Soil fertility regulates invasive herbivore performance and top-down control in tropical agroecosystems of Southeast Asia

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ABSTRACT

In terrestrial ecosystems, changes in soil nutrient availability, plant growth or natural enemies can generate important shifts in abundance of organisms at various trophic levels. In agroecosystems the performance of (invasive) herbivores and their impacts on crops is of particular concern. Scientists are presently challenged with making reliable inferences on invader success, natural enemy performance and efficacy of biological control, particularly in tropical agroecosystems. In this study, we assess how trophic regulatory forces (bottom-up vs. top down) influence the success of three globally important pests of cassava. We examine the mealybug species (Hemiptera: Pseudococcidae) of differing host breadth and invasion history: *Phenacoccus manihoti*, *Paracoccus marginatus*, and *Pseudococcus jackbeardsleyi*. Potted plant fertilizer trials were combined with a regional survey in Vietnam, Laos and Cambodia of 65 cassava fields of similar size and age, but with varying soil fertility. Relative abundance of each mealybug invader was mapped along a soil fertility gradient, and contrasted with site-specific measures of parasitism. Potted plant trials revealed strong bottom-up effects for *P. manihoti*, such that impacts of nitrogen and potassium additions were propagated through to higher trophic levels and substantially boost development and fitness of its specialist parasitoid, *Anagyrus lopezi* (Hymenoptera: Encyrtidae). Field surveys indicate that mealybug performance is highly species-specific and context-dependent. For example, field-level abundance of *P. jackbeardsleyi* and *P. marginatus*, was related to measures of soil fertility parameters, soil texture and plant disease incidence. Furthermore, for *P. manihoti*, in-field abundance is equally associated with soil texture (i.e., silt content). Principal component analysis (PCA) and regression suggested that *P. manihoti* and *P. marginatus* are disproportionately favored in low-fertility conditions, while *P. jackbeardsleyi* prospers in settings with high organic carbon and phosphorus. Parasitism of *P. manihoti* by *A. lopezi* varied greatly with field and soil fertility conditions, and was highest in soils with intermediate fertility levels and where management practices include the addition of fertilizer supplements. Our characterization of the relative performance of invasive mealybugs and strength of parasitism across variable soil fertility conditions will help guide parasitoid release programs and soil management practices that enhance mealybug biological control.

1. Introduction

Around the globe, impacts of human-mediated biodiversity loss, land-use change, and global warming are proceeding at an unrelenting pace, with profound effects on ecosystems and associated food webs (e.g., Vitousek et al., 1997; Newbold et al., 2016). Such changes are particularly relevant for smallholder agriculture in the tropics, where soil fertility (and resulting plant communities) is drastically altered by a variety of management practices and larger-scale patterns in land-use change. In Southeast Asia, cassava (*Manihot esculenta*) production has expanded considerably over the past few decades and now occupies more than 4 million ha throughout the region (Cramb et al., 2016; Mahanty and Milne, 2016). Cassava is typically managed as an annual crop and grown under a range of biophysical and socio-economic

conditions, from shifting cultivation in the uplands of Laos and Cambodia, to large-scale monocultures in the lowlands of southern Vietnam (e.g., Howeler et al., 2011). This crop produced especially well in the early years of cultivation, due to an overall absence of limiting pests and diseases. However, over the past decade, a series of non-native mealybug (Hemiptera: Pseudococcidae) species have colonized Asia's prime cassava-growing regions (Graziosi et al., 2016). These include (1) *Phenacoccus manihoti* Matile-Ferrero, a Neotropical parthenogenetic, oligophagous herbivore (9 host records) with broad climatic adaptability (Yonow et al., 2017) and global distribution (33 countries); (2) *Paracoccus marginatus* Williams & Granara de Willink, a Nearctic sexual, polyphagous herbivore (133 host genera), reported from 33 different countries; and (3) *Pseudococcus jackbeardsleyi* Gimpel & Miller, a Neotropical polyphagous species (98 host genera), found in 46 countries worldwide. Invasion history is variable between species, with respective colonization processes in mainland SE Asia presumably initiated around 2008, 2010, and 1987 respectively (Ben-Dov et al., 2012), and biological control with parasitic wasps such as *Anagyrus lopezi* De Santis (for *P. manihoti*, released in 2009), *Acerophagus papayae* Noyes & Schauff (for *P. marginatus*, colonized post-2010) and a set of endemic and exotic generalists wasps for *P. jackbeardsleyi* (Muniappan et al., 2009).

Soil fertility and overall quality has been shown to be a principal determinant of plant health and resistance to pests and disease (e.g., Amtmann et al., 2008), however, the impact of belowground processes on aboveground interactions is varied and often difficult to predict (Wardle et al., 2004). Understanding how these invasive herbivores and their associated parasitoids interact and respond to soil fertility conditions offers a number of possible benefits for managing pests. For example, such information could help target parasitoid releases, identify context-specific needs for integrated pest management and help improve our overall understanding of linkages between above and below-ground processes. So far, little research has been conducted on trophic regulation and associated invader success along gradients of ecosystem productivity or soil fertility (e.g., Zarnetske et al., 2013). While some suggest that highly fertile sites disproportionately favor invaders, regardless of top-down forces such as parasitoids (see Hovick and Carson, 2015), evidence also exists to the contrary.

Alterations in resource availability or species abundance are transmitted through trophic chains, and affect the relative role of resource ("bottom-up") versus consumer ("top-down") forces in the structuring of ecological communities (Hunter and Price, 1992; Ives and Carpenter, 2007). Changes in top predators or basal resources, e.g., through fertilizer addition, can shift the equilibrium abundances of various trophic levels and affect the relative success of certain species (native or exotic) Comparatively few empirical studies have concurrently assessed the relative effect of top-down, bottom-up and interactive processes on ecological communities (Moran and Scheidler, 2002; Gruner, 2004; Garibaldi et al., 2010) and population-level processes under field conditions are rarely considered in addressing such issues (Walker et al., 2008; Zaugg et al., 2013; Rzanny et al., 2013). Success rates of invasive species are explained through a range of hypotheses linked to trophic processes, in which community productivity, disturbance, species diversity and natural enemy action are all posed as important determinants. As these hypotheses are non-exclusive, interactions between mechanisms are increasingly employed to predict invasion outcomes and invader success (e.g., Parepa et al., 2013; Mallon et al., 2015; Peltzer et al., 2016). Certain theories simultaneously account for the role of resource availability (e.g., soil fertility) and natural enemies (Blumenthal, 2005; Center et al., 2014).

Particularly for sessile invasive herbivores, such as mealybugs, plant nutritional quality strongly determines species abundance and performance, shaping entire herbivore feeding guilds (Shurin et al., 2002; Carcamo et al., 2005; Rzanny et al., 2013). Also, soil fertility and plant nutrients may lead to differential, species-specific responses amongst invaders (Peltzer et al., 2016). Invader success and trophic regulation

have previously been linked to single-nutrient (e.g., soil N, P, K, Zn) measures (e.g., Walter and DiFonzo, 2007; Chen et al., 2010). However, increasing attention is being paid to overall plant quality and more universal measures of soil fertility (e.g., Ode, 2006; Bardgett and van der Putten, 2014). Thus, composite soil fertility indices potentially can help explain relative success of invasive mealybugs and associated biological control processes in fields with differing resource availability.

In this study, we assess soil-plant-herbivore-parasitoid interactions through both manipulative and observational approaches to better understand the relative influence of top-down vs. bottom up forces on herbivore pest performance. We evaluate the effect of resource quality on the success of invasive mealybug species, in a controlled laboratory setting as well as, in cassava fields along a soil fertility gradient. More specifically, we address the following three research questions: (1) do fertilizer supplement studies reveal the effects of single-element additions of nitrogen (N) and potassium (K) on *P. manihoti* performance and top-down forces (i.e., parasitism by a recently-introduced natural enemy); (2) does abundance of different invasive species vary along a soil fertility gradient, and do particular measures of soil fertility explain invader success; (3) do top-down forces (i.e., parasitism by a recently-introduced natural enemy) shift in importance between contexts of varying resource quality, as determined by soil fertility.

