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Continental-scale suppression of an invasive pest by a host-specific parasitoid heralds a new era for arthropod biological control

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Biological control constitutes one of the world's prime ecosystems services, and can provide long-term and broad-scale suppression of invasive pests, weeds and pathogens in both natural and agricultural environments. Following (very few) widely-documented historic cases that led to sizeable environmental up-sets, the discipline of insect biological control has -over the past three decades- gone through much-needed reform. Now, by deliberately taking into account the ecological risks associated with insect biological control, immense environmental and societal benefits can be gained. In this study, we document and analyze a rare, successful case of biological control against the invasive mealybug, *Phenacoccus manihoti* (Hemiptera: Pseudococcidae) which invaded Southeast Asia in 2008, where it caused substantial crop losses and triggered 2- to 3-fold surges in

agricultural commodity prices. In 2009, the host-specific parasitoid *Anagyrus lopezi* (Hymenoptera: Encyrtidae) was released in Thailand and subsequently introduced into neighboring Asian countries. Drawing upon continental-scale insect surveys, multi-year population studies and (field-level) experimental assays, we show how *A. lopezi* attained intermediate to high parasitism rates across diverse agro-ecological contexts. Driving mealybug populations below non-damaging levels at a continental scale, *A. lopezi* allowed yield recoveries up to 10.0 t/ha and provided biological control services worth several hundred dollars per ha (at local farm-gate prices) in Asia's 4-million ha cassava crop. Our work provides lessons to invasion science and crop protection worldwide, heralds a new era for insect biological control, and highlights its potentially large socio-economic benefits to agricultural sustainability in the face of a debilitating invasive pest. In times of unrelenting insect invasions, surging pesticide use and accelerating (invertebrate) biodiversity loss across the globe, this study unequivocally demonstrates how biological control – as a pure public good – constitutes a powerful, cost-effective and environmentally-responsible solution for invasive species mitigation.

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12 **new era for arthropod biological control**

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14 Running head: Biocontrol of the cassava mealybug in Asia

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42 parasitism; sustainable agriculture; invasion biology

43 **Abstract**

44 Biological control features as one of the world's prime ecosystems services, and can provide
45 long-term and broad-scale suppression of invasive pests, weeds and pathogens in both natural
46 and agricultural environments. Following (very few) widely-documented historic cases that led
47 to sizeable environmental up-sets, the discipline of arthropod biological control has -over the
48 past three decades- gone through much-needed reform. Now, by deliberately taking into account
49 the ecological risks associated with the deliberate introduction of insect natural enemies,
50 immense environmental and societal benefits can be gained. In this study, we document and
51 analyze a rare, successful case of biological control against the invasive cassava mealybug,
52 *Phenacoccus manihoti* (Hemiptera: Pseudococcidae) which invaded Southeast Asia in 2008,
53 where it caused substantial crop losses and triggered 2- to 3-fold surges in agricultural
54 commodity prices. In 2009, the host-specific parasitoid *Anagyrus lopezi* (Hymenoptera:
55 Encyrtidae) was released in Thailand and subsequently introduced into neighboring Asian
56 countries. Drawing upon continental-scale insect surveys, multi-year population studies and
57 (field-level) experimental assays, we show how *A. lopezi* attained intermediate to high parasitism
58 rates across diverse agro-ecological contexts. Driving mealybug populations below non-
59 damaging levels at a continental scale, *A. lopezi* allowed yield recoveries up to 10.0 t/h and
60 provided biological control services worth several hundred dollars per ha (at local farm-gate
61 prices) in Asia's 4-million ha cassava crop. Our work provides lessons to invasion science and
62 crop protection worldwide, heralds a new era for insect biological control, and highlights its
63 potentially large socio-economic benefits to agricultural sustainability in the face of a debilitating
64 invasive pest. In times of unrelenting insect invasions, surging pesticide use and accelerating
65 (invertebrate) biodiversity loss across the globe, this study unequivocally demonstrates how

66 biological control – as a pure public good – constitutes a powerful, cost-effective and
67 environmentally-responsible solution for invasive species mitigation.

68

69

70 **Introduction**

71

72 Biological control is one of the world's prime ecosystem services, and plays a pivotal role in the
73 functioning and broader resilience of agricultural and natural ecosystems alike (Costanza *et al.*
74 1997). For US agriculture alone, insect-mediated biological control is conservatively valued at
75 \$4.5 billion per year, and a diversity of natural enemies helps alleviate pressure from herbivores
76 and other crop antagonists (Losey and Vaughan, 2006). However, rapid depletion of animal
77 populations and progressive ecosystem simplification compromise the strength and stability of
78 this vital ecosystem service (Oliver *et al.*, 2015; Hallmann *et al.*, 2017). In tropical terrestrial
79 ecosystems, these trends might be even more pronounced though they routinely remain un-
80 documented (Melo *et al.*, 2013; Barnes *et al.*, 2014).

81 Across the globe, arthropod pests reduce agricultural productivity by 10-16% and constitute
82 key impediments to food security and (indirectly) poverty alleviation (Oerke, 2006; Bebber *et*
83 *al.*, 2013). Though native pests continue to pose major problems for the world's agriculture, non-
84 native species are of increasing significance as a result of trade globalization and human
85 movement (Bradshaw *et al.*, 2016; Paini *et al.*, 2016). Importation biological control (IBC; also
86 known as 'classical biological control'), or the judicious selection and subsequent introduction of
87 a specialized natural enemy from the pest's region of origin, has been repeatedly shown to
88 effectively reduce invasive pests (van Driesche *et al.*, 2008; Heimpel and Mills, 2017).

89 Particularly in the developing-world tropics, IBC can be a “silver bullet” option for destructive
90 agricultural pests, being largely self-sustaining and requiring little or no stakeholder intervention
91 (Andrews *et al.*, 1992). Since the late 1800s, more than 2,000 natural enemy species have been
92 released against approximately 400 invasive pests worldwide, occasionally resulting in complete
93 pest control but regularly causing limited or no impact (van Lenteren *et al.*, 2006; Cock *et al.*,
94 2016b). Though economic impacts are not routinely assessed for IBC, levels of pest suppression
95 and ensuing benefit:cost ratios can be exceptionally favorable (5:1 to >1,000:1) (Heimpel and
96 Mills, 2017; Gutierrez *et al.*, 1999; Naranjo *et al.*, 2015). Yet, IBC is marred with remarkably low
97 rates of success (Greathead & Greathead, 1992; Cock *et al.*, 2016a), and consequently biological
98 control as a whole is habitually undervalued and all too often taken for granted (Daily *et al.*,
99 2009). Furthermore, over the past three decades, IBC initiatives have been met with stringent
100 regulations and a heightened emphasis on potential ecological risks or unintended side-effects
101 (Heimpel & Cock, 2018). The latter was triggered by a provocative yet necessary account by
102 Howarth (1983, 1991), built around misguided biological control releases that were conducted
103 decades earlier, and in which the long-established paradigm of IBC as ‘ecologically-safe’
104 practice was challenged.

