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### **Landscape context does not constrain biological control of *Phenacoccus manihoti* in intensified cassava systems of southern Vietnam**

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**Landscape context does not constrain biological control of *Phenacoccus manihoti* in intensified cassava systems of southern Vietnam**

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**Abstract**

In 2008, the cassava mealybug, *Phenacoccus manihoti* (Homoptera: Pseudococcidae) was inadvertently introduced to Southeast (SE) Asia, where it inflicted severe damage on cassava and impacted countless farming families and rural agro-industries. The host-specific endophagous parasitoid *Anagyrus lopezi* (Hymenoptera: Encyrtidae) was imported into Thailand in 2009, yet nothing is known about the degree to which *A. lopezi* establishment, in-field colonization and impact on *P. manihoti* populations is shaped by local agro-landscape context. In this study, we contrasted temporal population fluctuations of *P. manihoti*, *A. lopezi*, and associated hyperparasitoids within low- and high-diversity landscapes in Tay Ninh (Vietnam). Across years and landscape types we found  $24.8 \pm 17.7\%$  (mean  $\pm$  SD) plants infected with *P. manihoti* and on average  $5.6 \pm 5.3$  mealybugs per cassava tip. High parasitism levels were attained across both years, with season-long averages of 49.9-52.1% in either low- or high-diversity settings. Hyperparasitism levels were on average  $2.8 \pm 5.4\%$ , and a total of three hyperparasitoid species were recorded. Cassava age was a significant predictor of *P. manihoti* incidence, abundance, parasitism rate and hyperparasitism rate. Landscape type significantly affected *P. manihoti* incidence and hyperparasitism rate (at particular ages), but not *P. manihoti* abundance or parasitism rate. At the scale of individual cassava tips and entire fields, *A. lopezi* expressed a strong density-dependent response to *P. manihoti* during the early season. This work constitutes the first, comprehensive assessment of *A. lopezi* establishment, parasitism rates, and parasitoid x host dynamics from a key cassava-growing region in SE Asia. Our study underlines how this exotic parasitic wasp effectively suppresses a globally-important insect pest in its newly invaded range, thus providing cost-free, environmentally-sound and lasting control across the developing-world tropics.

**Keywords:** natural enemy; tropical agriculture; ecosystem services; landscape fragmentation; arthropod biological control; landscape simplification

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## 1. Introduction

The cassava mealybug, *Phenacoccus manihoti* Matile-Ferrero (Homoptera: Pseudococcidae) is a prominent pest of cassava (*Manihot esculenta* Crantz; Euphorbiaceae) and one of the world's most notorious invasive species. Endemic to the Paraguay River basin, *P. manihoti* was inadvertently introduced into Africa during the early 1970s and subsequently spread through the continent's extensive cassava belt (Herren & Neuenschwander, 1991; Bellotti et al., 2012). Capable of inflicting yield losses up to 58-84% (Nwanze, 1982; Schulthess et al., 1991), *P. manihoti* devastated local cassava production and impacted food security for underprivileged rural populations across sub-Saharan Africa. In late 2008, this same pest was detected in Thailand, where it was reportedly causing root yield reductions up to 50% and economic losses over US \$30 million nationally (Muniappan et al., 2009; TTTA 2011). By 2014, *P. manihoti* had spread extensively into neighboring countries and several Indonesian islands (Sartiami et al., 2015; Graziosi et al., 2016). Climate-based niche modeling revealed that other key production areas in eastern Indonesia and the Philippines are also climatically suitable for *P. manihoti* (Yonow et al., 2017). As Southeast Asia houses a multi-billion dollar cassava industry and accounts for nearly 95% of the world's cassava exports (Cramb et al., 2017), the (socio-)economic impacts of this pest were projected to be exceptionally large.

With the 1981 introduction of *Anagyrus lopezi* (De Santis) (Hymenoptera: Encyrtidae) in West Africa, a globally-acclaimed biological control program against *P. manihoti* was started (Neuenschwander et al., 2001). This solitary, host-specific parasitoid had earlier been collected in Paraguay and southern Brazil from small *P. manihoti* colonies on cassava (Lohr et al., 1990). Following its release in Nigeria, *A. lopezi* promptly established and suppressed *P. manihoti* population levels from more than 100 to fewer than 10-20 individuals per tip (Hammond et al.,

1987). In less than three years following its release, *A. lopezi* had effectively dispersed over 200,000 km<sup>2</sup> and colonized the vast majority of cassava fields within this range (Herren et al., 1987). Though multiple endemic primary parasitoids and hyper-parasitoids were recorded in mealybug-invaded areas in Africa (Neuenschwander et al., 1987a; Neuenschwander & Hammond, 1988), these largely did not impede the success of *A. lopezi* as biological control agent (Neuenschwander, 2001). Overall, the parasitic wasp successfully established in 26 different African countries, prevented wide-spread famine and generated long-term economic benefits of US\$ 9.4-20.2 billion (Zeddies et al., 2001).

In late 2009, *A. lopezi* was introduced from West Africa into Thailand and subsequently into Indonesia, through a joint endeavor between the Food and Agriculture Organization (FAO), CGIAR centers and Thai governmental institutions (Winotai et al., 2010; Wyckhuys et al., 2015). Other methods promoted for *P. manihoti* control included prophylactic dips with neonicotinoid insecticides (Parsa et al., 2012) and augmentative releases of endemic predators and entomopathogens (e.g., Saengyot & Burikam, 2012; Sattayawong et al., 2016). However, it has largely been deemed that *A. lopezi* effectively suppressed local mealybug populations. In a first regional assessment during 2014-2015, *A. lopezi* was routinely found in *P. manihoti*-affected fields at parasitism levels of 10-57% (Wyckhuys et al., 2017a). Yet, from smallholder fields in Cambodia, a diverse and speciose complex of hyperparasitoids or mummy parasitoids was equally recorded (Wyckhuys et al., 2017b).

Natural enemy abundance and performance, as much as pest pressure, are shaped by a wide range of variables at a field, farm, and agro-landscape level. In Asian cassava fields, patch-level characteristics, such as soil parameters and a plant's phytopathogen infection status, readily modulate *A. lopezi* × *P. manihoti* interactions (Wyckhuys et al., 2017a, b). Landscape-dependent

impacts on cassava mealybug biological control have rarely been inferred in past studies, and so far have not been studied in-depth. Though the effects of landscape structure on natural enemy abundance, diversity, and activity have been relatively well investigated (e.g., Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Veres et al., 2013; Schellhorn et al., 2015b), much less is known about its impacts on pest pressure or (natural) biological control. Yet, for specialist parasitoids such as *A. lopezi*, habitat loss and landscape simplification could be particularly disruptive (Cagnolo et al., 2009). Also, while landscape-level interactions have been assessed to a fair extent for annual cropping systems under temperate conditions, they have only received scant attention in (semi-)perennial cropping systems in the tropics (but see Tylanakis et al., 2007; Pak et al., 2015). Lastly, fourth-trophic level organisms, such as hyperparasitoids, have only received peripheral attention in landscape ecology studies (Rand et al., 2012; Plecas et al., 2014), even though they are highly responsive to landscape complexity, are connected to arthropod population dynamics across habitats, and may release herbivores, such as *P. manihoti*, from biological control (Sullivan & Volk, 1999).