2. Materials and methods

2.1. Potted plant fertilizer trials

2.1.1. Plant cultivation

In this set of trials, we assessed the extent to which single-element nutrient additions affected different development parameters of *P. manihoti*, and its primary parasitoid, *A. lopezi*. During 2014–2015, assays were established at Hue University of Agriculture and Forestry (HUAF), in Hue, Vietnam. Soil was collected from an uncultivated plot at the HUAF experimental campus, and was homogenized for use in a controlled pot experiment. A sub-sample of this soil analyzed at the HUAF laboratory of Agronomy was determined to have a pH of 5.2, an organic carbon (C) content of 1.5%, and available concentrations of K_2O, N and P_2O_5 of 4.59 mg, 0.65 mg and 10.5 mg per 100 g of soil, respectively. Approximately 10 kg of this soil was placed in pots (30 dia. x 20 cm deep) and a single vegetative cutting (approx. 20 cm in length) of cassava (variety KM94, a popular cassava variety, widely cultivated across the region) was planted vertically in each pot. KM94 is. Pots were placed outside in a screen-house and watered daily. After two weeks, plants were randomly assigned to five fertilizer treatments: 1) no fertilizer (i.e., untreated controls), 2) low N addition (90 kg N ha^{-1}), 3) high N addition (180 kg N ha^{-1}), 4) low K addition (90 kg K_2O ha^{-1}), and 5) high K addition (180 kg K_2O ha^{-1}). This was equivalent to application rates of 0.65 g and 1.30 g N and 0.50 and 1.00 g K_2O per pot (respectively for medium and high fertilizer treatments) and represents fertilizer rates commonly applied by Asian cassava growers (e.g., Howeler, 2011). We focused on N and K additions in the potted plant fertilizer trials, as cassava is most responsive to these nutrients and has comparatively high capacity to mobilize P from tropical soils via root association with mycorrhizae and other mechanisms (Nguyen et al., 2002; Howeler, 2011). Both N (as urea) and K (as K_2O) were dissolved in water and applied in liquid form. After six weeks, the plants were moved into a climate-controlled chamber (ambient RH, 30 ± 1 °C and 12L: 12D).

2.1.2. Mealybug and parasitoid colony maintenance

In mid-2014, a starter laboratory culture of *P. manihoti* was established from field-collected individuals from Hue and Quang Tri, central Vietnam and reared on cassava stems grown in glass jars with a diluted fertilizer solution inside 60 × 160 × 180 cm cages. Prior to initiation of the trials, a total of five *P. manihoti* sub-colonies were concurrently

established in a climate-controlled chamber, on plants subjected to each of the above five experimental fertilizer treatments. Each sub-colony was initiated at the same time with approx. 100 mealybugs (mixed-age population), as obtained from the starter colony. Mealybug populations were maintained on these plants for two to three generations prior to use in experiments, to mitigate the influence of parental trophic feeding history and eventual other maternal effects. A colony of *A. lopezi* was established with field collected individuals obtained in mid-2015 from fields near Hue, Vietnam. The laboratory colony was kept on cassava plantlets infected with *P. manihoti* in cages with the following dimensions: $40 \times 50 \times 60$ cm. All of the mealybug and parasitoid colonies were maintained at 30 ± 1 °C and 12L: 12D photoperiod, and colonies were regularly refreshed by adding (unspecified, yet small numbers of) field-collected individuals. Voucher specimens of mealybugs and *A. lopezi* wasps were deposited at Hue University of Agriculture and Forestry (VNUA), Vietnam.

2.1.3. Experimental assays & data processing

At the onset of the experiment, a *P. manihoti* ovisac (egg batch) was collected from each mealybug sub-colony and allowed to hatch. Upon emergence, ten first-instar nymphs were transferred to the 3rd youngest leaf of an experimental plant grown in the same fertilizer treatment as the sub-colony. We used 20 un-fertilized control plants and 10 plants for each of the N and K-addition treatments (N = 60). Nymphs on each experimental plant were enclosed in one single $5 \times 10 \times 20$ cm clip-cage. Clip-cages were constructed out of transparent, plastic poly-propylene (PP) containers and equipped with a mesh lid to allow sufficient ventilation. Development and embryonic mortality of all nymphs (N = 600) was thus assessed within each fertility regime, following protocols by Tertuliano et al. (1993). Development parameters were thus recorded for ten different cohorts (i.e., replicate clip-cages) under each fertilizer treatment, and cohort trials for the separate treatments were run simultaneously. Size and weight measures were recorded for young females (stage L4, prior to oviposition) obtained from ten un-fertilized plants and five plants for each of the N and K-addition treatments (N = 300).

Adult reproduction and mortality were recorded for each of the plant fertilizer treatments in a separate experiment, using a new set of experimental potted cassava plants. Young females (stage L4) were collected from each of the five sub-colonies, and transferred to clip cages on the 3rd youngest leaf of an experimental plant with the same fertilizer treatment as the sub-colony, thus establishing a cohort of 10 females per clip-cage. Daily reproduction and mortality were recorded for all females per fertilizer treatment (N = 600). Furthermore, duration of the pre-reproductive period, fecundity and adult weight were assessed on 10 unfertilized control plants and five plants for each of the fertilizer treatments (N = 300) (e.g., Tertuliano et al., 1993). Reproductive output for each adult was recorded on a daily basis by removing newly-laid ovisacs from the clip cage and counting the number of eggs under a stereomicroscope.

In a second set of laboratory assays, we assessed *A. lopezi* parasitoid fitness, development and survival rates under the same fertilizer treatments used above. *P. manihoti* ovisacs were collected from each mealybug colony/fertilizer treatment combination, and one ovisac was placed in a $5 \times 10 \times 20$ cm clip-cage on 10 unfertilized control plants and five plants for each of the fertilization treatments (N = 300). At nymphal emergence, a total of 70 first-instar nymphs were allowed to establish within the cage, and the number was then reduced to 50 at the L3 stage (e.g., Van Driesche et al., 1987). Subsequently, a 1-day old adult, mated and naïve female *A. lopezi* wasp was introduced into each clip-cage together with one adult male *A. lopezi* for a 24 h period and allowed to oviposit. After the allotted time, the adult female parasitoid was transferred to another clip cage with another 50 third-instar nymphs on a different plant, but at the same fertilizer treatment. By transferring each parasitoid on a daily basis to a new clip-cage with ample new hosts, we were able to assess total lifetime reproductive

output. A total of 20 female *A. lopezi* were assessed on unfertilized controls, and 10 for each of the fertilization treatments (N = 60). This process was repeated on a daily basis until death of the female, regularly replacing male wasps that had died. Daily parasitism rate was calculated as the average parasitism (number of mummies/50 nymphs) within each cage every day, until death of the female. For each wasp, lifetime fecundity (# mummies), oviposition period (d) and rate (mummy/d) were calculated. After removal of the parasitoid from the clip-cage, each cassava plant was incubated at 30° C and mealybug mortality, parasitoid development time (egg deposition-mummification, and adult emergence) and sex ratio were recorded. A total of 10 replicate female wasps were assayed from each fertilizer treatment and 20 replicates for the non-fertilized controls. Upon offspring emergence, a subset of 60 wasps of each sex for the fertilized treatments, and 120 for the controls, were isolated in Eppendorf vials and provided daily access to honey mixed with water (50%). To assess longevity of wasps from each fertilizer treatment, we recorded daily mortality rates

2.2. Observational studies

2.2.1. Field-level arthropod survey

In a second experiment, a geographically widespread survey was conducted to assess the extent to which mealybug abundance relates to soil fertility in a set of cassava fields, representative of each of the target regions. During February-March 2015, a total of 65 fields were randomly chosen across three countries, with 20 fields in southern Vietnam, 18 in eastern Cambodia, and 27 in southern and south-central Laos. Fields were chosen within primary cassava-growing regions in each of the above countries, with assistance from local extension personnel. Plants within each field were 6–9 months old, and were located in the countries' primary cassava-growing regions. Survey activities covered two provinces in Vietnam (Binh Thuan/Ba Ria Vung Tau, Dak Lak), two in Cambodia (Kracheh, Tboung Khmum), and four in Laos (Bolikhamxay, Vientiane, Salavanh, Champasak). All survey work was carried out during the region's main dry season, when mealybug populations are generally increasing (e.g., Graziosi et al., 2016). Nearly 80% of the fields were planted with one of two popular cassava varieties (KM94 and Rayong 72), while in the other fields, less common varieties were cultivated or varietal mixes were used. Five representative linear transects (approx. 10 m in length; covering 10 plants) were assessed for the presence of arthropods, and the number of resident mealybug species per field transect. We also examined plants for symptoms of cassava witches broom disease (CWB), a phytoplasma disease that is commonly found in local fields (Alvarez et al., 2013; Graziosi et al., 2016). Mealybug species identity was determined according to morphological characteristics such as coloration and presence of abdominal waxy filaments (i.e., short- or long-tailed). This permitted field identifications of the most common invasive mealybugs in Asia's cassava crops, including *P. manihoti*, *P. marginatus*, and *P. jackbeardsleyi*. Also, in mixed-species infestations of long-tailed mealybugs, *P. jackbeardsleyi* tends to be the prevalent species in Vietnam and Laos (Graziosi et al., 2016). Average abundance or incidence levels for each of the different species were then calculated at a field level and used for subsequent analyses.

