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

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 ± 15.8% (mean ± 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 ±

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 ± 3.4% in coastal Vietnam, versus 52.9 ± 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 ± 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 ($F_{7,57} = 269\ 4.06$; $P < 0.0001$). 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 $= 0.47 \pm 0.09$) (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 ± 51,425 (n= 4;

343   mean ± SD) and 7,256 ± 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 ±

345   32,456 CMD in a 'full cage' treatment, and 1,782 ± 1,073 CMD in 'sham cage'. This compared

346   to CMD measures in a 'no cage' control of 1,378 ± 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, χ^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, χ^2= 8.344, p= 0.039; χ^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^{-1}year^{-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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546 **References**
547

548 Andrews KL, Bentley JW & Cave RD (1992) Enhancing biological control's contributions to
549   integrated pest management through appropriate levels of farmer participation. *Florida*
550   *Entomologist*, **75**, 429-439.
551 Bale JS, van Lenteren JC & Bigler F (2008) Biological control and sustainable food production.
552   *Philosophical Transactions of the Royal Society of London B*, **363**, 761-776.
553 Barnes AD, Jochum M, Mumme S, Haneda NF, Farajallah A, Widarto TH & Brose U (2014)
554   Consequences of tropical land use for multitrophic biodiversity and ecosystem functioning.
555   *Nature Communications*, **5**, 5351.
556 Bebber DP, Ramotowski MAT & Gurr SJ (2013) Crop pests and pathogens move polewards in a
557   warming world. *Nature Climate Change*, **3**, 985-988.
558 Bradshaw CJ, Leroy B, Bellard C, Roiz D, Albert C, Fournier A, Barbet-Massin M, Salles JM,
559   Simard F & Courchamp F (2016) Massive yet grossly underestimated global costs of invasive
560   insects. *Nature Communications*, **7**, 12986.
561 Cock JH (2012) Cassava growth and development. In: Howeler RH (Ed.), The cassava
562   handbook: a reference manual, pp. 39-61. International Center for Tropical Agriculture CIAT,
563   Cali (Colombia).
564 Connor DJ, Cock JH, Parra GE (1981) Response of cassava to water shortage. I. Growth and
565   yield. Field Crops Research 4: 181-200.
566 Cock MJW, Day RK, Hinz HL, Pollard KM, Thomas SE, Williams FE, Witt ABR & Shaw RH
567   (2016a) The impacts of some classical biological control successes. *CAB Reviews*, 10(42), 58
568   pp.
569 Cock MJ, Murphy ST, Kairo MT, Thompson E, Murphy RJ & Francis AW (2016b) Trends in
570   the classical biological control of insect pests by insects: an update of the BIOCAT database.
571   *BioControl*, **61**, 349–363.
572 Costanza R, d'Arge R, De Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S,
573   O'Neill RV, Paruelo J & Raskin RG (1997) The value of the world's ecosystem services and
574   natural capital. *Nature*, **387**, 253-260.
575 Costamagna AC, Landis DA & DiFonzo CD (2007) Suppression of soybean aphid by generalist
576   predators results in a trophic cascade in soybeans. *Ecological Applications*, **17**, 441-451.
577 Crooks JA & Soulé ME (1999). Lag times in population explosions of invasive species: causes
578   and implications. In Sandlund, Schei, Viken (eds.): Invasive Species and Biodiversity
579   Management, pp. 103-125.
580 Culliney TW (2005) Benefits of classical biological control for managing invasive plants.
581   *Critical Reviews in Plant Sciences*, **24**, 131-150.
582 Daily GC, Polasky S, Goldstein J, Kareiva PM, Mooney HA, Pejchar L, Ricketts TH, Salzman J
583   & Shallenberger R (2009) Ecosystem services in decision making: time to deliver. *Frontiers in*
584   *Ecology and the Environment*, **7**, 21-28.

