we ranked rodent damage in both seasons. Yellowing was also ranked each season. Rodent damage, and the proportions of tillers with blast damage, yellowing, and flowering at the time of damage assessments were all analyzed using GLM for the split-split plot design as described above. Tungro incidence was determined only for low-density plots and was not detected in the dry season. Tungro was therefore analyzed using a two-factor GLM (variety, nitrogen) and was ranked before analysis. Lodging during the WS was also ranked before analysis.

We examined factors affecting arthropod communities at two levels. First, we assessed the effects of nitrogen, transplanting density, and variety on the richness and abundance of guilds using univariate analyses; and secondly, we assessed which factors affected guild community structure using multivariate analyses (below). We analyzed arthropod richness, abundance, and density (i.e., abundance per unit of rice biomass) using GLM models for the split-split plot design. For the GLM models, analyses were separate for each season (because the season was not replicated). For richness and abundance, we initially included quadrat rice biomass as a covariate in the analyses, but in all cases, this was removed because there was no effect. For the analyses, we separated leafhoppers, planthoppers, all herbivores combined, all decomposers, parasitoids, and all predators (without parasitoids). Parasitoids were not included in the analyses of predators because the most abundant

parasitoids were species that respond to egg densities, but the predator species mainly respond to free-living prey items (although many predators do also feed on arthropod eggs) and we used prey items as a covariate to analyze predators in the univariate and multivariate analyses (see below). We ranked the abundances of some arthropod groups because of low numbers in some plots (e.g., leafhoppers and parasitoids). For analyses of guilds (herbivores, decomposers, predators) we used the original, non-transformed data. To estimate predation pressures, we assessed the ratios of phloem-feeders (planthoppers and leafhoppers) to all predators. This index may appear crude because many of the predators that we caught might not feed on phloem-feeders; however, the most abundant predator species in our samples have all been positively associated with planthopper or leafhopper predation [3,32,57]. We present the results from the univariate analyses of planthoppers and leafhoppers, as well as predation pressures in the main text. Results for other components of the arthropod communities are presented with the supplementary information to support findings from the multivariate analyses. Lists of the most abundant herbivore, parasitoid and predator species are also included with the supplementary information.

Permutational multivariate analysis of variance (PERMANOVA) [58] was used to test for differences across factors in species composition based on blow-vac samples for three arthropod guilds: herbivores (leafhopper and planthopper species), predators, and decomposers. Four factors were included in each analysis: 'season' was treated as a random factor with two levels (DS and WS); 'plant density' (fixed factor) with two levels (high density (HD) and low density (LD) rice planting); 'variety' (fixed factor) had two levels (IR62 and IR64), and; 'nitrogen' (fixed factor) had three levels (0 = 0 added N, 60 = 60 Kg N ha<sup>-1</sup>, and 150 = 150 Kg N ha<sup>-1</sup>). An additional fixed factor ('prey abundance') was included to assess the effect of prey abundance on predator species composition. Four levels of prey abundance were calculated based on the quartiles of the total invertebrate abundance distribution of all samples (low ≤ 51 individuals, moderate = 51–95 individuals, high = 96–169 individuals, very high = 170–456 individuals). Whenever significant results were found, PERMANOVA pair-wise tests were used to check for differences between levels. PERMANOVA analyses were based on Bray-Curtis similarity resemblance matrices of square root-transformed data; each analysis was permuted 9999 times. Canonical Analysis of Principal Coordinates (CAP) was used to visualize the differences between arthropod samples across factors [59]. Each CAP ordination analysis was calculated based on significant results obtained with PERMANOVA. PERMANOVA and CAP routines were performed with PRIMER (v. 6.1.16) and the PERMANOVA + extension (v. 1.0.6).

### 3. Results

#### 3.1. Plant Biomass at Mid Tillering

At 30 DAT, rice plants were at the mid-tillering stage in both low- and high-density plots. Tiller numbers and plant height increased linearly with increasing nitrogen levels (tiller linear contrasts DS,  $p < 0.001$ ; WS  $p = 0.004$ ; height linear contrast DS and WS,  $p < 0.001$ ), but were not affected at this crop stage by variety or density (Table 1). Plant biomass (root biomass in the DS and shoot biomass in DS, and WS; all linear contrasts  $p < 0.05$ ) increased with increasing nitrogen, with the effects most apparent in the DS (Table 1). Plants grown under high density were significantly ( $p < 0.001$ ) smaller than plants in the low-density plots (see total plant weight in Table 1). Root: shoot ratios tended to decline under increasing nitrogen levels with significant linear reductions ( $p = 0.001$ ) noted during the WS (Table 1). IR62 plants tended to have lower root: shoot ratios compared to IR64, with a significant effect of variety noted during the WS (Table 1). Based on plant weights, the total plant biomass per plot during suction sampling was greater in the high-density plots and increased linearly with added nitrogen (Table 1).

**Table 1.** Rice plant condition at 30 DAT during the 2013 dry and wet seasons. Numbers are means  $\pm$  SEM.

Variety	Density <sup>1</sup>	Nitrogen (Kg ha <sup>-1</sup> )	Tiller Number <sup>4</sup>	Plant Height (cm) <sup>4</sup>	Root Weight (g plant <sup>-1</sup> ) <sup>2,4</sup>	Shoot Weight (g plant <sup>-1</sup> ) <sup>2,4</sup>	Total Plant Weight (g plant <sup>-1</sup> ) <sup>2,4</sup>	Root:Shoot Ratio	Plant Weight per Quadrat (g) <sup>2,3,4</sup>
<b>Dry Season</b>									
IR62	LD	0	6.68 $\pm$ 0.98 <sup>a</sup>	49.26 $\pm$ 1.57 <sup>a</sup>	0.50 $\pm$ 0.09 <sup>a</sup>	5.48 $\pm$ 0.72 <sup>a</sup>	5.97 $\pm$ 0.73 <sup>a</sup>	0.10 $\pm$ 0.03	29.87 $\pm$ 3.64 <sup>a</sup>
	LD	60	12.68 $\pm$ 1.37 <sup>b</sup>	55.31 $\pm$ 1.50 <sup>b</sup>	0.77 $\pm$ 0.10 <sup>b</sup>	9.91 $\pm$ 1.01 <sup>b</sup>	10.68 $\pm$ 1.01 <sup>b</sup>	0.09 $\pm$ 0.02	53.39 $\pm$ 5.03 <sup>b</sup>
LD	150	13.58 $\pm$ 1.19 <sup>b</sup>	58.36 $\pm$ 2.13 <sup>c</sup>	0.93 $\pm$ 0.14 <sup>b</sup>	10.57 $\pm$ 0.88 <sup>c</sup>	11.50 $\pm$ 1.00 <sup>c</sup>	0.09 $\pm$ 0.01	57.51 $\pm$ 4.99 <sup>c</sup>	
	HD	0	7.19 $\pm$ 1.00 <sup>a</sup>	49.91 $\pm$ 1.90 <sup>a</sup>	0.44 $\pm$ 0.10 <sup>a</sup>	4.91 $\pm$ 0.73 <sup>a</sup>	5.36 $\pm$ 0.77 <sup>a</sup>	0.10 $\pm$ 0.02	53.58 $\pm$ 7.72 <sup>a</sup>
HD	60	9.19 $\pm$ 1.01 <sup>b</sup>	54.52 $\pm$ 1.28 <sup>b</sup>	0.50 $\pm$ 0.05 <sup>b</sup>	6.39 $\pm$ 0.74 <sup>b</sup>	6.89 $\pm$ 0.74 <sup>b</sup>	0.08 $\pm$ 0.01	68.88 $\pm$ 7.41 <sup>b</sup>	
	HD	150	12.35 $\pm$ 1.15 <sup>b</sup>	56.44 $\pm$ 1.63 <sup>c</sup>	0.66 $\pm$ 0.11 <sup>b</sup>	8.71 $\pm$ 0.85 <sup>c</sup>	9.36 $\pm$ 0.88 <sup>c</sup>	0.08 $\pm$ 0.01	93.65 $\pm$ 8.84 <sup>c</sup>
IR64	LD	0	4.46 $\pm$ 0.95 <sup>a</sup>	49.17 $\pm$ 0.59 <sup>a</sup>	0.48 $\pm$ 0.03 <sup>a</sup>	4.36 $\pm$ 0.48 <sup>a</sup>	4.84 $\pm$ 0.50 <sup>a</sup>	0.12 $\pm$ 0.01	24.22 $\pm$ 2.51 <sup>a</sup>
	LD	60	12.40 $\pm$ 1.33 <sup>b</sup>	53.98 $\pm$ 1.24 <sup>b</sup>	0.97 $\pm$ 0.14 <sup>b</sup>	8.40 $\pm$ 0.68 <sup>b</sup>	9.37 $\pm$ 0.68 <sup>b</sup>	0.12 $\pm$ 0.02	46.84 $\pm$ 3.42 <sup>b</sup>
LD	150	14.41 $\pm$ 2.36 <sup>b</sup>	60.03 $\pm$ 1.86 <sup>c</sup>	0.80 $\pm$ 0.21 <sup>b</sup>	9.42 $\pm$ 1.20 <sup>c</sup>	10.22 $\pm$ 1.32 <sup>c</sup>	0.09 $\pm$ 0.01	51.10 $\pm$ 6.59 <sup>c</sup>	
	HD	0	4.87 $\pm$ 1.16 <sup>a</sup>	48.37 $\pm$ 1.69 <sup>a</sup>	0.39 $\pm$ 0.01 <sup>a</sup>	4.34 $\pm$ 0.51 <sup>a</sup>	4.73 $\pm$ 0.50 <sup>a</sup>	0.10 $\pm$ 0.01	47.34 $\pm$ 5.03 <sup>a</sup>
HD	60	9.73 $\pm$ 1.96 <sup>b</sup>	53.47 $\pm$ 2.19 <sup>b</sup>	0.49 $\pm$ 0.07 <sup>b</sup>	6.45 $\pm$ 0.85 <sup>b</sup>	6.94 $\pm$ 0.84 <sup>b</sup>	0.09 $\pm$ 0.02	69.44 $\pm$ 8.39 <sup>b</sup>	
	HD	150	12.66 $\pm$ 1.84 <sup>b</sup>	52.67 $\pm$ 4.38 <sup>c</sup>	0.68 $\pm$ 0.14 <sup>b</sup>	7.73 $\pm$ 0.80 <sup>c</sup>	8.41 $\pm$ 0.83 <sup>c</sup>	0.09 $\pm$ 0.02	84.10 $\pm$ 8.28 <sup>c</sup>
F-variety (1,71) <sup>5</sup>			3.26	0.03	0.00	4.05	3.67	1.29	3.62
F-density (1,71) <sup>5</sup>			2.23	0.92	13.25 ***	11.95 ***	14.22 ***	1.29	62.67 ***
F-nitrogen (2,71) <sup>5</sup>			33.96 ***	26.96 ***	10.32 ***	40.26 ***	42.33 ***	1.29	41.77 ***
<b>Wet Season</b>									
IR62	LD	0	5.73 $\pm$ 0.37	51.58 $\pm$ 0.45 <sup>a</sup>	0.82 $\pm$ 0.08	4.78 $\pm$ 0.28	5.60 $\pm$ 0.35	0.17 $\pm$ 0.01 <sup>a</sup>	27.98 $\pm$ 1.74
	LD	60	5.34 $\pm$ 0.84	52.07 $\pm$ 1.18 <sup>a</sup>	0.50 $\pm$ 0.09	4.49 $\pm$ 0.62	4.99 $\pm$ 0.70	0.11 $\pm$ 0.01 <sup>b</sup>	24.93 $\pm$ 3.51
LD	150	6.34 $\pm$ 0.85	53.91 $\pm$ 0.76 <sup>b</sup>	0.53 $\pm$ 0.05	5.23 $\pm$ 0.63	5.76 $\pm$ 0.67	0.10 $\pm$ 0.01 <sup>b</sup>	28.80 $\pm$ 3.33	
	HD	0	5.21 $\pm$ 0.25	50.79 $\pm$ 0.83 <sup>a</sup>	0.57 $\pm$ 0.07	3.46 $\pm$ 0.19	4.02 $\pm$ 0.24	0.16 $\pm$ 0.01 <sup>a</sup>	40.21 $\pm$ 2.39
HD	60	5.82 $\pm$ 0.70	53.53 $\pm$ 1.22 <sup>a</sup>	0.45 $\pm$ 0.06	3.91 $\pm$ 0.52	4.69 $\pm$ 0.36	0.13 $\pm$ 0.02 <sup>b</sup>	43.16 $\pm$ 5.51	
	HD	150	5.85 $\pm$ 0.23	54.18 $\pm$ 1.26 <sup>b</sup>	0.52 $\pm$ 0.05	3.92 $\pm$ 0.17	4.44 $\pm$ 0.15	0.14 $\pm$ 0.02 <sup>b</sup>	44.44 $\pm$ 1.52
IR64	LD	0	3.49 $\pm$ 0.60	50.94 $\pm$ 0.86 <sup>a</sup>	0.72 $\pm$ 0.12	3.86 $\pm$ 0.31	4.58 $\pm$ 0.41	0.19 $\pm$ 0.02 <sup>a</sup>	22.92 $\pm$ 2.06
	LD	60	5.22 $\pm$ 0.91	53.52 $\pm$ 1.73 <sup>a</sup>	0.64 $\pm$ 0.11	4.74 $\pm$ 0.46	5.39 $\pm$ 0.53	0.14 $\pm$ 0.02 <sup>b</sup>	26.94 $\pm$ 2.66
LD	150	5.90 $\pm$ 1.12	54.82 $\pm$ 1.14 <sup>b</sup>	0.75 $\pm$ 0.16	5.09 $\pm$ 0.57	5.84 $\pm$ 0.71	0.14 $\pm$ 0.02 <sup>b</sup>	29.22 $\pm$ 3.56	
	HD	0	3.76 $\pm$ 0.71	51.54 $\pm$ 1.02 <sup>a</sup>	0.57 $\pm$ 0.04	3.52 $\pm$ 0.28	4.25 $\pm$ 0.28	0.16 $\pm$ 0.01 <sup>a</sup>	42.51 $\pm$ 2.77
HD	60	5.79 $\pm$ 1.07	52.02 $\pm$ 1.40 <sup>a</sup>	0.56 $\pm$ 0.06	4.10 $\pm$ 0.22	4.65 $\pm$ 0.26	0.14 $\pm$ 0.01 <sup>b</sup>	46.55 $\pm$ 2.58	
	HD	150	6.59 $\pm$ 1.31	56.57 $\pm$ 1.13 <sup>b</sup>	0.61 $\pm$ 0.11	4.06 $\pm$ 0.21	4.67 $\pm$ 0.23	0.15 $\pm$ 0.03 <sup>b</sup>	46.70 $\pm$ 2.33
F-variety (1,71) <sup>5</sup>			3.95	0.58	2.37	0.13	0.01	3.64 *	0.09
F-density (1,71) <sup>5</sup>			0.14	0.17	5.08 *	11.04	10.58 ***	0.05	78.59 ***
F-nitrogen (2,71) <sup>5</sup>			3.33	8.36 *	2.54	2.29	1.57	6.49 *	1.27

