

1 **A major subtropical fruit pest accumulates in**
2 **crop fields and spills over to a wild host**

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21 **Abstract**

22 Wild plant species are often considered a source of crop pests in mixed
23 landscapes but this view rarely considers pest spillover in the opposite
24 direction (from crop fields to natural vegetation), or spatiotemporal
25 variability in resources between crop and wild habitats. We investigate
26 how infestation of mango crop (*Mangifera indica*, Anacardiaceae) and a
27 related wild host (marula, *Sclerocarya birrea*, Anacardiaceae) by a major
28 subtropical fruit crop pest (*Ceratitis cosyra*, Diptera: Tephritidae) varies
29 with distance from the boundary between crop and natural vegetation. We
30 determined how infestation of marula is associated with proximity to
31 mango crops at field and landscape scales over two fruiting seasons on
32 three farms in north-eastern South Africa. This is one of few studies to
33 date to consider pest spillover from crop fields to natural vegetation and
34 the only one performed in a biodiverse region with relatively little habitat
35 transformation. Over three sampling periods, *C. cosyra* infestation of
36 marula always decreased with distance from mango fields. At the
37 landscape scale, marula alongside crop fields were 30 times more likely
38 to be infested than in distant vegetation (1.3 – 6 km from mango),
39 suggesting that spillover occurs from crop fields to natural vegetation.
40 During late mango and marula fruiting, twice as many flies infested
41 marula than mango. However, over the two months post-mango fruiting,
42 up to 25 times more *C. cosyra* were trapped in mango fields than in
43 bordering natural vegetation. Although pests spillover from crop fields
44 into natural vegetation to use marula as an alternate host, biological
45 control in the natural vegetation may eliminate this habitat as a pest

46 reservoir outside the crop season. Other nearby crops may be more
47 important than wild hosts for maintaining *C. cosyra* out of mango season.
48 Landscape planning should consider proximity and arrangement of fields
49 containing crops that host shared pests at different times of the year.

50 **Keywords:** agroecology, pest control, polyphagous pests, population
51 reservoir, related plant hosts, spatiotemporal variability

52

53 **1. Introduction**

54 Agriculture has fragmented natural ecosystems worldwide, leaving mixed
55 landscapes with patches of natural vegetation interspersed among human-
56 managed agroecosystems (Benton et al., 2003). Biological communities
57 in these landscapes are spatially and temporally dynamic (Thies et al.,
58 2005); if consumer species are supported by resources in both crop and
59 non-crop patches, they may move freely between the two habitats
60 (Tscharrntke et al., 2005). This spillover has been widely studied, with
61 much focus on its effect on ecosystem services and disservices in
62 agroecosystems (Blitzer et al., 2012 and Rand et al., 2006). Many insect
63 herbivores are crop pests responsible for large-scale production and
64 economic losses in agricultural systems (Oerke, 2006), so understanding
65 insect spillover informs how habitat transformation affects ecological
66 functioning in these systems.

67 Studies on spillover have tended to focus on movement of pests from
68 natural vegetation to crop fields because this research is of most interest
69 to farmers. Over 100 studies reviewed by Norris and Kogan (2009) show
70 that natural vegetation is a source of insect herbivores that shift into crop
71 fields. In natural vegetation, host plants are dispersed, making them
72 difficult for pests to locate, but crop monocultures provide a concentrated
73 resource on which pests may accumulate in high densities (Root, 1973).
74 Crops are only available at certain times of the year, however, and
75 resource alteration after crop harvesting often forces pests onto alternate
76 hosts in nearby natural vegetation (Altieri and Letourneau, 1982).