585 DeBach P & Huffaker CB (1971) Experimental techniques for evaluation of the effectiveness of
586   natural enemies. In: Huffaker CB (Ed.) Biological Control. Springer, Boston, MA, pp. 113-
587   140.
588 Delaquis E, de Haan S & Wyckhuys KAG (2017) On-farm diversity offsets environmental
589   pressures in tropical agro-ecosystems: a synthetic review for cassava-based systems.
590   *Agriculture, Ecosystems and Environment*, **251**, 226-235.
591 Enserink M, Hines PJ, Vignieri SN, Wigginton NS & Yeston JS (2013) The pesticide paradox.
592   *Science*, **341**, 728-729.
593 Gardiner MM, Landis, DA, Gratton, C, DiFonzo, CD, O'Neal, M, Chacon, JM et al. (2009)
594   Landscape diversity enhances biological control of an introduced crop pest in the north-central
595   USA. *Ecological Applications*, **19**, 143–154.
596 Graziosi I, Minato N, Alvarez E, Ngo DT, Hoat TX, Aye TM, Pardo JM, Wongtiem P &
597   Wyckhuys KAG (2016) Emerging pests and diseases of South-east Asian cassava: a
598   comprehensive evaluation of geographic priorities, management options and research needs.
599   *Pest Management Science*, **72**, 1071–1089.
600 Greathead DJ & Greathead AH (1992) Biological control of insect pests by insect parasitoids and
601   predators: the BIOCAT database. *Biocontrol News and Information*, **13**, 61N–68N.
602 Gutierez AP, Caltagirone LE & Meikle W (1999) Evaluation of results. Economics of biological
603   control. In: Bellows TS & Fisher TW (Eds.) Handbook of biological control. Academic Press,
604   San Diego, CA, USA, pp. 243-252.
605 Hairston NG, Smith FE, Slobodkin LB (1960). Community structure, population control and
606   competition. *American Naturalist*, **94**, 421–425.
607 Hajek AE, Hurley BP, Kenis M, Garnas JR, Bush SJ, Wingfield MJ, Van Lenteren JC & Cock
608   MJ (2016) Exotic biological control agents: a solution or contribution to arthropod invasions.
609   *Biological Invasions*, **18**, 953-969.
610 Hallmann CA, Sorg M, Jongejans E, Siepel H, Hofland N, Schwan H, Stenmans W, Müller A,
611   Sumser H, Hörren T & Goulson D (2017) More than 75 percent decline over 27 years in total
612   flying insect biomass in protected areas. *PLoS ONE*, **12**, e0185809.
613 Hammond WNO & Neuenschwander P (1990) Sustained biological control of the cassava
614   mealybug *Phenacoccus manihoti* (Homoptera: Pseudococcidae) by *Epidinocarsis lopezi*
615   (Hymenoptera: Encyrtidae) in Nigeria. *Entomophaga*, **35**, 515-526.
616 Hawkins BA & Cornell HV (1994) Maximum parasitism rates and successful biological control.
617   *Science*, **266**, 1886.
618 Heimpel GE & Mills NJ (2017) Biological control: ecology and applications. Cambridge
619   University Press, Cambridge UK, 386 p.
620 Heimpel GE & Cock MJW (2018) Shifting paradigms in the history of classical biological
621   control. *BioControl*, **63**, 27–37.
622 Herren HR & Neuenschwander P (1991) Biological control of cassava pests in Africa. *Annual
623   Review of Entomology*, **36**, 257-283.