<sup>1</sup>: LD = low density, HD = high density; <sup>2</sup>: All weights are presented as dry weights; <sup>3</sup>: Plant weight per quadrat was estimated based on average plant weights per subplot multiplied by the number of plants per 60 cm<sup>2</sup> in each plot; <sup>4</sup>: Lowercase letters indicate homogenous nitrogen groups based on Tukey pairwise comparisons ( $p > 0.05$ ); <sup>5</sup>: F-values are based on GLMs for a split-split plot design; numbers in parentheses are degrees of freedom; \* =  $p \leq 0.05$ , \*\*\* =  $p \leq 0.001$ ; interaction terms were not significant.

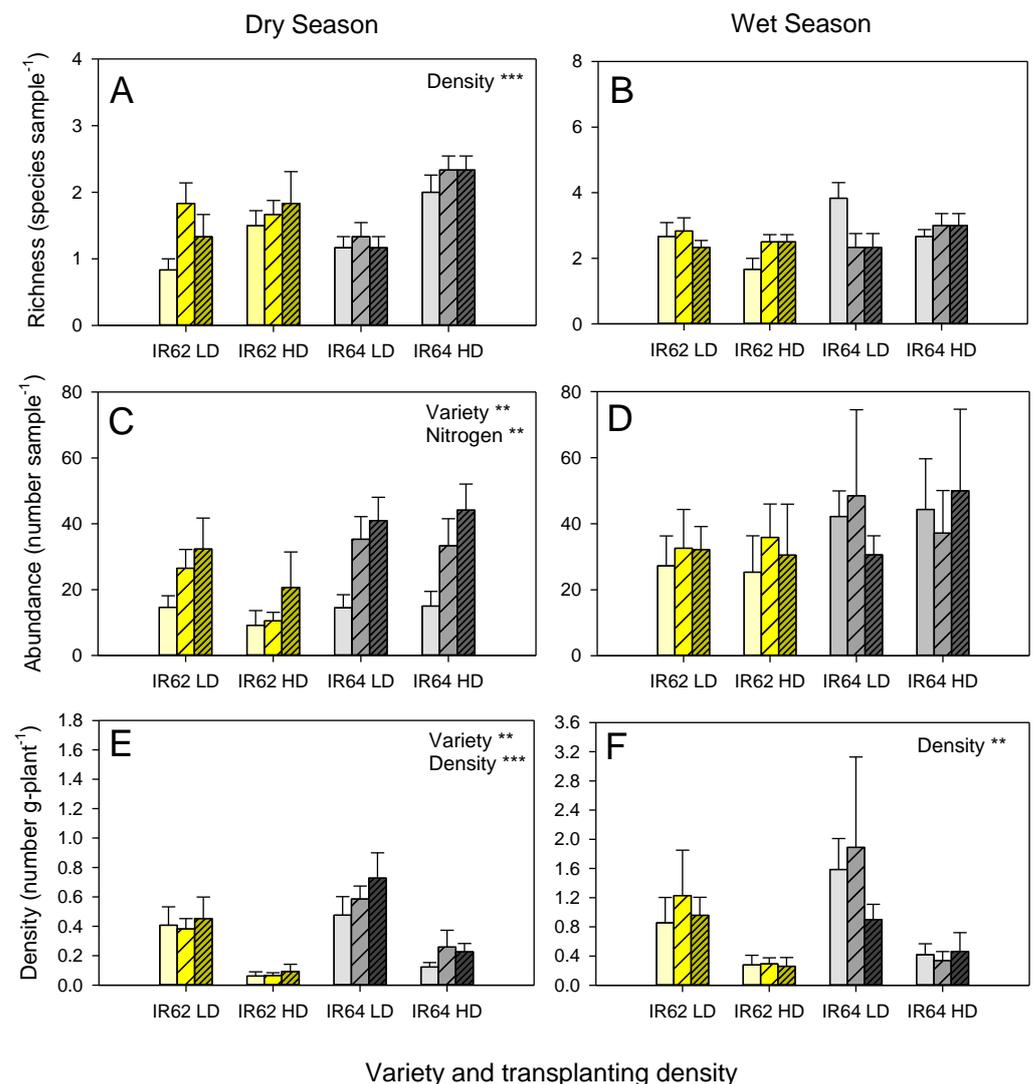
### 3.2. Planthopper and Leafhopper Densities

During DS sampling, 11 planthopper and leafhopper species were collected, of which *S. furcifera* and *N. lugens* were the most abundant planthoppers and *N. virescens* was the most abundant leafhopper (Table S1). Despite a lower planthopper richness per sample (Figure 1A,B), a total of 19 phloem-feeding species were collected during the WS. *Sogatella furcifera* and *N. lugens* were the most abundant planthoppers in the WS and *N. virescens* the most abundant leafhopper. *Nephotettix nigropictus* (Stål) was also relatively abundant during the WS (Table S1).

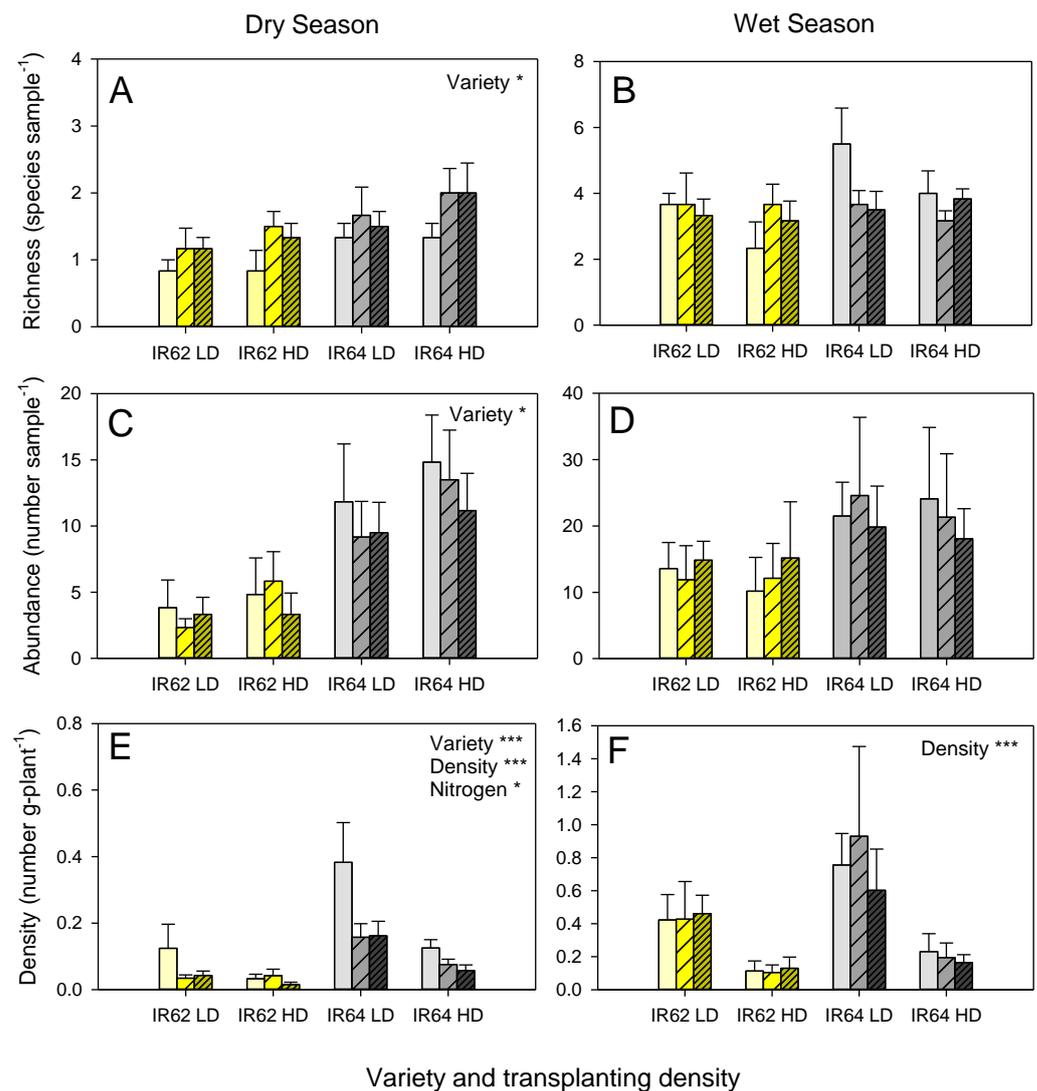
High transplanting density was associated with a greater richness ( $F_{1,71} = 17.77$ ,  $p < 0.001$ ) of planthopper species during the DS sampling and lower planthopper densities in both the DS ( $F_{1,71} = 42.91$ ,  $p < 0.001$ ) and WS ( $F_{1,71} = 8.93$ ,  $p = 0.009$ ) (Figure 1A,B). Planthoppers were more abundant ( $F_{1,71} = 9.10$ ,  $p = 0.009$ ) and attained higher densities ( $F_{1,71} = 8.25$ ,  $p = 0.012$ ) on the susceptible variety during the DS sampling, but not the WS (Figure 1C–F). Planthopper abundance increased linearly with increasing nitrogen levels ( $F_{3,71} = 6.96$ ,  $p = 0.013$ ; linear contrast = 0.001), but the effect was not apparent for planthopper densities, and nitrogen effects were not apparent during WS sampling (Figure 1C–F).

