1 **Natural vegetation benefits synergistic control of the three main insect and**

2 **pathogen pests of fruit crop in southern Africa**

3 **Dominic. C. Henri [1**]; Owen Jones*[1]; Ariana Tsiattalos* [1]; Elisa Thébault[2];**

4 **Colleen L. Seymour[3]; F. J. Frank van Veen[1]**

5 *these authors contributed equally to this paper

6 1. Centre of Ecology and Conservation, College of Life and Environmental Sciences,

7 University of Exeter, Penryn Campus, Penryn, Cornwall, TR10 9FE, UK

8 ** Current address: School of Biological, Biomedical & Environmental Sciences,

9 University of Hull, Hull, HU6 7RX, UK.

10 2. Institute of Ecology and Environmental Sciences - Paris, UMR 7618 (UPMC,

11 CNRS, IRD, INRA, UPEC, Paris Diderot), Université Pierre et Marie Curie, 7 quai St

12 Bernard, 75005 Paris, France

13 3. South African National Biodiversity Institute, Kirstenbosch Gardens, PVT Bag X7,

14 Claremont, 7735, South Africa

15

16 DCH is the corresponding author: email d.henri@hull.ac.uk; telephone 07719743511

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Summary

30 1   Most studies of the potential for natural habitat to improve agricultural productivity have been conducted in transformed, temperate regions, but little is known of the importance of agroecosystem services in biodiverse developing countries.

34 2   Natural vegetation may promote the density and/or diversity of natural enemies of crop pests, but the strength of the effect varies, and few studies directly measure concurrent impacts on pest density. Considering multiple pest species within the same agroecosystem may help explain why some pests are more affected than others by landscape complexity. Here, we investigated multiple pest species (leaf-galling flies, three species of Tephritidae fruit fly and pathogenic fungi *Fusarium spp.*) and their enemies in cultivated mango *Mangifera indica*, in North-Eastern South Africa.

42 3   The density of generalist Tephritidae fruit flies increased with distance from natural vegetation during harvesting months, and predation rate of pupae sharply decreased from ~50% at the edge with natural vegetation to 0% at 250m into the crop. Parasitism rates of the cryptic, gall-forming fly increased with proximity to natural vegetation but pest density was unrelated to distance from natural vegetation. Incidence of the fungal pathogen disease increased with distance from natural vegetation, possibly due to decreased predation of commensal mites.

49 4   Although the relationship with distance to natural vegetation was significant for all species considered, the strength of this relationship varied across pest species and type of natural enemy studied, suggesting the benefits of natural vegetation depends on each natural enemy species' ability to disperse into the agricultural environment.

54 5   *Syntheses and applications.* Our results suggest that natural vegetation is a net source of natural enemies in a region of South Africa that still contains much of its natural biodiversity. However, the decline in natural enemies, and increase in pests, with distance from natural habitat indicates that this biocontrol is limited by natural enemy dispersal. In landscapes like these that are still dominated by natural habitat, conservation biocontrol can still be improved by management aimed at providing corridors of key plants and habitat elements into to the crops, to facilitate natural enemy dispersal.

63   **Keywords**: agroecology, *Ceratitis*, conservation biological control, ecosystem
64   services, integrated pest management, mango malformation disease, natural
65   enemies, natural vegetation, pest control

66   **Introduction**

67   Native predators and parasitoids can contribute significantly to control of insect pest
68   populations, a process known as 'conservation biological control' (Thies *et al.* 2011).
69   The presence and state of local natural habitat could be instrumental in supporting
70   this ecosystem service, because species at higher trophic levels are generally more
71   sensitive to land-use intensity and habitat fragmentation than the insect pests they
72   attack (Chaplin-Kramer *et al.* 2011). A recent meta-analysis found a positive effect of
73   proximate natural/semi-natural vegetation on the intensity of pest suppression by
74   native predators and parasitoids (i.e., natural enemies; Veres *et al*. 2013). However,
75   natural enemy effectiveness can be unrelated to, or even negatively affected by,
76   proximate natural habitat (Macfadyen *et al.* 2009; Thies *et al.* 2011; Shackelford *et*
77   *al.* 2013), because natural enemy effectiveness is influenced by the crop type of the
78   agroecosystem, the geographic location and the ecology of both pest and natural
79   enemy.

80   To date, most studies relating land-use to pest suppression have been conducted in
81   developed, ecologically-transformed temperate regions, particularly Europe and
82   North America (Chaplin-Kramer *et al*. 2011; Shackelford *et al.* 2013; Veres *et al.*
83   2013). Therefore, the importance of natural habitat for ecosystem service provision
84   remains poorly understood where habitat complexity remains high (Tscharntke *et al.*
85   2012). In complex landscapes, natural vegetation harbours greater, more diverse
86   populations of service-providing species associated with greater agricultural yields
87   (Tscharntke *et al.* 2005; Bianchi *et al.* 2006). A recent review hypothesised that
88   ecosystem services in complex habitats (>20% untransformed) may be no stronger
89   than in simple habitats (1-20% untransformed), although the authors conceded this
90   may not apply outside of temperate ecosystems and called for more studies in high
91   diversity regions (Tscharntke *et al.* 2012). Ultimately, to provide predictive, trait-
92   based hypotheses linking landscape composition and biological control efficiency,
93   quantitative analyses of real systems from many different habitats and geographic
94   locations are required (Thies *et al.* 2011).

95   Our study system is situated within the subtropical, biologically-diverse Kruger to

96   Canyons Biosphere in South Africa, ~55% of which is intact vegetation, unimpacted

97   by human development (Mucina & Rutherford 2006; Coetzer *et al.* 2013). Our target

98   crop, mango *Mangifera indica* (L.) [Anacardiaceae], is economically important in the

99   region, and the dominant tropical fruit produced globally (FAO 2003). Previous

100   analysis of our study system found that productivity (kg of mangos per tree) declined

101   with distance from natural vegetation (Carvalheiro *et al.* 2010). This decline in yield

102   was only partly explained by concurrent reductions in pollinator diversity and density,

103   and we hypothesise that there is an additional effect of natural vegetation on pest

104   densities. There is a dearth of studies identifying the effect of proximate natural

105   vegetation on multiple pest and natural enemy species within the same

106   agroecosystem (Veres *et al.* 2013). Given that natural vegetation can be a source of

107   pests and natural enemies, it is important to evaluate both pest densities and natural

108   enemy activity to ascertain the net effect of natural vegetation on conservation

109   biological control (Chaplin-Kramer & Kremen, 2012).

110   Natural vegetation may benefit natural enemies by increasing local habitat

111   heterogeneity or by acting as a population reservoir that increases local density and

112   resistance to environmental stochasticity (Macfadyen *et al.* 2011). Landscape

113   complexity may also benefit natural enemies by providing food sources (e.g. pollen,

114   nectar, & protein and lipids from other insects) or by providing shade and shelter

115   (Heimpel & Jervis 2005). Reservoirs of predators and parasitoids in natural

116   vegetation are only effective if individuals can disperse to the target pests (Hossain

117   *et al.* 2002; Werling & Gratton 2010). Similarly, vegetation that provides shelter or

118   nutrition is only beneficial to pest control if it is sufficiently close to target pest

119   populations (Vollhardt *et al.* 2010). Thus, with increasing distance into agricultural

120   fields, natural enemy density and diversity should decrease, resulting in reduced

121   pest control. This effect could have contributed to the productivity declines found in

122   Carvalheiro *et al.* (2010).

123   Herein, we consider the effect of proximity to natural vegetation on the conservation

124   biological control of two types of Dipteran pest and a fungus on cultivated mangos .

125   We consider a suite of closely-related Tephritidae fruit flies (*Ceratitis spp.*), the non-

126   native Mango leaf-gall-forming fly *Procontarinia matteiana* and a pathogenic fungus

127   *Fusarium sp.*. Using these three pest types, whose control depends upon different

128   groups of natural enemies, we ask (i) does the density of these pests/pathogens
129   increase with distance from natural vegetation, and (ii) for the insect pests, does this
130   correspond to a decline in natural enemy action with distance from natural
131   vegetation?