77 Spillover from crop fields to natural vegetation is far less understood; a
78 recent review by Blitzer et al. (2012) identified only three studies that
79 investigated spillover in this direction (Kaiser et al., 2008, Mckone et al.,
80 2001 and Squires et al., 2009). Nevertheless, spillover from crop fields to
81 natural vegetation is likely common given that many insect herbivores are
82 polyphagous habitat generalists (Tscharntke et al., 2005), with many
83 using both crops and wild plants as hosts (Norris and Kogan, 2009). Such
84 spillover suggests that wild hosts may act as a refuge for pests outside the
85 crop season (Mckone et al., 2001).

86 Opposing predictions have been made for whether insect pests shift from
87 habitats of low to high resource concentration (i.e. from natural
88 vegetation to crop) or vice versa, with evidence of pest spillover across
89 the crop-non-crop interface suggesting that natural vegetation can be
90 either a source or a sink (a population “reservoir” or secondary host
91 source) in mixed agricultural landscapes (reviewed by Tscharntke et al.,
92 2005). Cultural pest-control schemes often target wild hosts in natural
93 vegetation by managing or removing wild plants before the crop season,
94 without considering these conflicting findings and the broader
95 spatiotemporal dynamics of mixed agricultural landscapes (Herzog and
96 Funderburk, 1986). Removing alternate hosts in surrounding natural
97 vegetation can reduce crop-pest infestation by encouraging dispersal of
98 natural enemies into crop fields, promoting biological pest control (e.g.
99 Cottrell and Yeargan, 1999). However, some wild hosts may provide
100 crops with “associational resistance” to infestation by retaining pests in
101 natural vegetation (reviewed by Barbosa et al., 2009), where predation

102 rates can be higher (Henri et al., 2015). Removing these wild hosts may
103 encourage pest spillover onto nearby crops.

104 A major pest of mango (*Mangifera indica* L. Anacardiaceae), the mango
105 fruit fly, *Ceratitis cosyra* (Walker) (Diptera: Tephritidae), also uses
106 marula fruits (*Sclerocarya birrea* (A. Rich) Hochst., Anacardiaceae) in
107 nearby natural vegetation. *Ceratitis cosyra* is polyphagous, using 33 other
108 crop and non-crop species as hosts throughout Sub-Saharan Africa (De
109 Meyer et al., 2002). Mango and marula fruiting overlap between
110 November and April and consequently, marula is considered an important
111 reservoir for *C. cosyra* (Copeland et al., 2006). Marula is often managed
112 by farmers at the start of mango season by spraying auxins to facilitate
113 early marula ripening, followed by burial, incineration or removal of
114 fruits from natural vegetation on farmlands.

115 Relative timing of the onset of mango and marula fruiting varies between
116 years, likely because marula fruiting is more coupled to rainfall than
117 mango, which receives irrigation throughout the year. This variation
118 results in marula fruiting earlier than mango in some years but later in
119 others. Given that the net direction of spillover depends on spatiotemporal
120 dynamics in productivity between habitats (Ries et al., 2004), marula
121 could be either a source or reservoir for *C. cosyra*, depending on relative
122 resource availability between habitats between seasons.

123 We investigated fruit infestation in mango and marula at increasing
124 distances from the habitat margin in crop fields and natural vegetation,
125 respectively, at field and landscape scales. Since related host species

126 display increased susceptibility to infestation when they occur in close
127 proximity (Barbosa et al., 2009), we expected that marula fruit infestation
128 would be highest in natural vegetation nearest to mango fields. In three
129 periods varying in relative marula-mango resource availability, we asked:

- 130 1. How is marula fruit infestation in natural vegetation associated with
131 distance to nearby mango fields (field scale)?
- 132 2. How is marula infestation associated with proximity to mango fields
133 at the landscape scale?
- 134 3. Does *C. cosyra* accumulate in mango fields or natural vegetation at
135 the end of the crop fruiting season?

