Continental-scale suppression of an invasive pest by a host-specific parasitoid underlines both environmental and economic benefits of arthropod biological control

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Biological control, a globally-important ecosystem service, can provide long-term and broad-scale suppression of invasive pests, weeds and pathogens in natural, urban and agricultural environments. Following (few) historic cases that led to sizeable environmental up-sets, the discipline of arthropod biological control has -over the past three decades- evolved and matured. Now, by deliberately taking into account the ecological risks associated with the planned introduction of insect natural enemies, immense environmental and societal benefits can be gained. In this study, we document and analyze a successful case of biological control against the cassava 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 over a broad geographical area, *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, accentuates the importance of (judiciously-implemented) biological control for insect pest management, 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 biodiversity loss across the globe, this study unequivocally demonstrates how biological control – as a pure public good endeavor – constitutes a powerful, cost-effective and environmentally-responsible solution for invasive species mitigation.

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10   **Continental-scale suppression of an invasive pest by a host-specific parasitoid underlines**
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13   Running head: Biocontrol of the cassava mealybug in Asia

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43   **Abstract**

44   Biological control, a globally-important ecosystem service, can provide long-term and broad-

45   scale suppression of invasive pests, weeds and pathogens in natural, urban and agricultural

46   environments. Following (few) historic cases that led to sizeable environmental up-sets, the

47   discipline of arthropod biological control has -over the past three decades- evolved and matured.

48   Now, by deliberately taking into account the ecological risks associated with the planned

49   introduction of insect natural enemies, immense environmental and societal benefits can be

50   gained. In this study, we document and analyze a successful case of biological control against the

51   cassava mealybug, *Phenacoccus manihoti* (Hemiptera: Pseudococcidae) which invaded

52   Southeast Asia in 2008, where it caused substantial crop losses and triggered 2- to 3-fold surges

53   in agricultural commodity prices. In 2009, the host-specific parasitoid *Anagyrus lopezi*

54   (Hymenoptera: Encyrtidae) was released in Thailand and subsequently introduced into

55   neighboring Asian countries. Drawing upon continental-scale insect surveys, multi-year

56   population studies and (field-level) experimental assays, we show how *A. lopezi* attained

57   intermediate to high parasitism rates across diverse agro-ecological contexts. Driving mealybug

58   populations below non-damaging levels over a broad geographical area, *A. lopezi* allowed yield

59   recoveries up to 10.0 t/ha and provided biological control services worth several hundred dollars

60   per ha (at local farm-gate prices) in Asia's 4-million ha cassava crop. Our work provides lessons

61   to invasion science and crop protection worldwide, accentuates the importance of (judiciously-

62   implemented) biological control for insect pest management, and highlights its potentially large

63   socio-economic benefits to agricultural sustainability in the face of a debilitating invasive pest. In

64   times of unrelenting insect invasions, surging pesticide use and accelerating biodiversity loss

65   across the globe, this study unequivocally demonstrates how biological control – as a pure public

66   good endeavor – constitutes a powerful, cost-effective and environmentally-responsible solution

67   for invasive species mitigation.

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70

71 **Introduction**

72

73 Biological control is a globally-important ecosystem service, and plays a pivotal role in the

74 functioning and broader resilience of agricultural and natural ecosystems alike (Costanza *et al.*

75 1997). For US agriculture alone, insect-mediated biological control is conservatively valued at

76 $4.5-17 billion per year, and a diverse community of natural enemies helps alleviate pressures

77 from herbivores and other crop antagonists (Losey and Vaughan, 2006). However, rapid

78 depletion of animal populations and progressive ecosystem simplification compromise the

79 strength and stability of this ecosystem service (Oliver *et al.,* 2015; Hallmann *et al.,* 2017). In

80 tropical terrestrial ecosystems with inherently high levels of biodiversity, these trends might be

81 even more pronounced yet routinely remain un-documented due to e.g., an overall lack of

82 sufficient funds, scientific interest and well-trained ecologists (Melo *et al.,* 2013; Barnes *et al.,*

83 2014).

84   Across the globe, arthropod pests reduce agricultural productivity by 10-16% and constitute

85 key impediments to food security and (indirectly) poverty alleviation (Oerke, 2006; Bebber *et*

86 *al.,* 2013). Though native pests continue to pose major problems for the world's agriculture, non-

87 native species are of increasing significance as a result of trade globalization and human

88 movement (Bradshaw *et al.,* 2016; Paini *et al.,* 2016). Importation biological control (IBC; also

89 known as 'classical biological control'), or the judicious selection and subsequent introduction of

90 a specialized natural enemy from the pest's region of origin, has been repeatedly shown to

91 effectively reduce invasive pest populations to less damaging levels (van Driesche *et al.,* 2008;

92 Heimpel and Mills, 2017). Particularly in the developing-world tropics, IBC can be a "silver

93 bullet" option for destructive agricultural pests, being largely self-sustaining and requiring little

94   or no stakeholder intervention (Andrews *et al.,* 1992). Since the late 1800s, more than 2,000

95   natural enemy species have been released against approximately 400 invasive pests worldwide,

96   occasionally resulting in complete pest control but regularly causing limited impact on target

97   pest populations (van Lenteren *et al.,* 2006; Cock *et al.,* 2016b). Though economic impacts are

98   not routinely assessed for IBC, levels of pest suppression and ensuing benefit:cost ratios can be

99   exceptionally favorable (5:1 to >1,000:1) (Heimpel and Mills, 2017; Gutierez *et al.,* 1999;

100   Naranjo *et al.,* 2015). Yet, IBC is marred with remarkably low rates of success (Greathead &

101   Greathead, 1992; Cock *et al.*, 2016a), and biological control as a whole is habitually undervalued

102   or even avoided while it should be promoted (Daily *et al.,* 2009). Furthermore, over the past

103   three decades, IBC initiatives have been met with stringent regulations and a heightened

104   emphasis on potential ecological risks or unintended side-effects (Heimpel & Cock, 2018). The

105   latter was triggered by a provocative yet necessary account by Howarth (1983, 1991), built

106   around misguided biological control releases that were conducted decades earlier, and in which

107   the long-established paradigm of IBC as 'ecologically-safe' practice was challenged.

108   One well-recognized IBC program is the Africa-wide initiative targeting the invasive cassava

109   mealybug, *Phenacoccus manihoti* (Hemiptera: Pseudococcidae), which led to a 50% yield

110   recovery resulting in long-term economic benefits up to US $20.2 billion as well as the likely

111   avoidance of widespread famine without negative side effects (Neuenschwander *et al.,* 1989;

112   Herren and Neuenschwander, 1991; Zeddies *et al.,* 2001). Key to the success of this program

113   was the carefully-selected host-specific and environmentally-adaptable parasitoid *Anagyrus*

114   *lopezi* (Hymenoptera: Encyrtidae), recovered in 1981 after foreign exploration from South

115   America, and introduced into Nigeria soon thereafter. As *A. lopezi* is considered to be a specialist

116   internal feeder on *P. manihoti*, no detrimental ecological impacts resulted from its continent-

117   wide release (Neuenschwander, 2001). Following its devastating passage through Africa's

118   cassava belt in the 1970s and 80s, *P. manihoti* was inadvertently introduced into Thailand in

119   2008, spread through mainland Southeast Asia, and made its appearance in Indonesia by 2010

120   (Graziosi *et al.,* 2016). As cassava is grown on >4 million ha by an estimated 8 million farming

121   families throughout tropical Asia, this pest had potential to cause massive socio-economic

122   impacts. As part of an internationally-coordinated management campaign for *P. manihoti*, *A.*

123   *lopezi* was promptly sourced from Benin, West Africa and 500 adult parasitoids were introduced

124   into Thailand in 2009 (Winotai *et al.,* 2010). Parasitoids were subsequently mass-reared by

125   multiple Thai institutions, released across the country during 2010-2012 (some by airplane) and

126   introduced into neighboring Laos, Cambodia (in 2011), Vietnam (in 2013) and Indonesia (in

127   2014) (Wyckhuys *et al.*, 2015).