In this study, we examine landscape-level effects on *P. manihoti* biological control in intensified cassava cropping systems of southern Vietnam (i.e., Tay Ninh province). We characterize overall *P. manihoti* population levels across two successive growing seasons, assess *A. lopezi* establishment and impact, and describe the resident hyperparasitoid community. Furthermore, we contrast mealybug-parasitoid-hyperparasitoid dynamics in fields embedded within simplified, large-scale landscapes vs. complex, small-scale settings. This study adopts a landscape ecology approach, yet is no landscape analysis *sensu stricto* as it is not guided by structural indicators of landscape composition or spatial configuration (Mühlner et al., 2010; Birkhofer et al., 2018). Our work constitutes the first, comprehensive assessment of *A. lopezi*



parasitism rates and parasitoid  $\times$  host dynamics from a key cassava-growing area in SE Asia, examines *P. manihoti* biological control through a (novel) landscape ecology lens, and provides valuable insights to guide further (invasive) pest mitigation programs.

## 2. Materials and methods

### 2.1. Study sites

Our study was conducted in several rural communes of Tay Ninh province, southern Vietnam (Fig. 1); an area characterized by highly-intensified cassava production, with staggered (overlapping) planting and near-continuous, year-long cultivation. Local cassava fields are routinely established with locally-sourced stem cuttings (i.e., stakes), receive ample fertilizer and herbicide inputs during the first 3-4 months, and are manually harvested at 9-12 months after planting. Overall, two different types of cassava fields and associated agro-landscapes could be identified in Tay Ninh. First, in certain areas, cassava fields are small (1-2 ha in size) and embedded within relatively complex and diverse landscape settings. Surrounding habitats consist of equally small-sized plots of cassava or semi-perennial crops such as rubber (*Hevea brasiliensis* (Willd. ex A. Juss.) Müll. Arg.; Euphorbiaceae), custard-apple (*Annona squamosa* L.; Annonaceae), sugarcane (*Saccharum sp.*; Poaceae), banana (*Musa sp.*; Musaceae) or plantation forest (here termed ‘high-diversity’ sites). Second, other landscape sectors are primarily made up of larger fields, ranging between 4-8 ha, surrounded by other cassava fields and thus creating simplified, homogeneous landscapes (here termed ‘low-diversity’ sites). In these settings, fields have lower perimeter-to-area ratios and less extended field boundaries.

Field work was initiated in January 2014, at the onset of the dry season, and continued over the course of two consecutive cassava-growing seasons. At the start of each season, fields were

selected by inspection of Google Maps and on-site ‘ground-truthing’. Landscape sectors were chosen with a radius of 1 km in size; a spatial scale that’s proven appropriate for the study of small-sized natural enemies such as aphid parasitoids and mirid bugs (e.g., Carriere et al., 2006; Plecas et al., 2014). A total of eight, newly-planted cassava fields were chosen of uniform age, crop variety, developmental stage and crop management, four in high-diversity and four in low-diversity settings. Particular care was taken to avoid confounding effects of biophysical or management variables such as fertilizer use, acaricide sprays or herbicide application rates (e.g., Bianchi et al., 2006). Fields were at least 1 km apart, and selection of fields was done in close collaboration with officials from the Plant Protection sub-Department of Tay Ninh province and with consent from individual growers. Each field was visited on a bi-monthly basis until late July 2015, thus covering a total of two consecutive seasons. Fields that were covered in our survey were typically planted in November, at the end of rainy season, and harvested between September and October. Field visits thus were conducted in January (2-month after planting), March (4 months), May (6 months) and July (8 months). Field visits were thus carried out during the regional dry season (November-April) and rainy season (May-October), over the course of two consecutive years.

## 2.2. Survey protocol & sample processing

Focal fields were sampled a total of 8 times, and insect surveys were done every two months to characterize *P. manihoti* (plant-field) abundance and (field-level) incidence and parasitoid species composition. Linear 10-15 m transects along which ten consecutive plants were screened were established in a random fashion in each focal field, at distances >2 m from the field border. Different transects were established at each subsequent field visit. By doing so, a total of 50

plants per field were assessed for presence of arthropods, *P. manihoti* infection status (and associated ‘bunchy top’ symptoms; Neuenschwander et al., 1987a), and per-plant *P. manihoti* abundance. In-field identification of mealybugs was based on morphological characters such as coloration and length of abdominal waxy filaments (see Graziosi et al., 2016). All mealybug species were collected and placed in 1.5 ml Eppendorf tubes filled with 70% or 90% ethanol and stored at -20°C until further processing. Mealybug samples were sent to Chamaiporn Buamas of the Thailand Department of Agriculture (DoA) in Bangkok, Thailand, where specimens were identified using morphological features and dichotomous keys. Field-level *P. manihoti* infestation was expressed both as the proportion of plants infested (i.e., incidence) and average number of *P. manihoti* per plant (i.e., abundance).

To assess *A. lopezi* parasitism rates and to describe the parasitoid community associated with *P. manihoti*, a total of 20 mealybug-infested tips or ‘bunchy tops’ were collected from each field and transferred to the laboratory. Sampling procedures were adapted from Neuenschwander & Hammond (1988), and consisted of breaking off a 20-cm upper section or ‘tip’ of each mealybug-infested plant, and placing those in sealed paper bags. Prior to bagging, tips were inspected and voracious predators such as coccinellids and lacewing larvae were removed. Next, bags with plant material were placed within a cooler box. Upon arrival in the laboratory, cassava tips were carefully examined, and the total number of *P. manihoti* were counted. As mixed mealybug colonies are regularly encountered in the field (e.g., Graziosi et al., 2016), other species were removed from the plant tips. Next, cassava tips were placed separately within transparent polyvinyl chloride (PVC) containers (40 cm in height, 25 cm diam.), and covered with fine cotton fabric mesh. Over the course of three weeks, containers were stored at ambient

conditions (25-30°C) and 12:12 L:D cycle, and inspected on a daily basis for emergence of parasitic wasps.

Parasitoids and possible hyperparasitoids were collected with a handheld aspirator and transferred to 1.5 ml Eppendorf tubes with 75% ethanol for subsequent identification. Prior to discarding the samples, each tip was carefully inspected for the presence of any un-enclosed parasitoid mummies. Primary parasitoids such as *A. lopezi* can be attacked by either hyperparasitoids or mummy parasitoids, but no distinction was made between these guilds. Our experimental protocol did not allow us to distinguish the exact (primary) parasitoid host of particular hyperparasitoids. Ecological role of each of the different parasitoid species was queried in the Universal Chalcidoidea Database and Taxapad (Noyes, 2003; Yu et al., 2012). Specimens of each of the parasitoid and possible hyperparasitoid species were labeled, and sent for identification to the USDA Systematic Entomology laboratory in Washington DC, USA. Hyperparasitoid generic determinations were made using Hayat (1998) and Gibson et al. (1997). Specimens were identified to species via primary literature followed by comparison with reliably identified material in the National Museum of Natural History (Washington, DC). Voucher specimens of mealybugs and parasitoid wasps were deposited at the Plant Protection Research Institute (PPRI) in Hanoi, Vietnam.

Percentage parasitism was calculated by dividing the total number of emerged parasitoids by the total number of mealybugs per tip, and percentage hyperparasitism was calculated as the number of emerged hyperparasitoids divided by number of emerged primary parasitoids. Parasitism rates were computed for individual cassava tips, and average field-level parasitism rates were calculated for each sampling date. The sex of emerged *A. lopezi* wasps was determined and sex ratio was expressed as the proportion of adults that were female. For each field and sampling

date, we also computed cumulative mealybug-days (CMD) as an adaptation of measures developed by Ragsdale et al. (2007) for evaluation of soybean aphid populations over time in North America. More specifically, we assessed mealybug population by converting the average number of mealybugs per plant on a given sampling date to CMD measures:

$$\sum_{n=1}^{\infty} = \left( \frac{x_{i-1} + x_i}{2} \right) \times (t_i - t_{i-1})$$

where  $n$  is the total number of days over which sampling took place,  $x_i$  is the number of mealybugs counted on day  $i$ , and  $t_i$  is the number of days since the initiation of sampling on day  $i$ . CMD indices were further adjusted by accounting for field-level incidence rates. This approach allowed us to compare *P. manihoti* population curves between years and landscape contexts.