105 One widely-acclaimed IBC program is the Africa-wide initiative targeting the invasive cassava
106 mealybug, *Phenacoccus manihoti* (Hemiptera: Pseudococcidae), which led to a 50% yield
107 recovery resulting in long-term economic benefits up to US \$20.2 billion as well as the likely
108 avoidance of widespread famine without negative side effects (Neuenschwander *et al.*, 1989;
109 Herren and Neuenschwander, 1991; Zeddies *et al.*, 2001). Key to the success of this program
110 was the carefully-selected host-specific and environmentally-adaptable parasitic wasp *Anagyrus*
111 *lopezi* (Hymenoptera: Encyrtidae), recovered in 1981 after foreign exploration from South

112 America, and introduced into Nigeria soon thereafter. As the *A. lopezi* wasp is considered to be a
113 specialist internal feeder on *P. manihoti*, no detrimental ecological impacts resulted from its
114 continent-wide release (Neuenschwander, 2001). Following its devastating passage through
115 Africa's cassava belt in the 1970s and 80s, *P. manihoti* was inadvertently introduced into
116 Thailand in 2008, spread through mainland Southeast Asia, and had made its appearance in
117 insular Indonesia by 2010 (Graziosi *et al.*, 2016). As cassava is grown on >4 million ha by an
118 estimated 8 million farming families throughout tropical Asia, this pest had ample potential to
119 cause massive socio-economic impacts. As part of an internationally-coordinated management
120 campaign for *P. manihoti*, *A. lopezi* was promptly sourced from Benin, West Africa and 500
121 adults of this wasp were introduced into Thailand in 2009 (Winotai *et al.*, 2010). Parasitoid
122 wasps were subsequently mass-reared by multiple Thai institutions, released across the country
123 during 2010-2012 (some by airplane) and introduced into neighboring Laos, Cambodia (in
124 2011), Vietnam (in 2013) and Indonesia (in 2014) (Wyckhuys *et al.*, 2015).

125 In this study, we characterized the degree to which *A. lopezi* has established in the highly-
126 heterogeneous cassava cropping environments of Southeast Asia. Field research was carried out
127 over the course of 2014-2017 by various country teams, each pursuing different objectives as
128 outlined below. We employed seasonal population surveys that extended from Myanmar's
129 Ayeyawaddy River delta to the uplands of Timor in eastern Indonesia, to quantify magnitude and
130 spatial extent of parasitoid-induced *P. manihoti* population suppression (*section i, ii*).
131 Furthermore, we employed well-established manipulative protocols to assess the effectiveness of
132 *A. lopezi* and subsequent yield benefits of biological control (De Bach *et al.*, 1971; van Lenteren
133 *et al.*, 1980; Luck *et al.*, 1988) (*section iii*). Finally, we conducted an analysis of production
134 statistics and cassava prices in one of Asia's main cassava-growing countries (Thailand) over a

135 time period spanning the 2008 *P. manihoti* invasion, the 2009 parasitoid introduction into
136 Thailand and the subsequent (natural, and human-aided) continent-wide distribution of *A. lopezi*
137 (*section iv*).

138 Our work uses original datasets to present a rare, continental-scale and multi-year assessment
139 of IBC-mediated insect pest suppression, and the cascading trophic and socioeconomic effects on
140 cassava yield loss reduction and commodity prices. We present a data-rich body of information
141 on the benefits of *A. lopezi* as a biological control agent, and lay the basis for further econometric
142 investigations. This study illustrates the potential value of an insect-driven ecosystem service to
143 agricultural sustainability, in the face of a potentially devastating invasive pest.

144

145

146 **Materials & Methods**

147

148 *i. Multi-country pest & natural enemy survey*

149

150 From early 2014 until late 2017, insect surveys were carried out in 634 cassava fields in
151 Myanmar, Thailand, Lao PDR, Cambodia, Vietnam, southern China and Indonesia. Survey
152 protocols are described in detail in Graziosi *et al.* (2016). In brief, we selected older fields (i.e.,
153 8-10 months of age) in the main cassava-growing areas of each country, with individual sites
154 located at least 1 km apart. Five linear transects were randomly chosen per site, with ten plants
155 (routinely spaced at 0.8-1.2 m) sampled in each transect. By doing so, a total of 50 plants per
156 field were assessed for *P. manihoti* infestation and per-plant mealybug abundance. In-field
157 identification of mealybugs was based on morphological characteristics such as coloration and

158 presence or length of abdominal waxy filaments, while samples were also taken to the laboratory
159 for identification by specialist taxonomists. Following transect walks we calculated average *P.*
160 *manihoti* abundance (number of individuals per infested tip) and field-level incidence
161 (proportion of *P. manihoti*-infested tips per field).

162 To assess local *A. lopezi* establishment and parasitism rates, we conducted dry-season sampling
163 from 2014 to 2017 at sub-sets of mealybug-invaded sites in Thailand ($n= 20$), Cambodia ($n = 10$,
164 15), southern Vietnam ($n= 20, 20, 6$) and Indonesia ($n = 10, 9, 21$) (total $n= 131$). Sampling
165 consisted of collecting 20 mealybug-infested tips from local fields and transferring them to a
166 laboratory to monitor subsequent parasitoid emergence (Neuenschwander *et al.*, 1989). Surveys
167 were carried out during January-May 2014 (dry season), October-November 2014 (late rainy
168 season), January-March 2015 (dry season) in mainland Southeast Asia, and during October-
169 November 2014 and 2017 (dry season) in insular Indonesia. Locations were recorded using a
170 handheld GPS unit (Garmin Ltd, Olathe, KS). In-field identification of mealybugs was based on
171 morphological characters, while samples were also transferred to the laboratory for further
172 taxonomic identification. Voucher specimens of *P. manihoti* were equally deposited at the Thai
173 Department of Agriculture (Bangkok, Thailand), Bogor Agricultural University (Bogor,
174 Indonesia) and Plant Protection Research Institute (Hanoi, Vietnam).

175 To assess local *A. lopezi* establishment and parasitism rates, mealybug-infected tips were
176 collected in the field and transferred to a laboratory. Upon arrival in the laboratory, each tip was
177 carefully examined, predators were removed and the total number of *P. manihoti* was
178 determined. Tips were then placed singly into transparent polyvinyl chloride (PVC) containers,
179 closed with fine cotton fabric mesh. Over the course of three weeks, containers were inspected
180 on a daily basis for emergence of parasitic wasps and *A. lopezi* parasitism levels (per tip and

181 field) were computed. Next, for fields where presence of *A. lopezi* was reported, we carried out a
182 regression analysis to relate field-level mealybug abundance with parasitism rate. Mealybug
183 infestation levels and parasitism rates were log-transformed to meet assumptions of normality
184 and homoscedasticity, and all statistical analyses were conducted using SPSS.

185

186 *ii. Multi-year mealybug and parasitoid population assessment in Vietnam*

187

188 From July 2013 until July 2015, we conducted population surveys in Tay Ninh province,
189 Vietnam; an area with near-continuous, all-year cassava cultivation (see also Le et al., 2018).
190 The cassava mealybug is assumed to have arrived in southern Vietnam during 2011-2012, and *A.*
191 *lopezi* was first detected from Tay Ninh province in early 2013. Eight newly-planted cassava
192 fields were selected of uniform age, crop variety, developmental stage and management. Every
193 two months, insect surveys were done within these fields, to characterize *P. manihoti* incidence,
194 infestation pressure and *A. lopezi* parasitism rate. In each field, a total of five linear 10-15 m
195 transects were screened (plants routinely spaced at 0.8-1.2 m) and, 50 plants were thus carefully
196 inspected for *P. manihoti*. *Phenacoccus manihoti* infestation was recorded as field-level
197 abundance (number of individuals per infected tip) and field-level incidence (proportion of
198 mealybug-affected tips) at each sampling date and location. To assess *A. lopezi* parasitism rates,
199 20 mealybug-infested tips were randomly collected from each field by breaking off the top parts
200 of individual plants, and transferred to the laboratory. Parasitism rates were estimated from these
201 samples as described above, and parasitism levels were computed for each individual field and
202 sampling date. We used analysis of variance (PROC MIXED, SAS version 9.1; SAS Institute,
203 Cary, NC) with field as random factor, and tested the effect of cassava age, sampling date and

204 year for *P. manihoti* incidence, abundance and *A. lopezi* parasitism. Means were compared with
205 least squares means approach. Mealybug abundance data were log-transformed while incidence,
206 parasitism and hyperparasitism data were arcsine-transformed to meet normality.