128   In this study, we characterized the degree to which *A. lopezi* has established in the highly-

129   heterogeneous cassava cropping environments of Southeast Asia. Field research was carried out

130   over the course of 2014-2017 by various country teams, each pursuing different objectives as

131   outlined below. We employed seasonal population surveys that extended from Myanmar's

132   Ayeyawaddy River delta to the uplands of Timor in eastern Indonesia, to quantify magnitude and

133   spatial extent of parasitoid-induced *P. manihoti* population suppression (*section i, ii*).

134   Furthermore, we employed well-established manipulative protocols to assess the effectiveness of

135   *A. lopezi* and subsequent yield benefits of biological control (De Bach *et al.,* 1971; van Lenteren

136   *et al.,* 1980; Luck *et al.,* 1988) (*section iii*). Finally, we conducted an analysis of production

137   statistics and cassava prices in one of Asia's main cassava-growing countries (Thailand) over a

138   time period spanning the 2008 *P. manihoti* invasion, the 2009 parasitoid introduction into

139   Thailand and the subsequent (natural, and human-aided) continent-wide distribution of *A. lopezi*

140   (*section iv*).

141   Our work uses original datasets to present a rare, continental-scale and multi-year assessment

142   of IBC-mediated insect pest suppression, and the cascading trophic and socioeconomic effects on

143   cassava yield loss reduction and commodity prices. We combine observational and manipulative

144   studies to exemplify the benefits of *A. lopezi* as a biological control agent, and lay the basis for

145   further econometric investigations. This study illustrates the value of an insect-driven ecosystem

146   service to support agricultural sustainability, in the face of a potentially devastating invasive

147   pest.

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149

150   **Materials & Methods**

151

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

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154   From early 2014 until late 2017, insect surveys were carried out in 601 cassava fields in

155   Myanmar, Thailand, Lao PDR, Cambodia, Vietnam, southern China and Indonesia. Survey

156   protocols are described in detail in Graziosi *et al.* (2016). In brief, we selected older fields (i.e.,

157   8-10 months of age) in the main cassava-growing areas of each country, with individual sites

158   located at least 1 km apart. Five linear transects were randomly chosen per site, with ten plants

159   (routinely spaced at 0.8-1.2 m) sampled in each transect. By doing so, a total of 50 plants per

160   field were assessed for *P. manihoti* infestation and per-plant mealybug abundance. In-field

161   identification of mealybugs was based on morphological characteristics such as coloration and

162   presence or length of abdominal waxy filaments, while samples were also taken to the laboratory

163   for identification by specialist taxonomists. Following transect walks we calculated average *P.*

164   *manihoti* abundance (i.e., number of individuals per infested tip) and field-level incidence (i.e.,

165   proportion of *P. manihoti*-infested tips per field).

166   To assess local *A. lopezi* establishment and parasitism rates, we conducted dry-season sampling

167   from 2014 to 2017 at sub-sets of mealybug-invaded sites in Thailand (n= 20), Cambodia (n = 10,

168   15), southern Vietnam (n= 20, 20, 6) and Indonesia (n = 10, 9, 21) (total n= 131). Sampling

169   consisted of collecting 20 mealybug-infested tips from local fields and transferring them to a

170   laboratory to monitor subsequent parasitoid emergence (Neuenschwander *et al.,* 1989). Surveys

171   were carried out during January-May 2014 (dry season), October-November 2014 (late rainy

172   season), January-March 2015 (dry season) in mainland Southeast Asia, and during October-

173   November 2014 and 2017 (dry season) in insular Indonesia. Locations were recorded using a

174   handheld GPS unit (Garmin Ltd, Olathe, KS). In-field identification of mealybugs was based on

175   morphological characters, while samples were also transferred to the laboratory for further

176   taxonomic identification. Voucher specimens of *P. manihoti* were equally deposited at the Thai

177   Department of Agriculture (Bangkok, Thailand), Bogor Agricultural University (Bogor,

178   Indonesia) and Plant Protection Research Institute (Hanoi, Vietnam).

179   To assess local *A. lopezi* establishment and parasitism rates, mealybug-infected tips were

180   collected in the field and transferred to a laboratory. Upon arrival in the laboratory, each tip was

181   carefully examined, predators were removed and the total number of *P. manihoti* was

182   determined. Tips were then placed singly into transparent polyvinyl chloride (PVC) containers,

183   closed with fine cotton fabric mesh. Over the course of three weeks, containers were inspected

184   on a daily basis for emergence of parasitoids and *A. lopezi* parasitism levels (per tip and field)

185   were computed. Next, for fields where presence of *A. lopezi* was reported, we carried out a

186   regression analysis to relate field-level mealybug abundance with parasitism rate. Mealybug

187   infestation levels and parasitism rates were log-transformed to meet assumptions of normality

188   and homoscedasticity, and all statistical analyses were conducted using SPSS.

189

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

191

192   From July 2013 until July 2015, we conducted population surveys in Tay Ninh province,

193   Vietnam; an area with near-continuous, all-year cassava cultivation (see also Le et al., 2018).

194   The cassava mealybug is assumed to have arrived in southern Vietnam during 2011-2012, and *A.*

195   *lopezi* was first detected from Tay Ninh province in early 2013. Eight newly-planted cassava

196   fields were selected of uniform age, crop variety, developmental stage and management. Every

197   two months, insect surveys were done within these fields to characterize *P. manihoti* incidence,

198   infestation pressure and *A. lopezi* parasitism rate. In each field, a total of five linear 10-15 m

199   transects were screened (plants routinely spaced at 0.8-1.2 m) and, 50 plants were carefully

200   inspected for *P. manihoti*. *Phenacoccus manihoti* infestation was recorded as field-level

201   abundance (number of individuals per infected tip) and field-level incidence (proportion of

202   mealybug-affected tips) at each sampling date and location. To assess *A. lopezi* parasitism rates,

203   20 mealybug-infested tips were randomly collected from each field by breaking off the top parts

204   of individual plants, and transferred to the laboratory. Parasitism rates were estimated from these

205   samples as described above, and parasitism levels were computed for each individual field and

206   sampling date. We used analysis of variance (PROC MIXED, SAS version 9.1; SAS Institute,

207   Cary, NC) with field as the random factor, and tested the effect of cassava age, sampling date

208   and year for *P. manihoti* incidence, abundance and *A. lopezi* parasitism. Means were compared

209   with least squares means approach. Mealybug abundance data were log-transformed while

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

211   The intrinsic rate of mealybug population increase, *r*, over two months was calculated over

212   subsequent sampling events as $\ln(m_{t+1}/m_t)$ where m = the per-tip mealybug density. This growth

213   rate was regressed against the mealybug parasitism rate as a means of evaluating the role of the

214   parasitoids in suppressing mealybug population growth rates and also of estimating the

215   parasitism level that correlates with a decrease in mealybug population growth rate (for other

216   uses of this approach, see Lin & Ives 2003 and Plecas et al. 2014). The statistical significance of

217   the relationship between parasitism rate and mealybug population growth was assessed using a

218   generalized linear model incorporating normal error distribution with *r* as the response variable

219   and parasitism level and field identity as independent variables.