132

133   **Methods**

134   *Field site*

135   We carried out pest, pathogen and natural enemy surveys on sections of a mango
136   farming estate (~2km^2 in size) bordering large areas of natural vegetation that are
137   occasionally grazed by cattle. The vegetation type in this area is "Granite Lowveld"
138   savanna, dominated by large *Acacia (Senegalia) nigrescens* (Oliver) [Fabaceae] and
139   *Sclerocarya birrea* (A.Rich) [Anacardiaceae] (Mucina & Rutherford 2006).

140   The estate is split into blocks of mango trees, each ~70 x 150 m block contains trees
141   of a single cultivar, within a grid of non-native *Casuarina sp.* trees serving as
142   windbreaks. Pest, pathogen and natural enemy surveys were conducted across
143   multiple blocks bordering the natural vegetation; see below for detailed methods.
144   Natural vegetation is separated from the crop by narrow paths and the windbreak; so
145   the nearest mango trees are ~20 m from the natural vegetation edge. Within mango
146   blocks, the herbaceous cover is dominated by non-native agricultural weeds (e.g.
147   *Tridax procumbens* (L.) and *Bidens pilosa* (L.) [Asteraceae]).

148   *Study species and their surveillance*

149   *1. Tephritidae fruit flies* (Ceratitis spp.)

150   Locally, mangos are infested by three closely-related *Ceratitis* species: the Marula fly
151   *C. cosyra* (Walker), the Mediterranean fly *C. capitata* (Wiedemann), and the Natal fly
152   *C. rosa* (Karsch). Tephritid fruit flies are considered the most economically important
153   insect pest of mango globally (Chin *et al.* 2010). Females lay eggs under the fruit's
154   skin. The larvae eat the flesh and pupate in the soil. Larvae are vulnerable to
155   parasitoid wasps, whereas the sessile pupae are vulnerable to generalist predators
156   (Chin *et al.* 2010; Ovruski *et al.* 2000). Natural vegetation could be a source of
157   *Ceratitis* and their natural enemies, as all three *Ceratitis* spp. are polyphagous (see

158   De Meyer *et al.* 2002). Estate employees surveyed *Ceratitis* spp. density over four

159   mango fruiting seasons (December-April, 2009-2013), using 29 Sensus™ adult fly

160   traps containing Capilure™ (River Bioscience Ltd, Port Elizabeth, SA). Single traps

161   were placed in alternate blocks of mango trees and monitored/reset every two

162   weeks. Traps were placed 80m (n=9), 240m (n=7), 400m (n=6) & 560m (n=7) away

163   from the mango-natural vegetation boundary. Traps were used in 8 cultivars with

164   their relative representation reflecting the estate as a whole (Kent: 16; Tommy Atkins

165   (TA): 9; Sensation: 8; Heidi: 4; Keitt: 4; Joa: 1; Manzanillo: 1; Shelly:1). To test for

166   the effect of natural vegetation on adult fly density, we performed a Generalised

167   Linear Mixed Effect Model (GLMM) with the following structure:

168   *Total fly count per trap ~ Distance of trap from natural vegetation * Month of survey +*

169   *(1+Distance| Year / Month) + (1| Block number) + (1| Cultivar of block) +*

170   *(1| Observation level factor), family = poisson.*

171   An observation-level random factor was included to account for high levels of extra-

172   poisson variance associated with count data (Harrison 2014).

173   We reared *Ceratitis* clutches from mangos from 12 different tree blocks between

174   March and April, 2013 (n=64; 33 'ripe', 31 'unripe'); obtaining at least 5 mangos in

175   every 25m band (e.g. 0-25, 25-50, etc.) up to a distance of 300m from the mango-

176   natural   vegetation   boundary   (measured   using   Garmin   eTrex10®   GPS

177   device, Southampton, UK). Mangos were stored in separate, perforated plastic bags

178   with a portion of sand. Bags were checked daily for fly pupae for two weeks following

179   mango collection. Pupae were separated into eppendorf tubes (with small holes for

180   air-flow) and monitored for one month after pupation; eclosing flies or parasitoids

181   were recorded and identified. Pupae which failed to eclose within a month were

182   presumed dead, either due to parasitism or other causes; proportion of pupae failing

183   to eclose was calculated on a 'per mango' basis. We considered mango ripeness as

184   a fixed effect in our analyses as studies have shown fruitfly parasitoids prefer ripe

185   mangos (Eben *et al.* 2000). Ripeness was assessed by the predominant colour of

186   the mango at collection; ripe mangos were ≥50% orange and unripe mangos >50%

187   green. To test for an effect of distance to natural vegetation on proportion of fly

188   larvae successfully becoming adults, we performed a GLMM using the following

189   structure:

190 *Proportion of pupae eclosed per mango ~ Host mango distance from natural*
191 *vegetation * Host mango ripeness + (1| Day of mango collection) +*
192 *(1+Distance| Block) + (1| Observation level factor), family = binomial.*

193 We placed cohorts of eight fly pupae at 300, 150 and 10m into natural vegetation,
194 and 250, 150 and 10m into the estate, from the border between the two
195 environments. Cohorts were placed along three parallel transects running
196 perpendicular to the border between April and May, 2013. The study ran for three
197 weeks with one cohort being placed at each transect point each week, totalling three
198 cohorts per transect point (n=48). For each cohort, we recorded the proportion of
199 pupae that survived for 48 hrs. Pupae were considered predated if they were missing
200 upon return or showed obvious signs of feeding damage. We collected samples of
201 predators if predation was observed. All observed predators were ants, which were
202 identified by Caswell Munyai (University of Venda). To test for the effect of distance
203 from the natural/agricultural environment border on fruitfly pupae predation, we
204 performed a GLMM using the following structure:

205 *Proportion of cohort predated ~ Distance of cohort from border + (1+Distance| Date)*
206 *+ (1+Distance| Transect) + (1| Observation level factor), family = binomial.*

2. Mango leaf gall fly (Procontarinia matteiana)

208 Mango leaf gall fly *Procontarinia matteiana* (Kieffer and Cecconi), lays eggs on
209 young mango leaves, the larvae bore into the leaf tissue, creating leaf-galls in which
210 the larvae pupate to emerge as adults (Mahmood, Mahmood & Razaq 2013). The
211 gall fly appears to be primarily controlled by the specialist parasitoid *Chrysonotomyia*
212 *pulcherrima* (Kerrich) (Waite 2002). In the absence of the parasitoid, high gall fly
213 densities cause substantial reductions in mango crop (Augustyn *et al.* 2013). There
214 is no documented evidence of *P. matteiana* persisting on native vegetation in South
215 African savanna, nor records of native natural enemies attacking the gall fly.

216 We collected mango leaves across four parallel transects running perpendicular to
217 the border between natural and managed environments, two transects each within
218 the cultivars Kent and TA. Leaves were collected at distances of 0, 10, 50, 100 &
219 200 m from natural vegetation between March and June 2013. At each distance, we
220 surveyed two leaves below head-height and two above from the same tree. We

221   accounted for gall age by picking leaves with at least five galls exhibiting a
222   characteristic dark spot without signs of insect eclosure (4-10 weeks old [Augustyn *et*
223   *al.* 2013]). Leaves were randomly chosen until the requisite numbers fulfilling sample
224   criteria were obtained. Leaves were frozen for 24hrs before data collection. Number
225   of galls on each leaf was recorded and five randomly-chosen galls were dissected.
226   The contents were classified as either: *C. pulcherrima*, *P. matteiana*, or
227   Unidentifiable. To test for an effect of natural vegetation on gall fly infestation, we
228   performed a GLMM with the following structure:

229   *Sum gall count on two leaves ~ Distance of tree from natural vegetation * Cultivar +*
230   *(1+Distance|Date collected) + (1+Distance|Leaf height) + (1+Distance|Transect) +*
231   *(1| Observation level factor), family = poisson.*

232   To test for an effect of natural vegetation on gall fly parasitism, we performed a
233   GLMM with the following structure:

234   *Proportion galls containing parasitoids per tree ~ Distance of tree from natural*
235   *vegetation * Cultivar + (1+Distance|Date collected) + (1+Distance|Transect) +*
236   *(1| Observation level factor), family = binomial.*

3. Pathogenic mango malformation fungus (Fusarium sp.)

238   Mango malformation disease (MMD), caused by one or more fungi in the genus
239   *Fusarium, is* of growing concern: infection is irreversible and it has now been
240   described in most mango-growing countries (Chakrabarti 2011). Mango flowers are
241   small and occur in large numbers within inflorescences. The disease causes
242   malformed inflorescences, which do not fruit; yield losses up to 86% have been
243   recorded (Chakrabarti 2011).