During the DS, *S. furcifera* was more abundant on IR64 ( $F_{1,71} = 8.73$ ,  $p = 0.011$ ), in low-density plots ( $F_{1,71} = 14.15$ ,  $p = 0.002$ ) and in high-nitrogen plots ( $F_{2,71} = 7.09$ ,  $p = 0.012$ ). The abundance of *N. lugens* was not affected by variety or nitrogen level, but was significantly higher in the high-density plots ( $F_{1,71} = 62.51$ ,  $p < 0.001$ ). There were no significant variety, nitrogen, or density effects on either species during the WS sampling (Table S1).

Leafhopper captures were lower in the DS sample. At the time of DS sampling, the species richness ( $F_{1,71} = 5.70$ ,  $p = 0.031$ ), abundance ( $F_{1,71} = 34.94$ ,  $p < 0.001$ ) and densities ( $F_{1,71} = 41.32$ ,  $p < 0.001$ ) of leafhoppers were all lower on IR62 than IR64 (Figure 2). Leafhopper densities were higher in low-density plots ( $F_{1,71} = 12.36$ ,  $p = 0.003$ ) and declined linearly with increasing nitrogen ( $F_{2,71} = 4.13$ ,  $p = 0.049$ : linear contrast,  $p < 0.001$ ). There were no significant variety or nitrogen effects on leafhopper richness, abundance or density at the time of WS sampling. However, leafhopper densities were higher in the low-density plots ( $F_{1,71} = 27.52$ ,  $p < 0.001$ ) during the WS (Figure 2). The DS abundance of *N. virescens* was lower in plots of IR62 than IR64 ( $F_{1,71} = 32.44$ ,  $p < 0.001$ ) (Figure 2). During the WS, there was no significant variety effect on *N. virescens* abundance, but *N. nigropictus* was less abundant on the resistant variety ( $F_{1,71} = 4.33$ ,  $p = 0.055$ ) (Table S1).



**Figure 1.** Species richness (A,B), abundance (C,D), and density (E,F) of planthoppers (all species combined—see Table S1) in rice plots with resistant (IR62: yellow bars) and susceptible (IR64: grey bars) rice transplanted at low (LD) and high (HD) densities under varying nitrogen fertilizer treatments. Nitrogen was applied at 0 Kg ha<sup>-1</sup> (open bars), 60 Kg ha<sup>-1</sup> (hatched bars), and 150 Kg ha<sup>-1</sup> (densely-hatched bars). Factors that significantly affected planthopper parameters are presented with significance levels as \*\*  $p \leq 0.01$  and \*\*\*  $p \leq 0.005$ . Sampling was conducted during the dry (A,C,E) and wet (B,D,F) seasons using blow-vac samplers. Standard errors are indicated ( $N = 6$ ).



**Figure 2.** Species richness (A,B), abundance (C,D), and density (E,F) of leafhoppers (all species combined: Table S1) in rice plots with resistant (IR62: yellow bars), and susceptible (IR64: grey bars) rice transplanted at low (LD) and high (HD) densities under varying nitrogen fertilizer treatments. Nitrogen was applied at 0 Kg ha<sup>-1</sup> (open bars), 60 Kg ha<sup>-1</sup> (hatched bars) and 150 Kg ha<sup>-1</sup> (densely-hatched bars). Factors that significantly affected leafhopper parameters are presented with significance levels as \*  $p \leq 0.05$  and \*\*\*  $p \leq 0.005$ . Sampling was conducted during the dry (A,C,E) and wet (B,D,F) seasons using blow-vac samplers. Standard errors are indicated ( $N = 6$ ).

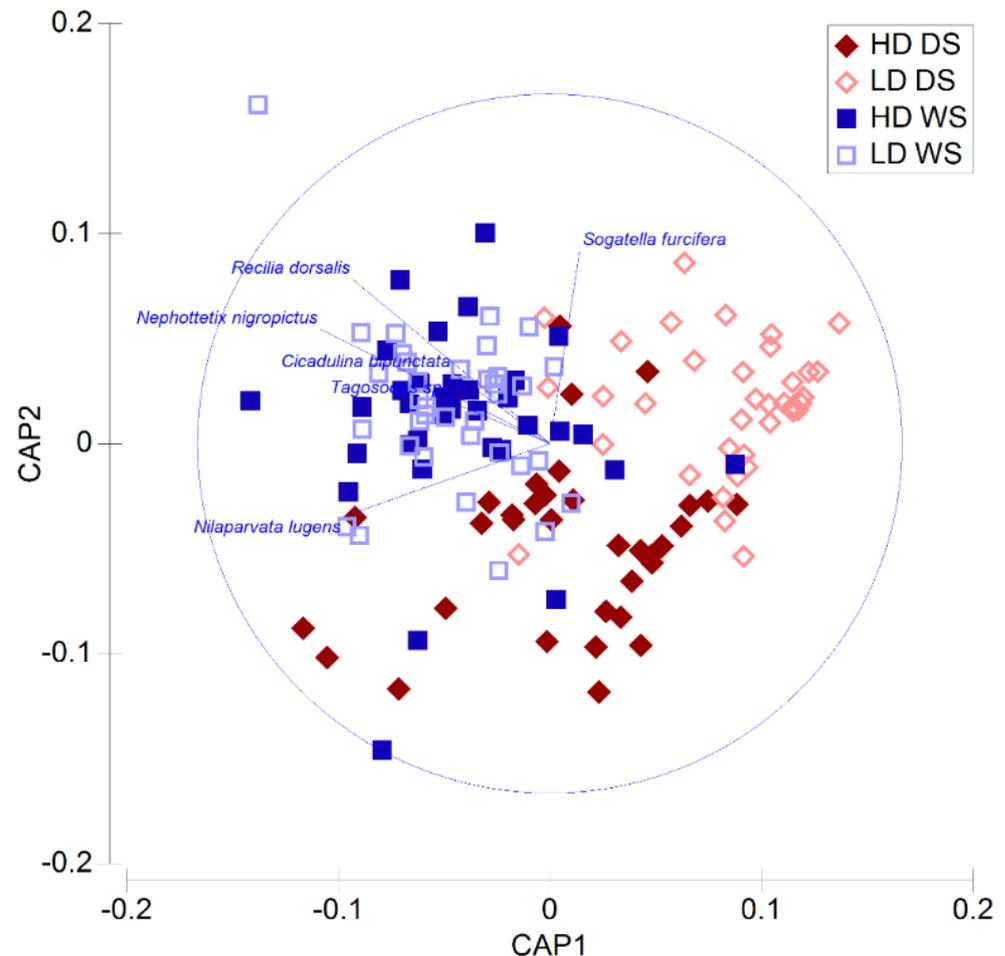
### 3.3. Arthropod Community Analysis

The species composition of all arthropod guilds significantly differed between seasons (herbivores: Pseudo-F = 21.309,  $p < 0.001$ ; decomposers: Pseudo-F = 27.612,  $p < 0.001$ ; predators: Pseudo-F = 5.232,  $p < 0.05$ ). However, each of the arthropod guilds was affected by different interactions between 'season' and other guild-specific factors as explained in the following sections.

#### 3.3.1. Factors Affecting Planthopper and Leafhopper Community Structure

We recorded 77 herbivore morphospecies during the study (Table S2); however, most occurred in relatively low numbers. Further information on species richness, abundance, and densities of all herbivores combined are presented in Figure S1. For planthoppers and leafhoppers, which were the most abundant herbivores, a significant interaction between 'plant density' and 'season' was found (Pseudo-F = 7.093,  $p < 0.001$ ) because

species composition differed significantly between high- and low-density rice planting during the DS ( $t = 4.274$ ,  $p < 0.001$ ), but not during the WS ( $t = 0.822$ ,  $p = 0.623$ ). These differences can be observed in the CAP ordination plot (Figure 3), where, for instance, the abundance of *S. furcifera* and *N. lugens* showed strong associations with low- and high-density planting, respectively, particularly during DS sampling (Table S1). Other factors, including rice variety and nitrogen levels, played no statistically significant role in determining planthopper and leafhopper community structure.

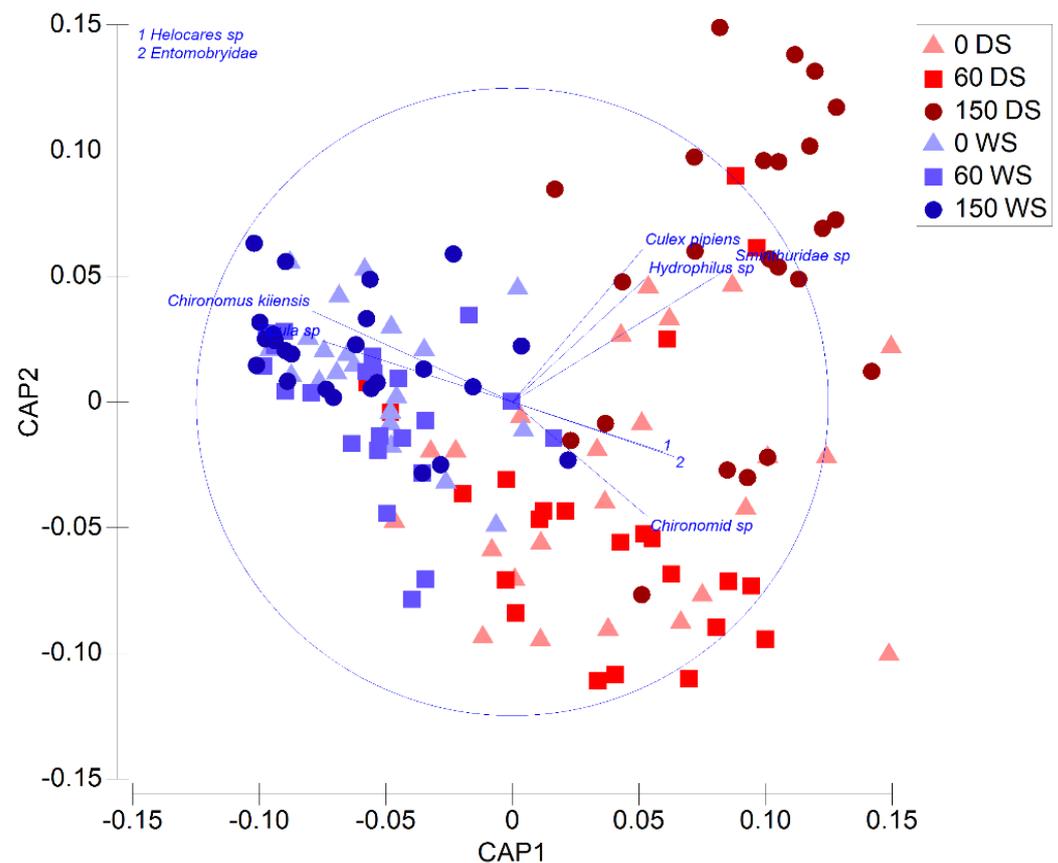


**Figure 3.** Canonical Analysis of Principal Coordinates (CAP) showing differences in herbivore (planthopper and leafhopper) species composition between blow-vac samples. Red colors indicate samples collected during the dry season (DS), whereas blue colors indicate samples collected during the wet season (WS). Filled and unfilled symbols represent high-density (HD) and low-density (LD) rice planting, respectively. Overlaid vectors (in blue) represent the correlations (Pearson's correlation coefficient  $> 0.3$ ) between herbivore species and the CAP axes, where vector length and direction reflect the increasing values of correlation and parameter values, respectively.