220

221   *iii. Exclusion cage assays*

222

223   In August 2014, a field study was initiated at the Rayong Field Crops Research Center

224   (RYFCRC) in Rayong, Thailand (see Thancharoen et al., 2018). To assess the relative

225   contribution of natural enemies such as *A. lopezi* to pest control, we employed exclusion assays

226   (Snyder and Wise, 2001; Costamagna *et al.,* 2007). More specifically, to determine separate and

227   joint effects of *P. manihoti* and *A. lopezi* on cassava crop yield, four different treatments were

228   established using two common cassava clones: Kasetsart 50 (KU50) and Rayong 72 (R72).

229   Treatments consisted of the following: 1) 'full cage' assays, in which a plant was entirely

230   covered by a mesh screen cage to exclude all natural enemies; 2) 'sham' cage assays, in which a

231 plant was covered by a screen cage to provide a microhabitat similar to that of the 'full cage', but

232 left open at the sides to allow natural enemy access; 3) 'no cage' assays, in which a plant was

233 kept without a cage as a 'real-world' benchmark. For the 'no cage' assay, two different

234 mealybug infestation modes were adopted: (1) one single infestation with 10 mealybug adults

235 per plot at the onset of the experiment; (2) a monthly infestation with 10 *P. manihoti* adults per

236 plot, to ensure a sustained mealybug population over the entire course of the experiment. Each

237 treatment (i.e., a single cage containing 4 replicated plants) was established with four replicates,

238 for two different cassava clones. The experimental field was established using locally-sourced

239 stem cuttings of KU50 or R72, planted at 1-m distances within plots.

240 Once plants had reached 4.5 months of age, 2 x 2 x 2 m polyvinylchloride (PVC) frame cages

241 were deployed, with four plants contained within each cage. Cages were covered with fine nylon

242 mesh screen to prevent entry by insects, including *A. lopezi* parasitoids. In January 2015, 10

243 adult female *P. manihoti* were gently brushed onto plants within each treatment. Mealybug

244 adults were obtained from a laboratory colony at RYFCRC that had been started in early 2014, in

245 which *P. manihoti* were maintained on potted cassava plants within a screen-house that were

246 regularly supplemented with field-collected individuals. Visual observations were carried out

247 within the cages on a monthly basis and *P. manihoti* abundance was recorded on each plant. On

248 September 7, 2015, once the crop had reached 12 months of age, cages were removed and plants

249 within the different experimental treatments were harvested manually. At harvest, fresh root

250 yield (FRY) was determined for each plant to determine treatment effects (Karlstrom *et al.,*

251 2016).

252 Mealybug population build-up under each experimental treatment was calculated, by

253 converting the average number of mealybugs per plant (averaged across plants within a given

254 treatment, as to avoid pseudo-replication) on a given sampling date to cumulative mealybug-days

255 (CMD) (Ragsdale *et al.,* 2007):

256

257 $$\sum_{n=1}^{\infty} = \left(\frac{x_{i-1} + x_i}{2} \right) \times \left(t_i - t_{i-1} \right)$$

258

259 where *n* is the total number of days over which sampling took place, x_i is the number of

260 mealybugs counted on day *i* and t_i is the number of days since the initiation of sampling on day *i*.

261   Mealybug population build-up under each treatment was computed, and average CMD

262 measures were compared between the respective treatments using a mixed modeling approach

263 with plot as the random factor and time as the repeated measure. A mixed modeling approach

264 was used to contrast fresh root yield (FRY), using treatment and variety as fixed factors. Plant

265 survival rates were compared between treatments, using a Chi-square analysis. Where necessary,

266 data were transformed to meet assumptions of normality and homoscedasticity, and all statistical

267 analyses were conducted using SPSS. In cases where data could not be transformed to normality,

268 non-parametric tests (e.g., Kruskal-Wallis) were used.

269

270   *iv. Country-wide yield changes*

271

272 Crop production statistics were obtained through the Office of Agricultural Economics, Ministry

273 of Agriculture & Cooperatives (Bangkok, Thailand). Yield measures were computed for 2006-

274 2016, for a total of 51 cassava-growing provinces within Thailand, and annual weighted means

275 were compared between successive years. Province-level yields were assigned different weights,

276 based upon the local extent of cassava cultivation (in terms of harvested area) during a given

277   year. Cassava crop yield can be impacted by agro-climatic conditions (e.g., temperature-related

278   variables) and by attack of pests such as *P. manihoti*. To assess the impact of sustained *A. lopezi*

279   releases from the 2011 cropping season onward, mean values of yields across all the cassava-

280   growing provinces were regressed with explanatory variables which included rainfall, minimum

281   and maximum temperature (obtained from Thai Meteorological Department, Bangkok,

282   Thailand).. Additionally, time (year for which yield observations and agro-climatic data were

283   obtained) was also added as an explanatory variable to control for variation in the variables

284   across years. In addition, a categorical variable representing the introduction of *A. lopezi*

285   (dummy-coded as 1 for 'presence' for the 2011 and 2012 growing seasons, and dummy-coded as

286   0 for 'absence' for growing seasons 2008, 2009 and 2010) was also added as an additional

287   explanatory variable in the regression model. Before proceeding for further analysis,, the

288   distribution of the response variable (i.e. yield) was tested, and was identified to be normal

289   (Shapiro test p < 0.05). A step-wise regression approach (forward and backward) using a linear

290   modeling approach was used to identify the model that best explains variation in yield. The

291   model with the lowest Akaike information criterion (AIC) was selected. In the next step, the

292   model with the lowest AIC score was compared with models containing interaction terms

293   between time and other explanatory variables (i.e. temperature minimum, rainfall and *A. lopezi*

294   introduction) both separately and simultaneously (see Table S1). Model with the least AIC score,

295   and the highest adjusted R^2 value was selected and is described in the Results section. Regression

296   analysis was performed in R (v 3.4.1) statistical computing environment. Additionally, R

297   package "gvlma" was used to assess if the assumptions of regression were met by the selected

298   model. Additional diagnostics of the selected model, such as determination of variance inflation

299   factor (VIF) for detection of multicollinearity, the Non-constant Variance Score Test (i.e. test for

300   heteroscedasticity of residuals over fitted values) was performed using R package "MASS" and

301   "car" respectively.

302

303

304   **Results**

305

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

307

308   During continental-scale insect surveys from 2014 until 2017 (i.e., 5-8 years following the initial

309   *A. lopezi* introduction), the mealybug complex on cassava largely comprised four non-native

310   species: (1) *P. manihoti*; (2) the papaya mealybug *Paracoccus marginatus* Williams & Granara

311   de Willink; (3) *Pseudococcus jackbeardsleyi* Gimpel & Miller; and (4) the striped mealybug

312   *Ferrisia virgata* Cockerell. *Phenacoccus manihoti* was the most abundant and widespread

313   mealybug species, and was reported from 37.0% (*n*= 549) and 100% fields (*n*= 52) in mainland

314   Southeast Asia and Indonesia, respectively. Among sites, *P. manihoti* reached field-level

315   incidence of 7.6 ± 15.9% (mean ± SD; i.e., proportion mealybug-affected tips) and abundance of

316   14.4 ± 31.0 insects per infested tip in mealybug-affected fields (or 5.2 ± 19.8 insects per tip

317   across all fields) in mainland Southeast Asia, and incidence rates of 52.7 ± 30.9% and 42.5 ±

318   67.7 individuals per tip in Indonesia. Field-level incidence and population abundance were

319   highly variable among settings and countries, reaching respective maxima of 100%, and 412.0

320   individuals per tip (Fig. 1).