2.2.2. Soil sampling and sample analysis

Leaf chemistry of mid- to late-season cassava is largely reflective of soil fertility status at early growth stages (e.g., Schulthess et al., 1997). In this experiment, we relate mealybug abundance to soil texture and fertility measures from samples collected at the time of the arthropod surveys (see Section 2.2.1; on 7–9 month old plants in the dry season). By doing so, we likely overlook eventual impacts of fertilizer supplementation at the time of planting, but do capture the effect of background soil fertility. This approach though is suitable given that fertilization practices are relatively uniform across the study region (except for Tay Ninh, Vietnam). One soil sample was collected along each of the

five survey transects in each field. For each transect, two soil sub-samples were collected from within the planting row (5–10 m apart) at two depths (0–20, 20–40 cm) using a 5 cm dia. corer. Soils from each transect were composited by depth, while rocks, roots and other debris were removed prior to air-drying of each composite sample. Once all samples were collected and dry, they were submitted to the soil diagnostics laboratory of the Soil and Fertilizer Research Institute (SFRI) in the Vietnam Academy of Agricultural Sciences (VAAS), in Hanoi, for nutrient analysis.

A suite of measurements of soil fertility and texture were conducted. Soil texture was assessed according to the Bouyoucos method (Gee and Bauder, 1986). Other variables include pH (1:1, soil:water solution), electrical conductivity (EC; 1:5, soil:water solution), and exchangeable Ca, Mg and K (extracted with ammonium acetate ($NH_4CH_3CO_2$)) at pH 7 and measured by atomic absorption spectrometry (AAS, Perkin Elmer 3100; Perkin Elmer, Norwalk, CT) and flame photometry (Elex 6361; Eppendorf, Hamburg, Germany) (Herrmann, 2005). Additionally, we measured total organic C using the Walkley-Black method and total N using the Kjeldahl method. Total P was measured using sulfuric acid-hydrogen peroxide-hydrofluoric acid digestion with 18 M H_2SO_4, while total K was determined using hydrofluoric acid (HF) and either H_2SO_4 or $HClO_4$ (Sparks, 1996). Finally, available P was determined using Bray and Kurt (Bray II) method and acidity (Al3+, H+) was measured through titration with a KCl 1M solution (Sparks, 1996).

2.3. Comparative evaluation of P. manihoti parasitism

2.3.1. Field sites

In a third set of experiments, we conducted a comparative field-level assessment of the strength of top-down regulation of *P. manihoti* by parasitism. Cassava fields of different developmental stages and varying soil fertility were selected. During 2014 and 2016, targeted sampling was performed during the dry season (January-March) in plots in Tay Ninh, Ba Ria Vung Tau and Binh Thuan (Vietnam) and Kracheh (Cambodia). In 2014, fields were visited as part of a larger, region-wide survey of *P. manihoti* parasitism, in which no particular attention was paid to soil variables. Fields that were visited in 2016 took into account observed trends in soil texture and fertility from earlier site visits (Section 2.2). In these surveys, soil fertility and crop intensification schemes were not specifically evaluated but rather inferred based on province- or district-level trends (as equally reflected in the PCA; Fig. 1). Cassava crops in Ba Ria Vung Tau and Binh Thuan were 7–9 months old, established at low-fertility sites with sandy soils. Cassava crops in Tay Ninh were either 2–3 months old (crop development status similar to the potted plant fertilizer assays) or 7–9 months old, and established at intermediate-fertility sites under intensified cropping schemes (i.e., with substantial input of fertilizer and herbicides). Lastly, crops in Kracheh were 7–9 months old, established under relatively high soil fertility conditions and with low-intensity management schemes (i.e., little or no fertilizer supplementation at planting). Multiple of the fields in Kracheh were equally visited for the 2015 arthropod survey (see Section 2.2).

2.3.2. Sample collection and assessment of parasitism levels

Within each region, up to eight different fields were visited and 10–20 mealybug-infested tips were collected from each field. Plant tips were placed in sealed paper bags and transferred to the laboratory. Before bagging, apparent predators such as ladybeetles and lacewing larvae were removed (see Meyhofer and Klug, 2002). Sample bags with plant material were kept in a cooler while being transported to the laboratory. In the laboratory, cassava tips were examined, the total number of *P. manihoti* was counted, and tips with > 10 individuals were further processed. Other mealybug species were discarded. Mealybug individuals from each tip were gently brushed onto a young cassava plant, placed in a transparent, 40 × 25 cm polypropylene (PP) plastic container that was provided with a mesh screen on the side. Daily

collections of emerging parasitoids were made with an aspirator for 18 days. In Ba Ria Vung Tau and Binh Thuan, local collaborators adopted a slightly modified methodology to record field-level parasitism rates that proved equally effective. Specifically, field-collected cassava tips were transferred to 95 mm diameter transparent PET plastic cups (390 ml), with each tip inserted into humidified floral foam. Each cup was closed with a lid, provided with a mesh screen to permit air circulation. Cassava tips with > 10 *P. manihoti* individuals were transferred to the cups, placed within a field laboratory at ambient temperature, and kept for 14 days (until full emergence of parasitoids). Parasitoid emergence was evaluated on a regular basis, and emerged wasps were removed from cups. For each site and field, *P. manihoti* abundance on field-collected cassava tips was recorded, and field-level parasitism rates and parasitoid sex ratio were subsequently computed.

2.4. Statistics

In experiment #1, *P. manihoti* and *A. lopezi* development, reproductive and survival measures were tested for normality (PROC UNIVAR) and Analysis of Variance (ANOVA) on log-transformed data was used to evaluate the effect of fertilization on these parameters (PROC GLM; SAS version 9.4).

In the first field study, bivariate relationships between each mealybug species, corresponding soil fertility parameters and *CWB* infection status were investigated (using Kendall's rank correlation analysis). Next, regression was performed to model the combined effect of soil fertility parameters and plant quality measures on the incidence of individual mealybug species. For *P. manihoti,* a general linear model based on negative binomial distribution was adopted, as the incidence data for this species was significantly zero-inflated. Simultaneous forward and reverse stepwise selection on all 14 parameters up to 2-way interaction was performed on a saturated model, starting with a null model (i.e., a model containing only the intercept), so as to select the best models for each species. This analysis yielded only two models in total for *P. marginatus* and *P. manihoti*, while for *P. jackbeardsleyi*, three models were identified. To select the best model, among the ones identified in the previous step, we employed a similar strategy as in Noma et al. (2010). A model with the lowest Akaike information criterion (AIC) (Model 1, i.e. "best-fit" model in Table 4), and another model (Model 2, i.e. "competing-model" in Table 4), with an AIC score that is within 2 units of the AIC score of Model 1 were selected. Diagnostic checks such as assessment of heteroscedasticity (using Nonconstant Variance Score Test) and auto-correlating factors was also performed on the selected models. Correlation analysis, was performed using the base function "cor" with the Kendall tau b method in R (version 3.3.1) statistics environment (R Development Core Team, 2013). Regression modeling and the associated model fitting diagnostics was performed using the base function "step", the MASS package (http://cran.r-project.org/web/packages/MASS) and the CAR package (https://cran.r-project.org/web/packages/car) in R (version 3.3.1) statistics environment (R Development Core Team, 2013).