207 The intrinsic rate of mealybug population increase, r , over two months was calculated over
208 subsequent sampling events as $\ln(m_{t+1}/m_t)$ where m = the per-tip mealybug density. This growth
209 rate was regressed against the mealybug parasitism rate as a means of assessing the role of the
210 parasitoids in suppressing mealybug population growth rates and also to estimate the parasitism
211 level needed to suppress population growth rate. The statistical significance of the relationship
212 between parasitism rate and mealybug population growth was assessed using a generalized linear
213 model incorporating normal error distribution with r as the response variable and parasitism level
214 and field identity as independent variables.

215

216 *iii. Exclusion cage assays*

217

218 In August 2014, a field study was initiated at the Rayong Field Crops Research Center in
219 Rayong, Thailand (Thancharoen et al., under review). To assess the relative contribution of
220 natural enemies such as *A. lopezi* to pest control, we employed exclusion assays (Snyder and
221 Wise, 2001; Costamagna *et al.*, 2007). More specifically, to determine separate and joint effects
222 of *P. manihoti* and *A. lopezi* on cassava crop yield, three different treatments were established
223 using two common cassava varieties: Kasetsart 50 (KU50) and Rayong 72 (R72). Treatments
224 consisted of the following: 1) ‘full cage’ assays, in which a plant was entirely covered by a mesh
225 screen cage to exclude all natural enemies; 2) ‘sham’ cage assays, in which a plant was covered
226 by a screen cage to provide a microhabitat similar to that of the ‘full cage’, but left open at the

227 sides to allow natural enemy access; 3) ‘no cage’ assays, in which a plant was kept without a
228 cage, as a ‘real-world’ benchmark. Each treatment was established with four replicates. The
229 experimental field was established using locally-sourced stem cuttings of KU50 or R72, planted
230 at 1-m distances within plots. In experimental plots, weeding was done manually, fertilizer was
231 used at conventional rates and insecticide use was avoided throughout the assay.

232 Once plants had reached 4.5 months of age, 2 x 2 x 2 m polyvinylchloride (PVC) frame cages
233 were deployed, with four plants contained within each cage. Cages were covered with fine nylon
234 mesh screen to prevent entry by insects, including *A. lopezi* parasitoids. In January 2015, 10
235 adult female *P. manihoti* were gently brushed onto plants within each treatment (shared among
236 the four plants). Mealybug adults were obtained from a laboratory colony at Rayong Field Crops
237 Research Center that had been started in early 2014, in which *P. manihoti* were maintained on
238 potted cassava plants within a screen-house that were regularly supplemented with field-
239 collected individuals. Visual observations were carried out within the cages on a monthly basis
240 and *P. manihoti* abundance was recorded on each plant. On September 7, 2015, once the crop
241 had reached 12 months of age, cages were removed and plants within the different experimental
242 treatments were harvested manually. At harvest, fresh root yield (FRY) was determined for each
243 plant: (Karlstrom *et al.*, 2016).

244 Mealybug population build-up under each experimental treatment was calculated, by
245 converting the average number of mealybugs per plants on a given sampling date to cumulative
246 mealybug-days (CMD) (Ragsdale *et al.*, 2007):

247

248
$$\sum_{n=1}^{\infty} = \left(\frac{x_{i-1} + x_i}{2} \right) \times (t_i - t_{i-1})$$

249

250 where n is the total number of days over which sampling took place, x_i is the number of
251 mealybugs counted on day i and t_i is the number of days since the initiation of sampling on day i .

252 Mealybug population build-up under each experimental treatment was computed, and average
253 CMD measures were compared between the respective treatments using a mixed modeling
254 approach with plot as random factor and time as repeated measure. A mixed modeling approach
255 was equally used to compare different yield parameters, using treatment and variety as fixed
256 factors. Plant survival rates were compared between treatments, using a Chi-square analysis.
257 Where necessary and feasible, data were transformed to meet assumptions of normality and
258 homoscedasticity, and all statistical analyses were conducted using SPSS.

259

260 *iv. Country-wide yield changes*

261

262 Crop production statistics were obtained through the Office of Agricultural Economics, Ministry
263 of Agriculture & Cooperatives (Bangkok, Thailand). Yield measures were computed for 2006-
264 2016, for a total of 51 cassava-growing provinces within Thailand, and annual weighted means
265 were compared between successive years. Cassava crop yield can be impacted by agro-climatic
266 conditions (e.g., temperature-related variables) and by attack of pests such as *P. manihoti*. To
267 assess the impact of the sustained, broad-scale *A. lopezi* releases from the 2011 cropping season
268 onward, mean values of yields across all the cassava-growing provinces were regressed with
269 explanatory variables which included rainfall, minimum and maximum temperature (obtained
270 from Thai Meteorological Department, Bangkok, Thailand) and time (year). In addition, a
271 categorical variable representing the introduction of *A. lopezi* ('present' for the 2011 and 2012
272 growing seasons, and 'absent' for growing seasons 2008, 2009 and 2010) was equaled entered as
273 an explanatory variable in the regression model. Specifically for regression analysis, the

274 distribution of the response variable (i.e. yield) was identified to be normal (Shapiro test $p <$
275 0.05). A step-wise regression approach (forward and backward) using a linear modeling
276 approach was used to identify the model that best explains variation in yield. The model with the
277 lowest Akaike information criterion (AIC) was selected. In the next step, the model with the
278 lowest AIC score was compared with models containing interaction terms between time and the
279 remaining explanatory variables (i.e. temperature minimum, rainfall and *A. lopezi* introduction)
280 separately. The regression analysis was performed in R (v 3.4.1) statistical computing
281 environment. Additionally, R package “gvlma” was used to assess if the assumptions of
282 regression were met by the selected model. Additional diagnostics of the selected model, such as
283 determination of variance inflation factor (VIF) for detection of multicollinearity, the Non-
284 constant Variance Score Test (i.e. test for heteroscedasticity of residuals over fitted values) was
285 performed using R package “MASS” and “car” respectively. Significant variables, as identified
286 by the selected model were visualized using the “effects” package in R statistical computing
287 environment.

288

289

290 **Results**

291

292 *i. Multi-country pest & natural enemy survey*

293

294 During continental-scale insect surveys from 2014 until 2017 (i.e., 5-8 years following the initial
295 *A. lopezi* introduction), the mealybug complex on cassava largely comprised four non-native
296 species: (1) *P. manihoti*; (2) the papaya mealybug *Paracoccus marginatus* Williams & Granara

297 de Willink; (3) *Pseudococcus jackbeardsleyi* Gimpel & Miller; and (4) the striped mealybug
298 *Ferrisia virgata* Cockerell. *Phenacoccus manihoti* was the most abundant and widespread
299 mealybug species, and was reported from 37.0% ($n= 582$) and 100% fields ($n= 52$) in mainland
300 Southeast Asia and Indonesia, respectively. Among sites, *P. manihoti* reached field-level
301 incidence of $7.4 \pm 15.8\%$ (mean \pm SD; i.e., proportion mealybug-affected tips) and abundance of
302 14.3 ± 30.8 insects per infested tip in mainland Southeast Asia, and incidence rates of $52.7 \pm$
303 30.9% and 42.5 ± 67.7 individuals per tip in Indonesia. Field-level incidence and population
304 abundance were highly variable among settings and countries, reaching respective maxima of
305 100%, and 412.0 individuals per tip (Fig. 1).