321   When examining *P. manihoti* parasitism rates from a select set of sites, *A. lopezi* was present

322   in 96.9% of mealybug-affected fields (n= 97) in mainland Southeast Asia, yet were only found in

323   27.5% sites (*n*= 40) across Indonesia. Among sites, highly variable parasitism rates were evident

324   with dry-season rates of 16.3 ± 3.4% in coastal Vietnam, versus 52.9 ± 4.3% in intensified

325   systems of Tay Ninh (also in Vietnam). In Indonesia, *A. lopezi* was found in 22.0% fields in

326   Lombok (*n*= 9) and was absent from prime growing areas in Nusa Tenggara Timur (NTT). In

327   sites where *A. lopezi* had successfully established, dry-season parasitism ranged from 0% to

328   97.4%, averaging 30.0 ± 24.0% (*n*= 110) (Fig. S1). In fields where *A. lopezi* had effectively

329   established, mealybug pest pressure exhibited a negative regression with parasitism rate ($F_{1,98}$=

330   13.162, p< 0.001; R^2= 0.118).

331

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

333

334   Over the course of three years, we monitored *P. manihoti* abundance, field-level incidence and

335   associated *A. lopezi* parasitism rates in Tay Ninh, southern Vietnam. Field-level incidence of *P.*

336   *manihoti* ranged from 0% to 82%, averaging 24.8 ± 17.7% (mean ± SD) plants infested over two

337   consecutive crop cycles. Mealybug incidence was significantly higher on older crops ($F_{7,57}$ = 9.9;

338   p<0.0001), and rapidly increased during the dry season. Similarly, mealybug abundance (average

339   5.6 ± 5.0 individuals per tip) was higher during the dry season ($F_{1,63}$ = 9.10; P = 0.0037), and in

340   crops older than six months, when compared to younger crops ($F_{7,57}$ =269 4.06; P < 0.0001).

341   From mid-2014 onward, mealybug populations remained at field-level abundance below 10-15

342   individuals per infested tip (Fig. 2). Furthermore, *A. lopezi* attained mean parasitism rates of 42.3

343   ± 21.7%, with maxima of 76.7 ± 28.9% during the early rainy season (Fig. 2). Overall,

344   parasitism gradually increased over the dry season, up until crops were 4-6 months old.

345   Mealybug growth rates were significantly and negatively correlated with parasitism levels

346   across the 8 sites studied (GLM w/ Normal error distribution and corrected for field: χ^2_1 = 125.4;

347   P = 0.0017; the field term was not significant; χ^2_7 = 0.2; P =1) (Fig. 3). The x-intercept of each

348   per-field regression represents the parasitism level above which mealybug growth rates are

349   negative and this value ranged between 0.38 and 0.69 for the 8 sites (average = 0.47 ± 0.09) (Fig.

350   3). Whilst *A. lopezi* was the sole primary parasitoid at this location, three hyperparasitoid species

351   attacked it at 2.79 ± 5.38% levels (as % of parasitized hosts).

352

353   *iii. Exclusion cage assays*

354

355   Over the entire assay, *P. manihoti* populations under 'full cage' attained 48,318 ± 51,425 (*n*= 4;

356   mean ± SD) and 7,256 ± 8,581 cumulative mealybug days (CMD) in 'sham cage' for one

357   popular variety (i.e., R72) (Thancharoen et al., 2018; Fig. 4). For a second variety, KU50, *P.*

358   *manihoti* attained 28,125 ± 32,456 CMD in a 'full cage' treatment, and 1,782 ± 1,073 CMD in

359   'sham cage'. This compared to CMD measures in a 'no cage' control of 1,378 ± 1,039 and 342 ±

360   252, for R72 and KU50 respectively. CMD measures were significantly affected by treatment

361   ($F_{3,189}$= 240.752, p< 0.001) and time ($F_{6,189}$= 113.347, p< 0.001), and the interaction term time x

362   treatment ($F_{18,189}$= 2.012, p= 0.011). Also, total CMD measures at the end of the trial

363   significantly differed between treatments for both R72 and KU 50 ($F_{3,12}$= 6.767, p= 0.006; $F_{3,12}$=

364   11.152, p= 0.001, respectively).

365   Cassava yield parameters varied considerably under the four experimental treatments, and for

366   both crop varieties (see Thancharoen et al., 2018). For Rayong 72, plant survival attained 37.5%

367   under 'full cage' as compared to 75% and 87.5% under 'no cage' or 'sham cage' conditions,

368   respectively (Chi square, χ^2= 10.473, p= 0.015). Fresh root yield (FRY) was significantly

369   affected by treatment ($F_{3,27}$= 4.104, p= 0.016) and variety ($F_{1,27}$= 4.364, p= 0.046). For R72 and

370   KU50, FRY under 'full cage' was 74.6% or 71.2% lower than under 'sham cage' (Kruskal-

371   Wallis, χ^2= 8.344, p= 0.039; χ^2= 19.134, p< 0.001, respectively), and respective yield reductions

372   for both varieties were 77.2% and 67.8% compared to 'no cage' treatments.

373

374   *iv. Country-wide yield changes*

375

376   During the 2009 dry season, *P. manihoti* attained its peak population in Thailand, with field-level

377   incidence near 100% and abundance rates of hundreds of *P. manihoti* per plant on at least

378   230,000 ha (Rojanaridpiched *et al.* 2013). Over the subsequent 2009-10 cropping season,

379   province-level crop yields dropped by 12.59 ± 9.78% nationwide (weighted mean: -18.2%) (Fig.

380   5). Furthermore, country-wide aggregate yields declined from 22.67 t/ha to 18.57 t/ha, and total

381   production dropped by 26.86% to 22,005,740 tonnes of fresh root. Following the lowered crop

382   output, prices for Thai cassava starch increased 2.38-fold at domestic prices in Thailand, and

383   2.62-fold at export prices (US$ FOB, Free On Board) (Fig. S2). However, in the following

384   growing seasons (i.e., 2011 and 2012), there was a marked improvement in yield across all

385   regions, as compared to previous years (Fig. 5). It was also from mid-2010 onward that country-

386   wide mass releases of *A. lopezi* were carried out. To test if the *A. lopezi* introduction was

387   responsible for this improvement in yield, and to differentiate *P. manihoti*-induced yield drops

388   from agro-climatic climatic impacts and changes across years, regression analyses were carried

389   out with yield as response variable and agro-climatic parameters, year ("time"), and *A . lopezi*

390   presence as explanatory variables. Multiple regression analysis revealed that a model with

391   interaction terms between time and all explanatory variables, i.e. time of introduction of *A. lopezi*

392   and rainfall had the lowest AIC score and the higest explanatory power (adjusted R^2) (Table S1).

393   The model showed a significantly positive effect ($F_{7,183}$= 8.641) of the interaction term Time x

394   Presence (i.e., 'presence' of *A. lopezi* and time , $p < 0.01$) on observed yields. The best model

395   indicated that the introduction of *A. lopezi* (and not agro-climatic variables or changes in those

396   variables over time) significantly increased yields across all cassava-growing regions during the

397   2011 and 2012 cropping seasons.