### 3.3.2. Factors Affecting Decomposer Community Structure

For decomposers, a significant interaction between 'nitrogen' and 'season' was observed (Pseudo-F = 7.093,  $p < 0.001$ ) because nitrogen addition affected species composition only during the DS. Samples from plots with the highest nitrogen levels were significantly different from samples under the other two levels (0 and 150:  $t = 1.958$ ,  $p < 0.001$ ; 60 and 150:  $t = 2.018$ ,  $p < 0.001$ ). Such differences are visualized in the CAP ordination plot (Figure 4), where a number of species showed contrasting associations with either high nitrogen (150) addition (e.g., *Culex pipiens* L., Sminthuridae sp., *Hydrophilus* sp.) or no (0) to medium (60)

nitrogen addition (e.g., *Helocares* sp., Entomobryidae species) during the DS. (See Figure S2 for details of decomposer species richness and abundance during the DS and WS sampling.)



**Figure 4.** Canonical Analysis of Principal Coordinates (CAP) showing differences in decomposer species composition between blow-vac samples. Red colors indicate samples collected during the dry season (DS), whereas blue colors indicate samples collected during the wet season (WS). Nitrogen regimes (0 = 0 added N, 60 = 60 Kg N ha<sup>-1</sup>, and 150 = 150 Kg N ha<sup>-1</sup>) are represented by increasing color darkness. Overlaid vectors (in blue) represent the correlations (Pearson's correlation coefficient > 0.3) between decomposer species and the CAP axes, where vector length and direction reflect the increasing values of correlation and parameter values, respectively.

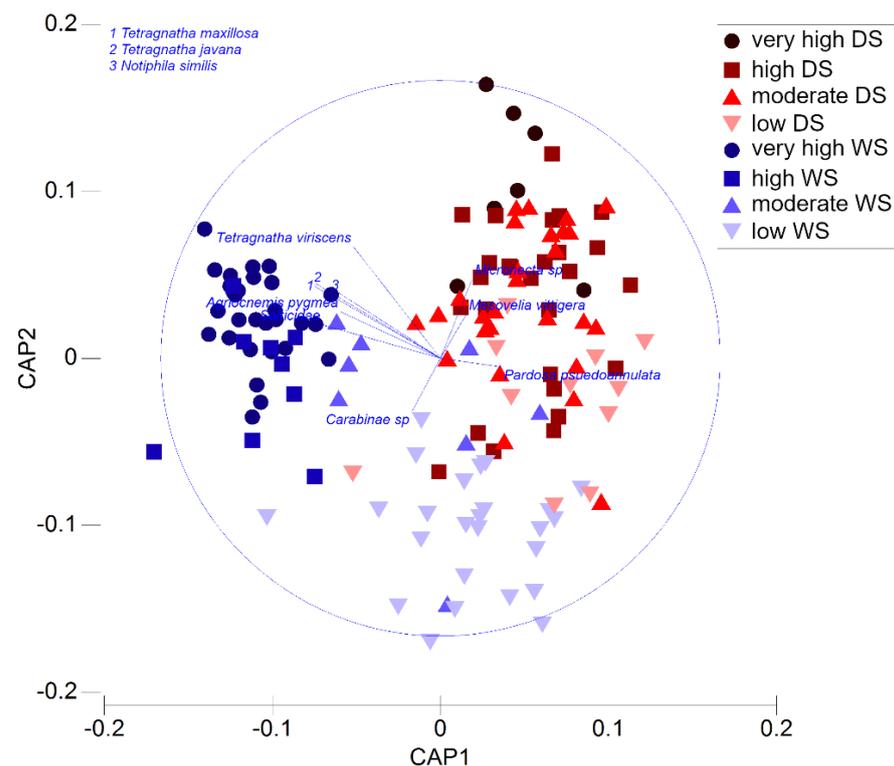
### 3.3.3. Factors Affecting Parasitoid Community Structure

We recorded 61 parasitoid morphospecies; however, only 15 of these morphospecies were represented by >10 individuals in both samples combined. Trends in parasitoid species richness, abundance, and densities are presented in Figure S3 with further details on selected species in Table S2. The abundant species were mainly the egg parasitoids of planthoppers and leafhoppers including *Oligosita* sp., *Anagrus* spp., and *Gonatocerus* spp.; or parasitoids of the eggs of Lepidoptera pests such as *Telenomus* spp. and *Trichogramma japonicum* Ashmead (Table S2). Further information related the egg parasitoids of planthoppers and leafhoppers in the low-density plots can be found in a recent paper by Peñalver-Cruz and Horgan (2022) [48]. The parasitoids of planthopper and leafhopper eggs were more abundant in plots of IR64 than IR62 during DS sampling (IR62 = 8.33 ± 1.50, IR64 = 15.50 ± 1.54: F<sub>1,55</sub> = 11.865, p < 0.001), but there was no significant variety effect during WS sampling. No other factors had significant effects on parasitoid abundance (Table S2). The parasitoids of Lepidoptera eggs responded to transplanting density, with higher numbers collected in the low-density plots in both the DS (LD = 7.00 ± 0.97, HD = 1.67 ± 0.20: F<sub>1,55</sub> = 11.526, p < 0.001) and WS (LD 21.38 ± 1.65, HD = 11.38 ± 1.97: F<sub>1,55</sub> = 5.036, p = 0.029) (Table S2).

### 3.3.4. Factors Affecting Parasitoid Community Structure

We separated predators into 72 morphospecies of which nine occurred at between 40 and 100 individuals during sampling (Table S2). These were: *Microcanthia ornatula* (Reuter), *Solenopsis geminata* (Fabricius), *Dyschiriognatha* sp., *Cyrtorhinus lividipennis* Reuter, *Araneus inustus* (L. Koch), *Atypena formosana* (Oi), and *Micraspis crocea* (Mulsant), as well as an unidentified Mesovellidae and unidentified Salticidae; five species occurred at between 100 and 300 in the samples. These were: *Mesovelia vittigera* (Horváth), *Pardosa psuedoannulata* (Bösenberg & Strand), *Microvelia douglasi atrolineata* (Bergroth), *Tetragnatha maxillosa* Thorell, and *Micronecta* sp.; The spider *Tetragnatha virescens* Okuma occurred more than 400 times in the samples (Table S2).

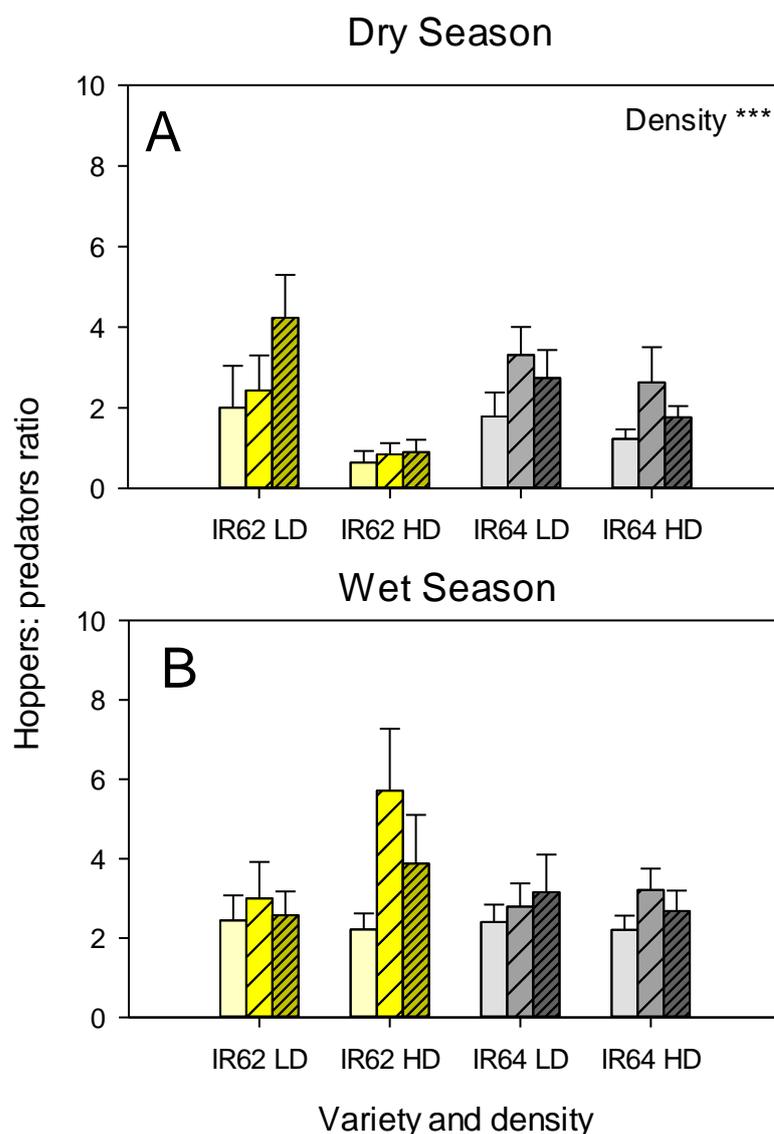
For predators, the interaction term prey abundance  $\times$  season was significant (Pseudo-F = 7.093,  $p < 0.001$ ) since prey abundance had an effect on species composition only during the WS, causing significant differences between all abundance levels ( $p \leq 0.05$ ) except between 'high' and 'very high' levels ( $t = 1.301$ ,  $p = 0.108$ ). Such statistical differences are observed in the CAP ordination plot (Figure 5), in which a number of spider species (e.g., *Tetragnatha virescens*, *T. maxillosa*, and *T. javana* (Thorell)) in particular, were strongly associated with samples that also had high or very high prey abundance during the WS, whereas other predators (e.g., Carabinae species) were associated with WS samples that had low prey abundance. Microvelliidae and Mesovelliidae were most abundant during the dry season sampling (Figure 5). (Further details related to experimental effects on predators are available in Figure S4.)



**Figure 5.** Canonical Analysis of Principal Coordinates (CAP) showing differences in predator species composition between blow-vac samples. Red colors indicate samples collected during the dry season (DS), whereas blue colors indicate samples collected during the wet season (WS). Prey abundance levels are represented by increasing color darkness. Prey (including all herbivores and decomposers) abundance is based on the quartiles of the total invertebrate abundance of all samples (low = <51, moderate = 51–95, high = 96–169, very high = 170–456). Overlaid vectors (in blue) represent the correlations (Pearson's correlation coefficient > 0.3) between predator species and the CAP axes, where vector length and direction reflect the increasing values of correlation and parameter values, respectively.

### 3.4. Predation Pressure

The ratios of planthoppers and leafhoppers to all predators were affected by transplanting density in the DS ( $F_{1,71} = 10.16$ ,  $p = 0.006$ ), with fewer hoppers per predator in the high-density plots (Figure 6). This effect was largely due to lower numbers of *S. furcifera* in the high-density plots where Microvellidae and Mesovellidae occurred at high numbers. There were no significant variety, density, or nitrogen effects on hopper: predator ratios during the WS sampling (Figure 6).