306 When examining *P. manihoti* parasitism rates from a select set of sites, *A. lopezi* wasps were
307 present in 96.9% of mealybug-affected fields ($n= 97$) in mainland Southeast Asia, yet were only
308 found in 27.5% sites ($n= 40$) across Indonesia. Among sites, highly variable parasitism rates
309 were evident with dry-season rates of $16.3 \pm 3.4\%$ in coastal Vietnam, versus $52.9 \pm 4.3\%$ in
310 intensified systems of Tay Ninh (also in Vietnam). In Indonesia, *A. lopezi* was found in 22.0%
311 fields in Lombok ($n= 9$) and was absent from prime growing areas in Nusa Tenggara Timur
312 (NTT). In sites where *A. lopezi* had successfully established, dry-season parasitism ranged from
313 0% to 97.4%, averaging $30.0 \pm 24.0\%$ ($n= 110$) (Fig. S1). In fields where *A. lopezi* had
314 effectively established, mealybug pest pressure was lower at increasing levels of parasitism
315 ($F_{1,98}= 13.162$, $p< 0.001$; $R^2= 0.118$).

316

317 *ii. Multi-year mealybug and parasitoid population assessment in Vietnam*

318

319 Over the course of three years, we monitored *P. manihoti* abundance, field-level incidence and
320 associated *A. lopezi* parasitism rates in Tay Ninh, southern Vietnam. Field-level incidence of *P.*
321 *manihoti* ranged from 0% to 82%, averaging $24.8 \pm 17.7\%$ (mean \pm SD) plants infested over two
322 consecutive crop cycles. Mealybug incidence was significantly higher on older crops ($F_{7,57} = 9.9$;
323 $p < 0.0001$), and rapidly increased during the dry season. Similarly, mealybug abundance (average
324 5.6 ± 5.0 individuals per tip) was higher during the dry season ($F_{1,63} = 9.10$; $P = 0.0037$), and in
325 crops older than six months compared to younger crops ($F_{7,57} = 269.406$; $P < 0.0001$). Mealybug
326 population levels were comparable to those in Nigeria in 1982 (Fig. 2a), where *P. manihoti*
327 attained 23% incidence and field-level abundance < 10 individuals per tip soon after the release
328 of *A. lopezi* (Hammond & Neuenschwander, 1990) (Fig. 2b). In Tay Ninh, *A. lopezi* attained
329 mean parasitism rates of $42.3 \pm 21.7\%$, with maxima of $76.7 \pm 28.9\%$ during the early rainy
330 season (Fig. 2b). Overall, parasitism gradually increased over the dry season, up until crops were
331 4-6 months old.

332 Mealybug growth rates were significantly negatively correlated with parasitism levels across
333 the 8 sites studied (GLM w/ Normal error distribution and corrected for field: $\chi^2_{87} = 125.4$; $P =$
334 0.0017 ; the field term was not significant) (Fig. 3). The x-intercept of each per-field regression
335 represents the parasitism level above which mealybug growth rates are negative and this value
336 ranged between 0.38 and 0.69 for the 8 sites (average = 0.47 ± 0.09) (Fig. 3). Whilst *A. lopezi*
337 was the sole primary parasitoid at this location, three hyperparasitoid species attacked it at $2.79 \pm$
338 5.38% levels (as % parasitized hosts).

339

340 *iii. Exclusion cage assays*

341

342 Over the entire assay, *P. manihoti* populations under ‘full cage’ attained $48,318 \pm 51,425$ ($n= 4$;
343 mean \pm SD) and $7,256 \pm 8,581$ cumulative mealybug days (CMD) in ‘sham cage’ for one
344 popular variety (i.e., R72) (Fig. 4). For a second variety, KU50, *P. manihoti* attained $28,125 \pm$
345 $32,456$ CMD in a ‘full cage’ treatment, and $1,782 \pm 1,073$ CMD in ‘sham cage’. This compared
346 to CMD measures in a ‘no cage’ control of $1,378 \pm 1,039$ and 342 ± 252 , for R72 and KU50
347 respectively. CMD measures were significantly affected by treatment ($F_{3,189}= 240.752$, $p< 0.001$)
348 and time ($F_{6,189}= 113.347$, $p< 0.001$), and the interaction term time x treatment ($F_{18,189}= 2.012$, $p=$
349 0.011). Furthermore, total CMD measures at the end of the trial significantly differed between
350 treatments for both R72 and KU 50 ($F_{3,12}= 6.767$, $p= 0.006$; $F_{3,12}= 11.152$, $p= 0.001$,
351 respectively).

352 Cassava yield parameters varied substantially under the four experimental treatments, and for
353 both crop varieties (see also Thancharoen et al., *under review*). For Rayong 72, plant survival
354 attained 37.5% under a ‘full cage’ set-up as compared to 75% and 87.5% under ‘no cage’ or
355 ‘sham cage’ (Chi square, $\chi^2= 10.473$, $p= 0.015$). Fresh root yield (FRY) was significantly
356 affected by treatment ($F_{3,27}= 4.104$, $p= 0.016$) and variety ($F_{1,27}= 4.364$, $p= 0.046$). For R72 and
357 KU50, FRY under ‘full cage’ was 74.6% or 71.2% lower than under ‘sham cage’ (Kruskal-
358 Wallis, $\chi^2= 8.344$, $p= 0.039$; $\chi^2= 19.134$, $p< 0.001$, respectively), and respective yield reductions
359 for both varieties were 77.2% and 67.8% compared to ‘no cage’ treatments.

360

361 *iv. Country-wide yield changes*

362

363 During the 2009 dry season, *P. manihoti* attained its peak population in Thailand, with field-level
364 incidence near 100% and abundance rates of hundreds of *P. manihoti* per plant on at least

365 230,000 ha (Rojanaridpiched *et al.* 2013). Over the subsequent 2009-10 cropping season,
366 province-level crop yields dropped by $12.59 \pm 9.78\%$ nationwide (weighted mean: -18.2%) (Fig.
367 5). Furthermore, country-wide aggregate yields declined from 22.67 t/ha to 18.57 t/ha, and total
368 production dropped by 26.86% to 22,005,740 tonnes of fresh root. Following the lowered crop
369 output, prices for Thai cassava starch increased 2.38-fold at domestic prices in Thailand, and
370 2.62-fold at export prices (US\$ FOB) (Fig. S2). To differentiate *P. manihoti*-induced yield drops
371 from climatic impacts, regression analyses were carried out. Multiple regression analysis
372 revealed that a model with interaction terms between time and all other explanatory variables,
373 i.e. time of introduction of *A. lopezi* and rainfall had the lowest AIC score and lowest residual
374 deviance values. The model showed a significantly positive effect ($F_{7,183} = 8.641$) of the
375 interaction term Time x Presence (i.e. 'presence' of *A. lopezi* and time, $p < 0.01$) on observed
376 yields. Over 2009-2010, annual yield shifts in 51 cassava-growing provinces were not affected
377 by changes in average monthly temperature and rainfall ($F_{3,33} = 0.036$, $p = 0.991$). By 2012,
378 province-level yields were partially restored and then steadily increased to 21.42 ± 1.96 t/ha in
379 2015.