398

399

400   **Discussion**

401

402   In 2008, the invasive mealybug *P. manihoti* accidentally arrived in Thailand. Through its

403   extensive spatial spread, rapid population build-up and unrestricted feeding on plants (this lead to

404   stunting and plant death), *P. manihoti* caused significant yield declines and a 27% drop in the

405   nation's cassava production. This study shows how the neotropical parasitoid, *A. lopezi*, released

406   throughout Thailand for mealybug control in 2010, had effectively established in 97% mealybug-

407   affected fields in mainland Southeast Asia by 2014, and colonized 27% sites across insular

408   Indonesia by late 2017. Attaining average dry-season parasitism rates of 30% across sites, *A.*

409   *lopezi* populations readily oscillate with those of its mealybug host and suppress *P. manihoti* to

410   incidence levels of 7% and background infestation pressure of a mere 14 individuals per

411   (infested) tip. Experimental assays using two widely-grown cassava varieties reveal how

412   biological control secures approximate yield gains of 5.3-10.0 t/ha. Our work clearly

413   demonstrates how *A. lopezi* downgrades the invasive *P. manihoti* to non-economic levels at a

414   continental scale, without any known detrimental side-effects. Offering a quantitative assessment

415   of IBC's contribution to (the restoration of) primary productivity in Asia's cassava crop, our

416   work illuminates the broader societal value of biological control in a geographical region where

417   there is heavy and increasing use of pesticides (Schreinemachers *et al.,* 2015).

418   Aside from featuring as a 'beacon of hope' in Asia's pesticide-tainted farming systems, our

419   work heralds a new era for the discipline of insect biological control. Since the late 1800s,

420   biological control has permitted the complete or partial suppression of 226 debilitating insect

421   pests globally, it has formed the crux of founding ecological theories (e.g., Hairston et al., 1960),

422   and was widely deemed to be a safe, dependable and preferred means for (invasive) pest control

423   for most of its history. Following the release of Rachel Carson's 1962 *Silent Spring*, biological

424   control was met with unrestrained enthusiasm and a firm belief in its potential as a dependable

425   alternative to pesticide-centered practices. Yet, as concerns over its ecological risks rose

426   following Howarth's (1983, 1991) denunciation of few historic cases of malpractice, regulatory

427   hurdles surfaced, public funding lowered and the practice of insect biological control went

428   through trying yet necessary reform (Strong & Pemberton, 2000; Hoddle, 2004; Messing &

429   Brodeur, 2018). Over the past three decades, IBC implementation has centered on ecological

430   safety and increasingly strives to balance environmental benefits and risks (Heimpel & Cock,

431   2018). Though weed biological control indeed has a 99% safety record (Suckling & Sforza,

432   2014), scientists are conscious that ecological risk will never be zero and that certain risk factors

433   are difficult to anticipate and predict (Crooks & Soule, 1999; Sexton et al., 2017). In the

434   meantime, it's well-recognized that invasive pests tend to present far higher threats to native

435   biota than judiciously-selected natural enemies with a narrow dietary breadth (Culliney, 2005).

436   Though the 1980s Africa campaign against *P. manihoti* was implemented during times when the

437   primary focus of insect biological control was on benefits (but see Neuenschwander, 2001), risks

438   were considered to be minimal and did not delay implementation. The fact that *A. lopezi* was

439   both effective and highly host-specific vindicated this. As a result, the implementation of IBC in

440   Southeast Asia more than 30 years later was greatly facilitated by recognizing that (*i*) IBC had

441   been effective across Africa's cassava-belt, and (*ii*) widespread benefits were amplified because

442   of an absence of negative environmental side-effects on non-target species.

443   In light of the above, *A. lopezi* attained consistently high parasitism rates across most of the *P.*

444   *manihoti* range of climatic suitability in tropical Asia (Yonow and Kriticos, 2017), except for

445   insular Indonesia where it was only introduced at one site in late 2014. The far superior *P.*

446   *manihoti* infestation pressure in eastern Indonesia (i.e., NTT, Lombok), where *A. lopezi* waits to

447   be introduced, further emphasize the contribution of this parasitoid to mealybug control. Across

448   locations, *A. lopezi* attained maximum parasitism levels of 98% (in late dry season, at Tay Ninh),

449   which greatly surpassed the 33-36% established threshold (of maximum parasitism rate) for

450   successful biological control – i.e., which results in lasting pest population suppression (Hawkins

451   and Cornell, 1994). At multiple sites, parasitism rates equally surpassed (max. 30%) levels from

452   smallholder plots in Africa's savanna (Hammond and Neuenschwander, 1990). Factors ensuring

453   this exceptional parasitoid efficacy and resulting pest control are a) unique features of the

454   cassava crop, including prolonged durational stability, vegetational complexity and a constitutive

455   secretion of energy-rich nectar for foraging parasitoids (Pinto-Zevallos *et al.,* 2016); b) spatio-

456   temporal continuity of mealybug-infested crops at a landscape level (Schellhorn *et al.,* 2014),

457   especially in locations where farmers employ staggered planting and piece-meal harvesting; c)

458   favorable ecological traits of *A. lopezi*, including high dispersal ability, environmental

459   adaptability and density-dependent parasitism (Neuenschwander *et al.,* 1989); d) non- or limited

460 use of (prophylactic) insecticides, except for Thailand and parts of southern Vietnam; and e)

461 human-assisted dispersal of *A. lopezi*, via (parasitized) mealybug-infested planting material

462 (Herren *et al.*, 1987). Furthermore, substantial fertilizer inputs and suitable water management in

463 areas with intensified cassava production -e.g., Vietnam's Tay Ninh province, or parts of eastern

464 Thailand such as Nakhon Ratchassima- likely benefited biological control further by boosting *A.*

465 *lopezi* development and fitness (Wyckhuys *et al.,* 2017a). All of the above factors may have

466 contributed to the stabilization of mealybug populations at 25% incidence and field-level

467 abundance below 10-15 individuals per infested tip, similar to what was observed in Africa

468 during the 1980s campaign (Fig 2; Hammond and Neuenschwander, 1990).

469 Exclusion cage assays illustrated how biological control enabled a root yield recovery of 5.3-

470 10.0 t/ha in two main cassava varieties, and how 2015 yields under 'no cage' (i.e., 'real-world')

471 conditions were in line with historic in-country yield tendencies. Though no direct field-level

472 measurements were made of *A. lopezi* parasitism during the cage trials, biological control was

473 found to occupy a central role in lowering *P. manihoti* populations (Thancharoen *et al.*, 2018),

474 and *A. lopezi* is a determining factor in ensuring mealybug suppression in other key cassava-

475 growing areas in Southeast Asia (Le et al., 2018). Cage trials also showed large variability in

476 responses between the two cassava clones, likely reflective of differences in plant vigor and an

477 individual clone's photosynthetic capability (Connor et al., 1981; Cock et al., 2012). The cassava

478 plant does possess a unique set of features to sustain root production under (a)biotic stress,

479 including the adaptive mobilization of biomass and a highly-effective use of resources (Cock et

480 al. 2012). Yet, the pronounced production losses - under cage conditions, especially for R72 -

481 can be ascribed to continuous (unrestrained) attack of the active apex, direct damage to stems

482 and high rates of plant death.