244   In August 2013, we surveyed five parallel transects running perpendicular from the
245   natural vegetation boundary ~300 m into mango; each transect was in a different
246   block of cultivar Kent. Within each transect, eight mango trees were selected at
247   distances of 5, 9, 15, 27, 51, 99, 195 and 303 m from the edge. For each tree, total
248   number of inflorescences and number of malformed inflorescences were counted.
249   Only inflorescences displaying the typical cauliflower appearance of advanced MMD
250   were scored as malformed. To test for an effect of natural vegetation on MMD
251   severity, we performed a GLMM using the following structure:

252   *Proportion of malformed inflorescences per tree ~ log Distance from natural*

253   *vegetation + (1+logDistance|Transect number), family = binomial.*

254   **Statistics**

255   All Generalised Linear Mixed Effect Models (GLMM) were performed in R (R Core

256   Team 2014) using glmer in the lme4 package (Bates *et al*. 2014). Initial exploration

257   to assess GLMM assumptions were performed following guidelines in Zuur *et al*.

258   (2010). Prior to analyses we assessed the data for collinearity using pairwise

259   scatterplots to assess fixed effect correlations >0.7 (Dormann *et al*. 2013). Random

260   slope analyses were used for transect effects due to high type I error rates of GLMM

261   random intercept analyses, where distance effects were unlikely to be consistent

262   between transects (Barr *et al*. 2013). The Minimum Adequate Model was established

263   via log-likelihood ratio comparisons using Maximum Likelihood approximation, for

264   which X^2 results indicating significance are reported; fixed effect parameters were

265   estimated using Restricted Maximum Likelihoods. GLMM models account for

266   pseudoreplication in time and space, where survey dates and locations were

267   included as random effects (Bates 2010). Observation level random factors were

268   included to account for overdispersion, identified by greater than expected variation

269   with all models, and to improve R^2 estimation accuracy (Harrison 2014). Poisson

270   error structures were used for count data and binomial error structures for proportion

271   data. We also assessed variance explained by the models, reporting marginal R^2

272   values for fixed effects alone and conditional R^2 for both fixed and random effects

273   (Johnson 2014).

274

275   **Results**

276   **i) Does the density of pests/pathogens increase with distance from natural**

277   **vegetation?**

278   *Tephritid fruit flies*

279   Multi-year trapping suggested that the relationship between adult fly counts and

280   distance from natural vegetation varied significantly with month, with fly density

281   decreasing with distance from natural vegetation in December (slope= -0.00063x)

282   and January (-0.00065x), the reverse being true in February (0.00020x), March

283   (0.00033x) and April (0.00035x) (X^2_5 = 16.644, P < 0.01; R^2 marginal = 0.08; R^2

284   conditional = 0.83; Fig 1).

285   *Mango leaf gall fly*

286   Gall counts per tree were not significantly related to distance from natural vegetation

287   (X^2_1 = 1.39, P = 0.24; Fig 2a). However, there were significantly more galls on TA

288   than Kent trees (X^2_1 = 11.25, P < 0.001; R^2 marginal = 0.18; R^2 conditional = 0.24;

289   Fig 2b).

290   *Pathogenic fungi* (Fusarium *spp.*)

291   The proportion of malformed inflorescences per tree increased with distance from

292   natural vegetation (X^2_1 = 10.61, P = 0.001; R^2 marginal = 0.28; R^2 conditional = 0.34;

293   Fig 3). Only one of the 40 trees surveyed exhibited no MMD; on average 17% of

294   inflorescences were malformed.

295   **ii) Does mortality of dipteran pests decline with distance from natural**

296   **vegetation?**

297   *Successful tephritid fruit fly emergence*

298   The proportion of pupae not eclosing decreased with distance from natural

299   vegetation in green (unripe) mangos, the opposite was true in orange (ripe) mangos

300   (interaction term; X^2_1=8.72, P < 0.01; R^2: marginal = 0.21, conditional = 0.52; Fig

301   4). The negative relationship between distance and fly mortality in unripe mangos

302   was ~three times as steep as the positive effect of distance for ripe mangos,

303   suggesting the distance effect was stronger on larvae in unripe mangos.

304   *Predation of tephritid pupae placed in soil*

305   Mortality rates of fly pupae were highest in natural vegetation and lowest in mango,

306   and intermediate at the border between the two environments (X^2_1=9.97, P = 0.001;

307   R^2: marginal = 0.51, conditional = 0.92; Fig 5). *Pheidole cf megacephala* (big-headed

308   ant), was the only visually verified predator.

309   *Mango leaf-gall fly*

310   Rates of gall parasitism were significantly lower in trees further from natural

311   vegetation (X^2_1 = 6.69, P < 0.01; R^2 Marginal = 0.07, R^2 Conditional = 0.42; Fig 6),

312   but did not vary between Kent and TA cultivars (X^2_1 = 2.21, P = 0.14).

313

314   **Discussion**

315   **Biological control services provided by natural vegetation in this study**

316   **system.**

317   This is one of the few studies considering 'conservation biological control' of multiple

318   pest and natural enemy species in the same study system simultaneously, and the

319   only one performed in a relatively untransformed, biodiverse subtropical region

320   (Chaplin-Kramer *et al*. 2011). Our results suggest that natural vegetation

321   characteristic of 'Granite Lowveld' provided a net positive pest control service to

322   mango growers, that was significantly reduced by ~200m into the crop (average

323   pest mortality was 25-80% lower compared to the edge). Across studied pest,

324   predator and pathogen species in this study, benefits declined with distance from

325   natural vegetation, supporting hypotheses that beneficial ecosystem services are

326   limited by dispersal distance from source vegetation (Hossain *et al.* 2002; Werling &

327   Gratton 2010). Similar studies performed in temperate countries suggest that

328   benefits of natural vegetation dissipate by ~80 m into the agricultural environment

329   (Collins *et al.* 2002; Thomson & Hoffman, 2013); compared to 200 m herein. It is

330   unclear whether this difference is because of the limited spatial scale considered in

331   prior studies or because of greater immigration by service providing organisms into

332   agroecosystems in high complexity landscapes (Bianchi *et al.* 2006). Tscharntke *et*

333   *al.* (2012) hypothesised that conservation management practices are less effective

334   in high complexity regions; however, strong dispersal limitation could explain

335   potential for natural vegetation patches within crops to improve ecosystem service

336   provision (Carvalheiro *et al.* 2012).

337

338   In this study, we observed distance-dependent effects of natural vegetation on

339   mortality and infestation severity by pests known to cause significant reductions in

340   mango yields, which could account for declines beyond those associated with

341 pollination loss (Carvalheiro *et al*., 2010). However, as observed in prior studies,
342 there was significant variability in the strength of the effect of natural vegetation
343 across study species (Chaplin-Kramer *et al.* 2011; Thies *et al.* 2011; Shackelford *et
344 al.* 2013). Below, we discuss possible mechanisms behind distance effects in each
345 focal species.