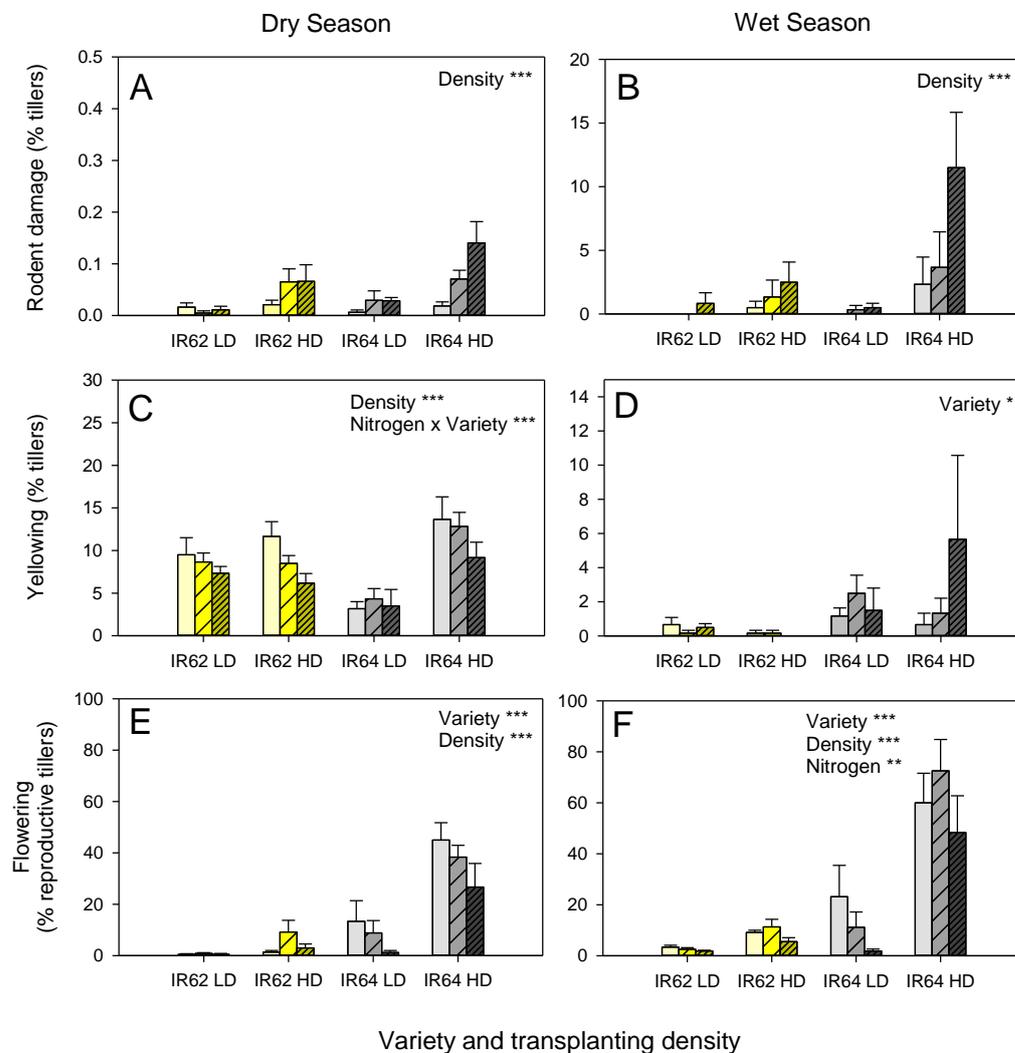


**Figure 6.** Hopper: predator ratios in rice plots with resistant (IR62: yellow bars) and susceptible (IR64: grey bars) rice transplanted at low (LD) and high (HD) densities under varying nitrogen fertilizer treatments. Nitrogen was applied at 0 Kg ha<sup>-1</sup> (open bars), 60 Kg ha<sup>-1</sup> (hatched bars), and 150 Kg ha<sup>-1</sup> (densely-hatched bars). The factors that significantly affected ratios are presented with significance level as \*\*\*  $p \leq 0.005$ . Sampling was conducted during the dry (A) and wet (B) seasons using blow-vac samplers. Standard errors are indicated ( $N = 6$ ).

### 3.5. Rodent Damage and Other Plant Health Issues

Rodents damaged less than 0.2% of tillers at the time of DS sampling. Damage was higher at the time of WS sampling, with over 10% of tillers cut by rodents in some plots (Figure 7A,B). Rodent damage was significantly affected by transplanting density in both seasons (DS:  $F_{1,71} = 14.75$ ,  $p < 0.001$ ; WS:  $F_{1,71} = 11.21$ ,  $p < 0.01$ ), with consistently higher

proportions of damaged tillers in high-density plots irrespective of variety (DS:  $F_{1,71} = 1.78$ ,  $p > 0.05$ ; WS:  $F_{1,71} = 3.84$ ,  $p > 0.05$ ) or nitrogen level (DS:  $F_{2,71} = 3.74$ ,  $p > 0.05$ ; WS:  $F_{2,71} = 5.59$ ,  $p > 0.05$ ). However, for both seasons, damage increased linearly with increasing nitrogen levels (linear contrasts,  $p < 0.005$ ).

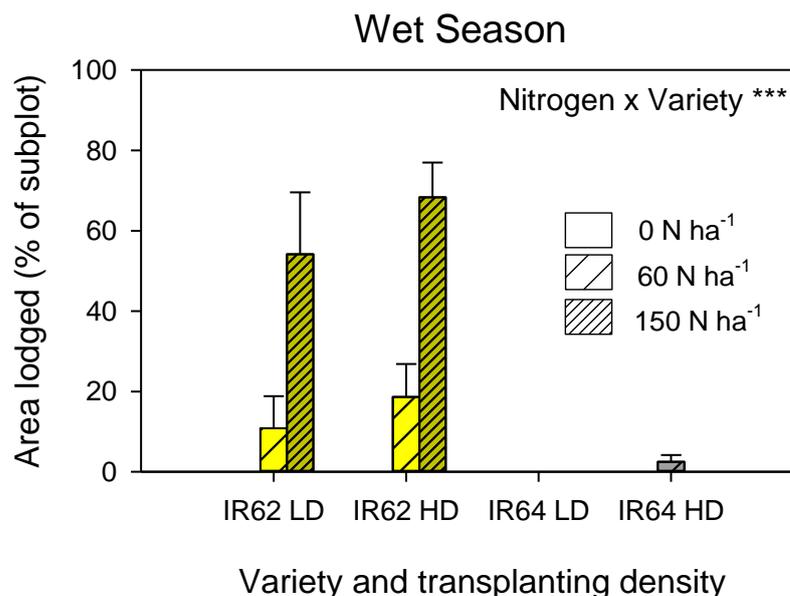


**Figure 7.** Rodent damage (i.e., % cut tillers: **A,B**), the percentage of tillers that were yellowing (**C,D**) and the percentage of reproductive tillers that were flowering at the time sampling was conducted (**E,F**) in plots with resistant (IR62: yellow bars) and susceptible (IR64: grey bars) rice transplanted at low (LD) and high (HD) densities under varying nitrogen fertilizer treatments. Nitrogen was applied at 0 Kg ha<sup>-1</sup> (open bars), 60 Kg ha<sup>-1</sup> (hatched bars), and 150 Kg ha<sup>-1</sup> (densely-hatched bars). Factors that significantly affected each parameter are presented with significance levels as \*  $p \leq 0.05$ , \*\*  $p \leq 0.01$  and \*\*\*  $p \leq 0.005$ . Sampling was conducted during the dry (**A,C,E**) and wet (**B,D,F**) seasons. Standard errors are indicated ( $N = 6$ ).

The occurrence of yellowing tillers was more prominent during our DS sampling, with most plots having over 5% of tillers evaluated at  $\geq 3$  using the SES (Figure 7C,D). Yellowing during the DS was more prominent in high density plots ( $F_{1,71} = 16.85$ ,  $p < 0.001$ ) and decreased with increasing nitrogen (linear contrast,  $p = 0.016$ ) mainly in the IR62 plots (interaction  $F_{2,71} = 14.09$ ,  $p < 0.001$ ). During the WS, fewer tillers had signs of yellowing, and yellowing was not affected by density ( $F_{1,71} = 3.57$ ,  $p > 0.05$ ) or nitrogen levels ( $F_{2,71} = 0.15$ ,  $p > 0.05$ ), but was higher among IR64 plants ( $F_{1,71} = 4.87$ ,  $p < 0.05$ : Figure 7). We detected spherical and bacilliform tungro virus particles at higher levels among yellowing IR64 tillers ( $0.069 \pm 0.025\%$ ) than IR62 tillers ( $0.021 \pm 0.011\%$ ) ( $F_{1,20} = 4.414$ ,  $p = 0.049$ ) with no

significant effect of nitrogen ( $F_{1,20} = 0.218, p = 0.646$ ), suggesting that yellowing included some plants with tungro virus, but that much of the yellowing was due to other factors including nutrient and water deficiencies or rodent damage.

Lodging during the WS occurred almost exclusively in the IR62 plots that had added nitrogen (Figure 8). The very low levels of lodging in IR64 plots produced a significant variety  $\times$  nitrogen interaction ( $F_{2,71} = 27.874, p < 0.001$ ). During the same season, rice in the high nitrogen plots ( $F_{2,71} = 6.28, p < 0.05$ ) showed signs of blast infection ( $3.17 \pm 2.44\%$  of tillers infected), irrespective of planting density ( $F_{1,71} = 0.01, p > 0.05$ ) or variety ( $F_{1,71} = 0.01, p > 0.05$ ).



**Figure 8.** The percentage area of subplots with lodged rice plants following a tropical storm. Subplots were transplanted with resistant (IR62: yellow bars) and susceptible (IR64: grey bars) rice at low (LD) and high (HD) densities under varying nitrogen fertilizer treatments. Nitrogen was applied at 0 Kg ha<sup>-1</sup> (open bars), 60 Kg ha<sup>-1</sup> (hatched bars) and 150 Kg ha<sup>-1</sup> (densely-hatched bars). The factors that significantly affected lodging are presented with significance levels as \*\*\*  $p \leq 0.005$ . Lodging was noted only during the wet season. Standard errors are indicated ( $N = 6$ ).

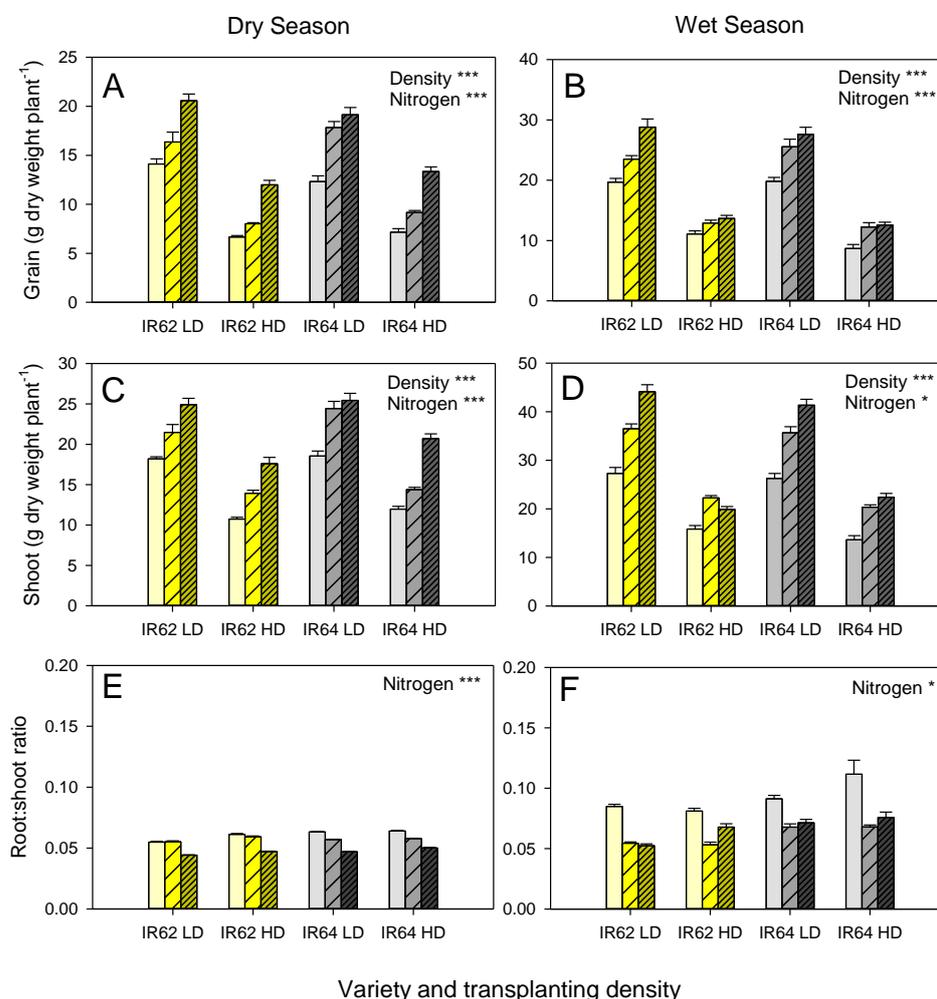
### 3.6. Plant Development and Yields

Plants at high density were phenologically more advanced (indicated by the proportion of reproductive tillers that were flowering) than plants at low density in both seasons (DS:  $F_{1,71} = 17.20, p < 0.001$ ; WS:  $F_{1,71} = 55.26, p < 0.001$ ) (Figure 7E,F). IR64 plants also flowered significantly earlier (DS:  $F_{1,71} = 17.20, p < 0.001$ ; WS:  $F_{1,71} = 17.37, p < 0.001$ ) (Figure 7E,F). Increasing levels of nitrogen tended to delay flowering, but the effect was only statistically significant when we sampled during the WS (DS:  $F_{2,71} = 2.31, p > 0.05$ ; WS:  $F_{1,71} = 5.73, p < 0.01$ , WS linear contrast,  $p < 0.001$ ) (Figure 7E,F).