483   As *P. manihoti* currently occurs at low infestation pressure across mainland Southeast Asia,

484   cage assays lend themselves to further extrapolation to a broader geographical scale. Yet, local

485   environmental conditions may still affect parasitoid abundance, efficacy and (biological control)

486   impact. For example, slightly higher *P. manihoti* population levels were recorded in settings with

487   sandy, low-fertile soils (Wyckhuys *et al.*, 2017a) and biological control under those conditions

488   merits closer research attention. Also, as landscape composition and plant disease infection status

489   equally modulate *P. manihoti* performance and efficacy of biological control at local scale

490   (Wyckhuys *et al.,* 2017b; Le *et al.,* 2018), further replicated trials could be warranted to validate

491   the robustness of our findings under varying agro-ecological contexts. Despite the above

492   confounding factors, careful analysis of production statistics and commodity market fluxes (as in

493   *section iv*) support our empirical results and confirm *A. lopezi* to be the major biotic factor

494   affecting mealybug population growth. In the meantime, Indonesian sites where *A. lopezi* has not

495   yet established now constitute a 'natural laboratory' to refine and validate existing projections on

496   *A. lopezi*-mediated yield gain (and crop recovery), in advance of the natural arrival / introduction

497   of the parasitoid.

498   In tropical Asia, cassava underpins a multi-billion dollar starch sector, constitutes a key source

499   of farm income and provides an (oftentimes indirect) means to food security for poor, under-

500   privileged populations (Howeler, 2014; Delaquis *et al.,* 2017). On the one hand, the *P. manihoti*-

501   induced yield shocks, as recorded during 2009-2011, can have major implications for rural

502   livelihoods. Sustained pest attack can aggravate food security issues in areas where cassava is a

503   prime food staple or progress into chronic 'poverty traps' (Tittonell *et al.,* 2013), all of which is

504   counteracted through *A. lopezi*-mediated biological control. Aside from restoring FRY, *A. lopezi*

505   equally helped recover a plant's total dry matter or 'biological yield' (Thancharoen *et al.,* 2018),

506 which is particularly relevant in various parts of tropical Asia where cassava leaves and shoots

507 constitute part of the local diet of rural communities. On the other hand, the net productivity loss

508 of 5.14 million ton of fresh root equaled a respective loss of revenue of US$ 267.5-591.7 million

509 (at 2009-10 factory price) for Thailand's cassava sector and the Asia-based starch industry.

510 Hence, aside from its manifest (direct, indirect) contribution to local food security, socio-

511 economic benefits of the *P. manihoti* campaign are deemed to be substantial and potentially

512 equal or even surpass those recorded previously in Africa (Zeddies *et al.,* 2001).

513   Yield recovery levels in our cage assays were considerably higher than the 2.5 t/ha yield

514 increase recorded through on-farm measurements in sub-Saharan Africa (Neuenschwander *et al.,*

515 1989). At Thai farm-gate prices, *A. lopezi*-mediated yield recovery equals to US$200-704 per ha

516 (Thancharoen *et al.*, 2018), though this does not take into account changes in production costs,

517 local elasticities of supply and demand, or (often substantial) insecticide / fertilizer expenditures.

518 Though we do call for caution in extrapolating our findings, the approximate value of *P.*

519 *manihoti* biological control in Asia could thus be hundreds of dollars higher than existing

520 estimates of $63 ha^{-1} year^{-1} across global biomes including natural systems (Costanza *et al.*

521 1997), $33 ha^{-1} year^{-1} for (natural) biological control of the soybean aphid in the US Midwest

522 (Landis *et al.,* 2008), or $75 to $310 ha^{-1}year^{-1} for bird-mediated pest control in Costa Rican

523 coffee (Karp *et al.,* 2013). From the above it can equally be deduced that the potential of insect

524 biological control has been significantly under-valued (Landis *et al.*, 2008; Naranjo *et al.*, 2015),

525 and that comprehensive cost-benefit analyses are urgently needed to raise (or restore) societal

526 recognition of this important and safe ecosystem service.

527   These substantial economic benefits of (naturally-occurring, cost-free) biological control need

528 to be contrasted with the unrelenting global increase in the use of insecticides for the mitigation

529   of (domestic and, increasingly invasive) pests (Enserink et al., 2013). Following the *P. manihoti*

530   invasion, pesticides have equally become pervasive in Thailand's cassava crop and growers have

531   embraced the (prophylactic) use of neonicotinoid insecticides. Yet, given the omnipresence of *A.*

532   *lopezi* and the largely low mealybug population levels in pesticide-free cassava plots across

533   Southeast Asia, cost-effectiveness of such approaches needs closer scrutiny. Though pesticides

534   do bring certain benefits to society, they tend to simplify ecological communities, adversely

535   impact natural enemies and thus accelerate pest proliferation (Lundgren and Fausti, 2015). On

536   the other hand, our work shows how a carefully-selected, specialist natural enemy constitutes a

537   viable alternative to insecticide-centered approaches. Hence, potential (non-target ecological)

538   risks of classical biological control have to be viewed in terms of refraining from action and thus

539   creating room for far-less environmentally-friendly tactics such as (systemic) pesticides

540   (Messing and Wright, 2006; Suckling and Sforza, 2014; Hajek *et al.,* 2016).

541

542

543   **Conclusions**

544

545   This study provides a quantitative assessment of how importation biological control (IBC)

546   helped restore primary productivity in Asia's cassava crop, following the arrival and extensive

547   spread of an invasive sap-feeding pest, i.e., the cassava mealybug. We demonstrate that IBC can

548   provide durable and cost-effective control of the invasive *P. manihoti*, and delivers substantial

549   and sustainable socio-economic and environmental benefits (Bale *et al.,* 2008; Naranjo *et al.,*

550   2015). Furthermore, we emphasize that by recognizing the minimal ecological risks associated

551   with the introduction of a highly host-specific parasitoid and by deliberately balancing benefits

552 and risks of biological control (see Heimpel & Cock, 2018), the transformative potential of IBC

553 can be fully exploited. In a world typified by massive declines in insect numbers, extreme

554 biodiversity loss, and dwindling public interest in biological control (Bale *et al.,* 2008; Hallmann

555 *et al.,* 2017; Warner *et al.,* 2012), our research underlines the immense yet largely untapped

556 potential of ecologically-based approaches to resolve (invasive) pest problems. We advocate that

557 (judiciously-implemented) IBC can positively assist with intensifying global agriculture and help

558 feed a growing world population in the 21st century.