346 **Tephritid Fruit Flies (*Ceratitis spp.*)**

347 Natural vegetation can be a source of both pests and natural enemies (Chaplin-
348 Kramer & Kremen, 2012; MacFadyen & Muller 2013). *Ceratitis spp*. use a wide
349 range of native species as host plants (De Meyer *et al*. 2002). Early in mango
350 harvesting season (December and January) we observed higher densities of adult
351 flies close to natural vegetation (Fig. 1). This suggests that host plants within natural
352 vegetation may provide nursery sites for *Ceratitis spp.* outside the mango growing
353 season. Pest population increases generally preceed significant natural enemy-
354 driven mortality (Chaplin-Kramer & Kremen, 2012; MacFadyen & Muller 2013). Later
355 in the season (February, March and April) adult fly counts were lower closer to
356 natural vegetation (Fig 1). In March and April, juvenile fly mortality was greater near
357 natural vegetation (Figs 4 & 5); suggesting that natural enemies could have driven
358 this negative relationship between proximity to natural vegetation and adult fly
359 density. Across all months, mean fly counts increased with distance from natural
360 vegetation (Table 1), suggesting that, on balance, natural vegetation favours natural
361 enemies over Tephritidae pest populations as predicted elsewhere (Chaplin-Kramer
362 *et al*. 2011). The relatively shallow slopes for adult fly count with distance could have
363 arisen because of the high number of zero-values (counts where there were no flies)
364 which reduced average fly-count, thus underestimating the strength of distance
365 effects. Alternatively, shallow slopes could indicate a weak effect of natural
366 vegetation on fly density or an effect that was only weakly limited by dispersal.

367 The effect of proximity to natural vegetation on mortality of larvae and pupae reared
368 under controlled conditions could have been caused by parasitoids prior to collection
369 of fruits from orchards. After collection, all fruit, larvae and pupe were treated
370 identically. Parasitoid wasps ovipositing in *Ceratitis spp*. larvae are well documented
371 (Ovruski *et al.* 2000); however, we only reared a single, Opinine parasitoid wasp
372 during the study. This may be because parasitoid development generally takes

373   longer (Courtney Moxley, personal communication, February 2015), extending

374   beyond our field season or, alternatively, that larval and pupal mortality was caused

375   by a currently unknown agent (e.g., a pathogen). Greater pupal predation in natural

376   vegetation compared to within the crop suggests that highly effective natural

377   enemies within natural vegetation could not inhabit crop fields despite prey being

378   available. *Pheidole cf megacephala* was the only predator observed, seen carrying

379   study pupae away on multiple occasions. Although we found consistent effects of

380   natural vegetation on pest mortality, few causative agents were identified, limiting

381   conclusions on the relative importance of natural enemy density or biodiversity

382   (Tscharntke *et al*. 2005). This gap highlights the need for network ecology analyses

383   that identify key biological control agents and the habitat features that aid their

384   dispersal into agricultural environments.

385

386   **Mango Leaf Gall fly *Procontarinia matteiana***

387   Benefits of natural vegetation tend to be much weaker for specialist (e.g.,

388   parasitoids) than generalist natural enemies (Chaplin-Kramer *et al.* 2011; Rand *et al.*

389   2012). This may partly be because specialist natural enemies are less likely to have

390   population reservoirs in the natural environment, particularly if the preferred

391   prey/host is a specialist feeder itself (Shackelford *et al.* 2013). However, parasitism

392   rates of mango leaf gall fly by its parasitoid were significantly higher closer to natural

393   vegetation despite there being no records of the pest or the parasitoid persisting on

394   species other than mango (Fig 6). Increased parasitism closer to natural vegetation

395   may have resulted from direct provisioning effects; for example, flowers provide

396   nectar and pollen for local parasitoids, increasing their longevity and parasitism rates

397   (Heimpel & Jervis 2005). We did not find a concurrent, significant effect on gall

398   density (Fig 2), either because the effect of increased parasitism was too weak to

399   affect local gall fly populations, or because of population effects of high local

400   parasitism being evenly distributed over the area through fly dispersal.

401   Whereas landscape complexity is generally correlated with natural enemy density, its

402   effect on pest density is far more variable (Chaplin-Kramer *et al.* 2011; Veres *et al.*

403   2013). Our study, in conjunction with others, suggests two pest traits that may be

404   important. Firstly, densities of pest species primarily controlled by a single, relatively

405   specialist natural enemy, such as *P. matteiana* and *Empoasca vitis* in viticulture

406   systems, were not reduced by the presence of proximate semi-natural vegetation

407   (Van Helden, Pain & Pithon 2008). This is despite positive effects on respective

408   natural enemies, *C. pulcherrima* in this study and *Trichogramma spp.* in viticulture

409   systems (Thomson & Hoffman, 2010). Similarly, studies of other pest species

410   controlled by few natural enemy species, such as cereal aphids, find little evidence

411   of benefits to control associated natural enemy diversity (MacFadyen *et al.* 2009).

412   Comparatively, pest species attacked by multiple natural enemies (e.g., *Ceratitis*

413   spp. in this study), are more prone to control associated with biodiverse systems,

414   where natural enemy complementarity and redundancy are supported by proximate

415   natural vegetation, and thus associated with reduced pest density (Tscharnkte

416   2005). Secondly, densities of hidden pest species, for which there may be fewer

417   potential natural enemy species, such as *P. matteiana* herein or stem-weevils

418   *Ceutorhynchus spp.* in oil-seed rape, do not respond to natural vegetation proximity

419   (Zaller *et al.* 2008). Further studies of multiple pests within the same study system

420   whose control is dependent upon a broad or narrow range of enemies is required to

421   elucidate the degree to which biodiversity could explain variation in response of pest

422   species to landscape complexity (Chaplin-Kramer *et al.* 2011; Veres *et al.* 2013).

423

424   Mango Malformation Disease *Fusarium spp*.

425   Severity of mango malformation disease (MMD) increased significantly with distance

426   from natural vegetation. The percentage of malformed inflorescences increased from

427   10% on mango field edges to ~40% at 250m into the crop (Fig 3). Spread of the

428   disease within estates is thought to occur via cutting (Kumar, Singh & Beniwal 1993)

429   but severity of MMD has also been shown to correlate with density of mango bud

430   mite *Aceria mangiferae* (Sayed) (Gamliel-Atinsky *et al.* 2010; Lindquist, Sabelis &

431   Bruin 1996). It is possible that predators originating from natural vegetation reduce

432   *A. mangiferae* density, reducing severity of MMD closer to natural vegetation; the

433   likelihood of which should be the subject of further study. MMD is a growing problem

434   globally (Chakrabarti 2011) and was a topic of concern during personal

435   communication with local farmers. We found that over a third of inflorescences

436   (maximum ~60%) were infected at ~250m into the agricultural environment. Because

437   we only scored severe advanced stages of malformation these figures are likely an

438   underestimation.

439   **Factors other than proximity to natural vegetation**

440   Average variance in pest or natural enemy presence explained by distance effects in

441   this study was 22%. Spatial and temporal influences were marked, given that

442   random factors (which captured position and date) explained a further 27% of the

443   variation. This may be because ecosystem service provision often originates from a

444   particular or small group of species or microhabitats (Bianchi & Wäckers 2008; De

445   Meyer *et al*. 2002), which are not ubiquitous or uniformly dispersed spatially or

446   temporally within the natural environment. Thus, some of the variance explained by

447   spatial and temporal random effects may have arisen from unequal distances to key

448   plant species, which occur at different densities and change over the season,

449   because of differing phenologies. We would also expect some spatial and temporal

450   autocorrelation associated with pest population dynamics and dispersal. *Fusarium*

451   *spp.*, which cause MMD, is particularly slow spreading, and its incidence (not

452   severity) may exhibit strong spatial aggregation (Gamliel-Atinsky *et al.* 2010).

453   We found a significant effect of tree cultivar on mango leaf gall fly infestation,

454   corroborating previous studies (e..g. Augustyn *et al*. 2013). Different cultivars also

455   flower and fruit at different times of year, altering spatial aggregation of

456   pests/pathogens and natural enemies, and we found a significant effect of month on

457   the relationship between natural vegetation proximity and adult fruit fly density (Fig

458   1). We tried to limit our investigations to the Kent cultivar and have included tree

459   cultivar as a random or independent model variable when this was not possible.