136 **2. Methods and materials**

137 **2.1 Study site and species**

138 The study was conducted on three mango farming estates (Bavaria Fruit
139 Estates, Mohlatsi and Venden) in the Kruger to Canyons Biosphere
140 Region, a biodiverse area of north-eastern South Africa, of which half is
141 set aside for conservation (Coetzer et al., 2010). Mango are farmed in
142 single cultivar blocks (~70 x 150 m) separated by a single row of
143 *Casuarina* sp. trees serving as windbreaks. Other subtropical fruits,
144 including several *Citrus* spp., passion fruit (*Passiflora edulis*) and
145 avocado (*Persea americana*) are also cultivated on these farms over the
146 year. Farms practise conventional pest control using chemical pesticides
147 throughout the year.

148 The farms have patches of natural vegetation alongside some crop fields,
149 with the habitats separated by a 10-25 m margin. The natural vegetation is
150 “Granitic Lowveld” savanna, dominated by woody *Acacia* spp. and *S.*
151 *birrea* (marula) (Mucina and Rutherford, 2006). Marula is dioecious;
152 females bear small fruits (mass = ~20 g) with a large pit and soft, fleshy
153 skin when ripening on the ground.

154 *Ceratitis cosyra* is endemic to sub-Saharan Africa where it can cause up
155 to 73% losses to the annual mango crop in some countries (Vayssières et
156 al., 2009). Adult flies damage fruits by ovipositing their eggs beneath the
157 fruit skin, where larvae hatch and feed, later dropping to the soil to pupate
158 and eclose as adults (Hill, 1983).

159 **2.2 How is marula fruit infestation in natural vegetation** 160 **associated with distance to nearby mango fields?**

161 2.2.1 Fruit collection and processing

162 In natural vegetation alongside mango fields at the three farms we
163 sampled fruit from randomly distributed marula trees (>40 m apart) at
164 various distances (4-275 m) from the field-natural vegetation margin.
165 From 15 trees at Bavaria and 10 trees at Mohlatsi and Venden, we
166 collected up to 20 fruits from the ground surrounding each tree, wherever
167 possible (range: 1 – 20 fruits per tree). We sampled in three periods
168 differing in relative availability of marula and mango: 1) Late marula/ late
169 mango fruiting (March 2014, $n = 302$ marula fruits); 2) Early marula/peak
170 mango fruiting (January 2015, $n = 304$); 3) Late marula/post-mango (30
171 days later, February 2015, $n = 605$), when mango fruiting had ended and

172 crop fields had been cleared of all fruit. Bavaria was the only farm
173 sampled in 2014, while all farms were sampled in both seasons in 2015.
174 Marula fruits were placed into individual polystyrene cups with ~4 cm
175 depth dry, sterile sand as a substrate for fly pupation, covered with
176 chiffon secured with an elastic band to prevent emerged adult flies from
177 escaping while permitting air flow. Cups were stored at ambient
178 temperature (~27 °C) for at least 35 days before adult flies were counted
179 and identified as *C. cosyra*. Larvae and pupae that failed to develop and
180 eclose were considered dead due to parasitism or other causes and could
181 not be identified to species. These were assumed to be *C. cosyra* and
182 included in total fly count per fruit.

183 2.2.2 Data analysis

184 We ran two separate generalized linear mixed effects models (GLMMs) to
185 investigate how distance from the habitat margin is associated with 1) the
186 likelihood of marula infestation by *C. cosyra* and 2) infestation intensity.
187 GLMMs are suitable for analysing non-normal data that are pseudo-
188 replicated in space and time (Bolker et al., 2009).

189 The likelihood of marula infestation was investigated using a binomial GLMM
190 (with logit function) and *C. cosyra* presence/absence per fruit as the response
191 variable. Infestation intensity was investigated using a GLMM with negative
192 binomial error structure (with log function) and *C. cosyra* abundance per fruit as
193 the response variable. This error structure accounts for overdispersion without
194 the need to transform the count data (Zuur et al. 2009). We included a zero-
195 inflated parameter in the model to account for the excess zeros in the count data

196 (R package: glmmADMB, Bolker et al. 2012) and to reduce the risk of Type I
197 errors (Martin et al. 2015).