559

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561

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566

567

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569

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Figure 1

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

Doughnut charts in the left and right margins represent field-level incidence (i.e., red portion reflecting the proportion of *P. manihoti* affected tips, ranging from 0 to 1 for full circumference), and are complemented with bar charts indicative of plant-level *P. manihoti* abundance (i.e., average number of individuals per tip). The number inside each doughnut reflects the number of fields sampled per locale. Doughnut charts in the lower panel indicate average *A. lopezi* parasitism rate at six selected sites (depicted by the dark green section, reflecting proportion parasitism ranging from 0 to 1 for full circumference). The distribution map is created as overlay on a 2005 cassava cropping area (MapSpam, 2017). Photograph *Anagyrus lopezi* (credit G. Goergen, IITA).
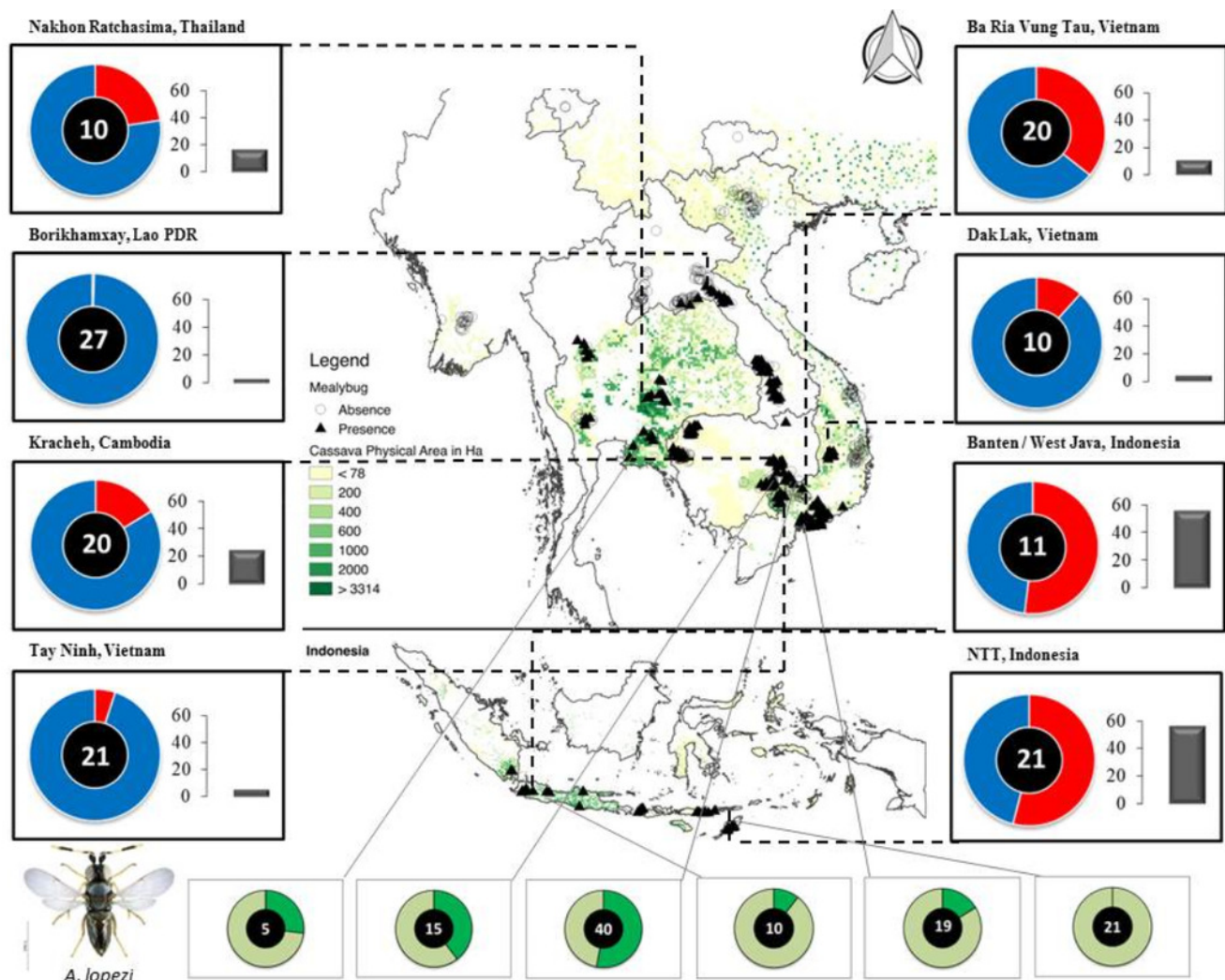
Figure 2

Bi-monthly mealybug population fluctuations in southern Vietnam, over a 2-year time period.

Phenacoccus manihoti dynamics are represented following the first record of *A. lopezi* presence in southern Vietnam, depicting field-level *P. manihoti* abundance (*n*= 8) as contrasted with respective *A. lopezi* parasitism rates, from July 2013 until July 2015.
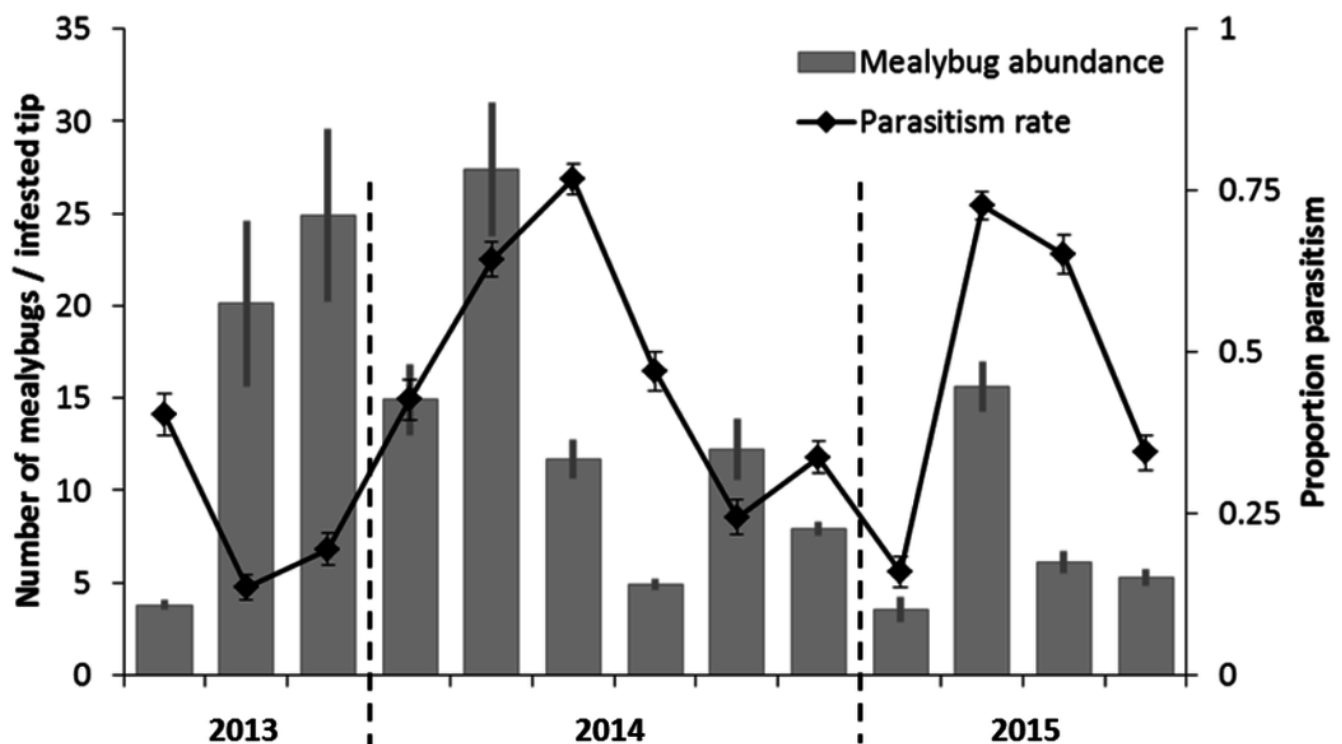
Figure 3