624 Herren HR, Neuenschwander P, Hennessey RD & Hammond WNO (1987) Introduction and
625   dispersal of *Epidinocarsis lopezi* (Hym., Encyrtidae), an exotic parasitoid of the cassava
626   mealybug, *Phenacoccus manihoti* (Hom., Pseudococcidae), in Africa. *Agriculture, Ecosystems*
627   *& Environment*, **19**, 131-144.
628 Hoddle MS (2004) Restoring balance: using exotic species to control invasive exotic species.
629   *Conservation Biology*, **18**, 38-49.
630 Howarth FG (1983) Classical biological control: panacea or Pandora's Box? *Proceedings of the*
631   *Hawaiian Entomological Society*, **24**, 239-244.
632 Howarth FG (1991) Environmental impacts of classical biological control. *Annual Review of*
633   *Entomology*, 36, 485-509.
634 Howeler R (2014) Sustainable soil and crop management of cassava in Asia. International Center
635   for Tropical Agriculture, CIAT. Cali, Colombia, 280 p.
636 Karlström A, Calle F, Salazar S, Morante N, Dufour D & Ceballos H (2016) Biological
637   implications in cassava for the production of amylose-free starch: Impact on root yield and
638   related traits. *Frontiers in Plant Science*, **7**, 604.
639 Karp DS, Mendenhall CD, Sandí RF, Chaumont N, Ehrlich PR, Hadly EA & Daily GC (2013)
640   Forest bolsters bird abundance, pest control and coffee yield. *Ecology Letters*, **16**, 1339-1347.
641 Landis DA, Gardiner MM, van der Werf W & Swinton SM (2008) Increasing corn for biofuel
642   production reduces biocontrol services in agricultural landscapes. *Proceedings of the National*
643   *Academy of Sciences USA*, **105**, 20552-20557.
644 Le TTN, Graziosi I, Cira TM, Gates MW, Wyckhuys KAG (2018) Landscape context does not
645   constrain biological control of *Phenacoccus manihoti* in intensified cassava systems of
646   southern Vietnam. Biological Control, **121**, 129-139..
647 Losey J & Vaughan M (2006) The economic value of ecological services provided by insects.
648   *BioScience*, **56**, 311-323.
649 Luck RF, Shepard BM & Kenmore PE (1988) Experimental methods evaluating arthropod
650   natural enemies. *Annual Review of Entomology*, **33**, 367-391.
651 Lundgren JG & Fausti SW (2015) Trading biodiversity for pest problems. *Science Advances*, **1**,
652   e1500558.
653 Melo FP, Arroyo-Rodríguez V, Fahrig L, Martínez-Ramos M & Tabarelli M (2013) On the hope
654   for biodiversity-friendly tropical landscapes. *Trends in Ecology and Evolution*, **28**, 462-468.
655 Messing RH & Wright MG (2006) Biological control of invasive species: solution or pollution?
656   *Frontiers in Ecology and the Environment*, **4**, 132-140.
657 Messing RH & Brodeur J (2018) Current challenges to the implementation of classical biological
658   control. *BioControl*, **63**, 1-9.
659 Naranjo SE, Ellsworth PC & Frisvold GB (2015) Economic value of biological control in
660   integrated pest management of managed plant systems. *Annual Review of Entomology*, **60**, 1-
661   25.
662 Neuenschwander P (2001) Biological control of the cassava mealybug in Africa: a review.
663   *Biological Control*, **21**, 214-229.

664   Neuenschwander P, Hammond WO, Gutierrez AP, Cudjoe AR, Adjakloe R, Baumgärtner JU &
665   Regev U (1989) Impact assessment of the biological control of the cassava mealybug,
666   *Phenacoccus manihoti* Matile Ferrero (Hemiptera: Pseudococcidae) by the introduced
667   parasitoid *Epidinocarsis lopezi* (De Santis) (Hymenoptera: Encyrtidae). *Bulletin of*
668   *Entomological Research*, **79**, 579-594.
669   Oerke EC (2006) Crop losses to pests. *The Journal of Agricultural Science*, **144**, 31-43.
670   Oliver TH, Isaac NJ, August TA, Woodcock BA, Roy DB & Bullock JM (2015) Declining
671   resilience of ecosystem functions under biodiversity loss. *Nature Communications*, **6**, 10122.
672   Paini DR, Sheppard AW, Cook DC, De Barro PJ, Worner SP & Thomas MB (2016) Global
673   threat to agriculture from invasive species. *Proceedings of the National Academy of Sciences*
674   *USA*, **113**, 7575-7579.
675   Pinto-Zevallos DM, Pareja M & Ambrogi BG (2016) Current knowledge and future research
676   perspectives on cassava (*Manihot esculenta* Crantz) chemical defenses: an agro-ecological
677   view. *Phytochemistry*, **130**, 10-21.
678   Ragsdale DW, McCornack BP, Venette RC, Potter BD, MacRae IV, Hodgson EW, O'Neal ME,
679   Johnson KD, O'Neil RJ, DiFonzo CD & Hunt TE (2007) Economic threshold for soybean
680   aphid (Hemiptera: Aphididae). *Journal of Economic Entomology*, **100**, 1258-1267.
681   Rojanaridpiched C et al. (2013) Rapid response to the accidental introduction of the mealybug,
682   *Phenacoccus manihoti*. In: Anonymous (ed) "Save and Grow": Cassava. A guide to sustainable
683   production intensification. Food and Agriculture Organization of the United Nations, FAO,
684   Rome, pp. 81-82.
685   Schellhorn NA, Bianchi FJJA & Hsu CL (2014) Movement of entomophagous arthropods in
686   agricultural landscapes: links to pest suppression. *Annual Review of Entomology*, **59**, 559-581.
687   Schreinemachers P, Afari-Sefa V, Heng CH, Dung PTM, Praneetvatakul S & Srinivasan R
688   (2015) Safe and sustainable crop protection in Southeast Asia: status, challenges and policy
689   options. *Environmental Science & Policy*, **54**, 357-366.
690   Sexton JP, Montiel J, Shay JE, Stephens MR & Slatyer RA (2017). Evolution of ecological niche
691   breadth. *Annual Review of Ecology, Evolution, and Systematics*, **48**, 183-206.
692   Snyder WE & Wise DH (2001) Contrasting trophic cascades generated by a community of
693   generalist predators. *Ecology*, **82**, 1571-1583.
694   Strong DR & Pemberton RW (2000) Biological control of invading species – risk and reform.
695   *Science*, **288**, 1969-1970.
696   Suckling DM & Sforza RFH (2014) What magnitude are observed non-target impacts from weed
697   biocontrol? *PLoS ONE*, **9**, e84847.
698   Tittonell P & Giller KE (2013) When yield gaps are poverty traps: The paradigm of ecological
699   intensification in African smallholder agriculture. *Field Crops Research*, **143**, 76-90.
700   van Driesche R, Hoddle M & Center T (2008) Control of pests and weeds by natural enemies.
701   Blackwell Publishing Limited, Malden, MA, USA, 484 p.
702   van Lenteren JC (1980) Evaluation of control capabilities of natural enemies: does art have to
703   become science? *Netherlands Journal of Zoology*, **30**, 369-381.