Full details of plant development prior to harvest are included in Table S3. Among the factors affected by variety, 100-grain weights were heavier for IR64 compared to IR62 (DS:  $F_{1,71} = 46.37, p < 0.001$ ; WS  $F_{1,71} = 21.18, p < 0.001$ ); and IR62 plants were taller than IR64 plants during the WS ( $F_{1,71} = 5.08, p < 0.05$ ) (Table S3). Increasing nitrogen levels were associated with higher tillering (DS:  $F_{2,71} = 18.81, p < 0.01$ , linear contrast  $p < 0.001$ ; WS:  $F_{2,71} = 14.53, p < 0.001$ , linear contrast  $p < 0.01$ ), taller plants (DS:  $F_{2,71} = 43.92, p < 0.001$ , linear contrast  $p < 0.001$ ; WS:  $F_{2,71} = 11.79, p < 0.001$ , linear contrast  $p < 0.001$ ) and a higher number of filled grain (DS:  $F_{2,71} = 7.30, p < 0.01$ , linear contrast  $p < 0.001$ ; WS:  $F_{2,71} = 6.25, p < 0.01$ , linear contrast  $p < 0.01$ ) (Table S3). Plants grown under high density had fewer tillers (DS:  $F_{1,71} = 119.12, p < 0.001$ ; WS:  $F_{1,71} = 113.49, p < 0.001$ ), less root biomass (DS:  $F_{1,71} = 36.55, p < 0.001$ ; WS:  $F_{1,71} = 29.22, p < 0.001$ ), were shorter during the DS (DS:

$F_{1,71} = 5.15, p < 0.05$ ; WS:  $F_{1,71} = 3.41, p > 0.05$ ), and had fewer filled grain (DS:  $F_{1,71} = 42.68, p < 0.001$ ; WS:  $F_{1,71} = 78.59, p < 0.001$ ). Grain tended to be heavier in the low-density plots (DS:  $F_{1,71} = 7.70, p < 0.05$ ) with more unfilled grain in the high-density plots (DS:  $F_{1,71} = 5.71, p < 0.05$ ) during the DS only (Table S3).

The final weights of plants did not differ between varieties; however, nitrogen was associated with larger plants (DS:  $F_{2,71} = 13.77, p < 0.001$ , linear contrast  $p < 0.001$ ; WS:  $F_{2,71} = 12.40, p < 0.001$ , linear contrast  $p < 0.001$ ) and higher yields per plant (DS:  $F_{2,71} = 13.58, p < 0.001$ , linear contrast  $p < 0.001$ ; WS:  $F_{2,71} = 5.84, p < 0.05$ , linear contrast  $p < 0.001$ ) in both seasons (Figure 9). Increasing levels of nitrogen were also associated with a decline in root: shoot ratios in both seasons (DS:  $F_{2,71} = 20.00, p < 0.001$ , linear contrast  $p < 0.001$ ; WS:  $F_{2,71} = 5.53, p < 0.05$ , linear contrast  $p < 0.001$ ) (Figure 9). Plants grown under high density were smaller than corresponding plants under low density (DS:  $F_{1,71} = 40.08, p < 0.001$ ; WS:  $F_{1,71} = 76.22, p < 0.001$ ) and yields per plant were lower (DS:  $F_{1,71} = 51.06, p < 0.001$ ; WS:  $F_{1,71} = 75.26, p < 0.001$ ) for plants grown under high density. Density did not significantly affect root: shoot ratios (DS:  $F_{1,71} = 2.00, p > 0.05$ ; WS:  $F_{1,71} = 0.85, p > 0.05$ ) (Figure 9).



**Figure 9.** The weight of filled grain (A,B), weight of non-reproductive plant parts (C,D) and root: shoot ratios (E,F) of R62 (yellow bars) and IR64 (grey bars) transplanted at low (LD) and high (HD) densities under varying nitrogen fertilizer treatments. Nitrogen was applied at 0 Kg ha<sup>-1</sup> (open bars), 60 Kg ha<sup>-1</sup> (hatched bars) and 150 Kg ha<sup>-1</sup> (densely-hatched bars). Factors that significantly affected each parameter are presented with significance levels as \*  $p \leq 0.05$  and \*\*\*  $p \leq 0.005$ . Plants were evaluated at harvest time for dry (A,C,E) and wet (B,D,F) season crops. Standard errors are indicated ( $N = 6$ ). The same data, together with other growth parameters are presented in Table S3.

Final yields per m<sup>2</sup> were not different between varieties and were not affected by transplanting density in either season (Table 2). Yields increased linearly with increasing nitrogen in both seasons (linear contrasts,  $p < 0.001$ ) (Table 2). IR62 plants, and plants in low-density plots had more unfilled grain per square m than IR64 or plants in high-density plots respectively, but only during the DS (Table 2). A higher proportion of IR62 grain also remained unfilled per square m compared to IR64 grain in the DS (Table 2). The same effects were not noted during the WS.

**Table 2.** Grain yields per m<sup>2</sup> quadrat at harvest. Numbers are means  $\pm$  SEM ( $N = 6$ ).

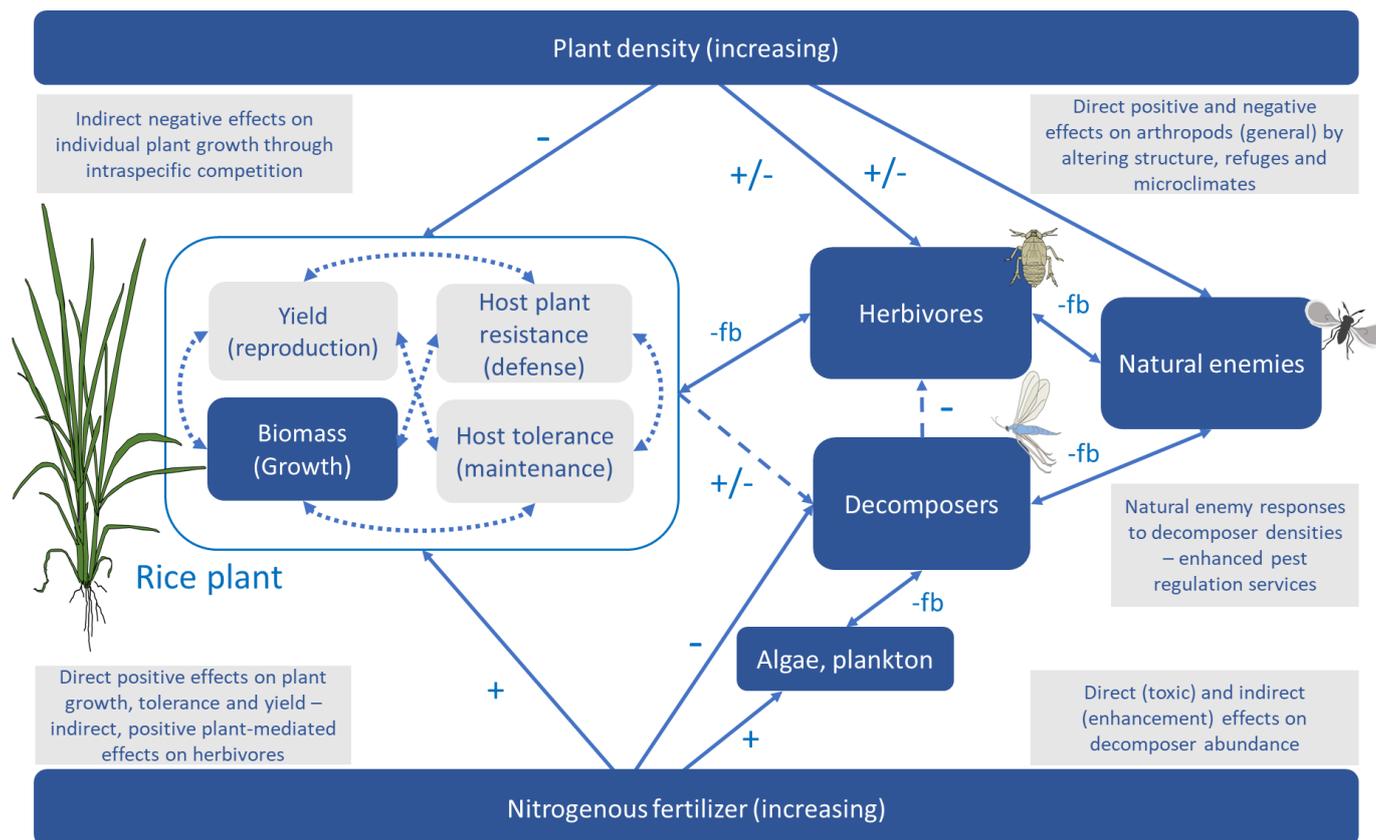
Variety	Density <sup>1</sup>	Nitrogen (Kg ha <sup>-1</sup> )	Number of Filled Grain <sup>3</sup>	Number of Unfilled Grain <sup>3</sup>	Proportion of Grain Unfilled <sup>3</sup>	Total Grain Weight (g m <sup>-2</sup> ) <sup>2,3</sup>
<b>Dry Season</b>						
IR62	LD	0	310.98 $\pm$ 19.61 <sup>a</sup>	18.99 $\pm$ 1.78 <sup>a</sup>	0.06 $\pm$ 0.01 <sup>a</sup>	329.98 $\pm$ 20.05 <sup>a</sup>
	LD	60	481.24 $\pm$ 23.74 <sup>b</sup>	50.77 $\pm$ 5.52 <sup>b</sup>	0.09 $\pm$ 0.01 <sup>b</sup>	532.01 $\pm$ 25.67 <sup>b</sup>
	LD	150	615.24 $\pm$ 23.86 <sup>c</sup>	85.95 $\pm$ 14.25 <sup>c</sup>	0.12 $\pm$ 0.02 <sup>b</sup>	701.19 $\pm$ 27.36 <sup>c</sup>
	HD	0	263.63 $\pm$ 13.80 <sup>a</sup>	14.82 $\pm$ 1.50 <sup>a</sup>	0.06 $\pm$ 0.01 <sup>a</sup>	278.45 $\pm$ 13.56 <sup>a</sup>
	HD	60	483.83 $\pm$ 61.00 <sup>b</sup>	41.46 $\pm$ 5.10 <sup>b</sup>	0.08 $\pm$ 0.01 <sup>b</sup>	525.29 $\pm$ 64.10 <sup>b</sup>
	HD	150	557.11 $\pm$ 38.19 <sup>c</sup>	69.29 $\pm$ 5.22 <sup>c</sup>	0.12 $\pm$ 0.01 <sup>b</sup>	626.39 $\pm$ 34.76 <sup>c</sup>
IR64	LD	0	289.78 $\pm$ 18.76 <sup>a</sup>	19.50 $\pm$ 2.71 <sup>a</sup>	0.06 $\pm$ 0.01 <sup>a</sup>	309.28 $\pm$ 20.62 <sup>a</sup>
	LD	60	467.58 $\pm$ 26.51 <sup>b</sup>	32.50 $\pm$ 3.93 <sup>b</sup>	0.06 $\pm$ 0.00 <sup>b</sup>	500.07 $\pm$ 29.60 <sup>b</sup>
	LD	150	689.53 $\pm$ 33.51 <sup>c</sup>	68.46 $\pm$ 6.68 <sup>c</sup>	0.09 $\pm$ 0.01 <sup>b</sup>	758.00 $\pm$ 33.11 <sup>c</sup>
	HD	0	272.66 $\pm$ 21.75 <sup>a</sup>	12.14 $\pm$ 1.02 <sup>a</sup>	0.04 $\pm$ 0.01 <sup>a</sup>	284.80 $\pm$ 21.76 <sup>a</sup>
	HD	60	474.06 $\pm$ 21.16 <sup>b</sup>	34.64 $\pm$ 3.04 <sup>b</sup>	0.07 $\pm$ 0.01 <sup>b</sup>	508.70 $\pm$ 21.34 <sup>b</sup>
	HD	150	656.46 $\pm$ 30.99 <sup>c</sup>	56.67 $\pm$ 2.86 <sup>c</sup>	0.08 $\pm$ 0.00 <sup>b</sup>	713.13 $\pm$ 33.61 <sup>c</sup>
F-variety (1,71) <sup>4</sup>			1.57	6.80 <sup>*</sup>	12.73 <sup>***</sup>	0.19
F-density (1,71) <sup>4</sup>			1.78	4.59 <sup>*</sup>	1.82	3.70
F-nitrogen (2,71) <sup>4</sup>			118.69 <sup>***</sup>	71.94 <sup>***</sup>	25.55 <sup>***</sup>	154.07 <sup>***</sup>
<b>Wet Season</b>						
IR62	LD	0	452.79 $\pm$ 17.44 <sup>a</sup>	16.22 $\pm$ 1.66 <sup>a</sup>	0.03 $\pm$ 0.00 <sup>b</sup>	469.02 $\pm$ 18.48 <sup>a</sup>
	LD	60	524.05 $\pm$ 28.11 <sup>b</sup>	35.63 $\pm$ 6.30 <sup>ab</sup>	0.06 $\pm$ 0.01 <sup>a</sup>	559.68 $\pm$ 32.89 <sup>b</sup>
	LD	150	670.62 $\pm$ 25.44 <sup>c</sup>	23.67 $\pm$ 0.74 <sup>b</sup>	0.04 $\pm$ 0.00 <sup>b</sup>	660.95 $\pm$ 37.30 <sup>c</sup>
	HD	0	383.64 $\pm$ 30.06 <sup>a</sup>	20.92 $\pm$ 2.88 <sup>a</sup>	0.04 $\pm$ 0.00 <sup>b</sup>	404.56 $\pm$ 29.84 <sup>a</sup>
	HD	60	519.57 $\pm$ 41.32 <sup>b</sup>	34.86 $\pm$ 7.58 <sup>ab</sup>	0.06 $\pm$ 0.02 <sup>a</sup>	554.42 $\pm$ 40.63 <sup>b</sup>
	HD	150	585.70 $\pm$ 14.28 <sup>c</sup>	27.76 $\pm$ 4.51 <sup>b</sup>	0.04 $\pm$ 0.01 <sup>b</sup>	613.46 $\pm$ 9.98 <sup>c</sup>
IR64	LD	0	394.77 $\pm$ 24.53 <sup>a</sup>	13.15 $\pm$ 2.75 <sup>a</sup>	0.03 $\pm$ 0.00 <sup>b</sup>	441.25 $\pm$ 27.37 <sup>a</sup>
	LD	60	517.11 $\pm$ 23.64 <sup>b</sup>	25.14 $\pm$ 2.31 <sup>ab</sup>	0.05 $\pm$ 0.01 <sup>a</sup>	542.25 $\pm$ 23.72 <sup>b</sup>
	LD	150	598.92 $\pm$ 17.93 <sup>c</sup>	18.57 $\pm$ 2.44 <sup>b</sup>	0.03 $\pm$ 0.00 <sup>b</sup>	616.66 $\pm$ 16.59 <sup>c</sup>
	HD	0	395.33 $\pm$ 23.76 <sup>a</sup>	23.68 $\pm$ 5.55 <sup>a</sup>	0.05 $\pm$ 0.01 <sup>b</sup>	519.01 $\pm$ 28.29 <sup>a</sup>
	HD	60	533.50 $\pm$ 18.02 <sup>b</sup>	22.07 $\pm$ 2.56 <sup>ab</sup>	0.04 $\pm$ 0.00 <sup>a</sup>	555.57 $\pm$ 18.68 <sup>b</sup>
	HD	150	578.99 $\pm$ 19.28 <sup>c</sup>	22.67 $\pm$ 1.93 <sup>b</sup>	0.04 $\pm$ 0.00 <sup>b</sup>	601.66 $\pm$ 17.74 <sup>c</sup>
F-variety (1,71) <sup>4</sup>			1.48	4.08	2.50	0.29
F-density (1,71) <sup>4</sup>			2.79	1.37	2.50	0.01
F-nitrogen (2,71) <sup>4</sup>			52.97 <sup>***</sup>	5.17 <sup>*</sup>	5.00 <sup>*</sup>	32.95 <sup>***</sup>