460   However, there may be additional effects unaccounted for, such as type of cultivar in

461   adjacent blocks.

462   **Limitations and future studies**

463   All of our data were collected on a single but sizeable (~ 2km^2) estate bordering a

464   large area of natural vegetation. We used GLMMs including date and position as

465   random effects to account for repeated transect sampling, and future extension of

466   this work over more estates and a wider geographic range are required to test the

467   generality of our results. At present we cannot distinguish whether weak distance

468 effects were due to weak effects of natural vegetation or lack of dispersal limitation.
469 Future studies could address this by quantifying effects of species mobility on the
470 interaction between natural and managed environments.

471

472 **Conclusions**

473 Our findings suggest that part of the decline in mango productivity with distance
474 from natural vegetation that cannot be explained by declines in pollination alone
475 (Carvalheiro *et al*. 2012) are attributable to changes in densities of adult *Ceratitis*
476 *spp*. during key mango harvesting months, and severity of Mango Malformation
477 Disease; both of which impact mango productivity (Chakrabarti, 2011; Chin *et al.*
478 2010). This corroborates previous studies suggesting that natural vegetation is only
479 important within an effective distance and that the scale of habitat structure is
480 important in determining ecosystem service strength (Hossain *et al.* 2002;
481 Tscharntke *et al*. 2005; Bianchi & Wäckers 2008; Werling & Gratton 2010).

482 It has been hypothesised that management aimed at generally increasing
483 biodiversity conservation will have little impact on the ecosystem service of pest
484 control in complex landscapes with high proportion of intact biodiversity (Tschartke *et*
485 *al.* 2012). However, our results indicate that in such landscapes, conservation
486 biocontrol is limited by natural enemy dispersal and can be improved by providing
487 corridors of key plants and habitat elements in crop fields to facilitate movement into
488 fields.

489 **Acknowledgements**

498

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631

632

633 Table 1. Average and standard error of *Ceratitis* spp. fly counts across all blocks,

634 months and years.

Distance from natural vegetation (m)	80	240	400	560
Mean adult count (+/- s.e.)	1.62 (+/- 0.09)	1.77 (+/- 0.12)	2.19 (+/- 0.15)	2.24 (+/- 0.14)

635

636

637　**Fig legends**

638　**Fig 1.** Counts of all adult *Ceratitis spp.* flies caught in Census™ traps against
639　distance from the natural/agriculture environment border. Data are separated
640　according to month of collection to illustrate the interaction between month and
641　distance. Lines illustrate median values +/- 1s.d. Equations are poisson glm fits of
642　median values.

643　**Fig 2.** (a) Leaf gall counts per tree against the log(distance) of the tree from natural
644　vegetation. (b) Leaf gall counts per tree for each cultivar studied.

645　**Fig 3.** Proportion of inflorescences per mango tree that exhibited pathogenic flower
646　malformation against the log(distance) of the tree from natural vegetation. Lines and
647　equations illustrate model best fit +/- 1s.e.

648　**Fig 4.** Proportion of reared *Ceratitis* pupae not eclosing against the distance of the
649　host mango from natural vegetation, for (a) ripe and (b) unripe mangos. Lines and
650　equations illustrate model best fit +/- 1s.e. Point size is weighted by log(number of
651　pupae collected from sampled mangoes).

652　**Fig 5.** Proportion of *Ceratitis* pupae predated within 48 hrs against distance from the
653　natural/agriculture environment border. Negative distances represent distance into
654　natural vegetation and positive ones indicate distance into the estate. Lines illustrate
655　model best fit +/- 1s.e. Point size is weighted according to the number of points at
656　that value; i.e. number of cohorts for which that particular proportion of pupae were
657　predated at that distance across all replicates and transects.

658　**Fig 6.** Proportion of parasitised galls per tree against the log(distance) of the tree
659　from natural vegetation. Lines and equations illustrate model best fit +/- 1s.e.

660

661
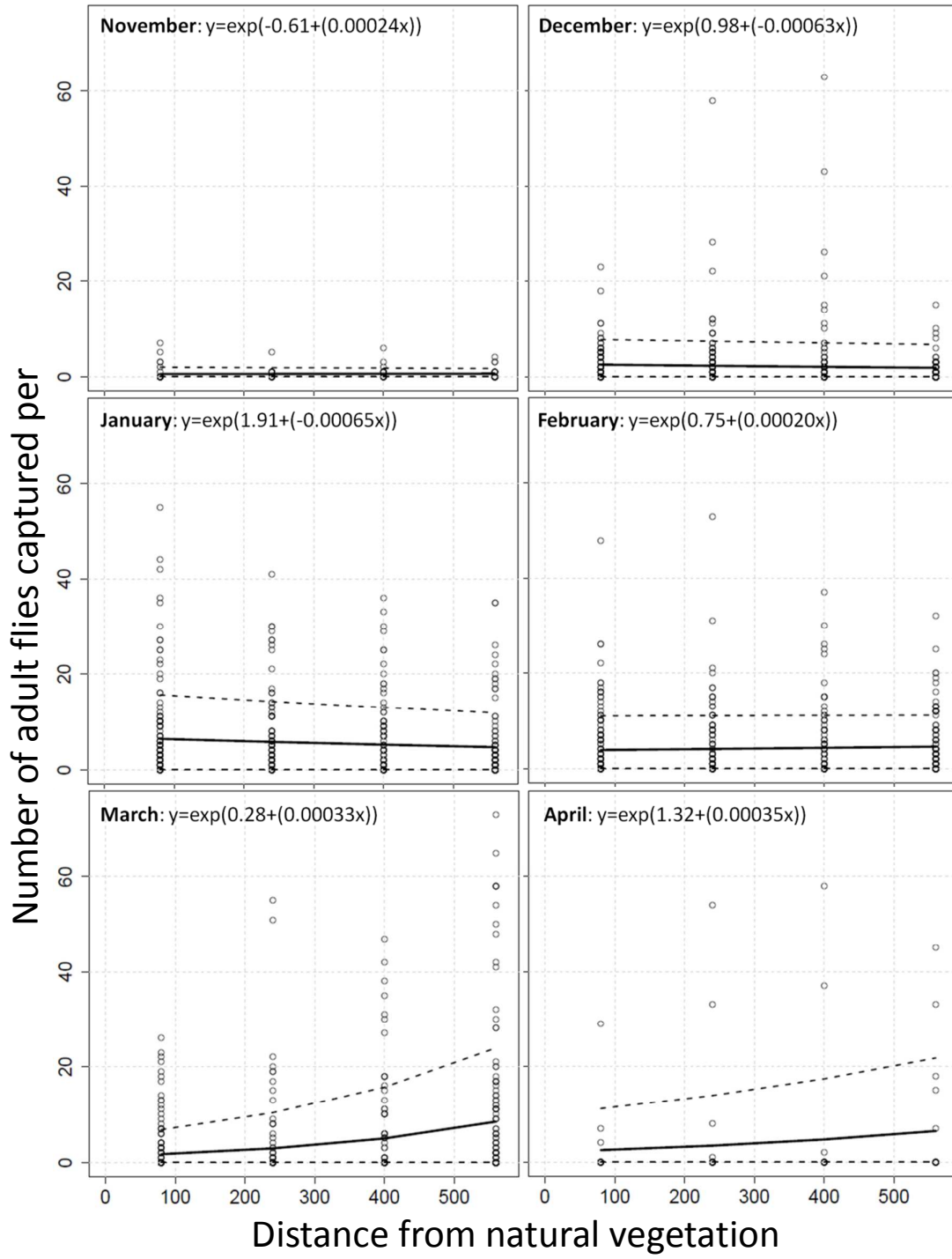
662

663   Fig 1

664

665   Fig 2

$y = 1/(1+1/exp(-3.19 + 0.47x)$

666
667   Fig 3

668

(a)   y = 1/(1+1/exp(-0.80 + 0.0037x)

(b)   y = 1/(1+1/exp(1.13 + -

Proportion of larvae failing to pupate

Distance from natural vegetation (m)