Since individual soil fertility measures tend to be strongly correlated (e.g., Fujita et al., 2013), we conducted Principal Component Analysis (PCA) to extract the main axes of variation. The dataset that was subjected to multivariate analysis was composed of a total of 13 soil fertility measures (i.e., crude sand, W silt, fine sand, pH, EC, Al, K, Ca, Mg, C, N, P, avail P) and field-level incidence of cassava witches broom (CWB) disease, the latter as an additional index for plant resource quality. Systemic pathogens can bring about important shifts in plant quality and secondary chemistry, which rarely get taken into account (Tack and Dicke, 2013). From the PCA, factor loading scores (i.e. scores for each field) were extracted for the two main axes of variation (PCA axis 1 and 2). A general linear model based on negative binomial distribution was used to relate field-level abundance measures of *P. manihoti*, *P. jackbearsleyi* and *P. marginatus* with the factor loading scores. In addition, a Chi-square based test was performed on residual
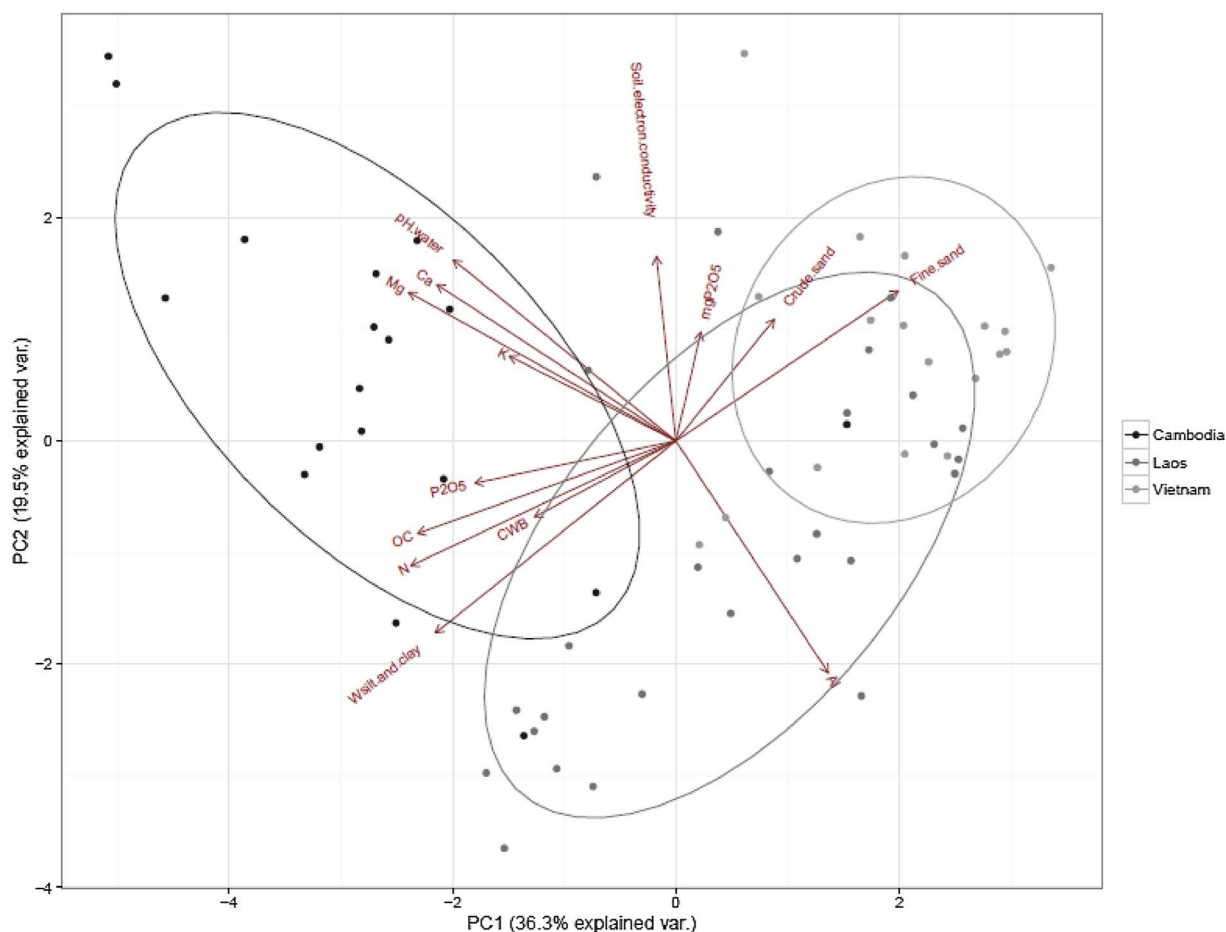
Fig. 1. Principal component analysis (PCA) of 65 cassava fields, based upon soil fertility status and CWB pathogen-infection of host plants. Soil fertility status was determined through a total of 13 different measures, and CWB infection was assessed by recording disease symptomatology. Fields are classified per country, and soil fertility measures are abbreviates as follows: crude sand (% particles 630 μm–2 mm); W silt (well-graded silt + clay); fine sand (% particles 63 μm–200 μm); pH (pH of soil suspension); EC (soil electron conductivity); Al (Al 3 + mg/100 g soil); K (K + mg/100 g soil); Ca (Ca2 + mg/100 g soil); Mg (Mg2 + mg/100 g soil); OC (% soil organic carbon); N (% nitrogen); P (% P_2O_5); P_2O_5 (mg P_2O_5/100 g soil).

deviance measures from the selected models, in order to obtain a goodness-of-fit measure. Multivariate analyses were performed using the base function "princomp", and the resulting biplot was visualized with the ggbiplot package (https://github.com/vqv/ggbiplot), within the R statistical environment. Eigen values for each component were extracted using the nFactors package (https://cran.r-project.org/web/packages/nFactors/). Components with an Eigen value lower than 2 were disregarded for further analysis. Regression modelling and model visualization was performed using the MASS and CAR packages within the R statistical environment. In order to identify the effect of aggregated groups, each consisting of multiple fertility measures on mealybug abundance, multivariate analysis of the 13 soil fertility measures and CWB incidence was performed.

In experiment #3, ANOVA or non-parametric tests (e.g., Kruskal-Wallis, for data that did not meet normality assumptions) was used to compare parasitism rates, sex ratio and mealybug abundance rates between different sites. Normality and homoscedasticity of the dataset was checked, and the necessary data transformations (i.e., SQRT) were conducted prior to statistical analysis.

3. Results

3.1. Potted plant fertilizer trials

Mealybugs feeding on fertilized plants developed more rapidly than those reared on the controls, with the high N and medium K addition treatments having the strongest effects (Table 1a). Nutrient addition did not affect *P. manihoti* survival, but N and the lower K regimes had positive effects on both insect weight and length. Total fecundity was highest for females on plants treated with the lower N dose and lowest on control plants (Table 1a), while oviposition rate did not vary among treatments. However, both pre-oviposition and oviposition periods were strongly affected by nutrient additions. Nitrogen additions led to the shortest pre-oviposition, followed by K and then the controls, but no differences were observed between the two application rates for either nutrient. Similarly, N applications extended the insects' oviposition period, but no clear impact of K on this parameter was recorded (Table 1a).

On N-fertilized plants, parasitism rates were significantly higher than for control or K-amended treatments (Table 1b). Parasitoid females in the fertilized treatments attained higher fecundity levels than with the un-fertilized controls, regardless of nutrient type and application rate. Parasitoid oviposition rate was significantly higher on N-fertilized plants. Fertilizer treatments also affected *A. lopezi* offspring, such that emergence rates were significantly higher in all fertilizer treatments, and sex ratio was far more female-biased for either nutrient supplement, particularly on N-fertilized plants (Table 1b).

3.2. Observational studies

All three species of mealybug were found in cassava fields across the surveyed region, with field-level incidence and abundance exhibiting significant differences between fields and countries. Mealybug incidence significantly varied between countries for *P. jackbeardsleyi*

Table 1a

Development and reproductive outputs of the cassava mealybug (*P. manihoti*) feeding on plants under different fertilizer treatments. Means (± SD) followed by the same letter do not differ (ANOVA, α = 0.05).

Parameter (*P. manihoti*)	N	control	N90	N180	K$_2$O90	K$_2$O180	Test statistic; P-value
Development time (d)	527	15.5 ± 0.06 a	15.0 ± 0.06 b	14.2 ± 0.07 d	14.3 ± 0.07 d	14.8 ± 0.09 c	$F_{4,522}$ = 61.24; P < 0.0001*
Survival per plant (%)	60	85.5 ± 0.02	87.0 ± 0.03	91.0 ± 0.03	89.0 ± 0.02	89.0 ± 0.03	$F_{4,55}$ = 0.8; P = 0.53
Adult[a] weight (mg)	300	4.76 ± 0.26 b	5.85 ± 0.52 a	5.54 ± 0.69 ab	6.4 ± 0.16 a	5.00 +0.24 b	$F_{4,295}$ = 3.78; P = 0.016*
Adult length (mm)	300	2.01 ± 0.02 c	2.15 ± 0.02 b	2.14 ± 0.02 b	2.32 ± 0.04 a	1.98 ± 0.05 c	$F_{4,295}$ = 18.43; P < 0.0001*
Total fecundity (eggs)	279	369.0 ± 8.6 c	438.0 ± 11.3 a	419.6 ± 9.0 ab	403.8 ± 10.3 b	395.8 ± 10.8 b	$F_{4,274}$ = 7.75; P < 0.0001*
Oviposition rate (eggs/d)	279	23.4 ± 0.5	24.4 ± 0.5	24.0 ± 0.5	23.9 ± 0.8	23.6 ± 0.5	$F_{4,274}$ = 1.04; P = 0.389
Pre-oviposition period (d)	279	5.4 ± 0.1 a	4.4 ± 0.1 c	4.0 ± 0.1 c	5.2 ± 0.2 b	4.9 ± 0.1 b	$F_{4,274}$ = 20.51; P < 0.0001*
Oviposition period (d)	279	16.0 ± 0.3 b	18.0 ± 0.3 a	17.7 ± 0.4 a	17.0 ± 0.3 ab	16.8 ± 0.4 b	$F_{4,274}$ = 5.13; P = 0.0005*

[a] Young females (stage L4, prior to oviposition).