<sup>1</sup>: LD = low density, HD = high density; <sup>2</sup>: All weights are presented as dry weights; <sup>3</sup>: Lowercase letters indicate homogenous nitrogen groups based on Tukey pairwise comparisons ( $p > 0.05$ ); <sup>4</sup>: F-values are based on GLMs for a split-split plot design; numbers in parentheses are degrees of freedom; \*  $p \leq 0.05$ , \*\*\*  $p \leq 0.005$ ; interaction terms were not significant.

#### 4. Discussion

Our results indicate how rice plasticity combined with a range of negative feedback mechanisms that are inherent to the rice ecosystem determine the stability and resilience of the rice crop in plots without pesticide applications (Figure 10). Despite different planting densities and differences in host resistance, rice yields were stable within seasons and fertilizer regimes. For example, relatively higher densities of *N. lugens* and *S. furcifera* (species that are frequently targeted in insecticide applications) on IR64 and, particularly, under high nitrogen had no apparent effects on yields in either season. Increasing plant density reduced the growth rates of individual plants, which probably reduced their susceptibility and tolerance to herbivores. Herbivore densities were lower in high-density plots. Herbivore and decomposer abundance responded positively to nitrogen levels during the dry season (Figures S1 and S3). Predators responded numerically to herbivore and decomposer

numbers in the dry season (Figure S4), and predator communities were strongly influenced by the abundance of potential prey items during the wet season (Figure 5). Parasitoids in particular were more abundant in plots of IR64, where planthoppers were most abundant. Therefore, maintaining a diversity of arthropods in the rice ecosystem can avoid potential yield losses from rice pests such as planthoppers. For example, natural enemies played a greater role than host plant resistance in protecting rice yields, as was indicated by similar yields in plots irrespective of functioning resistance. Furthermore, planthopper densities have been shown to rapidly decline over the rice growing season [46]. We discuss the dynamics of these interactions in the following sections.



**Figure 10.** Schematic representation of some of the main interactions of planting density, nitrogenous fertilizer, and host plant resistance with arthropod communities in tropical rice. Interactions are indicated as mainly positive (+), mainly negative (−), conditionally positive or negative (+/−; depending on arthropod species or levels of exposure), and part of a negative-feedback, regulatory mechanism (−fb). Lines indicate prominent directions of energy flow: solid arrows are direct effects, dashed arrows are indirect effects, and dotted arrows (within the rice plant) are trade-offs. Based on the results of the present study, nitrogenous fertilizer increases rice plant growth and can positively impact decomposer abundance (e.g., indirectly through increases in algal and plankton growth). Enhanced rice plant growth increases yields and tolerance against herbivores, but increases rice susceptibility to herbivores. Nevertheless, resistance against the brown planthopper is required if fertilizers are to increase tolerance to this pest. Increasing plant density decreases individual plant growth, potentially reducing tolerance and susceptibility to herbivores. High-density rice stands provide structural habitat for arthropods in general, but can negatively impact some arthropods (i.e., egg parasitoids in this study). High decomposer abundance in response to applied nitrogen increases natural enemy abundance through numerical and reproductive responses, thereby increasing herbivore vulnerability to generalist parasitoids and predators.

#### 4.1. Direct Effects of Planting Density and Nitrogen on Rice Plants

Rice planting density and nitrogenous fertilizer had significant effects on the growth and development of both rice varieties in our field experiment (Tables 1 and S3, Figure 9). During the experiment, nitrogenous fertilizer increased dry matter accumulation and improved yields without interacting significantly with planting density (Tables 1, 2 and S3). As predicted, higher densities created conditions for greater intraspecific competition and resulted in smaller rice plants with fewer tillers, and less root, shoot, and grain biomass (Table S3, Figure 9). By harvest time, more extensive tillering in the low-density plots meant that reproductive tiller densities were similar per unit area and yields were consequently similar under both high- and low-density planting for each of the three nitrogen levels and in both seasons (Table 2). During the early crop sampling, varying planting density had not yet affected tillering, but plants were smaller at the higher planting densities (Table 1). Several previous studies have shown similar patterns of increasing intraspecific competition affecting rice growth and development across gradients of planting density [24,40,41,60–62], which can sometimes affect yields per unit area (see below).

In previous studies that included a greater range of planting densities than in our study, and particularly where crops were established by direct seeding, intermediate seeding densities (tending toward higher densities) have generally resulted in higher yields. This often occurred with associated increases in the densities of panicles per unit area, but with fewer spikelets and often lower grain weights per panicle [26,35,37,43]. However, in some cases, trade-offs between panicle and spikelet densities per unit area meant that increasing plant/seeding densities had no significant effect on yields [23,34,36,39,62–66]; this also likely occurred each season in our study (Table 2). For transplanted rice, a small number of studies have indicated that high plant densities can reduce rice yields per unit area (i.e., 15 × 15 cm [67]; 12 × 8 cm, [24]). Declines in yield at high seeding densities may be due to lower photosynthesis rates and lower radiation use efficiency in stands with relatively high canopy closure [35,61]. Discrepancies between the effects of density on yields can depend on crop establishment method, seedling density per hill, plant type (i.e., hybrid versus inbred, or panicle shape), water management, tillage regime, and available nutrients in chemical and organic fertilizers, or derived from green mulches [40,41,68–76]. In direct-seeded systems, in particular, several researchers have shown that increasing seeding densities can compensate for reduced rates of nitrogenous fertilizer, thereby promoting sustainable resource use [41,73,75,76]. This was not observed in our study with transplanted rice.

We assessed root-to-shoot ratios in our study because large root systems can be associated with greater nutrient assimilation and improved tolerance to environmental stresses [68]. Our results indicated that root development was greater under low levels of soil nitrogen and that the root-to-shoot ratio of IR64 was greater than that of IR62 (Table 1; Figure 8). Although high-density planting significantly reduced root biomass, it did not reduce the root-to-shoot ratios (Table 1, Figure 8). Several studies have indicated how planting density can increase lodging potential in rice. Several varieties of rice are more vulnerable to lodging when grown under high nitrogen or planted at high densities [11,66,70,77,78]. This can be associated with a reduced light interception that affects the lignin and cellulose content of the rice stems [11] as well as changes to the stem structure (e.g., thickness, specific dry weight, etc. [70]). Furthermore, high nitrogen can reduce silicon assimilation in rice, thereby weakening the stem [4,78]. Zhao et al. (2020) [79] have shown that by reducing nitrogen levels, lodging rates in maize (*Zea Mays* L.) grown at high density can be reduced. In our experiments, a tropical storm during the wet season resulted in severe lodging (>50% under high nitrogen) of IR62 plants (Figure 8). There was a clear relationship between fertilizer use and lodging, but plant density had no apparent effect on lodging. We suggest that a lower root-to-shoot ratio in IR62, particularly under high nitrogen conditions, contributed to lodging in the variety.

#### 4.2. Effects of Host Variety and Nitrogen on Insect Herbivores

Increased rice herbivory due to nitrogenous fertilizers has been described in a number of previous studies (e.g., planthoppers, leafhoppers, black bug, stemborers, leaf folders, gall midge, and apple snails [5,7,17,19,20,22,80–82]) (Figure 10). We found that rodents also caused greater damage (Figure 7) and blast disease was most severe in our high nitrogen plots. Although we did not identify the rats in our study, simultaneous trapping studies noted *Rattus tatezumi* (Temminck) as the most abundant species in IRRI rice fields (Stuart, unpublished data). We also found a greater abundance of all arthropod herbivores (combined) in our high-nitrogen plots during the dry season (Figure S1), but trends for many of the individual species were generally weak in both seasons (Table S2). Planthopper numbers were higher in the high-nitrogen plots and in plots of IR64 in the dry season, but without any statistically significant interaction between these factors (Figure 1). In agreement with previous studies [19,22,82], this indicates that high nitrogen reduced the resistance of IR62 to planthoppers, but that the variety still maintained relatively low planthopper numbers compared to IR64 (Figure 1). In contrast to planthoppers, the densities of leafhoppers were actually lower under high nitrogen (Figure 2E). Because leafhoppers have been shown to respond positively to high nitrogen in greenhouse experiments [48,82], we suggest that the trend towards lower densities of leafhoppers in our high-nitrogen field plots was probably due to interspecific interactions with other herbivores (i.e., competition), or due to greater predation pressures in high-nitrogen plots (see for example, Figure 6, Figure S3). Overall, host resistance had several positive impacts: the abundance and density of planthoppers and leafhoppers were lower in plots of IR62 and leafhopper richness was also lower (Figure 1, Figure 2). Furthermore, *N. virescens* and *N. nigropictus* were less abundant on IR62 in the dry and wet seasons, respectively.