669

670   Fig 4

671
672   Fig 5.

$$y = 1/(1+1/exp(-0.89 - 0.18x))$$

673
674   Fig 6.
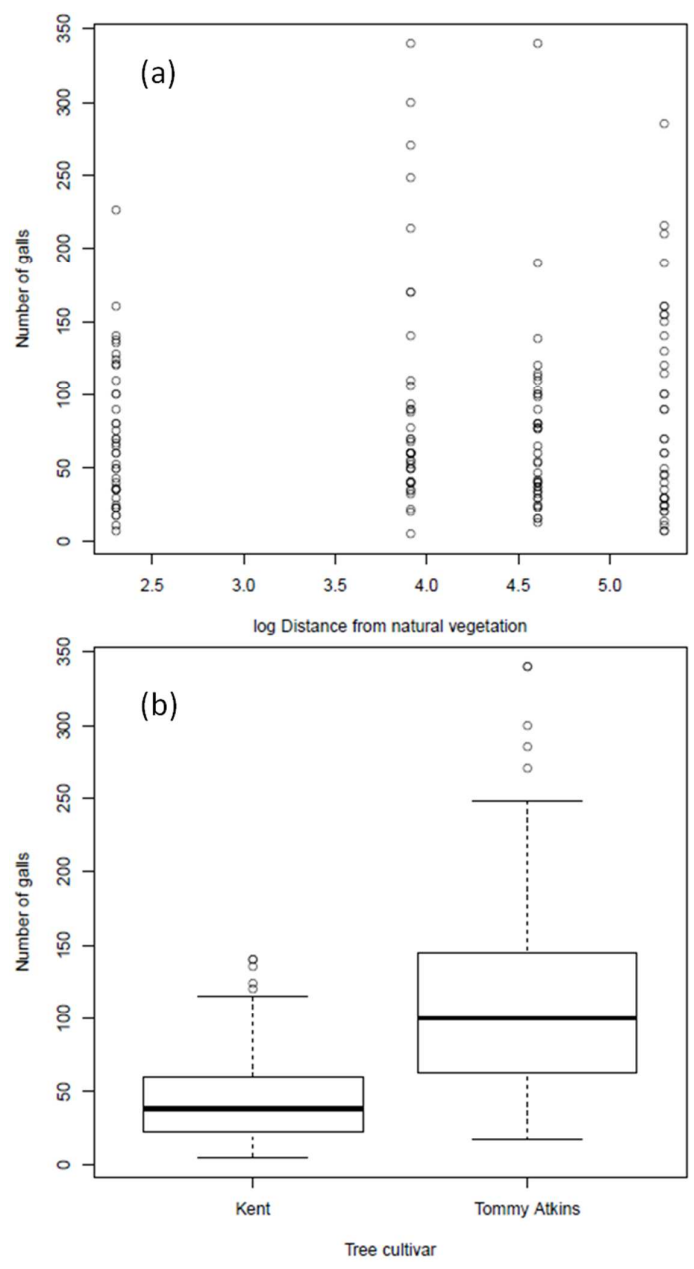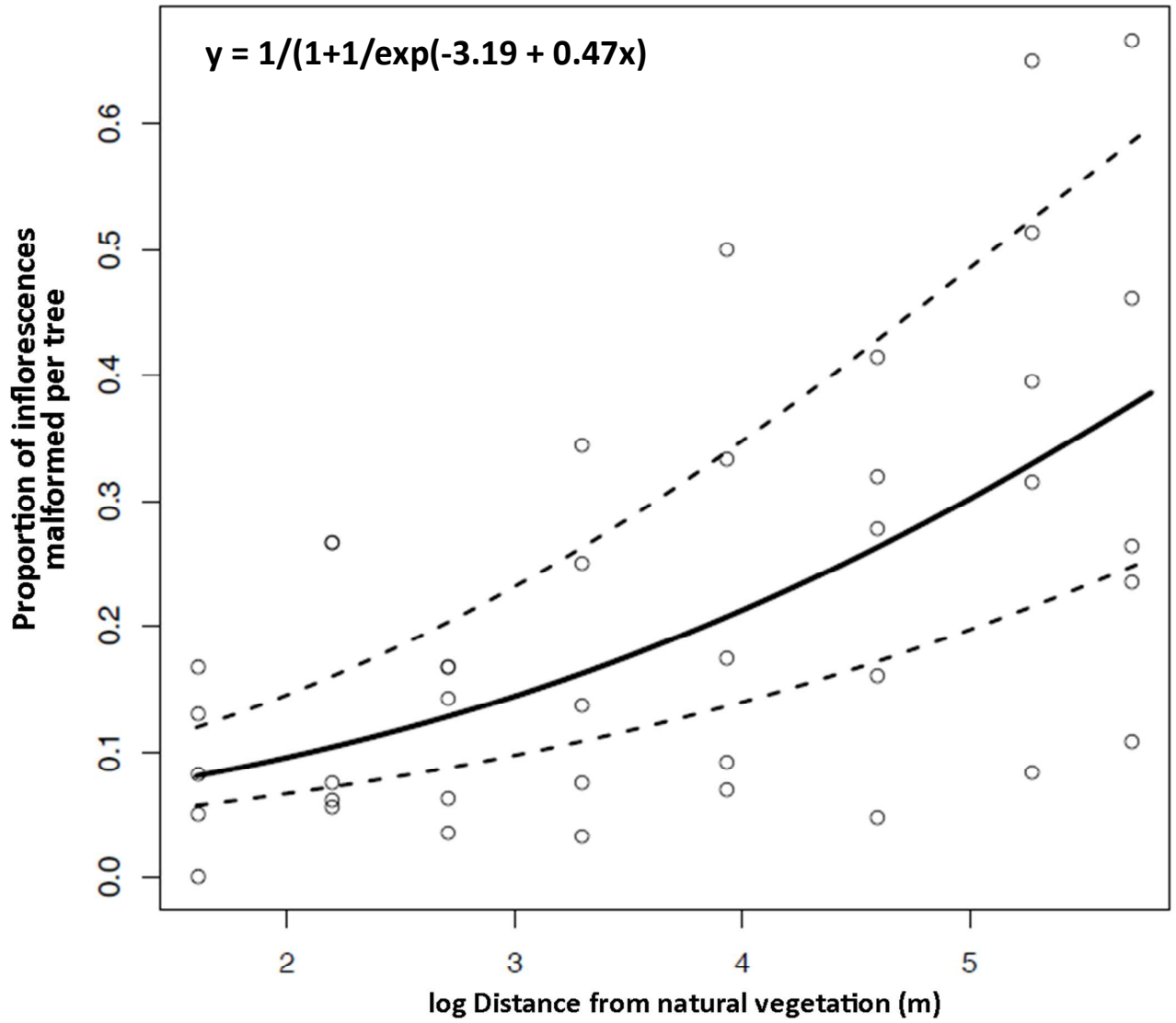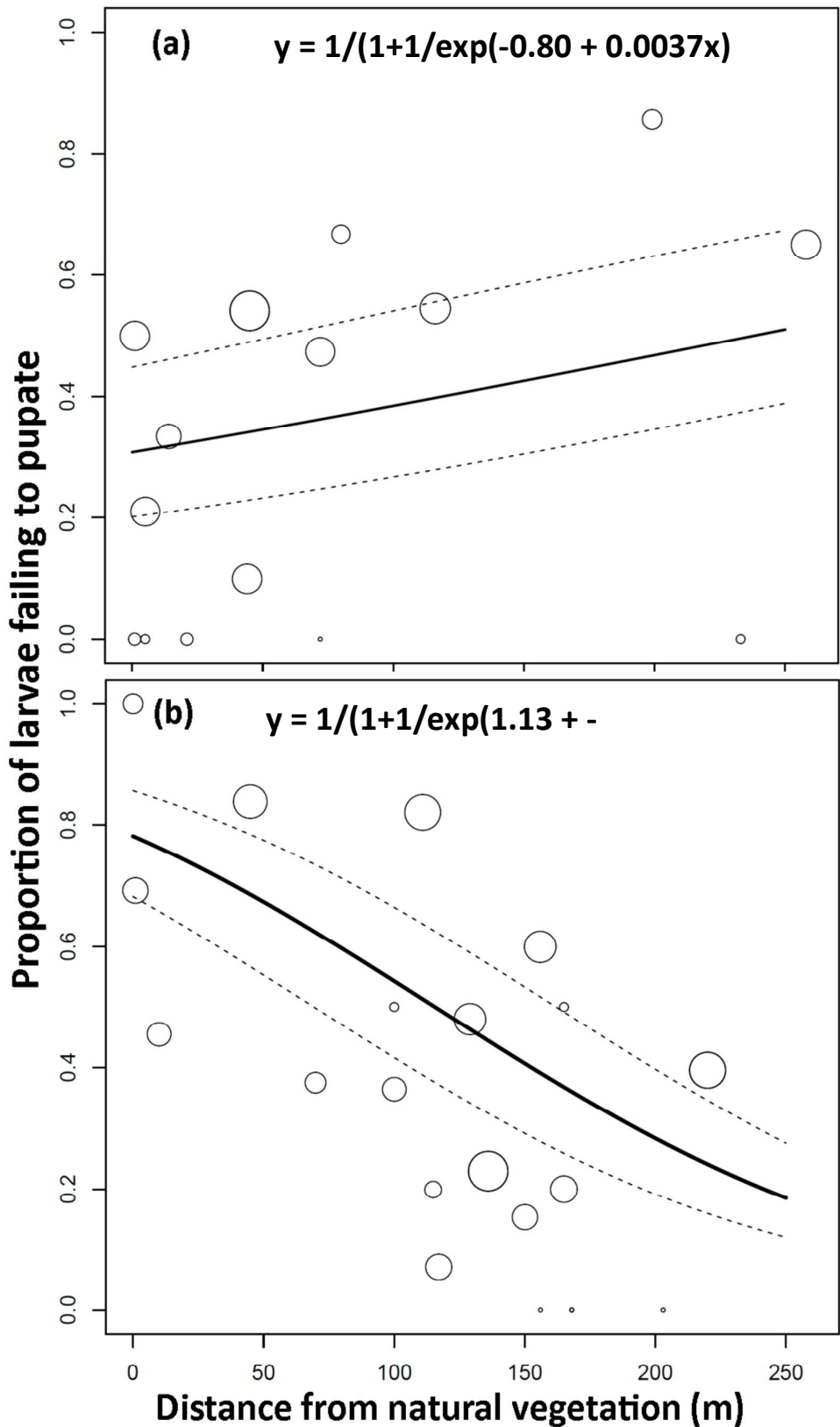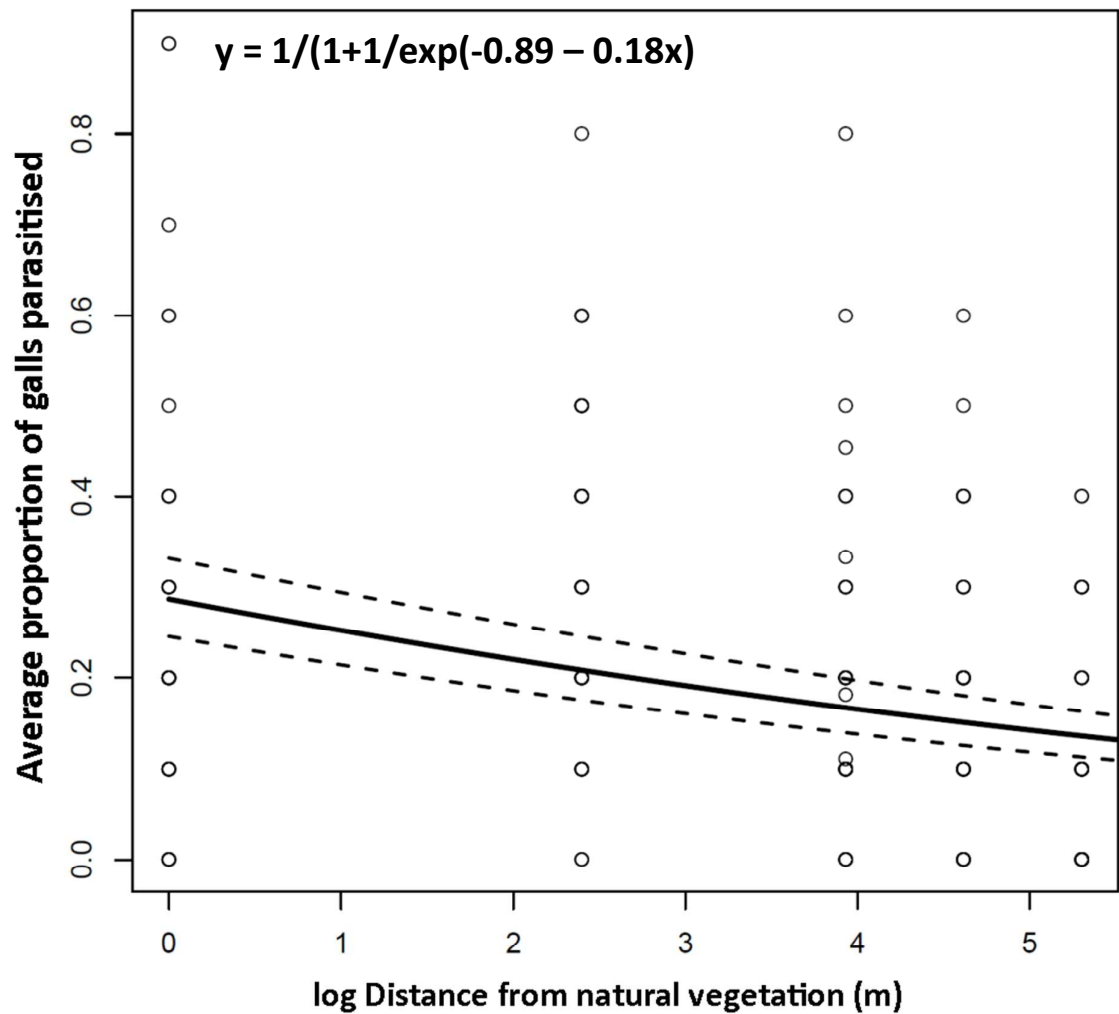
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Supplementary materials 1. Outputs of GLMER models applied to various data sets