### 2.3. Statistics

We used analysis of variance (PROC MIXED, SAS version 9.1; SAS Institute, Cary, NC) with field as random factor, and tested the effect of landscape type (high- or low-diversity) on mealybug incidence and abundance, *A. lopezi* parasitism and potential hyperparasitism. We also tested the effect of cassava age, sampling date and year, and their interaction with landscape type for *P. manihoti* incidence, abundance and *A. lopezi* parasitism using the same approach. Means were compared with least squares means approach. Repeated measures analysis of variance (ANOVA) was equally carried out to assess effects of the above variables on CMD measures. Regression analysis and curve fitting were employed to assess density-dependent parasitism at the level of individual cassava tips and at a field scale. Regression statistics were compared between sampling dates (or cassava age) and landscape types. Mealybug abundance data were

log-transformed while incidence, parasitism and hyperparasitism data were arcsine-transformed to meet normality.

### 3. Results

#### 3.1. Mealybug & parasitoid community composition

In field surveys from 2014 to 2015, a total of four different mealybug species were recorded from cassava fields: *P. manihoti*, *Pseudococcus jackbeardsleyi* Gimpel and Miller, *Paracoccus marginatus* Williams and Granara de Willink, and *Ferrisia virgata* (Cockerell). Across sites and years, *P. manihoti* constituted 91.4% of the mealybug complex, with other species representing 5.7%, 2.8% and 0.2%, respectively. Field-level incidence of *P. manihoti* ranged from 0% to 82% across both years, with an average of  $24.8 \pm 17.7\%$  (mean  $\pm$  SD) plants infected with at least one mealybug. Mealybug abundance ranged from 0 to 698 mealybugs per cassava tip, and on infected tips an average of  $5.56 \pm 5.03$  individuals were found. From 1,280 collected cassava tips (or 'bunchy tops'), we recorded a total of 14,547 *P. manihoti* at average infestation levels of 11.36 individuals per tip. A total of 7,673 *A. lopezi* wasps and 233 potential hyperparasitoids emerged from field-collected tips held in the laboratory. Hyperparasitism levels were on average  $2.79 \pm 5.38\%$ , with a maximum hyperparasitism rate of 26.4% (recorded in 2015 dry season; high-diversity site). The primary parasitoid community was entirely comprised of *A. lopezi*. Season-long *A. lopezi* sex-ratio was recorded as 36.9% (prop. female). The hyperparasitoid community was composed of *Chartocerus* sp. near *walkeri* Hayat (Signiphoridae; 46.0%), *Promuscidea unfasciiventris* (Eriaporidae; 53.7%) and *Prochiloneurus* sp. (Encyrtidae; 0.4%). In high-diversity setting, *P. unfasciiventris* was the main hyperparasitoid (61.2%) while *Chartocerus* sp. (85%) dominated the hyperparasitoid community in low-diversity settings.

### 3.2. *Host × parasitoid dynamics*

Mealybug incidence fluctuated greatly across sampling dates, and was affected by landscape type (Fig. 2a) and cassava age (Fig. 3a). Overall, *P. manihoti* incidence was significantly higher in high-diversity fields compared to low-diversity fields, with increasing incidence across the cropping season up until 6 months of age. Significant effects were recorded for landscape type ( $F_{1,45} = 16.69$ ;  $P = 0.0002$ ), collection date ( $F_{1,45} = 11.60$ ;  $P < 0.0001$ ) and age ( $F_{3,53} = 24.13$ ;  $P < 0.0001$ ), but not for their interaction. Season is reflected in the age of cassava fields, as dry season basically covered fields of ages 2-4 months, while the rainy season included 6-8 month old fields. In the dry season, *P. manihoti* field-level incidence was  $16.3 \pm 3.2\%$  and  $31.1 \pm 5.8\%$  (average  $\pm$  SE) in low- and high-diversity settings, respectively. In the rainy season, respective incidence was  $22.1 \pm 3.2\%$  and  $29.5 \pm 4.2\%$ . Incidence levels did not vary between the two years of sampling ( $F_{1,57} = 0.08$ ;  $P = 0.7802$ ).

Similarly, *P. manihoti* abundance per tip varied significantly across the study period (Fig. 2b) and with cassava age (Fig. 3b). Landscape diversity and sampling date significantly affected mealybug abundance ( $F_{1,780} = 11.2$ ;  $P = 0.0009$  and  $F_{7,780} = 6.63$ ;  $P < 0.0001$  respectively), as well as their interaction ( $F_{7,780} = 4.63$   $P < 0.0001$ ), with mealybug numbers significantly higher in high-diversity fields compared to low-diversity fields. Younger fields harbor significantly higher numbers of mealybug ( $F_{3,788} = 13.60$ ;  $P < 0.0001$ ) compared to older fields, but population abundance did not vary between the two years of sampling ( $F_{1,792} = 1.59$ ;  $P = 0.2074$ ). On average, dry-season mealybug abundance was  $5.9 \pm 1.3$  and  $8.7 \pm 1.7$  individuals per infested tip for low- and high-diversity settings, respectively. In the rainy season, *P. manihoti* abundance dropped to respective levels of  $3.8 \pm 0.6$  and  $3.7 \pm 0.4$  individuals per tip.

Mealybug population build-up varied between years and landscape types (Fig. 4), with season-long mealybug abundance being highest in high-diversity settings. Cumulative mealybug-days were significantly affected by landscape type ( $F_{1,54} = 23.491$ ,  $P < 0.001$ ), cassava age ( $F_{3,54} = 24.145$ ,  $P < 0.001$ ) and the interaction of landscape diversity  $\times$  year ( $F_{2,54} = 4.415$ ,  $P = 0.017$ ).

*Anagyrus lopezi* parasitism was higher in high diversity landscapes as compared to low diversity ones, and gradually increased over the dry season up until cassava was 4-6 months old (Fig. 2c and 3c). Parasitism levels were affected by diversity ( $F_{1,1261} = 5.01$ ;  $P = 0.0254$ ), collection date ( $F_{7,1261} = 51.39$ ;  $P < 0.0001$ ) and their interaction ( $F_{7,1261} = 4.33$ ;  $P < 0.0001$ ), and age ( $F_{3,1269} = 95.52$ ;  $P < 0.0001$ ). Parasitism levels were significantly higher in 2014 compared with 2015 ( $F_{1,1273} = 21.24$ ;  $P < 0.0001$ ). Parasitism rates were  $43.2 \pm 6.7\%$  and  $44.6 \pm 6.1\%$  for low- and high-diversity settings in the dry season, respectively. In the rainy season, respective rates were  $47.1 \pm 5.7\%$  and  $53.6 \pm 4.8\%$ . Variability in *A. lopezi* parasitism (coefficient of variation, CV) was  $1.00 \pm 0.73$  and  $0.82 \pm 0.63$  for low- and high-diversity settings, with CV rates significantly affected by cassava age ( $F_{1,62} = 23.299$ ,  $P < 0.001$ ).

Potential hyperparasitism varied significantly across sampling dates (Fig. 2d), with lowest levels in 2-month old cassava ( $F_{7,1261} = 3.62$ ;  $P = 0.0007$ ). Though landscape type did not affect potential hyperparasitism ( $F_{1,1261} = 2.86$ ;  $P = 0.0909$ ), the interaction between sampling date and landscape diversity was significant ( $F_{7,1261} = 3.32$ ;  $P = 0.0017$ ).