Although rice grown in plots under relatively high nitrogen is more attractive to herbivores, nevertheless, nitrogen also enhances the plant's ability to compensate for damage [4–7,18,19]. A notable exception occurs with *N. lugens*. This insect is attracted to plants with high phloem concentrations of the amino acid asparagine, as occurs in rice grown under high nitrogen [83]. Feeding by the planthopper reduces nitrogen uptake and assimilation by the rice plant [84], which often results in rapid mortality (known as 'hopperburn') in fields with high fertilizer use [1,18]. Host plant resistance can reduce planthopper fitness on high-nitrogen plants thereby allowing the plants to compensate for planthopper feeding [18,22]. We did not explicitly examine rice tolerance in our experiments. Tolerance is notoriously difficult to quantify, even under controlled conditions [18,22]. However, observations of plant health during the dry season suggest that nitrogen compensated for stress-related yellowing. This yellowing, which affected up to 10% of tillers in some plots (Figure 7C), was not associated with tungro virus during the dry season, but was more probably related to rodent damage (which potentially depletes nutrient resources to remaining, uncut tillers) and to water deficits. During the wet season, tungro virus was detected, but it was not widespread and was not associated with nitrogen levels. Tungro was more prevalent in IR64 than in IR62, which followed trends in the abundance of leafhopper vectors (Figure 2D) and yellowing (Figure 7D) in the wet season, and indicates how resistant varieties with the *Bph3* locus can be used to reduce tungro damage.

#### 4.3. Effects of Planting Density on Herbivores

We predicted that planthoppers and leafhoppers would attain higher densities on rice plants grown at low densities. We based our predictions on higher growth rates and delayed maturity of rice at low densities, particularly since intraspecific competition had not yet affected tiller densities at 30 DAT (Table 1, Figure 7). However, recent research has indicated that rice grown at low densities has greater antioxidant enzyme activity, which is associated with improved anti-herbivore defenses [85]. Furthermore, plants at high densities can create relatively humid microclimates [42] that are better suited to planthoppers and leafhoppers (Figure 10). As originally predicted, we found higher densities of planthoppers and leafhoppers in the low-density plots (Figures 1 and 2). However, commu-

nity analysis revealed that two of the most abundant planthopper species, *S. furcifera* and *N. lugens*, tended to segregate to low- and high-density plots, respectively (Figure 3). To our knowledge, ours is the first study to report possible rice density effects on these planthoppers. However, similar trends were noted by Ishii-Eiteman and Power (1997) [24] for rice leafhoppers in field-plots in Thailand. These authors found that leafhopper densities were highest where rice had been transplanted (as opposed to direct-seeded) and at low plant densities. Furthermore, *N. virescens* was more abundant in direct-seeded fields and *N. negropictus* in transplanted fields. The movement between plants by both species was also greater in low-density and in transplanted fields [24]. Way et al. (1983) [30] also found that the aster leafhopper (*Macrostelus fascifrons* (Stål)) was more abundant in rice planted at relatively low densities. These authors suggested that low planting densities allowed the development of aquatic weeds that supported high densities of the polyphagous leafhopper that moved between the weeds and the rice. In contrast, a study from Cote d'Ivoire by Oyediran and Heinrichs (2001) [26] found that leafhoppers (*Nephotettix* spp.) were more abundant in rice fields that were transplanted or direct-seeded at relatively high densities; however, these authors did not correct for differences in plant biomass in their study and, because samples were pooled over the growing season, it is likely that the leafhopper densities were higher in low-density plots. In our study, higher densities of planthoppers and leafhoppers in low-density plots may be partly related to increased mobility between rice plants at low densities [24]; however, based on partitioning of the two abundant planthoppers in this study, and the two abundant leafhoppers in the study by Ishii-Eiteman and Power (1997) [24], to fields under distinct crop establishment methods, it is probable that condition-dependent (i.e., plant density) interspecific competition between the species at least partially determined relative abundances [50,86,87]. Together, these results suggest that high planting density affects planthoppers and leafhoppers directly by restricting movement, and indirectly through condition-dependent interspecific competition.

We did not detect any plant-density effects on other insect herbivores (Table S2). However, rodent damage was strongly associated with high-density planting in both seasons. This was contrary to our prediction that herbivores would select fast-growing plants. One possible explanation is that rodents foraged for longer in our high-density plots because they perceived these plots provided a better refuge against predators (i.e., a response to the 'landscape of fear' [88]). Another explanation is that the rodents may have been attracted to the phenologically advanced rice in the high-density plots, which has a greater nutritional value for rodents [88–90]; however, rodent damage was high in plots of both varieties under high density, whereas flowering was accelerated more in IR64 and under low-nitrogen (Figure 7). For many herbivores, and particularly for rodents, our plots provided a choice of foraging. Therefore, greater damage observed in our high-density plots may not translate into increased vulnerability of rice fields under high-density planting at larger spatial scales. Nevertheless, by creating a more suitable environment for rodents, that provides better cover from perceived enemies, rice planted at high densities could reduce rodent displacement in the rice landscape and increase energy gains from rice foraging.

A small number of previous studies have examined plant-density effects on other rice herbivores. Results have not generally been consistent. For example, studies have indicated that high-density stands reduced damage by *Chilo partellus* (Swinhoe) and *Sesamia calamistis* Hampson in transplanted rice [21] but increased damage by Diopsidae stemborers in direct seeded rice [26]. Litsinger et al. (2003) [43] found that increasing densities of upland rice were associated with reduced oviposition by the rice seedling maggot (*Atherigona oryzae* Malloch), but because of lower tolerance or reduced cannibalism, damage was higher in high-density plots. Viajante and Heinrichs (1985) [29] also reported lower oviposition by rice whorl maggot (*Hydrelia philippina* Ferino) in high-density rice stands. Finally, several studies indicated higher oviposition, larval densities, and root scaring by the rice water weevil (*Lissorhoptrus oryzophilis* Kuschel) in low-density compared to high-density rice stands in the USA [23,27,28]; however, the effects on relative rice tolerance to weevil

damage at low and high planting densities remain unclear [23,27]. Planting density can also affect the incidences of rice diseases (generally higher disease levels under high planting density [91,92]) and weeds (generally lower weed biomass under high planting density [64,69,93]).

#### 4.4. Effects of Host Resistance, Nitrogen, and Planting Density on Arthropod Communities

Our analyses of arthropod communities highlighted distinct factors that influenced the structures of different guilds. Planthopper and leafhopper community structure was strongly affected by planting densities (dry season) (Figure 3); decomposer community structure by fertilizer levels (dry season) (Figure 4); and predator community structure by the availability of prey items (wet season) (Figure 5). These results support previous models of rice ecosystem functions that indicate decomposers, specifically, as influencing predation pressures for key rice herbivores at early rice crop stages [47]. Our results further suggest that decomposers respond to fertilizer levels in the rice ecosystem by increasing species richness and abundance (Figure 4, Figure S2). Most of the decomposer species we recorded were chironomid flies that have aquatic larval stages. Although fertilizers can kill aquatic organisms, once nitrogen is assimilated into the environment it often leads to increased densities of algae, zooplankton, and aquatic weeds that are food for decomposers [80,94]. These decomposer organisms in turn represent an important food for predators during early rice crop stages [95].

Our analyses indicated that predators, particularly spiders, were most abundant where prey abundance was highest (Figure 5) thereby depicting the role of predators as regulators of prey density (Figure 10). During the dry season, this resulted in higher predation pressures for planthoppers and leafhoppers in high-density rice stands. Furthermore, predation pressures were particularly high where IR62 was planted at high densities (Figure 6) because planthopper and leafhopper abundance was lower on the resistant variety (Figure 1, Figure 2). Despite higher predation pressures on IR62 in the dry season, the richness, abundance, and densities of parasitoids and predators were greater in plots of IR64 (Table S2, Figure S4). Peñalver-Cruz and Horgan (2022) [48] have previously discussed how these trends support the Optimal Defense Hypothesis for parasitoids, whereby vulnerable plants use volatiles or honeydew-related cues to draw in egg parasitoids. Although the densities of predators per plant biomass were lower in the high-density plots (Figure S4), spiders and other predators are highly mobile cursorial hunters and may more easily move between plants in high-density plots (thereby avoiding surface water) to encounter aggregations of herbivores (e.g., planthoppers and other herbivores generally have aggregated distributions in rice fields [1,96]). Therefore, rice planting density also probably indirectly determines planthopper and leafhopper abundance through its effects on predator densities and behavior. Previous studies with rice planthoppers have indicated that plant nitrogen can reduce aspects of egg parasitoid and predator efficacy [32,33]. However, despite such negative impacts of nitrogen, our analyses suggest that spiders in particular will protect vulnerable plants by responding to prey densities (e.g., planthoppers and leafhoppers were among the most abundant organisms in our samples) and, furthermore, that decomposer responses to nitrogen could counter fertilizer-induced susceptibility of the rice crop to herbivores by drawing-in predators.

## 5. Conclusions

We found that transplanting rice at relatively high densities reduced planthopper and leafhopper densities, but increased rodent damage. Planting density probably directly affected rodents by providing refuges for foraging animals. Host plant resistance reduced planthopper and leafhopper abundance, but nitrogenous fertilizers countered resistance. Nitrogen also increased damage from rodents and blast disease in both rice varieties, and was associated with lodging in IR62. However, nitrogen was associated with high numbers of decomposer organisms in the dry season, which can sustain natural enemy numbers. Furthermore, natural enemies, particularly spiders, responded positively to the availability

of prey items (including decomposers) in the wet season. Overall, predation pressures were greater for planthoppers and leafhoppers on resistant rice under high planting density as observed during the dry season. High planting density also probably reduces the movement of adult insect herbivores between plants, but facilitates movement by cursorial species such as spiders. The interrelations between different arthropod guilds and other emerging patterns from this study, support the idea that herbivore densities in rice ecosystems are regulated through several interacting negative feedback mechanisms. Our results indicate that plasticity in rice growth, together with diverse arthropod communities (including decomposers and natural enemies) support rice ecosystem resilience by diminishing the impacts of varying host resistance, fertilizer levels, and planting density on crop vulnerability to insect herbivores. Therefore, conserving arthropod diversity is vital to preserving the sustainability and resilience of rice production systems.

**Supplementary Materials:** The following are available online at <https://www.mdpi.com/article/10.3390/agriculture12122053/s1>, Table S1 Planthoppers and leafhoppers captured during blow-vac sampling; Figure S1: Species richness, abundance and density of herbivores (all species combined) in rice plots with resistant and susceptible rice transplanted at low and high densities under varying nitrogen fertilizer treatments; Figure S2: Species richness and abundance of decomposers (all species combined) in rice plots with resistant and susceptible rice transplanted at low and high densities under varying nitrogen fertilizer treatments; Figure S3: Species richness, abundance, and density of free-living parasitoids in rice plots with resistant and susceptible rice transplanted at low and high densities under varying nitrogen fertilizer treatments; Table S2: Abundant rice herbivores (other than planthoppers and leafhoppers) and natural enemies captured during blow-vac sampling; Figure S4: Species richness, abundance, and density of all predators in rice plots with resistant and susceptible rice transplanted at low and high densities under varying nitrogen fertilizer treatments; Table S3: Rice plant condition at harvest.

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