($F_{2,62}$ = 7.431, p < 0.001) and *P. marginatus* ($F_{2,62}$ = 11.832, p < 0.001), while plant-level abundance differed between countries only for *P. marginatus* ($F_{2,58}$ = 3.532, p = 0.036) (Table 2). On average, 31.2 ± 27.9 plants per field were affected and symptomatic for CWB, with disease incidence levels significantly different between countries ($F_{2,62}$ = 7.556, p = 0.001).

Bivariate correlations were found between field-level abundance levels of a given mealybug species, and a set of single soil fertility measures (Table 3). More specifically, statistically-significant negative correlations were found between *P. manihoti* abundance and silt content, organic C, N and available P, while crude sand content demonstrated a significant positive relationship. For *P. jackbeardsleyi*, in-field abundance was positively correlated with CWB incidence, soil pH, EC, and available P, but negatively correlated with Al^{3+} content. For *P. marginatus*, significant negative correlations were observed with Ca^{2+} content, Mg^{2+} content, soil organic C and total N. Above values correspond to Kendall tau b (τB) correlation coefficients (Table 3), indicating a measure of concordance between the measured variables.

When evaluating the combined effect of multiple soil fertility and plant quality measures, different species-specific patterns were found (Table 4). Both the best-fitting model, and the competing model showed that abundance of *P. marginatus* was negatively related to total soil N, available P and the fine sand soil fraction, and positively related to *CWB* incidence. Similar to *P. marginatus*, both CWB incidence (positive) and N (negative) were found to be related to *P. jackbeardsleyi* abundance. However, unlike in the case of *P. marginatus*, soil C was also positively associated with the abundance of *P. jackbeardsleyi*. In the stepwise multiple regression analysis, only silt + clay content of the soil was negatively related to the abundance of *P. manihoti*. Multiple R^2 values were not obtained for the selected models of *P. manihoti*, as the models were built using a negative binomial regression approach. For the regression analyses, variation partitioning showed that, for *P. marginatus*, 34% of the variability was explained by N, 15% by Ca^{2+} and 13–14% each by EC and fine sand. Meanwhile, for *P. jackbeardsleyi*, 31% of the variability was explained by CWB infection, 25% by Al^{3+} content, 20% by P, and < 10% each by N and K.

Principal component analysis extracted important degrees of variation and the associated loading values (Table 5) in a combined dataset of soil fertility profiles and CWB incidence levels (reflecting overall plant resource quality), with the first two components representing 55.8% of the overall variance. The first PCA axis represented 36.3% of variance and was largely reflective of overall nutrient availability, as determined by major (N, P, Ca, Mg) elements, organic C and soil texture (Fig. 1). Fields in the left side of the PCA panel (i.e., with negative PC1 values) were characterized by conditions of high soil fertility, including recently cleared and burned plots in Cambodia, where cassava had been grown for 2–5 years with limited external inputs. On the right side of the PCA were fields from Binh Thuan provinces with sandy soils. Plots with intermediate soil fertility, staggered growing cycles and occasionally more intensive agro-production schemes (i.e., ample N usage, high-quality planting materials, herbicide use) were located towards the center of the fertility gradient defined by PC1, and included fields from Dak Lak (Vietnam) and Laos.

The second PCA axis represented 19.5% of variance, and was largely reflective of Ca, Mg, Al, EC, sand content and pH. Fields in the upper side of the biplot (i.e., positive values) were characterized by sandy soils with high EC and high levels of elements such as Ca or Mg, while more weathered fine textured (silt or clay) soils with high levels of Al oxides were found in the lower part of the PCA panel. Incidence of CWB (as additional determinant of plant resource quality) was associated with N content, organic C levels and% silt and clay fractions. The PCA analysis also differentiated fields from the different countries, with Cambodia's flat alluvial soils generally high pH, Ca and Mg content, Vietnamese plots typified by sandy texture and low soil fertility, and Lao soil differentiated by comparatively higher levels of Al oxides (Fig. 1).

Principal component regression was then carried out on aggregate measure of soil fertility (as reflected by PC1 and PC2 axes). Given that several soil fertility measures (and plant disease infection status) exhibited high levels of correlation, abundance of specific mealybug invaders appears to be associated with a combination of several variables. Field-level incidence patterns of all three mealybug species were significantly related to the first PCA axis (Fig. 2), with positive relationships for *P. marginatus* and *P. manihoti*, and negative trends for *P. jackbeardsleyi*. The second PCA axis showed significantly positive relationship with only *P. manihoti* abundance and not with the other mealybug species.

Table 1b

Parasitism levels and reproductive output of *A. lopezi*, when developing on *P. manihoti* nymphs reared on plants with different fertilizer treatments. Means followed by the same letter do not differ (ANOVA, α = 0.05), while an asterisk indicates statistical significance.

Parameter (*A. lopezi*)	N	control	N90	N180	K2O90	K2O180	Test statistic; P-value
Parasitism rate (proportion)	413	0.27 ± 0.005 c	0.29 ± 0.008 ab	0.30 ± 0.008 a	0.27 ± 0.008 bc	0.27 ± 0.006 bc	$F_{4,408}$ = 3.42 P = 0.009*
Lifetime fecundity (# mummies)	60	87.3 ± 2.0 b	99.4 ± 2.9 a	100.6 ± 3.3 a	96.6 ± 3.8 a	96.4 ± 2.8 a	$F_{4,55}$ = 18.43; P < 0.0001*
Oviposition period (d)	60	6.5 ± 0.24	7 ± 0.21	6.8 ± 0.20	7.1 ± 0.23	7.1 ± 0.18	$F_{4,55}$ = 2.07 P = 0.097
Oviposition rate (mummy/d)	60	13.5 ± 0.3 b	14.2 ± 0.2 ab	14.8 ± 0.3 a	13.6 ± 0.2 b	13.6 ± 0.2 b	$F_{4,55}$ = 5.05 P = 0.002*
Emergence rate (adults/mumm)	413	0.64 +0.01 c	0.72 +0.01 ab	0.71 +0.01 a	0.89 ± 0.02 b	0.73 +0.01 ab	$F_{4,408}$ = 10.84 P < 0.0001*
Offspring sex ratio (f/m)	413	0.60 ± 0.02 c	0.69 ± 0.03 ab	0.71 ± 0.02 a	0.65 ± 0.03 b	0.67 +0.02 b	$F_{4,408}$ = 3.06 P = 0.017*
Offspring longevity (d)	360	10.41 ± 0.2	9.97 ± 0.3	9.97 ± 0.2	9.92 ± 0.2	10.35 ± 0.2	$F_{4,355}$ = 1.05 P = 0.38*

Table 2
Incidence frequency (% sampled plants) and plant-level infestation rates (mealybug densities per plant) of three invasive mealybug species (*P. jackbeardsleyi, P. manihoti, P. marginatus*) for 65 cassava plots that were visited during the 2015 dry season in Vietnam, Cambodia and Laos. Incidence and infestation levels are indicated as mean ± SD. Means followed by the same letter do not differ between countries (ANOVA, α = 0.05; Tukey post-hoc test).

Mealybug species	Field-level incidence (% sampled plants)			
	Vietnam n = 20	Cambodia n = 18	Lao PDR n = 27	Regional n = 65
P. jackbeardsleyi	12.8 ± 9.1a	33.7 ± 24.3b	15.6 ± 18.4a	19.7 ± 20.0
P. manihoti	10.4 ± 10.9a	3.2 ± 5.0a	8.6 ± 13.7a	7.7 ± 11.3
P. marginatus	56.5 ± 25.7a	24.0 ± 23.5b	26.9 ± 21.9b	35.2 ± 27.3
	Plant-level infestation (individuals/plant)			
P. jackbeardsleyi	3.2 ± 3.5a	61.6 ± 137.1a	2.6 ± 2.1a	10.1 ± 47.8
P. manihoti	5.1 ± 8.2a	56.8 ± 136.8a	14.6 ± 21.5a	17.4 ± 57.3
P. marginatus	29.0 ± 21.6a	38.7 ± 76.4ab	5.7 ± 11.3b	22.0 ± 43.2

Table 3
Bivariate relationships between the three invasive mealybug species and single soil fertility parameters and CWB pathogen infection status. Values correspond to Kendall *tau b* (τ_B) correlation coefficients, which indicate a measure of concordance between corresponding variables. A negative sign before the value indicates a negative relationship, while no sign indicates a positive correlation. Values marked with an asterisk are coefficients that were statistically significant (**P-value** < **0.05**) for that particular comparison, when tested against a null hypothesis of no correlation ($\tau_B = 0$) between the variables.