### 3.3. Density-dependent parasitism

At the level of individual cassava tips (see Segoli, 2016), a quadratic relationship was recorded between parasitism rate and mealybug abundance (Fig. 5c;  $F_{2,2077} = 36.700$ ,  $P < 0.001$ ). This regression pattern was sustained under low- and high-diversity landscape types ( $F_{2,1037} = 36.808$ ,



$P < 0.001$ ;  $F_{2,1037} = 6.619$ ,  $P = 0.001$ ). In early season (2-month old) fields, the quadratic regression was sustained for the overall data-set ( $F_{2,317} = 43.585$ ,  $P < 0.001$ ), and also for low- and high-diversity landscape contexts separately (Fig. 3a;  $F_{2,157} = 27.488$ ,  $P < 0.001$ ;  $F_{2,157} = 18.741$ ,  $P < 0.001$ , respectively). In late season (8-month old) fields, no relationship was recorded between parasitism rates and mealybug abundance in the full data-set (Fig. 5b), but statistically significant patterns were recorded for low- and high-diversity contexts separately ( $F_{1,238} = 11.015$ ,  $P = 0.001$ ;  $F_{2,237} = 7.181$ ,  $P = 0.001$ , respectively).

At the level of entire fields, highly-significant regression was recorded within the full two-year dataset between *A. lopezi* parasitism rate and mealybug density, under both low-diversity and high-diversity landscape contexts ( $F_{1,30} = 15.771$ ,  $P < 0.001$ ;  $F_{1,30} = 15.671$ ,  $P < 0.001$ ). Significant regression patterns were only found for 2-month old plots, under both low- and high-diversity landscape contexts (Fig. 6;  $F_{1,6} = 18.760$ ,  $P = 0.005$ ;  $F_{1,6} = 13.935$ ,  $P = 0.010$ , respectively).

#### 4. Discussion

As the stage for one of the world's greatest biological control successes (Neuenschwander, 2001), cassava cropping systems possess unique and noteworthy features. Being long-season crops exposed to comparatively few disturbances, cassava systems provide habitats of prolonged durational stability and vegetational complexity for myriad natural enemies. The secretion of extra-floral nectar by the cassava plant also constitutes a favorable trait for multiple beneficial organisms, including hymenopteran parasitoids (e.g., Pinto-Zevallos et al., 2016). *Anagyrus lopezi* itself equally possesses an exceptional dispersal potential of 20 km per generation, a high degree of adaptation to varying agro-ecological conditions, host-feeding capabilities and an

ability to persist at low *P. manihoti* densities (Neuenschwander et al., 1989). Thus are well-adapted to provide effective biological control in novel settings, including Asia's intensified and dynamic cassava production landscapes.

The above life history and ecological traits of *A. lopezi* help explain its sustained presence in settings with year-long staggered cassava planting, and the minimal differences in its population build-up between landscape types. Given the high mobility of *A. lopezi*, our choice of a 1-km radius to assess landscape composition likely did not effectively account for the insect's perceptual range (or the 'spatial extent at which movement decisions are made'; Olden et al., 2004), and the parasitoid is likely to face continuous spatiotemporal availability of resources irrespective of landscape context (Schellhorn et al., 2015a). Furthermore, *A. lopezi* readily encounters carbohydrate and other vital resources on mealybug-infested cassava plants, thus minimizing a need for landscape-level foraging (Burger et al., 2005; Roitberg & Gillespie, 2014). Also, adequate crop husbandry likely benefited wasp populations further by boosting *A. lopezi* development (Wyckhuys et al., 2017a) and possibly increasing secretion rates or amino acid content of cassava extrafloral nectar (Lundgren, 2009). These patch and landscape characteristics, coupled with the favorable life history traits of *A. lopezi*, could have contributed to the high mealybug parasitism levels in our study. Across both years, *A. lopezi* parasitism rates (i.e., season-long averages of 49.9 and 52.1% in low- and high-diversity settings) were markedly higher than the maximum 30% levels in smallholder-managed fields in Africa (Hammond & Neuenschwander, 1990).

Maximum field-level *P. manihoti* incidence of  $33.5 \pm 7.9\%$  and  $58.0 \pm 0.9\%$ , and plant-level *P. manihoti* abundance of  $8.9 \pm 5.1$  and  $16.3 \pm 4.0$  individuals per tip in low- and high-diversity settings, respectively was far below economic threshold levels. Local pest pressure is identical to

that in Africa, when *P. manihoti* populations collapsed after *A. lopezi* release and stabilized at 23% incidence and abundance <10 individuals per tip (Hammond & Neuenschwander, 1990). Similar to the African case, Vietnam's *P. manihoti* populations built up during the second half of the dry season and remained at low levels during the rainy season. As no quantitative assessments were made of *A. lopezi*-mediated pest suppression, exclusion trials could still reveal the strength and stability of biological control under varying landscape contexts (see Chisholm et al., 2014; Rusch et al., 2016). Also, though we did not record crop yields in this study, *P. manihoti* infestation rates of a similar magnitude did not affect yield or harvest indices in Thailand (Tancharoen et al., unpublished).

In both years, *P. manihoti* colonized fields earlier and attained higher incidence in small plots within high-diversity landscapes as compared to simplified settings. Nevertheless, mealybug abundance proved similar under both landscape types. Our findings underscore that small-field landscapes are not necessarily typified by low pest pressure (Roschewitz et al., 2005; Plecas et al., 2014), and that ecological traits of colonizing organisms and particularities of the crop environment can modulate the relationship between field size and pest pressure (Segoli & Rosenheim, 2012). Though island biogeography and resource-concentration hypotheses both imply that specialist herbivores, such as *P. manihoti*, attain superior densities in large-scale monocultures, this is only irregularly confirmed through empirical work (e.g., Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Schellhorn et al., 2015b). Higher perimeter-to-area ratios of small fields permit more effective and uniform colonization of pests, but concurrently favor immigration by natural enemies (Rusch et al., 2013). *Phenacoccus manihoti* is an efficient colonist that draws upon two main strategies: 1) airborne dispersal by crawlers, and 2) passive colonization with infested planting material (Nwanze et al., 1979). For airborne movement,

immigration rates are directly tied to the amount of potential colonizers in the surrounding landscape (e.g., Bianchi et al., 2017). In small-field landscapes, crop harvest extended over longer periods into the early dry season, and possibly allowed for a sustained movement of airborne *P. manihoti* nymphs through a so-called ‘green bridge’ effect. This greater inoculum pressure likely explained the higher season-long *P. manihoti* incidence under small-field or high-diversity settings.

Parasitism rates and host  $\times$  parasitoid dynamics did not show clear, consistent differences between landscape types. As in-field parasitism results from immigration and field-level reproduction, it is often challenging to distinguish landscape-level impacts (e.g., Schellhorn et al., 2015b). One possibility is that the host-specific *A. lopezi* does not respond to landscape complexity, as postulated above, thus opposing prevailing hypotheses (Chaplin-Kramer et al., 2011). An alternative option is that *A. lopezi* is actually responsive to landscape-level diversity, but these patterns are obscured through field-level disturbances. More specifically, in early 2015, certain fields in high-diversity landscapes were sprayed with broad-spectrum acaricides (i.e., propargite, fenpyroximate) to control tetranychid mite outbreaks. Although non-target effects of acaricides on parasitoids are rare (e.g., Urbaneja et al., 2008), their overhead application in newly-planted crops possibly might have affected *A. lopezi*  $\times$  mealybug dynamics during the subsequent cropping season. To obtain more conclusive insights into *A. lopezi* immigration rates under different landscape types, mark-release-recapture, rare-element labeling or interception traps could be used (e.g., Corbett & Rosenheim, 1996; Schellhorn et al., 2015b).