380

381

382 Discussion

383

384 In 2008, the invasive mealybug *P. manihoti* made its accidental arrival into Thailand. Through
385 its extensive spatial spread, rapid population build-up and unrestricted feeding on plants (this
386 leading to stunting and plant death), *P. manihoti* caused significant yield declines and a 27%
387 drop in the nation's cassava production. This study shows how the neotropical wasp *A. lopezi*,

388 released for mealybug control in 2010, had effectively established in 97% mealybug-affected
389 fields in mainland Southeast Asia by 2014, and colonized 27% sites across insular Indonesia by
390 late 2017. Attaining average dry-season parasitism rates of 30% across sites, *A. lopezi*
391 populations readily oscillate with those of its mealybug host and suppress *P. manihoti* to
392 incidence levels of 7% and background infestation pressure of a mere 14 individuals per infested
393 tip. Experimental assays using two widely-grown cassava varieties reveal how biological control
394 secures approximate yield gains of 5.3-9.4 t/ha. Our work clearly demonstrates how *A. lopezi*
395 downgrades the invasive *P. manihoti* to non-economic status at a continental scale and enables a
396 lasting yield-loss recovery. Offering a quantitative assessment of IBC's contribution to (the
397 restoration of) primary productivity in Asia's expansive cassava crop, our work illuminates the
398 broader societal value of biological control in a geographical region where there is heavy and
399 increasing use of pesticides (Schreinemachers *et al.*, 2015).

400 Aside from featuring as 'beacon of hope' in Asia's pesticide-tainted agro-landscapes, our work
401 heralds a new era for the discipline of insect biological control. Since the late 1800s, biological
402 control has permitted the complete or partial suppression of 226 debilitating insect pests globally,
403 formed the crux of transformative ecological theories (e.g., Hairston *et al.*, 1960), and was
404 widely deemed to be a safe, dependable and preferred means for (invasive) pest control.
405 Following the release of Rachel Carson's 1962 *Silent Spring*, biological control was met with
406 unrestrained enthusiasm and a firm belief in its potential as a reliable alternative to pesticide-
407 centered practices. Yet, as concerns over its ecological risks rose following Howarth's (1983,
408 1991) denunciation of few cases of historic malpractice, regulatory hurdles surfaced, public
409 funding lowered and the practice of insect biological control went through trying yet necessary
410 reform (Strong & Pemberton, 2000; Hoddle, 2004; Messing & Brodeur, 2018). Over the past

411 decades, IBC implementation has centered on ecological safety and increasingly strives to
412 balance environmental benefits and risks (Heimpel & Cock, 2018). Though weed biological
413 control has a 99% safety record (Suckling & Sforza, 2014), scientists are conscious that
414 ecological risk will never be zero and certain factors are difficult to anticipate (Crooks & Soule,
415 1999; Sexton et al., 2017). Also, invasive pests routinely present far higher threats to native biota
416 than judiciously-selected natural enemies with a narrow dietary breadth (Culliney, 2005).
417 Though the 1980s Africa campaign against *P. manihoti* was implemented during times when the
418 primary focus of insect biological control was on benefits (but see Neuenschwander, 2001), risks
419 were considered minimal and did not delay implementation. The fact that *A. lopezi* was both
420 effective and highly host-specific vindicated this. As a result, the implementation of IBC in
421 Southeast Asia more than 30 years later was greatly facilitated by recognizing that (i) IBC had
422 been effective across Africa's cassava-belt, and (ii) widespread benefits were gained in the
423 overall absence of negative side-effects.

424 In light of the above, *A. lopezi* attained consistently high parasitism rates across most of the *P.*
425 *manihoti* range of climatic suitability in tropical Asia (Yonow and Kriticos, 2017), except for
426 Indonesia where it was only introduced at one site in late 2014. The far superior *P. manihoti*
427 infestation pressure in eastern Indonesia (i.e., NTT, Lombok), where *A. lopezi* waits to be
428 introduced, further accentuate the role of the parasitoid in suppressing cassava mealybug. Across
429 locations, *A. lopezi* reached maximum parasitism levels of 98% (in late dry season, at Tay Ninh),
430 which greatly surpassed the established threshold of 33-36% maximum parasitism rate for
431 successful biological control (Hawkins and Cornell, 1994). At multiple sites, parasitism rates
432 equally surpassed (max. 30%) levels from smallholder plots in Africa's savanna (Hammond and
433 Neuenschwander, 1990). Factors ensuring this exceptional parasitoid efficacy and resulting pest

434 control are a) unique features of the cassava crop, including prolonged durational stability,
435 vegetational complexity and a constitutive secretion of energy-rich nectar for foraging
436 parasitoids (Pinto-Zevallos *et al.*, 2016); b) spatio-temporal continuity of mealybug-infested
437 crops at a landscape level (Schellhorn *et al.*, 2014), especially in sites where farmers employ
438 staggered planting and piece-meal harvesting; c) favorable ecological traits of *A. lopezi*,
439 including high dispersal ability, environmental adaptability and density-dependent parasitism
440 (Neuenschwander *et al.*, 1989); d) non-usage of (prophylactic) insecticides, except for Thailand
441 and parts of southern Vietnam; and e) the important human-assisted dispersal of *A. lopezi*, by
442 mealybug-infested planting material (Herren *et al.*, 1987). Furthermore, substantial fertilizer
443 inputs and suitable water management in areas with intensified cassava production -e.g.,
444 Vietnam's Tay Ninh province- likely benefited parasitoids further by boosting *A. lopezi*
445 development and fitness (Wyckhuys *et al.*, 2017a). All of the above factors may have resulted in
446 *P. manihoti* pest pressure that is largely identical to that observed during the Africa campaign, in
447 which mealybug populations stabilized following the *A. lopezi* release at 23% incidence and
448 field-level abundance below 10 individuals per tip (Hammond and Neuenschwander, 1990).

449 Exclusion cage assays illustrated how biological control enabled a root yield recovery of 5.3-
450 10.0 t/ha in two main cassava varieties and how 2015 yields under 'no cage' ('real-world')
451 conditions were in line with historic in-country yield tendencies. Though no direct field-level
452 measurements were made of *A. lopezi* parasitism during the cage trials, biological control was
453 found to occupy a central role in downgrading *P. manihoti* populations (Thancharoen *et al.*,
454 under review), and *A. lopezi* is a determining factor in ensuring mealybug suppression in a
455 similar fashion as in southern Vietnam (Le *et al.*, 2018). Cage trials also revealed large
456 variability in responses between the two cassava clones, likely reflective of differences in plant

457 vigor and a clone's photosynthetic capability (Connor et al., 1981; Cock et al., 2012). The
458 cassava plant possesses a unique set of features to sustain root production under (a)biotic stress,
459 including the adaptive mobilization of biomass and a highly-effective use of resources (Cock et
460 al. 2012). Yet, the pronounced production losses can be ascribed to continuous (unrestrained)
461 attack of the active apex, direct damage to stems and high rates of plant death, especially for
462 R72.

463 As *P. manihoti* currently occurs at low infestation pressure across mainland Southeast Asia, we
464 believe that the above cage assays lend themselves to further extrapolation to a far broader
465 geographical scale. Yet, slightly higher population levels were recorded in settings with sandy,
466 low-fertile soils (Wyckhuys *et al.*, 2017a) and in Indonesian sites where *A. lopezi* had not yet
467 made its arrival. The latter can now constitute a 'natural laboratory' to refine and validate
468 existing projections on *A. lopezi*-mediated yield gain. Also, as landscape composition and plant
469 disease infection status equally shape *P. manihoti* performance and efficacy of biological control
470 at local scale (Wyckhuys *et al.*, 2017b; Le *et al.*, 2018), further replicated trials could be
471 warranted to validate the robustness of our findings under varying agro-ecological contexts.
472 Despite the above shortcomings, careful analysis of production statistics and commodity market
473 fluxes (as in *section iv*) do lend support to our empirical results.