	P. manihoti	*P. jackbeardsleyi*	*P. marginatus*
crude_ sand	0.15*	−0.07	0.04
Silt	−0.30*	0.08	−0.13
fine_sand	0.21	−0.04	0.08
pH	0	0.27*	−0.15
EC	−0.02	0.10*	0
Al	−0.09	−0.30*	0
K	−0.18	0.10	−0.18
Ca	−0.14	0.26	−0.25*
Mg	−0.13	0.28	−0.20*
OC	−0.17*	0.07	−0.17*
N	−0.24*	0	−0.25*
P	−0.25*	0.16*	−0.16
P₂O₅	0.10	0.10	0.08
CWB[a]	−0.04	0.18*	−0.13

Soil fertility parameters are abbreviated as follows: coarse sand corresponds to% of > 0.02 mm soil particles, silt is well-graded silt + clay; fine sand is% soil particles 0.02-0.2 mm); pH is pH of soil suspension; EC is soil electron conductivity; Al is Al 3+ mg/ 100 g soil; K is K+ mg/100 g soil; Ca is Ca2+ mg/100 g soil; Mg is Mg2+ mg/100 g soil; OC is% of soil organic carbon); N is% nitrogen); P is% P₂O₅; P₂O₅ is mg P₂O₅/100 g soil.

[a] *CWB* corresponds to field-level incidence of cassava witches broom disease, as recorded during transect walks.

3.3. Comparative evaluation of top-down pressures

In the third experiment, we specifically examined parasitism rates of *P. manihoti* for three different sites as positioned along the soil fertility

Table 5
Loading values of all the measured soil variables and cassava witches broom −CWB-infestation (per field) obtained from the first two PCA components (PC1 and PC2) (see Fig. 1 legend for explanation of the variables).

Variables	PC1	PC2
CWB	0.192	0.141
Crude sand (> 0.02 mm)	−0.133	−0.225
Wsilt and clay	0.326	0.355
Fine sand (0.02–0.2 mm)	−0.302	−0.278
pH	0.302	−0.335
EC	−0.341	0.161
Al	−0.206	0.429
K	0.226	−0.157
Ca	0.324	−0.29
Mg	0.362	−0.275
OC	0.35	0.171
N	0.359	0.231
P	0.272	0.49
mgP2O5	−0.201	0.668

spectrum, reflective of the PC1 axis. Nearly 400 *P. manihoti*-infected cassava tips were collected over the course of the 2014 and 2016 dry seasons. Out of these, 205 tips had > 10 mealybug individuals and were monitored for parasitoid emergence. In 2-month old crops at intermediate soil fertility, mealybug abundance showed high levels of variability between individual tips, with a coefficient of variation (CV) of 1.77, especially as compared to the CV values of 0.73 in fields in low-fertility settings. Mealybugs reached average abundance levels of 41.0 ± 30.0, 50.6 ± 89.7, 71.5 ± 123.7 and 101.2 ± 158.9 individuals per tip in Binh Thuan on 7–9 month old cassava, Tay Ninh on 2–3 month old cassava, Tay Ninh on 7–8 month cassava, and Kracheh on 7–9 month old cassava, respectively. Associated parasitism levels (proportion) were 0.10 ± 0.15, 0.52 ± 0.40, 0.57 ± 0.32 and 0.32 ± 0.27, respectively, for the four samplings. Parasitoid
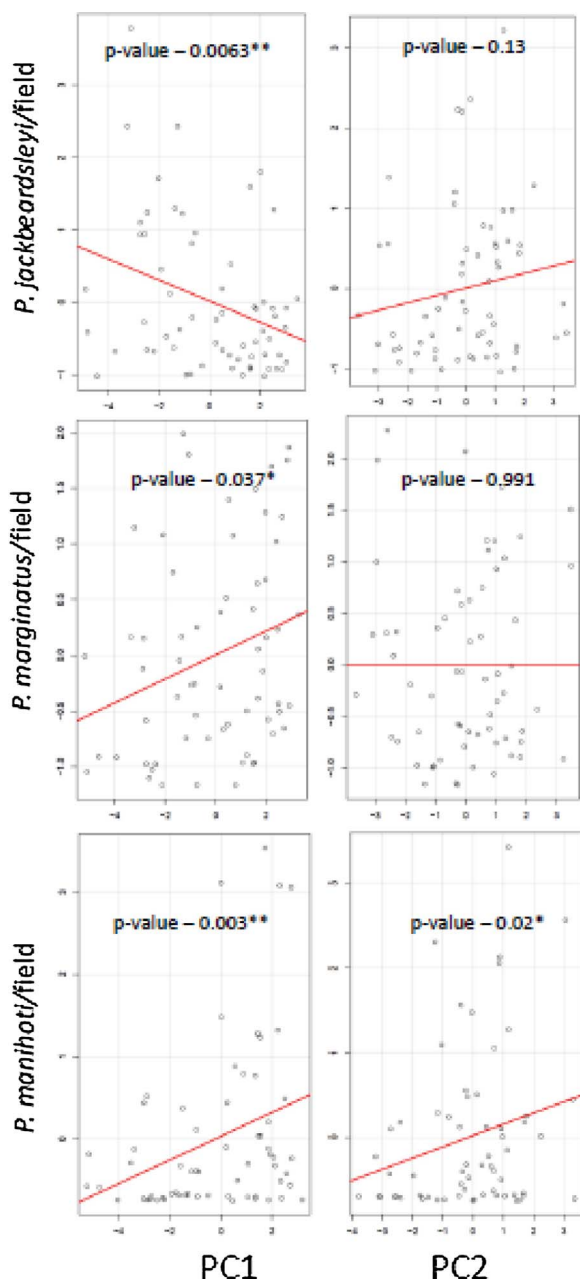
Table 4
Stepwise multiple regression models for abundance of three different species of mealybug, in relation to different soil fertility parameters and pathogen-infection status (both measures reflecting plant resource quality). For each of the invasive mealybug species, two statistical models are represented, with their respective Akaike information criterion (AIC) and R².

Mealybug species	Model equation[*]	AIC	Multiple R² value
Paracoccus marginatus	Model I[**]: 45.02–125.46 × N − 0.36 × fine_sand − 40.37 × P + 0.26 × CWB + 184.63 × EC − 1.09 × Ca	315.47	36.1%
	Model II[**]: 48.61–153.53 × N − 0.37 × fine_sand − 41.36 × P + 0.25 × CWB + 139.79 × EC	316.27	33.1%
Pseudococcus jackbeardsleyi	Model I[**]: 10.27–102.78 × N + 0.29 × CWB + 5.39 × OC + 21.42 × K	270.27	41.0%
	Model II[**]: 12.55–10.54 X Al + 0.27 × CWB + 24.77 × P − 87.75 × N + 4.61 × OC	270.42	38.9%
Phenacoccus manihoti	Model I[**]: 3.21–6.23 x silt − 15 × EC	293.31	−[***]
	Model II[**]: 2.70–5.82 × silt	293.46	−[***]

[*] Explanatory variables: N: nitrogen%; fine_sand: (0.02–0.2 μm fraction)%; P: P₂O₅%; CWB: field-level incidence of cassava witches broom disease; EC: soil electron conductivity; OC: soil organic carbon%; silt: W silt + clay.

[**] Model 1 corresponds to the model with the least AIC score ("best-fit model"), and model 2 ("competing model") corresponds to the model that obtained an AIC score, that is within 2 units of the AIC score of the "best-fit model".

[***] Multiple R² values for the selected models of *P. manihoti* are not available, as the models were built using a negative binomial regression approach (see Materials & Methods section for more details).

Fig. 2. Relationships between field-level abundance of *P. jackbeardsleyi*, *P. marginatus* and *P. manihoti*, and soil texture or fertility measures as obtained through principal component regression. For each mealybug species, regression patterns are represented with the first and second PCA axis (i.e., PC1, PC2). Lines represent regression curves, with associated p values. Goodness-of-fit was assessed for each regression model, by testing for significant difference between the residual deviances of an ideal model (where the predicted values are identical to the observed) and the selected model using a chi-square test. None of the models yielded a significant p-value in the chi-square test, indicating that the selected model fit the data well.

communities were largely dominated by the parasitic wasp *A. lopezi*. Mealybug numbers did not differ between sites and field conditions (Kruskal-Wallis, $X^2 = 5.96$, $p = 0.114$), but parasitism rates were significantly higher in the intermediate fertility site (i.e., Tay Ninh), than at other locales (Kruskal-Wallis, $X^2 = 74.41$, $p < 0.001$; Fig. 3).