One hint of *A. lopezi*'s responsiveness to landscape complexity though can be found in its density-dependent response to *P. manihoti* during the early season. In early season, parasitism rates are likely more reflective of landscape-level influxes and less obscured by numerical

increases from in-field reproduction (see Schelhorn et al., 2015b, Bianchi et al., 2017). Similar to Hammond & Neuenschwander (1990), positive density dependence was found at low host densities and parasitism rates declined rapidly at higher *P. manihoti* densities. Yet, density dependence patterns were slightly more pronounced in large-field landscapes. One hypothesis is that parasitoids aggregate more on host-rich patches under those conditions (e.g., Segoli, 2016; Morgan et al., 2017), or that *A. lopezi* that colonize plots from further afield become time-limited and exploit host patches differently (Dieckhoff et al., 2014). Irrespective of its underlying mechanism, the type of spatial aggregation under low-diversity settings could work in a stabilizing manner on mealybug  $\times$  parasitoid dynamics.

The local primary parasitoid community on *P. manihoti* exclusively consisted of *A. lopezi*, associated with at least three hyperparasitoid species: *Chartocerus* sp. near *walkeri* Hayat (Signiphoridae), *P. unfasciiventris* (Eriaporidae) and *Prochiloneurus* sp. (Encyrtidae). Across sites, hyperparasitism rates peaked at 26.4% during late dry season. Similar patterns were found across the African cassava belt, where a species-rich hyperparasitoid community initially reached 41% parasitism rates that gradually leveled off to 17-20% (Neuenschwander et al., 1987a). In our study, a more abundant and species-rich parasitoid community was recorded from small-field landscapes versus large-field settings, with hyperparasitoids likely colonizing fields from nearby cassava plots or from other agricultural or non-crop habitats. Yet, there is no evidence that this more diverse community reached higher parasitism rates (Rodriguez & Hawkins, 2000) or dampened mealybug biological control (e.g., Crowder & Yabour, 2014). It is not unexpected that diverse agro-landscapes differentially benefit higher trophic-level natural enemies, such as hyperparasitoids (Gagic et al., 2011; Rand et al., 2012; Frago, 2016). Within intensified cassava agro-landscapes of southern Vietnam, mealybug-parasitoid food webs are thus composed of very

few strong interactions and several weak links, also observed from other tropical settings by Tylianakis et al. (2007). In smallholder-managed systems or on low-fertility soils, parasitoid communities are thought to be vastly different (Wyckhuys et al., 2017a), and nothing is known about the magnitude of *P. manihoti* biological control under those conditions.

In conclusion, our work sheds light upon landscape-level impacts on host × parasitoid dynamics in intensified cassava systems. In those settings, *A. lopezi* effectively colonizes fields irrespective of landscape context and reaches high parasitism rates at comparatively low *P. manihoti* abundance. The main factors ensuring biological control are the favorable ecological traits of *P. manihoti* and its host-specific parasitoid. Furthermore, though not assessed in this study, *P. manihoti* control could benefit from the spatio-temporal continuity of host and food items at a landscape level (e.g., Vasseur et al., 2013; Schellhorn et al., 2014). This is the first report of *A. lopezi*-mediated suppression of *P. manihoti* in Asia's intensified cassava production systems. With >4 million ha of cassava cultivated by roughly 8 million Asian farming families, socio-economic impacts of *P. manihoti* biological control in this part of the globe are expected to be of a similar order of magnitude as those in Africa (Zeddies et al., 2001). With arthropod biological control receiving dwindling public interest and low cultural saliency in many corners of the globe (e.g., Warner et al., 2011), these monumental achievements now only wait to be further documented, communicated, and celebrated.

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**Figure legends:**

**Figure 1.** Map of the Southeast Asia region depicting *P. manihoti* geographical distribution during 2014-2015 cropping seasons (e.g., Graziosi et al., 2016), and the delineation of the survey site.

**Figure 2.** Bimonthly variations in *P. manihoti* incidence (A) and abundance (B), *Anagyrus lopezi* parasitism levels (C) and potential hyperparasitism levels (D), as recorded in 8 cassava fields of two different landscape types in Tay Ninh (Vietnam) during consecutive cropping seasons over 2014-2015. Cassava age (or field age) is indicated as the number of months after planting, sampling time are included in parenthesis, and dry (D) or rainy (R) season periods are equally indicated. Data reflect the mean  $\pm$  SE.

**Figure 3.** Effect of cassava age on *P. manihoti* incidence (A) and abundance (B), and *Anagyrus lopezi* parasitism levels (C), as recorded in 8 cassava fields of two different landscape types in Tay Ninh (Vietnam) during consecutive cropping seasons over 2014-2015. Field age is expressed as the number of months after planting, and dry (D) or rainy (R) season periods are indicated. P value indicates effect of cassava age. Data reflect the mean  $\pm$  SE.

**Figure 4.** Cumulative mealybug days (average  $\pm$  SE) in eight cassava fields over the 2014-15 growing season, within distinct landscape contexts (i.e., high-diversity, low-diversity) in Tay Ninh province, southern Vietnam.

**Figure 5.** Parasitism rates of *P. manihoti* on individual cassava tips sampled from fields in high-diversity and low-diversity settings, two months after planting (early season; A), eight months after planting (late season; B) and across all sampling events (C). Mealybug densities are transformed using  $\text{Log}_{10}(x+1)$ . Regression statistics are indicated in the text.

**Figure 6.** Mean field-level parasitism in relation to *P. manihoti* density during early season (month #2), in high-diversity and low-diversity settings. Host density records reflect average densities on 20 randomly-collected tips per field, and are transformed using  $\text{Log}_{10}(x+1)$ . Regression statistics are indicated in the text.