Adult fly data
glmer(Fly Count~Distance*Month+(1+Distance|Year:Month)
+(1|Block)+(1|obs)+(1|Cultivar), family= poisson)

Random factor

Groups	Variance	Std.Dev.
Observation level	2.70E+00	1.6429641
Block	2.02E-01	0.4498547
Distance|Year/Month	5.03E-01	0.7095413
	7.16E-08	0.0002675
Cultivar	2.39E-01	0.4885443

Number of observations	2117	Groups	Observation	2117		
			Block	29	Year/Month	19
			Cultivar	8		

Fixed effects	Estimate	Std.Error	Z-value	Pr(>|z|)	
(Intercept)	-2.4869377	0.9007367	-2.761	0.005762	**
Distance	0.0010492	0.0014367	0.73	0.465225	
Month[December]	2.2935921	0.9438696	2.43	0.015099	*
Month[January]	3.2404589	0.9416189	3.441	0.000579	***
Month[February]	2.1397982	0.9440194	2.267	0.023409	*
Month[March]	0.3821232	0.9500778	0.402	0.687535	
Month[April]	0.0863817	1.1387376	0.076	0.939533	
Distance:Month[December]	-0.0024232	0.0014453	-1.677	0.093623	.
Distance:Month[January]	-0.002363	0.0014308	-1.651	0.098646	.
Distance:Month[February]	-0.0001987	0.0014342	-0.139	0.889821	
Distance:Month[March]	0.0026	0.0014546	1.787	0.073879	.
DistanceMonth[April]	0.0022794	0.0020005	1.139	0.254539	