Total number of parasitoids (per tip) significantly differed between sites (Kruskal-Wallis, $X^2 = 52.05$, $p < 0.001$). Regression analyses revealed that parasitoid abundance was closely related to *P. manihoti* infestation pressure, with different patterns of density-dependence for each of the soil fertility conditions as such: Kracheh ($F_{1,18} = 10.781$,

$p < 0.01$), Tay Ninh 2 months ($F_{1,85} = 77.183$, $p < 0.01$), Tay Ninh 8 months ($F_{1,38} = 83.602$, $p < 0.001$) and Binh Thuan ($F_{1,54} = 8.625$, $p < 0.01$; Fig. 3). Positive density dependence was recorded in all sites, with the strongest parasitoid response at intermediate fertility sites (i.e., Tay Ninh). Although no data were obtained from Binh Thuan and Ba Ria Vung Tau provinces, parasitoid sex ratio from sites in Cambodia and Tay Ninh were not significantly different (Kruskal-Wallis, $X^2 = 3.13$, $p = 0.209$).

4. Discussion

Much remains to be learned about the regulatory forces that shape ecological communities in terrestrial systems (Gruner, 2004; Borer et al., 2006; Allen and Wesner, 2016). The agroecosystems studied here provide a unique and highly-relevant opportunity to evaluate trophic regulation processes. In tropical agroecosystems in particular, soils tend to be highly weathered and thus plant resource or bottom-up effects can exert strong effects on herbivore communities that may either overshadow the role of top-down regulation (Ritchie, 2000) or influence herbivores by affecting the strength of top-down forces. While past research has examined how fertilizer addition impacts particular feeding guilds and plant-herbivore interactions (Sipura, 1999; Forkner and Hunter, 2000; Ritchie, 2000; Garibaldi et al., 2010; Rzanny et al., 2013), much of this work has been conducted in perennial ecosystems. Our study is unique in the extent to which it relies upon community ecology approaches, to assess invader success mitigated by plant resource constraints in a rapidly-expanding tropical agricultural system.

4.1. Soil fertility impacts on herbivore and parasitoid performance

Plant chemistry, largely determined by soil fertility, affects life history and physical characteristics of herbivores as well as higher trophic orders (Ode, 2006; Chen et al., 2010; Stam et al., 2014). Plant stoichiometry, defense mechanisms (constitutive or induced), and primary productivity are all factors that affect plant-herbivore interactions and impacts on parasitoids or predators. Through our manipulated "microcosm" studies, we gained an initial appreciation of how soil fertility and/or availability of key limiting nutrients impacts such interactions between plants, the herbivore, *P. manihoti,* and the parasitoid, *A. lopezi*. Nitrogen fertilization led to a reduction in *P. manihoti* development time along with an increase in body size, adult weight and total fecundity. Meanwhile, K addition had less pronounced effects, and only intermediate fertilization levels seemed to benefit *P. manihoti* growth and reproduction. These findings are in line with results from other herbivore-plant systems, in which sap-feeders such as aphids increase their populations on short-season crops when soils are deficient in K, or under N supplements (Noma et al., 2010). While both nutrients influence phloem content of dietary N, a limiting nutrient for the development of homopterans such as mealybugs (Dixon, 1998), the effect of K fertilization may only be apparent when plants are K-stressed (e.g., Walter and DiFonzo, 2007). For *A. lopezi*, laboratory trials corroborate previous findings that its development rate and sex ratio are shaped by the size of its host (van Dijken et al., 1991; Schulthess et al., 1997). The microcosm studies conducted here, thus indicate that *P. manihoti* (and indirectly *A. lopezi*) abide to Price's (1991) 'plant vigor hypothesis', in which vigorously-growing plants are better hosts for herbivores and N disproportionally supports herbivore growth as it is the basis for protein synthesis. This is aligned with *P. manihoti* feeding habits, as this insect prefers nutrient-rich, actively growing tissues (White, 2009). Laboratory findings reported here are also reflected by the strong parasitoid response to high *P. manihoti* population levels that was evident from the field samplings in Tay Ninh (i.e., at settings with intermediate soil fertility and N enrichment, based on farmer discussions; Fig. 3). Our microcosm studies could thus constitute a first step towards defining a crop-specific range of N concentrations that benefit plant growth and boost a plant's immune responses or optimize biological control (Chen
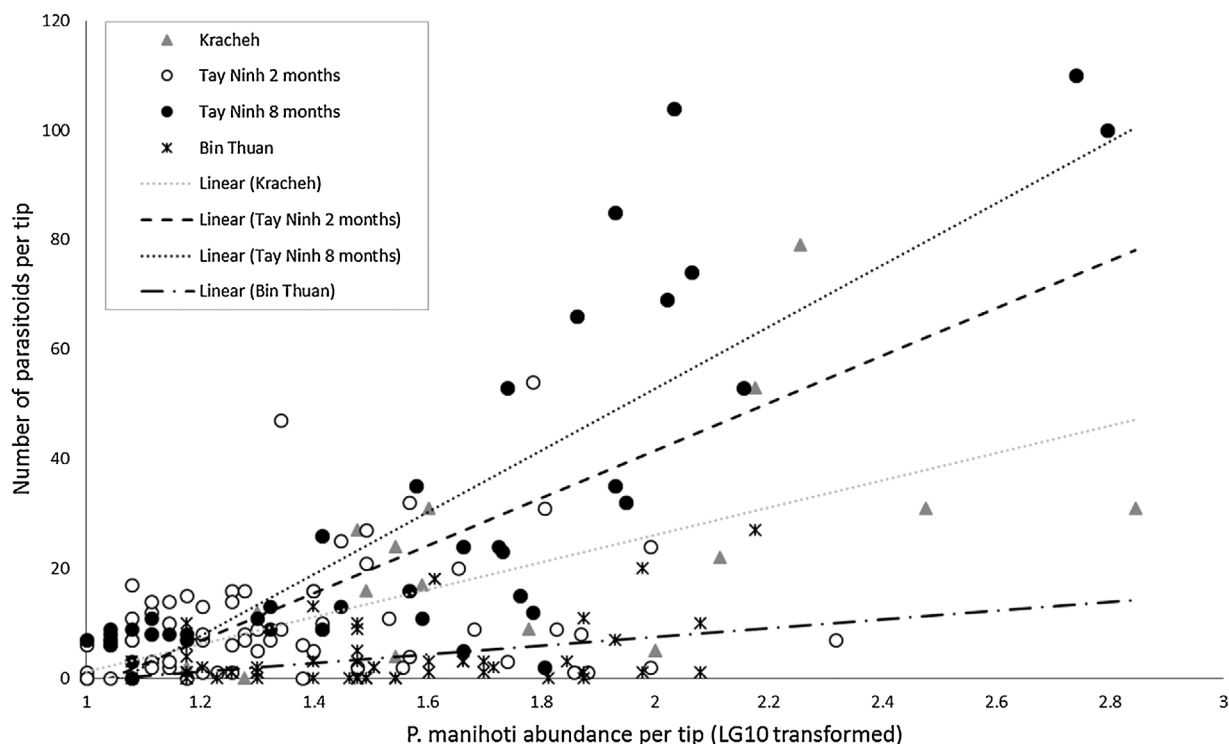
Fig. 3. Relationship between per-plant *P. manihoti* infestation level and parasitism rate in three different soil fertility contexts in four locations, as positioned along the PC1 axis. Locations include Kracheh (Cambodia) and Tay Ninh, Binh Thuan/Ba Ria Vung Tau (Vietnam), covering a high-fertility and intermediate fertility site, and a low-fertility site with sandy soils respectively. For the site in Tay Ninh, *P. manihoti* abundance and *A. lopezi* parasitism rates were assessed on 2-month and 8-months old crops. Regression curves represent statistically significant patterns, with the following coefficients of determination: Kracheh 7–9 months (R^2 = 0.375), Tay Ninh 2 months (R^2 = 0.476), Tay Ninh 8 months (R^2 = 0.688), and Binh Thuan 7–9 months (R^2 = 0.138). Parameter estimates for slopes of the regression curves were as follows: 56.44, 43.35, 24.87, and 7.95 respectively.

et al., 2010).