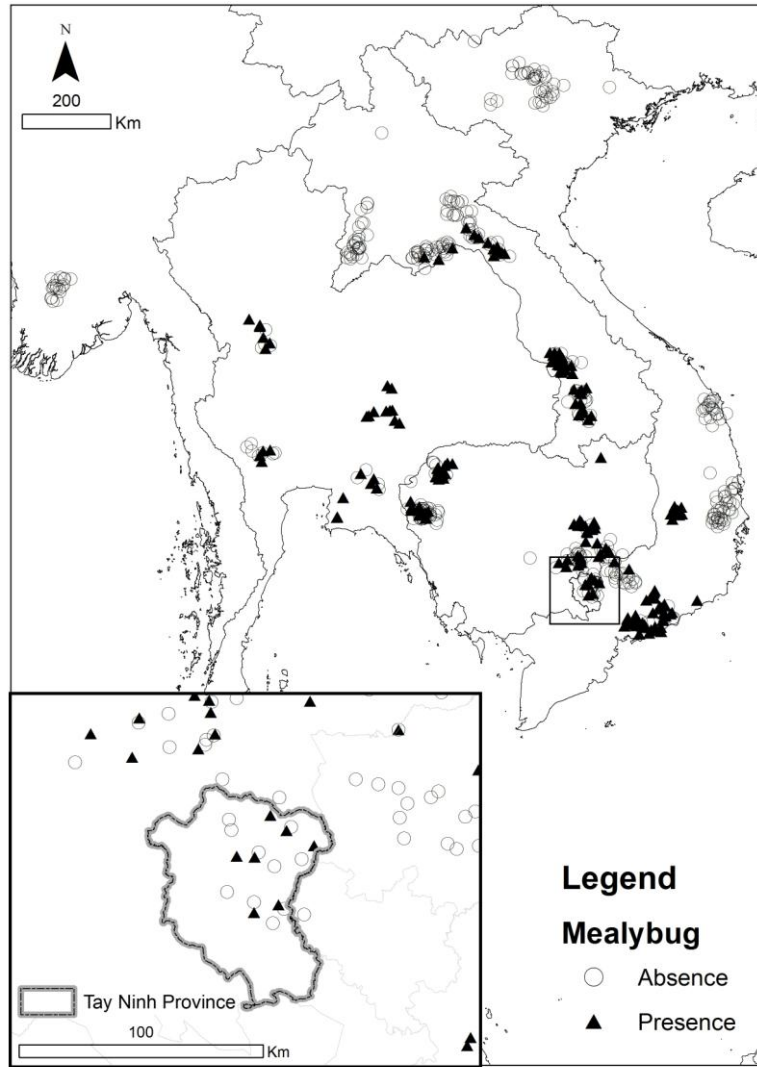
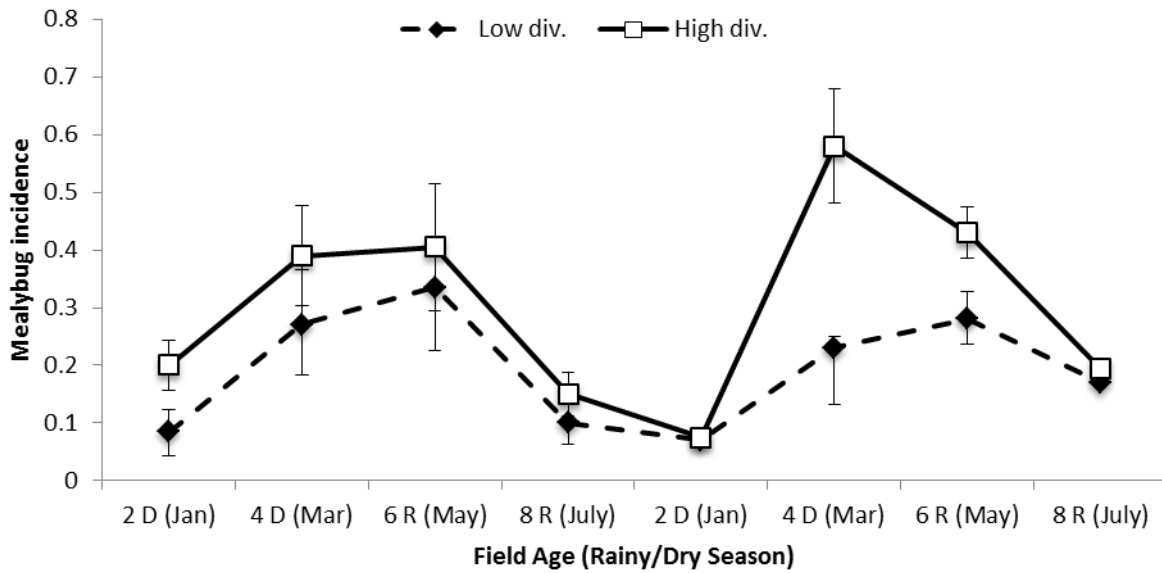


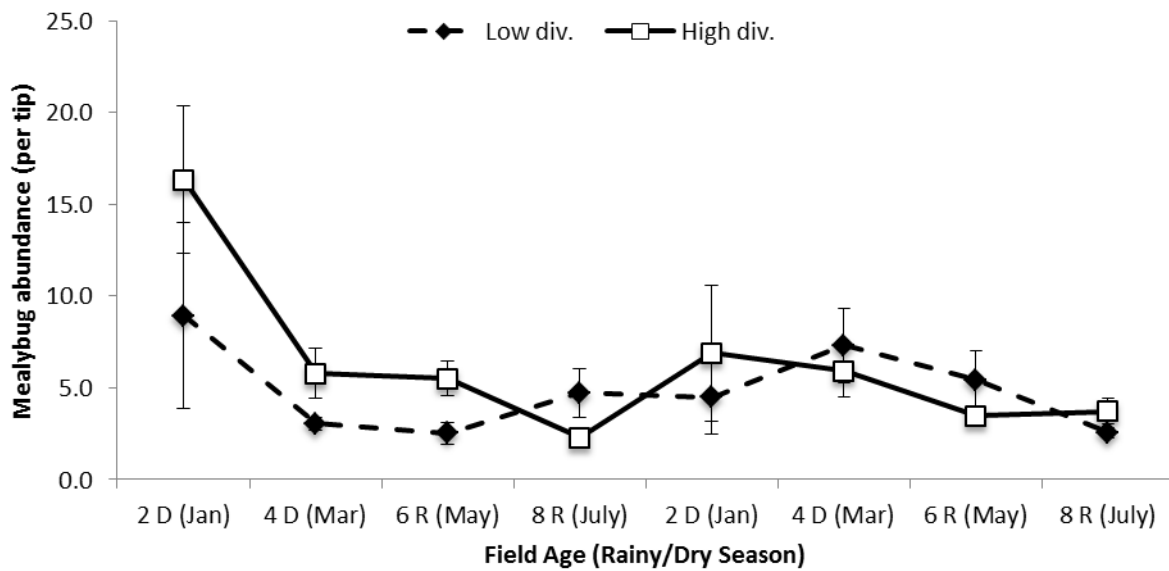
Figure 1.