704 Van Lenteren JC, Bale J, Bigler F, Hokkanen HMT & Loomans AJM (2006) Assessing risks of
705   releasing exotic biological control agents of arthropod pests. *Annual Review of Entomology*,
706   **51**, 609-634.
707 Warner KD, Daane KM, Getz CM, Maurano SP, Calderon S & Powers KA (2011) The decline
708   of public interest agricultural science and the dubious future of crop biological control in
709   California. *Agriculture and Human Values*, **28**, 483-496.
710 Winotai A, Goergen G, Tamò M & Neuenschwander P (2010) Cassava mealybug has reached
711   Asia. *Biocontrol News and Information*, **31**, 10N–11N.
712 Wyckhuys KAG, Burra DD, Tran DH, Graziosi I, Walter AJ, Nguyen TG, Trong HN, Le BV, Le
713   TTN & Fonte SJ (2017a) Soil fertility regulates invasive herbivore performance and top-down
714   control in tropical agro-ecosystems of Southeast Asia. *Agriculture, Ecosystems and
715   Environment*, **249**, 38–49.
716 Wyckhuys KAG, Graziosi I, Burra DD & Walter AJ (2017b) Phytoplasma infection of a tropical
717   root crop triggers bottom-up cascades by favoring generalist over specialist herbivores. *PLoS
718   ONE*, **12**, e0182766.
719 Wyckhuys KAG, Rauf A & Ketelaar J (2015) Parasitoids introduced into Indonesia: Part of a
720   region-wide campaign to tackle emerging cassava pests and diseases. *Biocontrol News and
721   Information*, **35**: 29N–38N.
722 Yonow T, Kriticos DJ & Ota N (2017) The potential distribution of cassava mealybug
723   (*Phenacoccus manihoti*), a threat to food security for the poor. *PloS ONE*, **12**, p.e0173265.
724 Zeddies J, Schaab RP, Neuenschwander P & Herren HR (2001) Economics of biological control
725   of cassava mealybug in Africa. *Agricultural Economics*, **24**, 209-219.
726