474 In tropical Asia, cassava underpins a multi-billion dollar starch sector, constitutes a key source
475 of farm income and provides an (oftentimes indirect) means to food security for poor, under-
476 privileged populations (Howeler, 2014; Delaquis *et al.*, 2017). On the one hand, the *P. manihoti*-
477 induced yield shocks, as recorded during 2009-2011, can have major implications for rural
478 livelihoods. Sustained pest attack can aggravate food security issues in areas where cassava is a
479 prime food staple or progress into chronic 'poverty traps' (Tittonell *et al.*, 2013), all of which is

480 counteracted through *A. lopezi*-mediated biological control. Aside from restoring FRY, *A. lopezi*
481 equally helped recover a plant's total dry matter or 'biological yield' (Thancharoen *et al.*, under
482 review), which is highly relevant as cassava leaves and shoots are widely consumed in tropical
483 Asia. On the other hand, the net productivity loss of 5.14 million ton of fresh root equaled a
484 respective loss of revenue of US\$ 267.5-591.7 million (at 2009-10 factory price) for Thailand's
485 cassava sector and the Asia-based starch industry. In any case, socio-economic impacts of the *P.*
486 *manihoti* campaign are deemed to be substantial and potentially equal or even surpass those
487 recorded in Africa (Zeddies *et al.*, 2001).

488 Yield recovery level in our cage assays were substantially higher than the 2.48 t/ha yield
489 increase recorded through on-farm measurements in sub-Saharan Africa (Neuenschwander *et al.*,
490 1989). At Thai farm-gate prices, *A. lopezi*-mediated yield recovery equals to US\$200-704 per ha
491 (Thancharoen *et al.*, under review), although this does not take into account changes in
492 production costs, local elasticities of supply and demand, or insecticide expenditures. Though we
493 call for caution in extrapolating our findings, the approximate value of *P. manihoti* biological
494 control could be hundreds of dollars higher than estimates of \$63 ha⁻¹ year⁻¹ across global biomes
495 including natural systems (Costanza *et al.* 1997), \$33 ha⁻¹ year⁻¹ for (natural) biological control
496 of the soybean aphid in the US Midwest (Landis *et al.*, 2008), or \$75 to \$310 ha⁻¹year⁻¹ for bird-
497 mediated pest control in Costa Rican coffee (Karp *et al.*, 2013). This strengthens arguments by
498 Landis *et al.* (2008) and Naranjo *et al.* (2015) that the potential of insect biological control has
499 been significantly under-valued, and that comprehensive cost-benefit analyses are urgently
500 needed to raise (or restore) societal recognition of this prime ecosystem service.

501 These substantial economic benefits of (naturally-occurring, cost-free) biological control need
502 to be contrasted with the unrelenting global increase in the use of chemically-synthesized

503 insecticides for the mitigation of (domestic and, increasingly invasive) pests (Enserink et al.,
504 2013). Following the *P. manihoti* invasion, pesticides have equally become pervasive in
505 Thailand's cassava crop and growers have embraced the (prophylactic) use of neonicotinoid
506 insecticides. Yet, given the omnipresence of *A. lopezi* and the largely low mealybug population
507 levels across Southeast Asia, cost-effectiveness of such approaches needs closer scrutiny.
508 Though pesticides do bring great benefits to society, they tend to simplify ecological
509 communities, impact natural enemies and accelerate further pest proliferation (Lundgren and
510 Fausti, 2015). On the other hand, our work shows that a carefully-selected, host-specific
511 parasitoid constitutes a viable, most lucrative alternative to insecticide-centered approaches.
512 Hence, potential (non-target ecological) risks of classical biological control clearly have to be
513 viewed in terms of refraining from action and thus creating room for far-less environmentally-
514 friendly tactics (Messing and Wright, 2006; Suckling and Sforza, 2014; Hajek *et al.*, 2016).

515

516

517 **Conclusions**

518

519 This study provides a quantitative assessment of how importation biological control helps restore
520 primary productivity in Asia's cassava crop, following the arrival and extensive spread of an
521 invasive sap-feeding pest. Our work reminds the reader of how IBC can provide durable and
522 cost-effective control of an invasive pest such as *P. manihoti*, and deliver huge socio-economic
523 and environmental benefits (Bale *et al.*, 2008). Aside from the concerns over its unintended
524 ecological impacts, disciplinary silos and attitudinal factors have prevented routine (economic)
525 valuation of biological control and a far broader recognition of its societal contributions (Naranjo

526 *et al.*, 2015; Bale *et al.*, 2008). Hence, our characterization and (approximate) valuation of *P.*
527 *manihoti* biological control is clearly not an end in itself, but should now become a starting point
528 for further awareness-raising, and efforts to guide and inform policy and agile decision-making
529 (Daily *et al.*, 2009). In a world typified by massive declines in insect numbers, extreme
530 biodiversity loss, and dwindling public interest in biological control (Bale *et al.*, 2008; Hallmann
531 *et al.*, 2017; Warner *et al.*, 2012), our research underlines the immense yet largely untapped
532 potential of ecologically-based approaches to resolve invasive species problems, intensify global
533 agriculture and feed a growing world population in the 21st century.

534

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536

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727 **Author contributions**

728

729 KAGW, AR, TTNL, AT and PW conceived and designed the experiments; AT, MZF, IG,
730 TTNL, performed trials and collected the data; KAGW, MZF, IG, AT, LKP, DDB and GH
731 analyzed the data; all authors co-wrote the paper

732

733

734 **Competing interests**

735

736 There are no competing interests.

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739 **Figure legends:**

740 **Figure 1. Map of Southeast Asia, depicting *P. manihoti* spatial distribution, infestation**
741 **pressure and *A. lopezi* parasitism rates.** Doughnut charts in the left and right margins represent
742 field-level incidence (i.e., red portion reflecting the proportion of *P. manihoti* affected tips,
743 ranging from 0 to 1 for full circumference), and are complemented with bar charts indicative of
744 plant-level *P. manihoti* abundance (i.e., average number of individuals per tip). The number
745 inside each doughnut reflects the number of fields sampled per locale. Doughnut charts in the
746 lower panel indicate average *A. lopezi* parasitism rate at six selected sites (depicted by the dark
747 green section, reflecting proportion parasitism ranging from 0 to 1 for full circumference). The
748 distribution map is created as overlay on a 2005 cassava cropping area (MapSpam, 2017).

749

750 **Figure 2. Bi-monthly mealybug population fluctuations in southern Vietnam, as contrasted**
751 **with those in 1982 Nigeria.** Vietnam's *P. manihoti* dynamics (*panel a*) are contrasted with those
752 in Nigeria following the 1982 release of *A. lopezi*. In *Panel b*, field-level *P. manihoti* abundance
753 (n= 8) is contrasted with respective *A. lopezi* parasitism rates, from July 2013 until July 2015.

754

755 **Figure 3. Effect of cassava mealybug parasitism rate on intrinsic rate of mealybug increase**
756 **over consecutive 2-month periods in Tay Ninh, Vietnam.** Lines are linear regressions per each
757 of the eight sites monitored. The red dotted line shows $r=0$; values above this on the y axis
758 indicate positive growth of mealybug populations and below it indicate negative population
759 growth. Parasitism level above which *P. manihoti* growth rates are negative ranged between 0.38
760 and 0.69 for the 8 sites. See text for statistical details.

761

762 **Figure 4. Mealybug abundance and subsequent yield parameters for two cassava varieties**
763 **under an exclusion cage assay at Rayong, Thailand.** Six weeks after experimental set-up,
764 mealybug abundance (n = 16; mean \pm SE) is compared between treatments for two common
765 varieties (R72, KU50), and is significantly higher under 'full cage' conditions (i.e., exclusion of
766 natural enemies, incl. *A. lopezi*), as compared to 'sham cage' and un-caged controls (ANOVA,
767 $F_{2,45} = 50.289$; $P < 0.001$). For each treatment, fresh root yield is determined at time of harvest, on
768 a 12-month old crop.