A



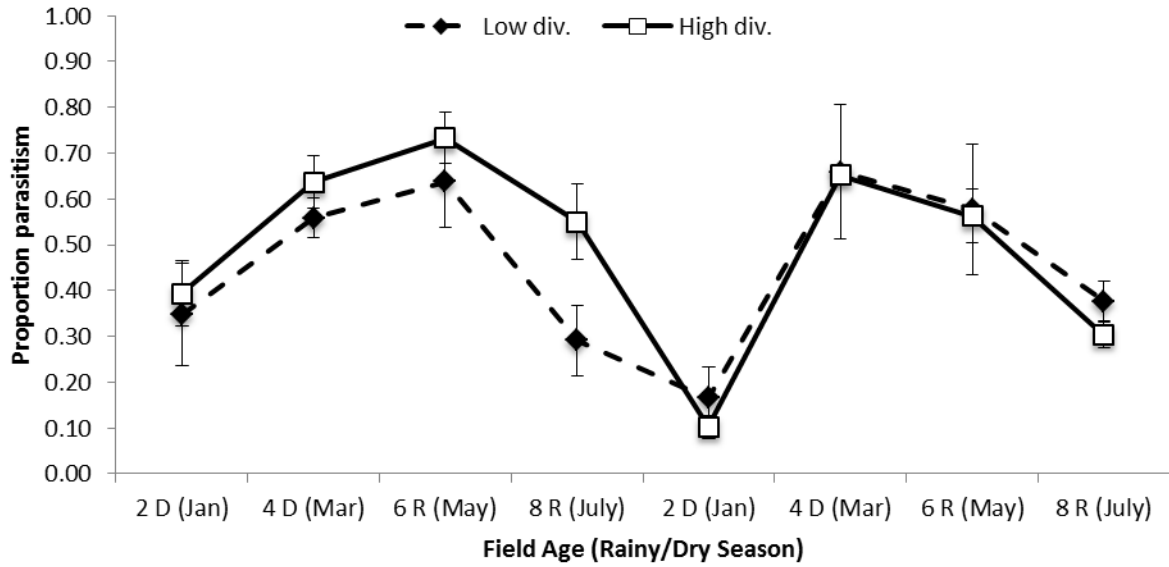
B



C

AC





D

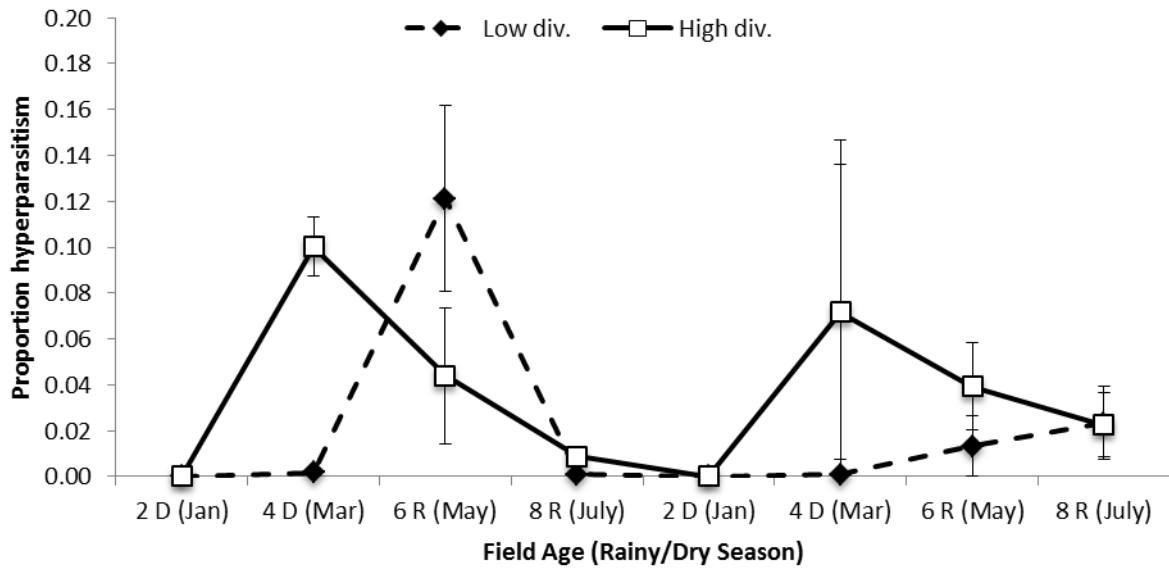


Figure 2

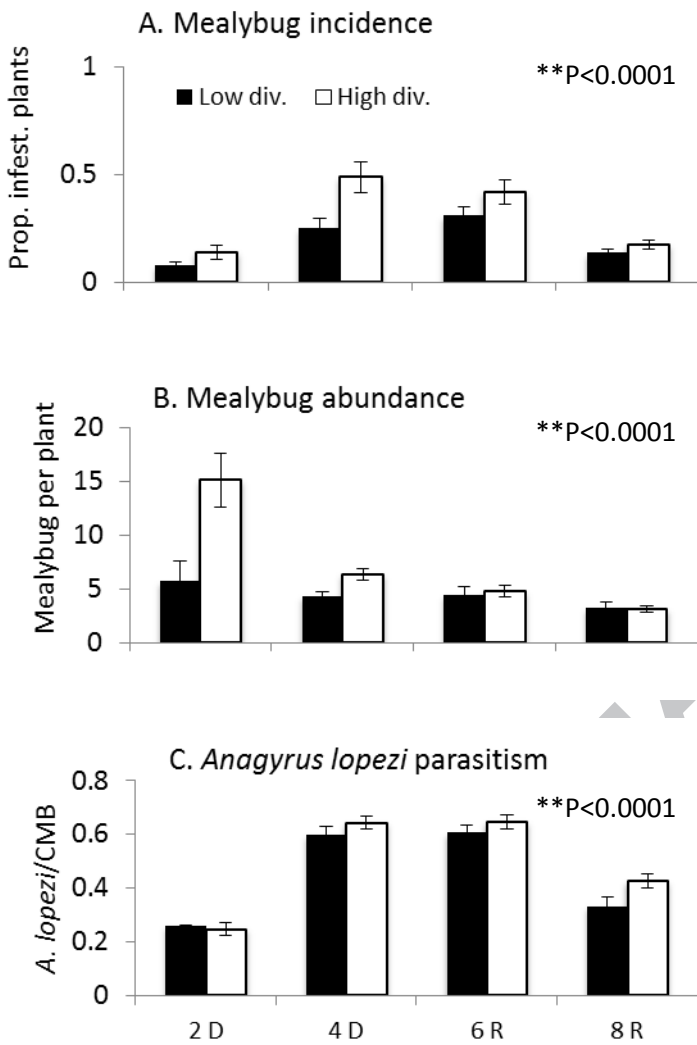


Figure 3

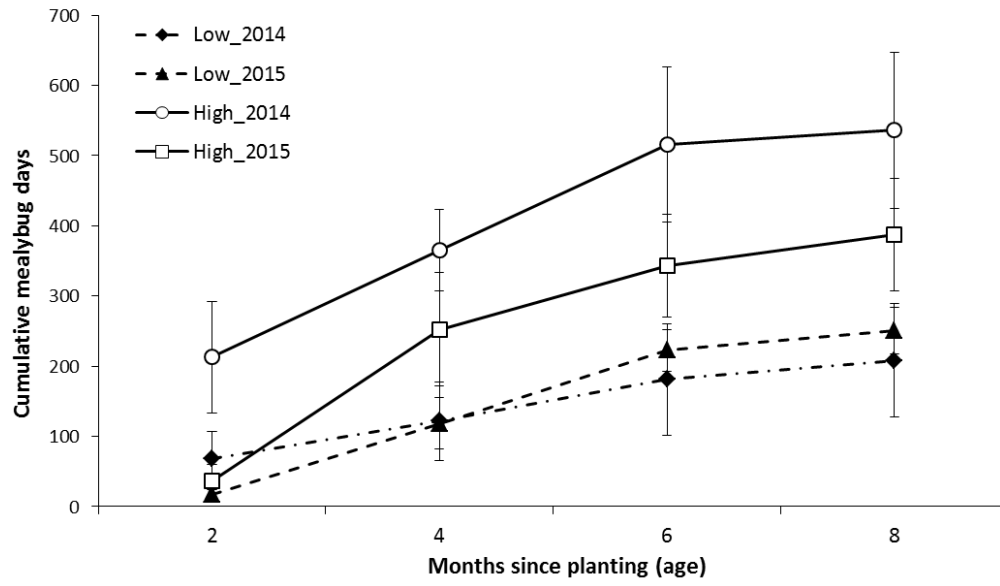
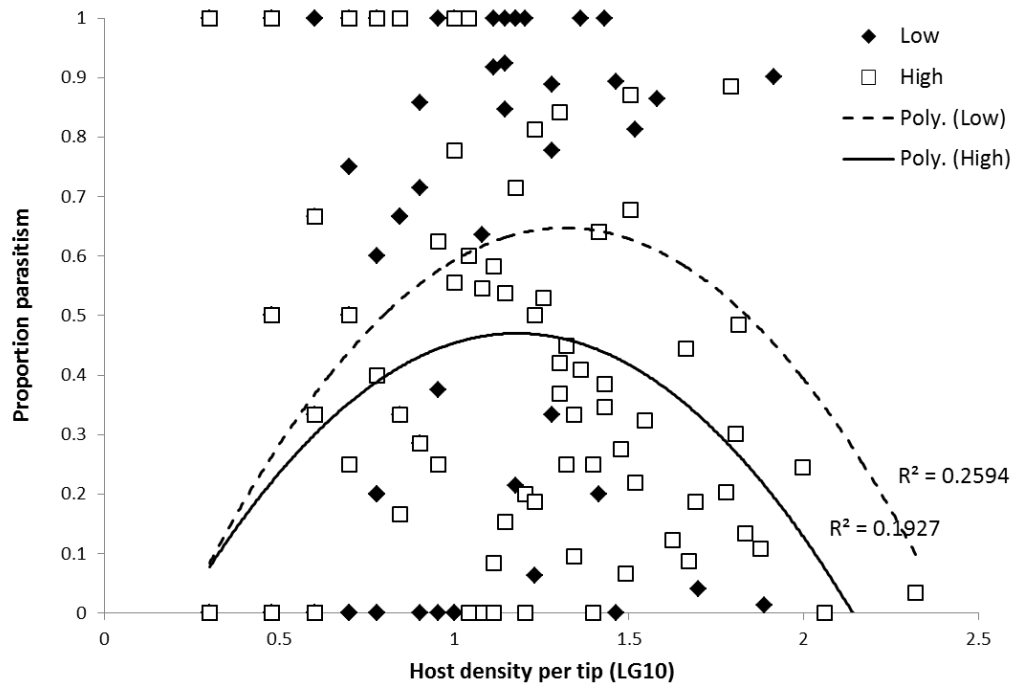
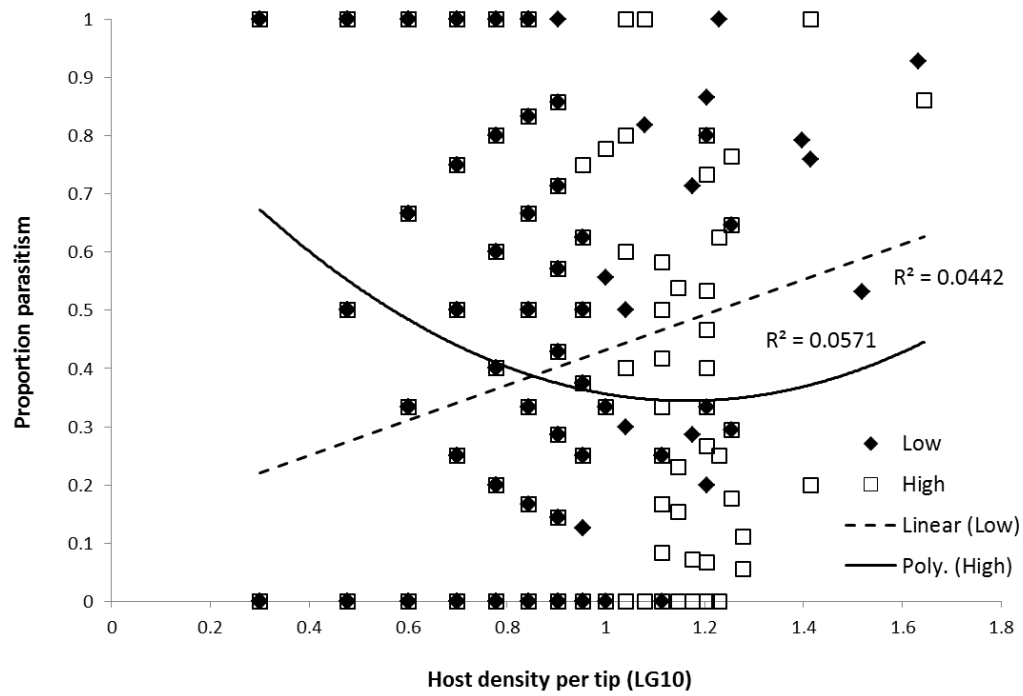