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

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733

734 **Competing interests**

735

736 There are no competing interests.

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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 ± 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.
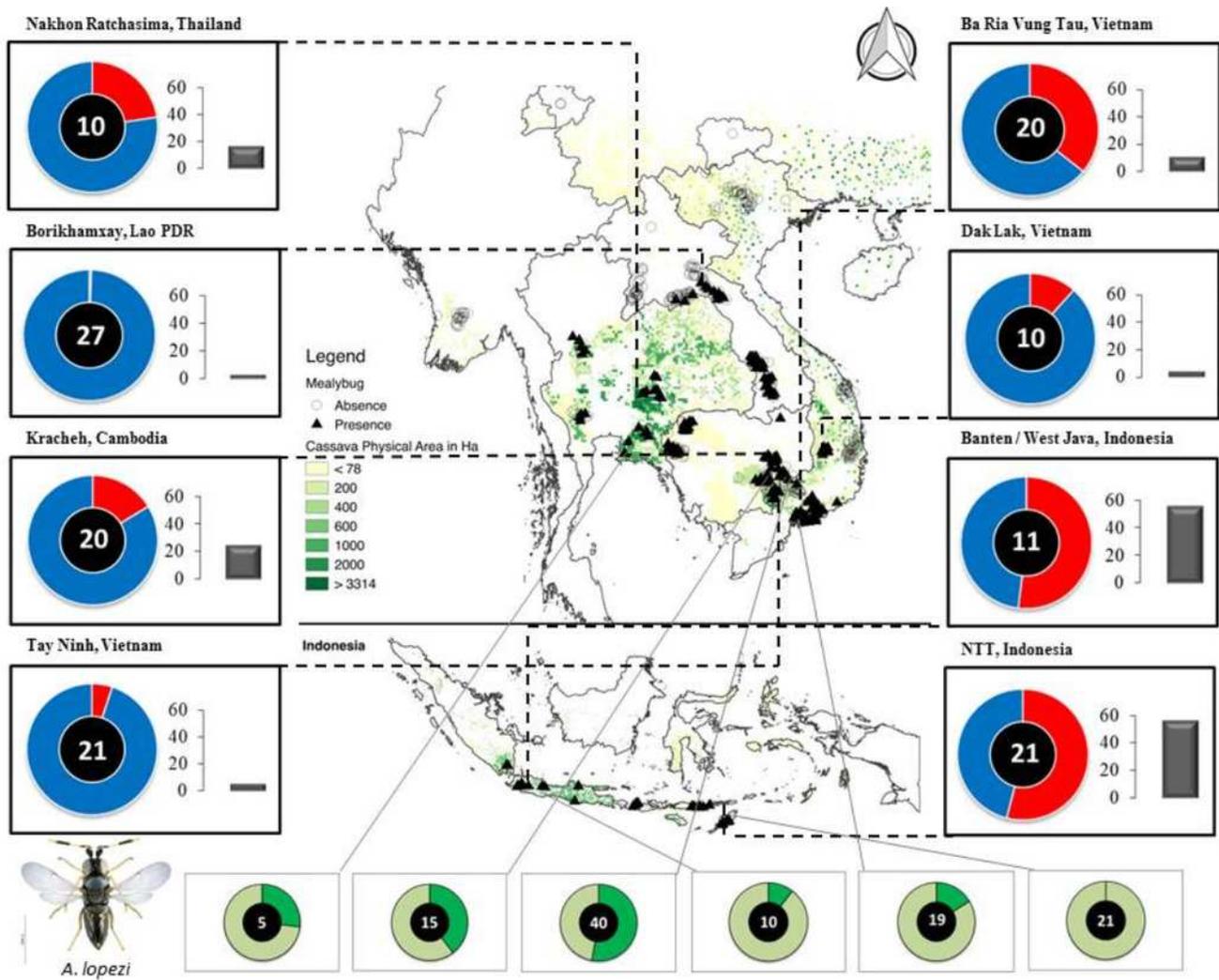
Figure 2