769

770 **Figure 5. Annual percent shifts in crop yield for 51 cassava-growing provinces in Thailand,**
771 **reflective of the mealybug invasion and ensuing biological control.** Shifts cover the country-
772 wide spread of *P. manihoti* from late 2008 until 2011, the first release of *A. lopezi* (Nov. 2009)
773 and subsequent nation-wide distribution of the parasitoid from June 2010 onward. Province-level
774 yield shifts depict the percent change of crop yield in one given year, as compared to the
775 previous year.

776

777

Figure 1

Map of Southeast Asia, depicting *P. manihoti* spatial distribution, infestation pressure and *A. lopezi* parasitism rates.

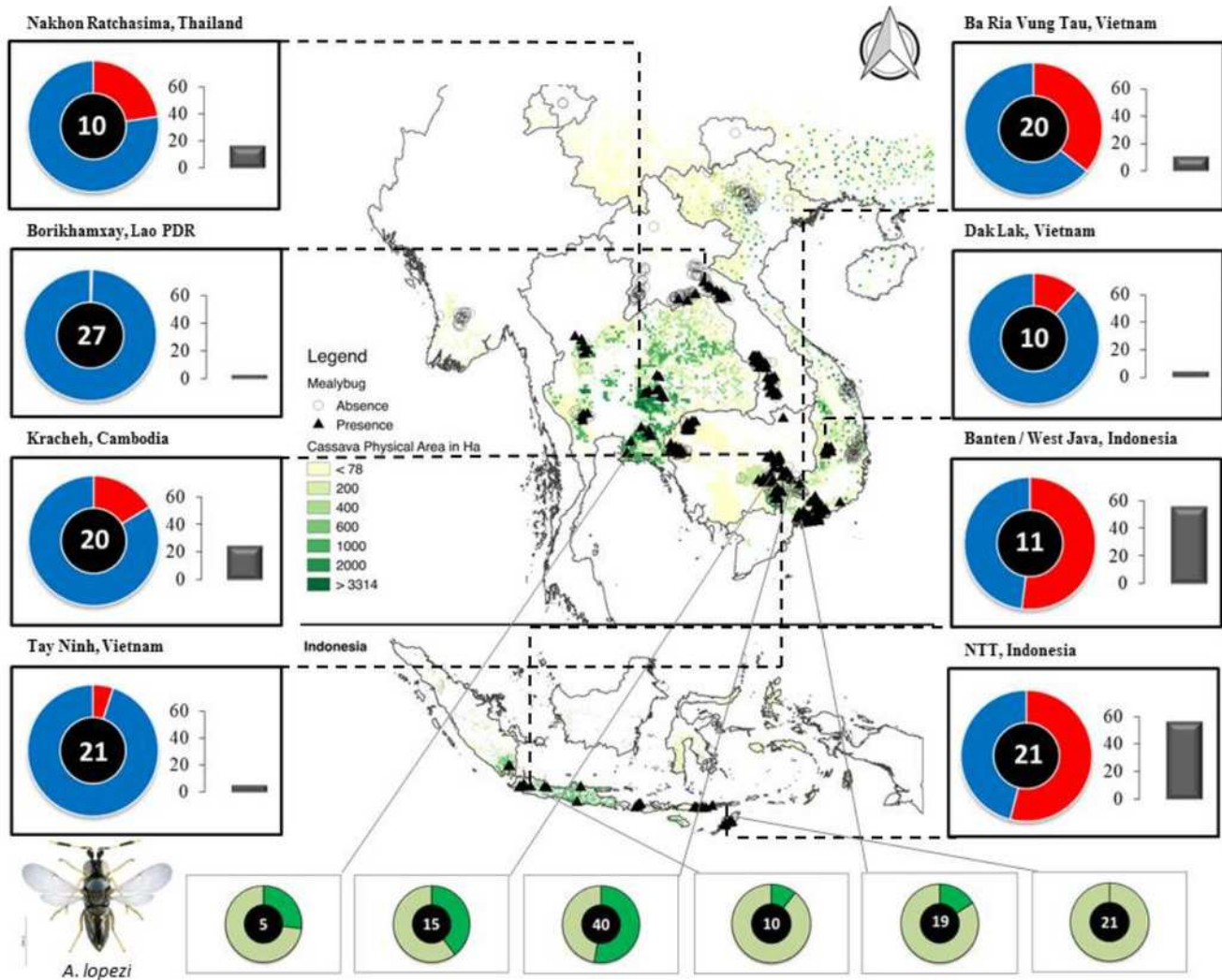


Figure 2

Bi-monthly mealybug population fluctuations in southern Vietnam, as contrasted with those in 1982 Nigeria.

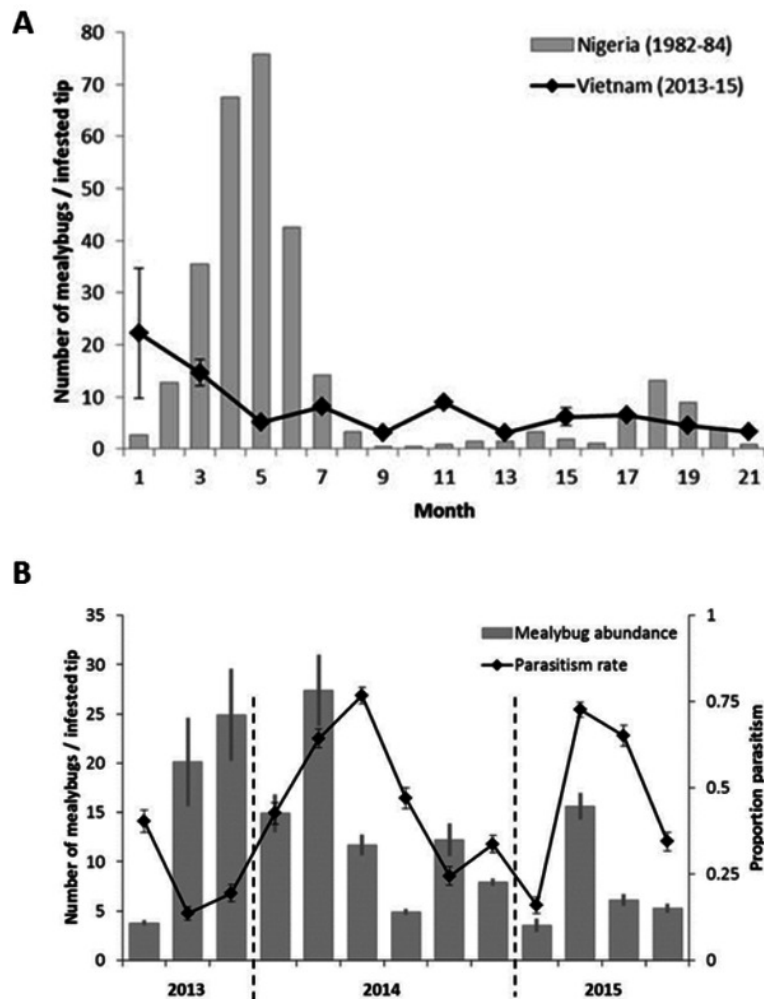


Figure 3

Effect of cassava mealybug parasitism rate on intrinsic rate of mealybug increase over consecutive 2-month periods in Tay Ninh, Vietnam.

Lines are linear regressions per each of the eight sites monitored. The red dotted line shows $r=0$; values above this on the y axis indicate positive growth of mealybug populations and below it indicate negative population growth. Parasitism level above which *P. manihoti* growth rates are negative ranged between 0.38 and 0.69 for the 8 sites. See text for statistical details.