Figure 4.

A



B



C

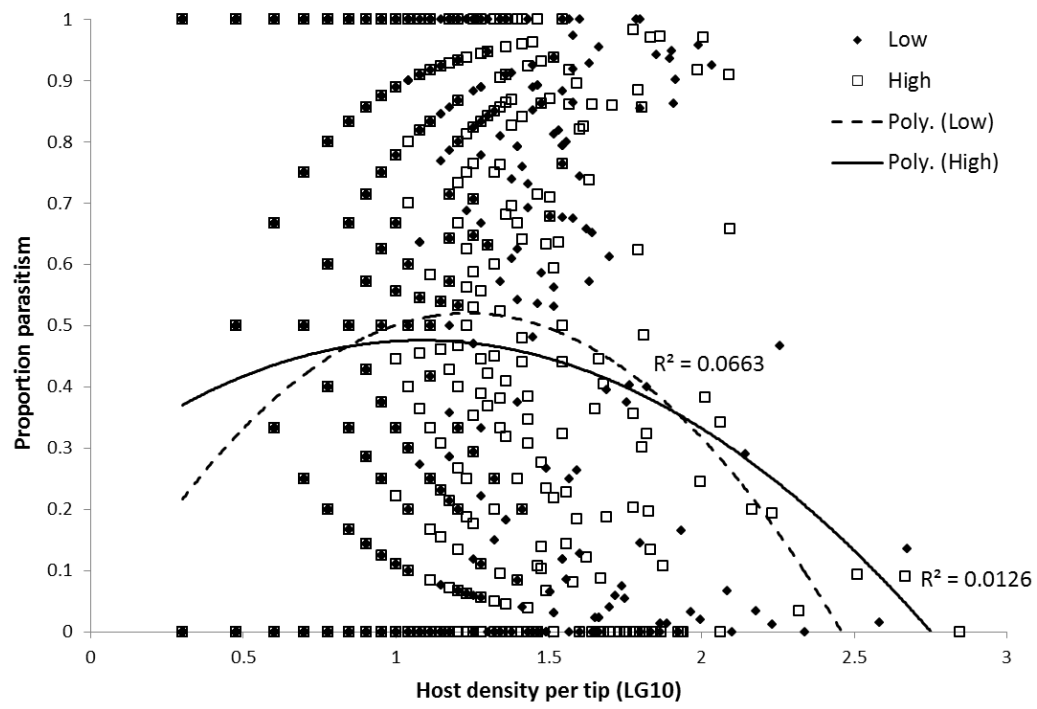


Figure 5.

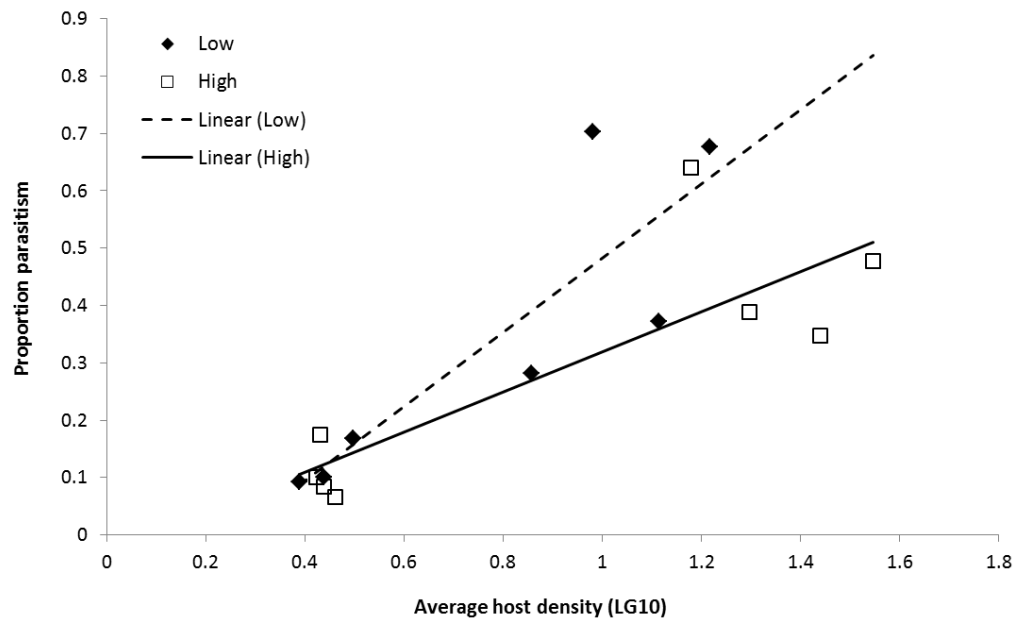


Figure 6.

**Highlights**

- Asia's cassava mealybug populations are suppressed following *A. lopezi* introduction
- Mealybug incidence, but not abundance, is highest in high-diversity settings
- Parasitism is unaffected by landscape context
- Hyperparasitism is enhanced in diverse settings at particular crop age
- Parasitoid density dependency is more pronounced in low-diversity settings

ACCEPTED MANUSCRIPT