AIC	BIC	logLik	deviance	df.resid
8702.3	8804.2	-4333.2	8666.3	2099

Pupae rearing data
glmer(Survival~Distance*Ripeness+(1|Date.Day)+(1+Distance|Plot)
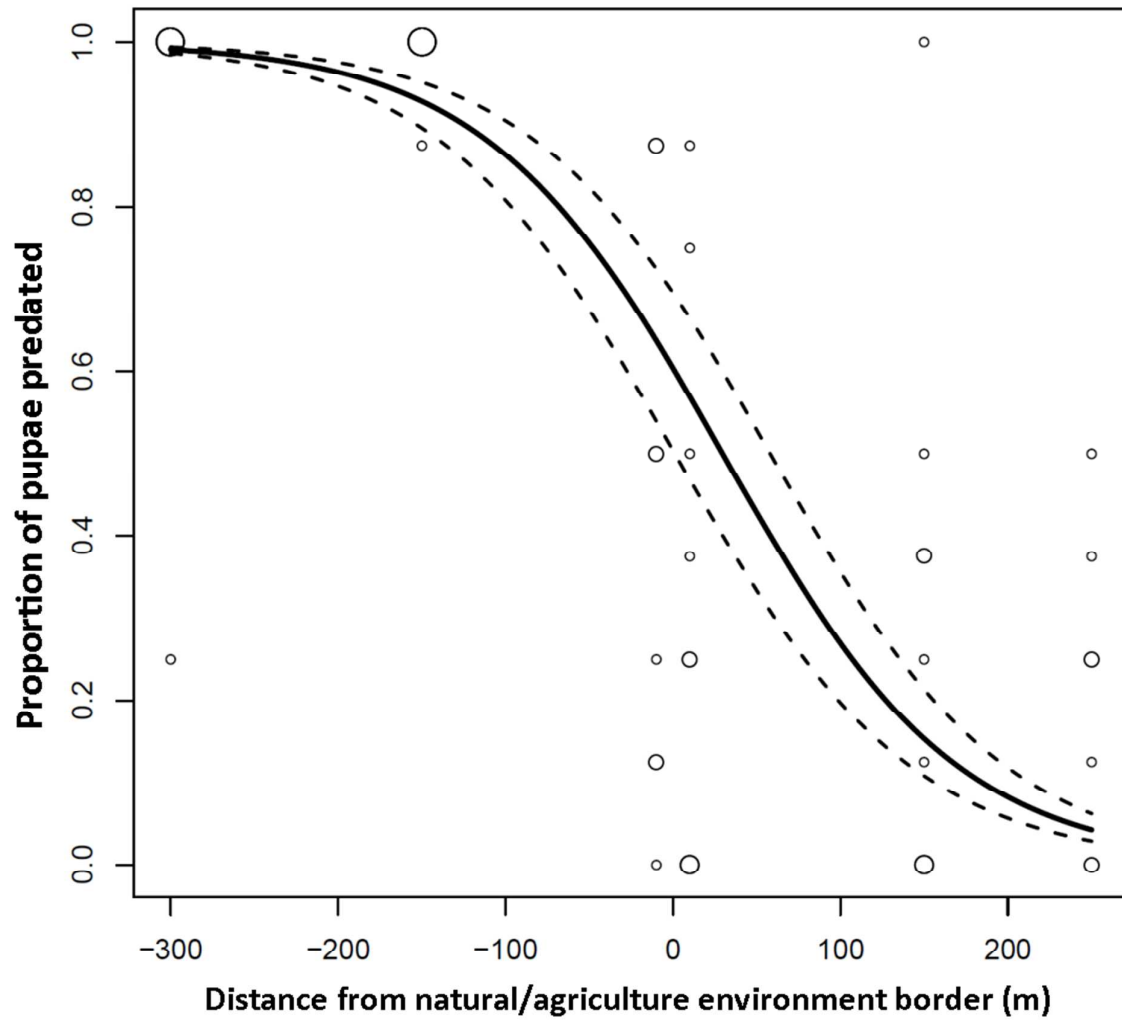*+(1|Observation level), family=binomial)*

Random effects

Groups	Variance	Std.Dev.
Observation level	3.94E-01	6.28E-01
Day of collection	2.51E-01	5.01E-01
Block of collection	5.83E-10	2.41E-05

Number of observations	64	Groups	Observation	64	Day	9
			Block	7		

Fixed effects	Estimate	Std.Error	Z-value	Pr(>|z|)	
(Intercept)	1.130935	0.513562	2.202	0.02766	*

Distance	-0.011007	0.003952	-2.785	0.00535 **
Ripeness[Ripe]	-1.926249	0.591277	-3.258	0.00112 **
Distance:Ripeness[Ripe]	0.014723	0.004892	3.009	0.00262 **

AIC	BIC	logLik	deviance	df.resid
169.8	189.2	-75.9	151.8	55

Pupae predation data

glmer(Proportion predated~Distance+(1+Distance|Transect)
+(1+Distance|Date cohort placed) + (1|Observation),family=binomial)

Random effects

Groups	Variance	Std.Dev.
Observation level	5.21E+00	2.28E+00
Distance|Date cohort placed	1.35E-09	3.67E-05
		1.01E-07
Distance|Transect	3.81E-10	1.95E-05
		6.42E-08

Number of observations	49	Groups	Observation	49	Date placed	7
					Transect	3

Fixed effects	Estimate	Std.Error	Z-value	Pr(>|z|)	
(Intercept)	0.419615	0.403388	1.04	0.298	
Distance	-0.014199	0.002857	-4.971	6.67E-07	***

Gall Density

glmer(Gall count~Cultivar+(1+logDistance|Date surveyed)+(1+logDistance|High.Low)
+(1|Observation level)+(1+logDistance|Transect),family=poisson)

Random effects

Groups	Variance	Std.Dev.
Observation level	3.83E-01	0.618714
logDistance|Date surveyed	5.07E-02	0.225062
	5.46E-03	0.075744
logDistance|Transect	1.62E-03	0.040235
	6.63E-05	0.008372
logDistance|High.Low	1.91E-03	0.043737
	9.18E-05	0.009584

Number of observations	199	Groups	Observation	199	Date surveyed	15
					Transect	4

Fixed effects	Estimate	Std.Error	Z-value	Pr(>|z|)	
(Intercept)	3.56002	0.09713	36.65	2.00E-16	***
Cultivar[TommyAtkins]	0.97299	0.12688	7.67	1.74E-14	***

AIC	BIC	logLik	deviance	df.resid
2038.6	2068.2	-1010.3	2020.6	190

Gall parasitoid density

glmer(Proportion parasitised~logDistance+(1+logDistance|Date surveyed)
+(1+logDistance|Transect)+(1|Observation level),family=binomial)

Random effects

Groups	Variance	Std.Dev.
Observation level	0.450315	0.67105
logDistance|Date surveyed	0.374802	0.61221
	0.008708	0.09332
logDistance|Transect	0.001855	0.04307
	0.002373	0.04872

Number of observations	199	Groups	Observation le	199	Date surveyed	15
					Transect	4

Fixed effects	Estimate	Std.Error	Z-value	Pr(>|z|)	
(Intercept)	-0.88904	0.21955	-4.049	5.13E-05	***
logDistance	-0.17858	0.05305	-3.366	0.000762	***

AIC	BIC	logLik	deviance	df.resid
745.1	774.8	-363.6	727.1	190

Malformed inflorescences

glmer(Proportion malformed~logDistance+(1+logDistance|Transect),family=binomial)

Random effects

Groups	Variance	Std.Dev.
logDistance|Transect	0.02218	0.1489
	0.1066	-1
Number of observations	40	Groups	Transect	5

Fixed effects	Estimate	Std.Error	Z-value	Pr(>|z|)	
(Intercept)	-3.19025	0.27778	-11.485	<2e-16	***
logDistance	0.46885	0.07905	5.931	3.00E-09	***

AIC	BIC	logLik	deviance	df.resid
226.7	235.2	-108.4	216.7	35