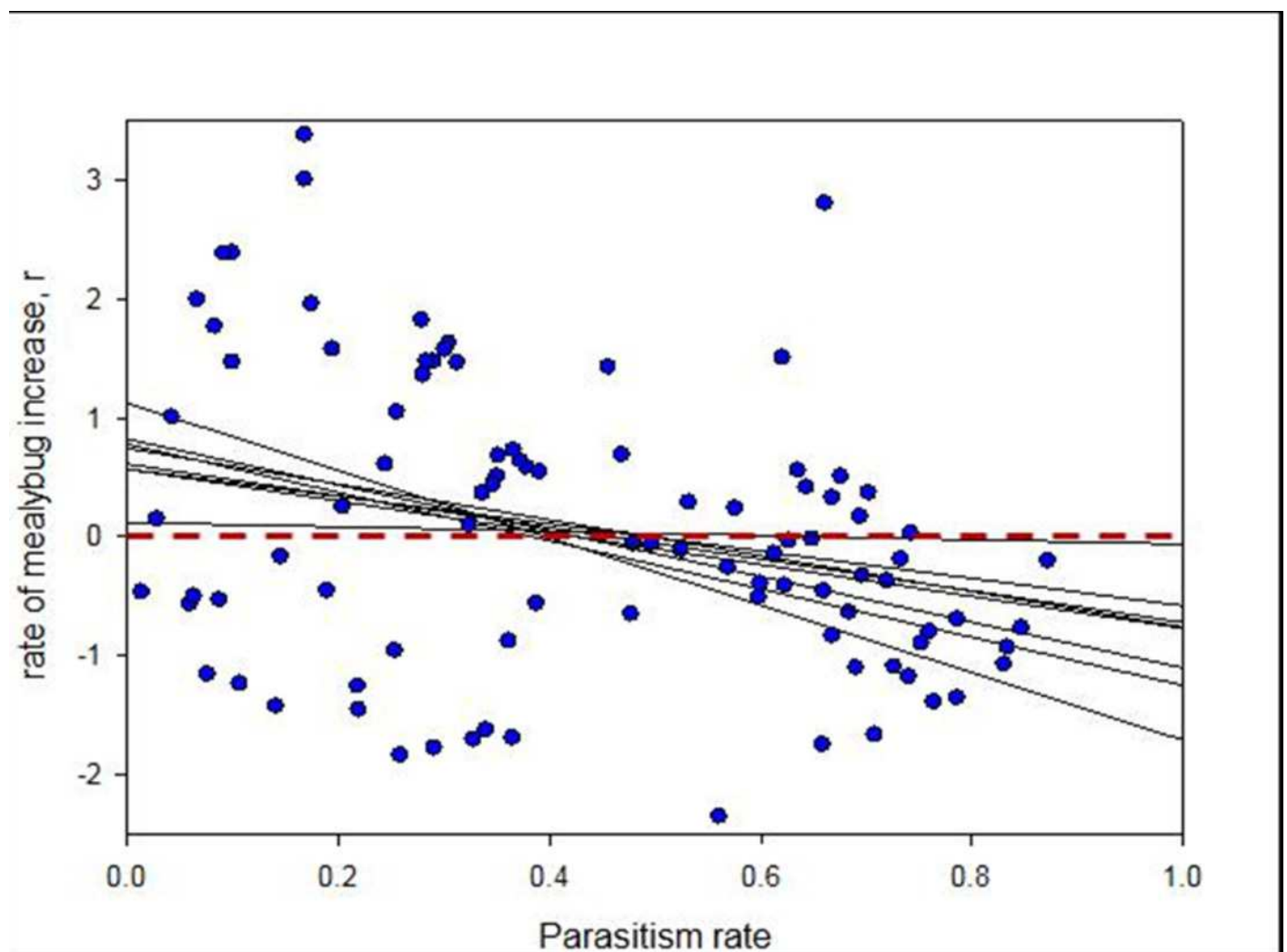


Figure 4

Mealybug abundance and subsequent yield parameters for two cassava varieties under an exclusion cage assay at Rayong, Thailand.

Six weeks after experimental set-up, mealybug abundance ($n = 16$; mean \pm SE) is compared between treatments for two common varieties (R72, KU50), and is significantly higher under 'full cage' conditions (i.e., exclusion of natural enemies, incl. *A. lopezi*), as compared to 'sham cage' and un-caged controls (ANOVA, $F_{2,45} = 50.289$; $P < 0.001$). For each treatment, fresh root yield is determined at time of harvest, on a 12-month old crop.

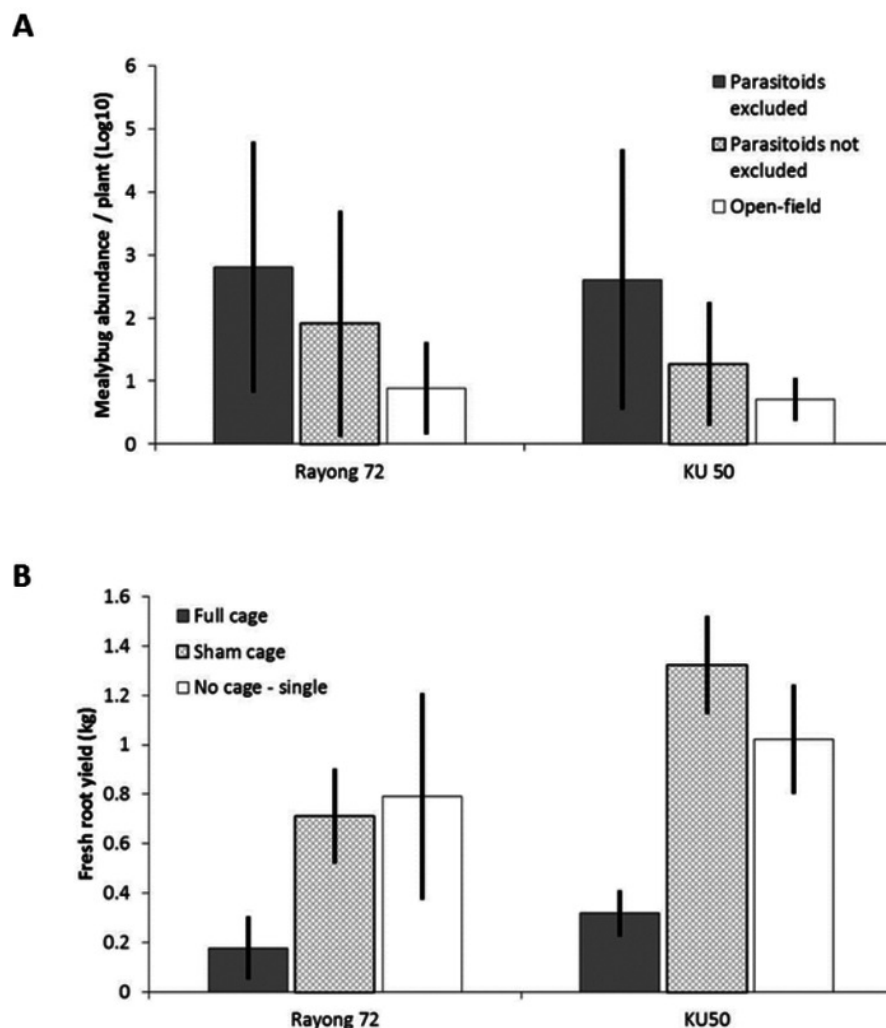


Figure 5

Annual percent shifts in crop yield for 51 cassava-growing provinces in Thailand, reflective of the mealybug invasion and ensuing biological control.

Shifts cover the country-wide spread of *P. manihoti* from late 2008 until 2011, the first release of *A. lopezi* (Nov. 2009) and subsequent nation-wide distribution of the parasitoid from June 2010 onward. Province-level yield shifts depict the percent change of crop yield in one given year, as compared to the previous year.