Bi-monthly mealybug population fluctuations in southern Vietnam, as contrasted with those in 1982 Nigeria.
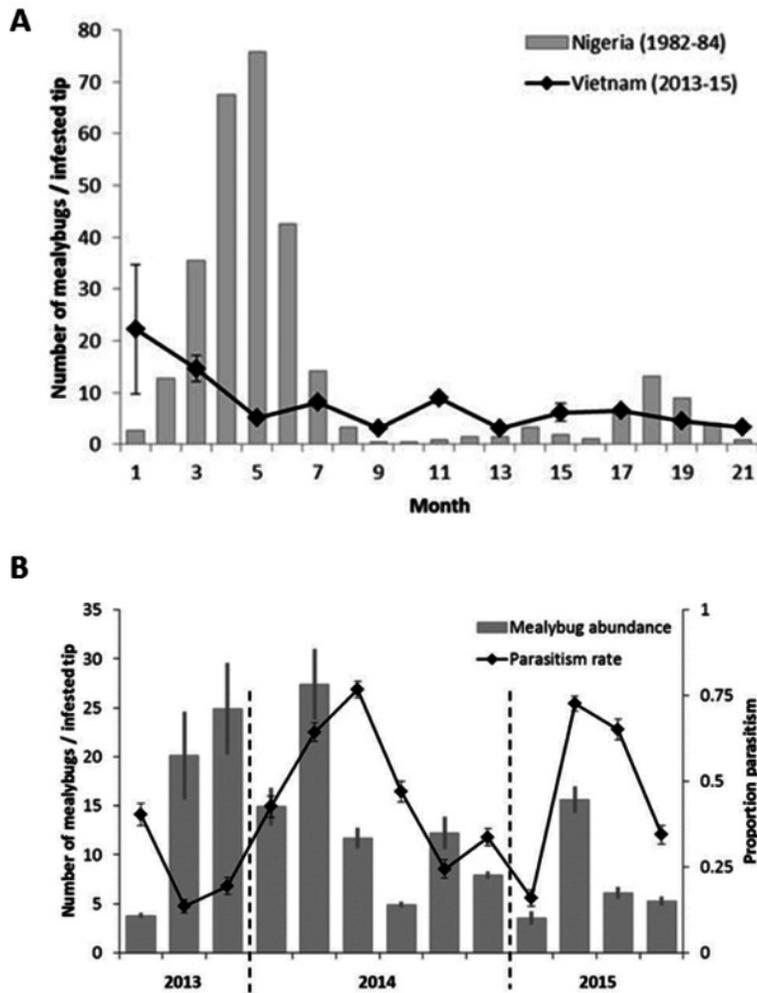
Figure 3

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.
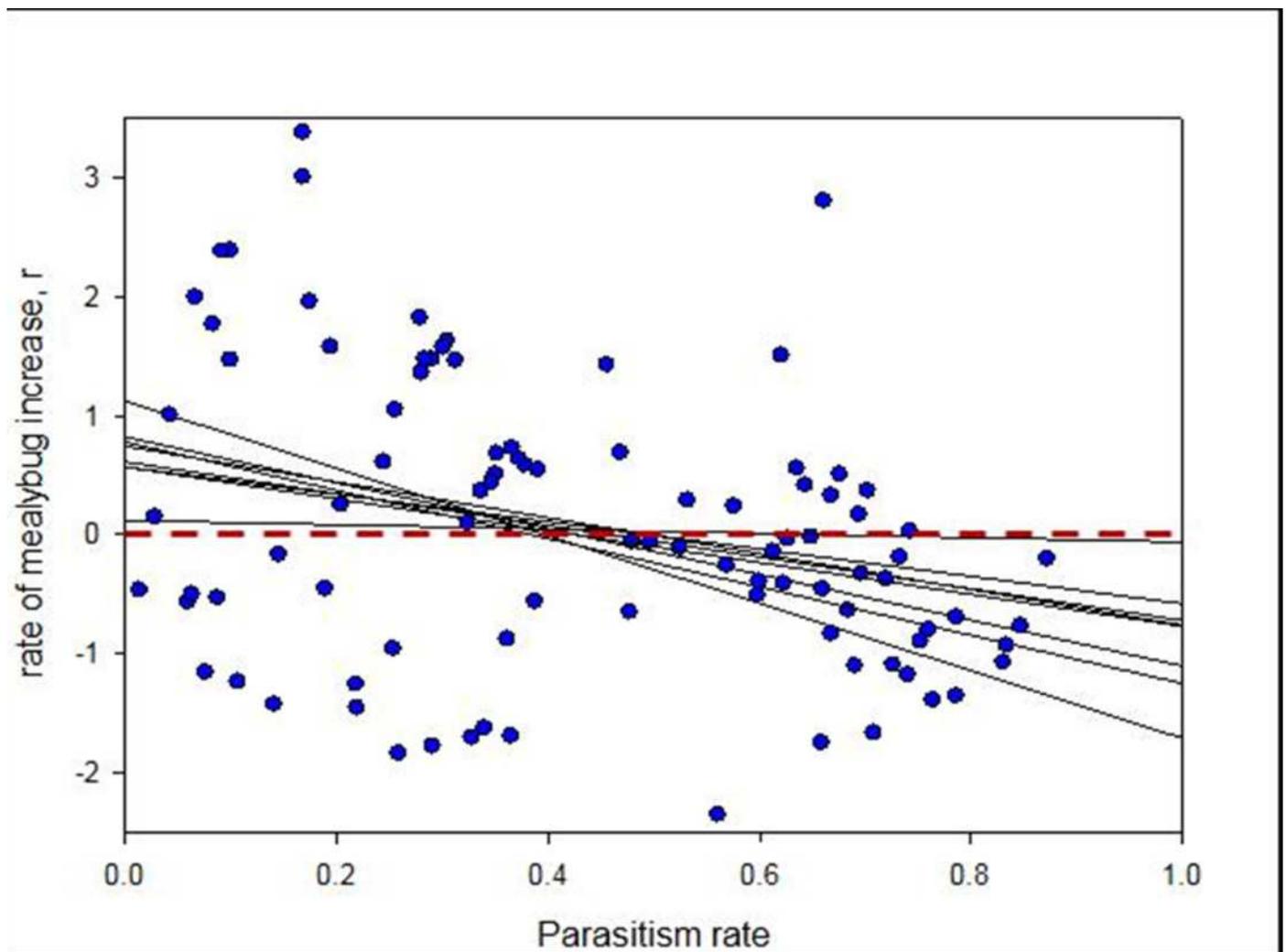
Figure 4