While microcosm studies are valuable and informative, it's often difficult to extrapolate their results to field conditions particularly when considering short-term pot assays for semi-perennial woody plants, such as cassava, which can have 2-m long roots (Connor et al., 1981). Also, performance of herbivores such as mealybugs is determined by the nutritional content and quality of above-ground plant parts, but addition of single-element fertilizer does not necessarily affect those. For example, K fertilization regularly causes minor variation in leaf nutrient content, while leaf N content can concurrently be controlled by multiple soil fertility parameters, e.g., soil pH, P content or water availability (e.g., Lower and Orians, 2003; Fujita et al., 2013). Hence, the effect of a single nutrient addition on host-parasitoid systems can easily be obscured by other plant growth-limiting factors. In fertilizer supplement studies, the strongest effects are often found when nutrient limitation is alleviated (see Elser et al., 2000). As our microcosm studies were conducted using relatively fertile, nutrient-rich soil instead of inert media (e.g., sand), thus some of the envisaged effects on herbivore-parasitoid complexes may have been dampened (see Guttierez et al., 1988). Similar to work by Denno et al. (2002), we observe a correspondence between laboratory studies and field surveys for *P. manihoti*, both of which suggest a dominance of bottom-up controls. While we cannot draw conclusions for the other two species of mealybugs, bottom-up impacts are likely determined by their particular traits and associated parasitoid (complex). We can infer that improved mealybug performance is related to increased leaf N content, though this was not measured, so this conclusion is somewhat speculative. In the meantime, it should be noted that individual-level measurements of the effect of soil fertility and plant nutritional quality on herbivore or parasitoid performance may not necessarily translate into population effects (Zaugg et al., 2013).

In our study, field observations indicated that population levels for the three invasive herbivores across the various sampling sites were correlated to a soil fertility with distinct soil fertility parameters. Our findings suggest species-specific relationships with single measures of soil fertility, texture and disease infection status. While correlations don't necessarily entail causality, observed patterns do differ substantially between the three invaders. For *P. manihoti*, in-field incidence was positively correlated with sand content, and negatively with silt, soil C, N and P (Table 3). This supports previous work in Africa suggesting that *P. manihoti* achieves high population levels on low-fertility, sandy soils, even in the presence of effective parasitoids (Neuenschwander et al., 1990). On the other hand, the abundance of *P. jackbeardsleyi* appeared to follow a distinct pattern and was largely associated with pH, EC and CWB-infestation status. Given the multi-dimensional usage of resources by plants, herbivores and parasitoids, an aggregate measure (e.g., obtained through PCA) may be more suitable to capture species' responses to soil- or resource-based conditions (see also Drenovsky et al., 2012; Fujita et al., 2013). Nevertheless, various single soil fertility measures did correlate significantly with field-level abundance for all three mealybug species (Table 3) and both approaches are likely valuable for understanding soil impacts on herbivore performance.

4.2. Life history and field management drivers for invader success

Differential life history traits and invasion history of the three invaders might help explain some of observed disparate response trends. As globally successful invaders, all three mealybug species could benefit from similar high phenotypic plasticity or adaptation potential (e.g., Dawson et al., 2012), but may still differ in myriad other aspects. Although there's no single trait that reflects invasiveness, so-called 'invader attributes' tend to comprise competitive ability, phenotypic plasticity, niche construction and phenological niche separation (e.g., Perkins and Nowak, 2013). Amongst others, the outcome of invasions is set by the interaction of the above species' traits with nutrient

availability over short and long time periods (Mata et al., 2013). Competitively-inferior invaders capable of rapid population growth, such as *P. manihoti*, can capitalize on short-term nutrient pulses, while competitively-superior or dominant invaders are easily disrupted by disturbance-related resource heterogeneity. In our study, such disturbance-related heterogeneity was indirectly measured through the soil fertility measurements in the field survey, but only qualitatively inferred for the specific case of *P. manihoti* and *A. lopezi*. Life history traits and feeding behavior can also explain comparative performance of specific herbivores in given varying resource quality or soil fertility (White, 2009). For *P. manihoti*, the 'plant vigor hypothesis' possibly may apply, with this species benefiting greatly under crop management schemes with important levels of nutrient addition. On the other hand, species such as *P. jackbeardsleyi* that feed preferentially on older senescing tissues and on CWB-affected plants, might follow the 'plant stress hypothesis' and experience a niche opportunity on debilitated plants with sub-optimum nutrition for other mealybug species. In studies with plant hoppers, Denno et al. (2002) also pointed at mobility as a prime mediator of top-down vs. bottom-up impacts for a given species. However, for largely sedentary species such as mealybugs, mobility and specifically a species' ability to elude aggregative responses of natural enemies may be of limited relevance. Lastly, history of the invasion process can bring about species-specific shifts in top-down forces. For a long-time invader such as *P. jackbeardsleyi* (first reported from Asia in 1987), parasitoid communities possibly have had comparatively more time to assemble, diversify or adapt (e.g., Shea and Chesson, 2002), and exert stronger top-down pressures. Also, recent invaders relatively less burdened by natural enemies, such as *P. manihoti* or *P. marginatus*, may outperform long-time invaders in high-resource settings (Blumenthal, 2005), or cassava might simply be a far superior host for them as compared to *P. jackbeardsleyi*.

Sites along the soil fertility continuum vary in historic land-use, current management practices, as well as a range of important environmental parameters (e.g., climate, landscape heterogeneity). More specifically, sites on the left side of the continuum (Fig. 1) include recently-cleared swidden agriculture plots and fields under rotation with other crops (e.g., soybean). Under less intensive agricultural systems, C storage and soil quality can be substantially higher than under continuous annual cropping systems (Bruun et al., 2009), although these patterns can also be greatly influenced by soil fertility management and inherent properties, such as soil texture. Land-use legacies can persist for decades and have profound impacts on herbaceous species composition, biodiversity and resulting parasitoid communities (Stahlheber et al., 2015; Stuhler and Orrock, 2016). This may be particularly relevant, as Lao and Cambodian fields under swidden agriculture regimes and less intensive management had far greater weed cover (Wyckhuys, unpublished). On the other hand, several plots in the central portion of the soil fertility continuum (Fig. 1) were under more intensive crop management practices (e.g., tillage, herbicide use, high-quality planting materials) and frequent additions of N-P-K fertilizers. Actions such as N fertilization are not necessarily reflected in soil fertility metrics, and fertilizer N additions are even likely to amplify N-loss pathways (see Lu et al., 2011). Nevertheless, they can augment plant nutritional status, and subsequent herbivore population growth and/or parasitoid development. Invader performance appeared to differ under these varying contexts, and suggests that soil fertility (measured), disturbance frequency (inferred, but not measured), and community composition or maturity (inferred, but not measured) all contributed to shape invasion and invader dynamics (e.g., Mattingly and Orrock, 2013). While certain species were more successful in plots with high soil fertility, others thrived under more resource-limited settings (see also Funk and Vitousek, 2007). Increased abundance of *P. marginatus* and *P. manihoti* at sites with intensified agro-production and intermediate (or low) soil fertility (Fig. 2) may hint that these species benefit primarily from nutrient pulses (inferred from pot trials, but not measured in the field) and disturbance regimes (largely inferred, but not measured). In

contrast, enhanced presence of *P. jackbeardsleyi* in high-fertility settings suggests a strong bottom-up effect and a substantially shortened "window of vulnerability" to resident natural enemies (see 'slow growth − high mortality' phenomenon; Benrey and Denno, 1997). For *P. manihoti*, bottom-up effects were evident and top-down forces appeared to be strengthened in high-fertility soils or plots with external nutrient enrichment (Fig. 3). Such increases of top-down forces with resource inputs have been recorded in several other systems (e.g., Hunter and Price, 1992; Forkner and Hunter, 2000; Walker et al., 2008). Our results also echo those of Ritchie (2000), in which bottom-up influences are quite pronounced in resource-limited settings, while some herbivores can experience far stronger top-down forces within environments with fertile soils and N-rich plant tissue. Though patterns are highly species-specific, soil nutrient profiles and fertilizer additions shape host plant quality and either enhance or reduce an individual mealybug's relative niche opportunity (Stiling and Moon, 2005).

5. Conclusions

Our work points at differential trophic regulation for three invasive mealybugs in tropical agroecosystems, and elucidates important species and context-specific patterns. The findings presented here emphasize how biological control is strongly dependent upon site fertility for the particular case of *P. manihoti* (see Hovick and Carson, 2015), and illuminate resource-mediated performance of two other key mealybug invaders. Microcosm experiments clearly emphasized the potential of plant nutrient availability, N in particular, for regulating the performance of multiple trophic levels in cassava systems. Meanwhile, results from regional field studies show important species-specific responses of invasive herbivores (and their parasitoids) to a gradient in soil fertility and texture, and management intensity. Our results support the notion that soil fertility and plant quality variables, either singly or as composite indices, should be taken into consideration when setting priorities for invasive species management or planning biological control interventions (Asiimwe et al., 2013; Mace and Mills, 2016). Last but not least, our findings from smallholder systems in the developing-world tropics provide renewed impetus for earlier calls to address agricultural pest management in a more holistic and integrated fashion (e.g., Lewis et al., 1997).

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