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

Each dot represents a 2-month period in one of 8 field plots. Thin lines are linear regressions per each of the eight sites monitored for illustrative purposes although the analysis was done on the entire data set. The thick black line shows the fit of the entire data set. 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.
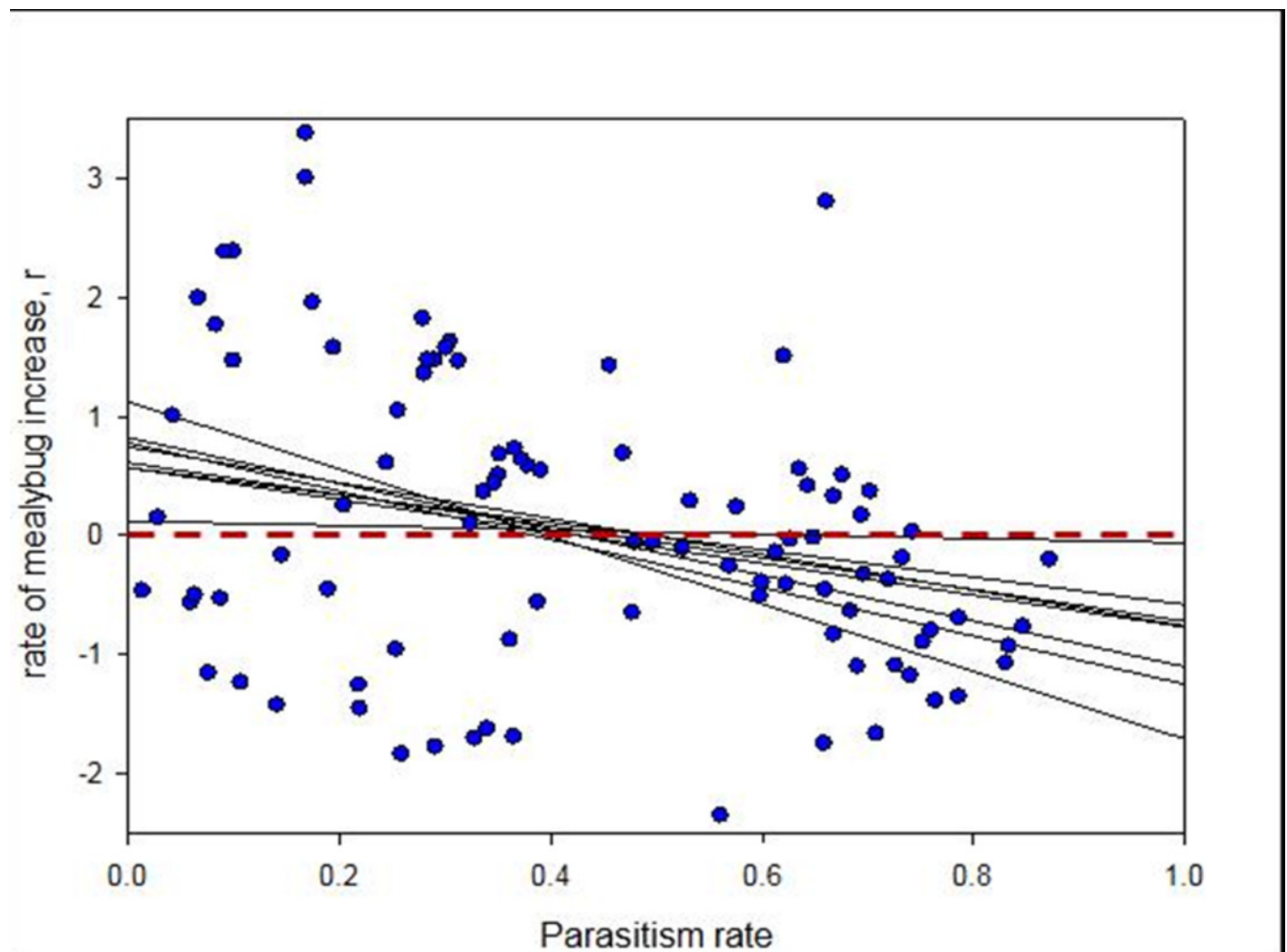
Figure 4

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

Six weeks after inoculation, mealybug abundance (n = 16; mean ± 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 R72; $F_{2,45}$= 9.807, P<0.001 for KU50). For each treatment, fresh root yield is determined at time of harvest, on a 12-month old crop.
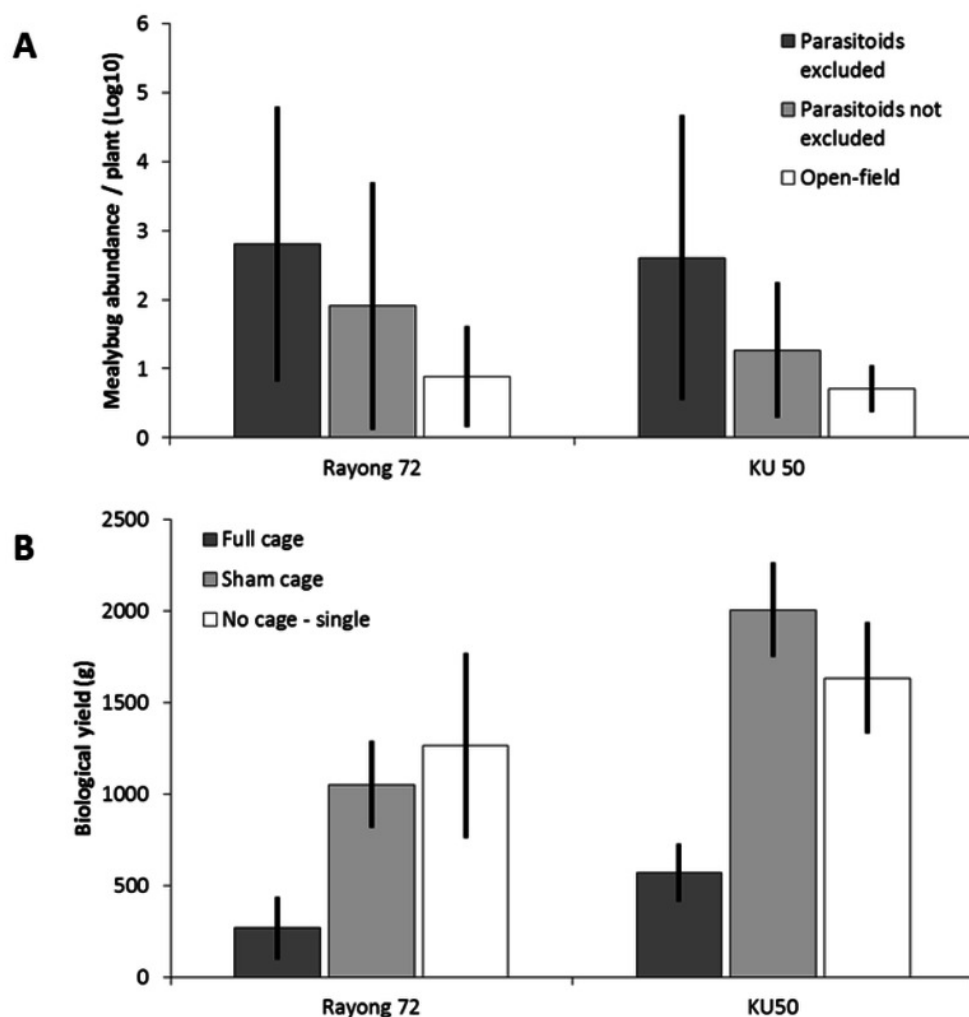
Figure 5

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

Shifts (A-D) cover the country-wide spread of *P. manihoti* from late 2008 until 2011, the first small-scale 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.