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 ± 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.
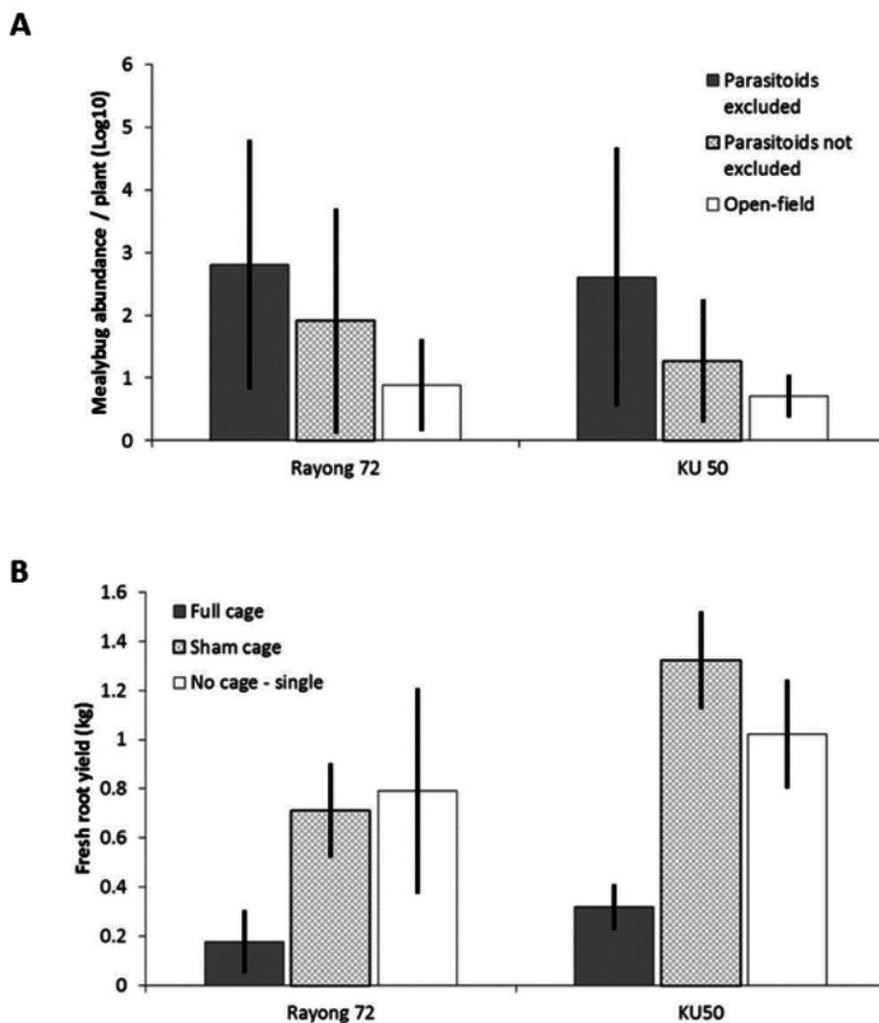
Figure 5

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.