198 Both models included distance from the habitat margin and sample season
199 as fixed effects. Tree and farm were included as random effects to
200 account for pseudoreplication, repeat sampling of trees between seasons
201 and non-independence of fruits sampled from the same tree.

202 **2.3 How is marula infestation associated with proximity to** 203 **mango fields at the landscape scale?**

204 2.3.1 Fruit collection and processing

205 To determine how marula infestation is associated with proximity to
206 mango at the landscape scale during (January 2015) and after mango
207 fruiting (February 2015), we collected marula in both periods from five
208 trees (>40 m apart) at distances of 4-275 m from the margin along two
209 parallel transects (~100 m apart) at each of Bavaria, Mohlatsi and Venden
210 Estates. In distant vegetation (1.3-6 km), we sampled five randomly-
211 distributed trees (>35 m apart) in each of two conservation areas with
212 relatively little human disturbance, Hoedspruit Wildlife Estate and
213 Raptor's View.

214 Marula availability and ripeness may influence *Ceratitis* population size
215 and distribution (Sciarretta and Trematerra, 2011). Therefore, we
216 recorded total fruit abundance within canopies and on the ground
217 surrounding each tree, and the number of fruiting marula trees within a 20
218 m radius of each tree. We also collected 10 fruit within three ripeness
219 categories per tree where possible: 1) “unfallen, unripe”: green fruit

220 within the canopy, 2) “fallen, unripe” and 3) “fallen, ripe”: green-white
221 and yellow fruit on the ground surrounding each tree, respectively.
222 Fruit were stored in polystyrene cups for 28-31 days before emerged flies
223 were counted and identified as *C. cosyra*. Pupae that failed to eclose were
224 assumed to be *C. cosyra* and included in the total fly count per fruit.

225 2.3.2 Data analysis

226 We used separate binomial and zero-truncated, negative binomial
227 GLMMs to determine how *C. cosyra* presence/absence and abundance
228 per fruit, respectively, differ alongside mango fields and in the distant
229 vegetation (Jan: $n = 675$, Feb: $n = 833$). Both models included a binary
230 factor for proximity to mango fields (nearby/distant), sample season, fruit
231 ripeness, the abundance of fruit in/surrounding the tree and the number of
232 surrounding trees as fixed effects, and tree nested within site (including
233 farms and distant conservation areas) as random effects.

234 **2.4 Does *C. cosyra* accumulate in mango fields or natural** 235 **vegetation at the end of the fruiting season?**

236 2.4.1 Fruit collection and processing

237 In March 2014, we collected between 2 – 10 mangoes (Kent cultivar,
238 mass = ~600 g) (depending on fruit availability) from trees at varying
239 distances from the natural vegetation along four parallel transect (>100 m
240 apart) in fields on Bavaria Fruit Estate: 0 m ($n = 18$ mangoes), 10 m ($n =$
241 21), 50 m ($n = 19$), 100 m ($n = 21$), 200 m ($n = 16$) and 500 m ($n = 13$).

242 These transects were mirrored in the natural vegetation opposite each
243 field, with five marula trees (>40 m apart) sampled at 8-370 m from the
244 margin along each transect. Twenty marula fruits were collected from the
245 ground around each tree where possible (range: 1-20 fruit per tree) ($n =$
246 399).

247 Mangoes were placed into separate perforated, plastic bags with a portion
248 of sand for 2-3 weeks. Emerged larvae and pupae were placed into
249 individual polystyrene cups containing sand and a piece of damp tissue to
250 retain moisture for pupation. Cups were covered with perforated plastic
251 film and stored for 2 weeks before eclosed adult flies were counted and
252 identified to species. Two other species also infest mango in addition to
253 *C. cosyra*: *C. rosa* and *C. capitata*. These two species are not known to
254 use marula as an alternative host and were excluded from analyses.

255 Marula were placed into individual polystyrene cups as above and stored
256 for at least 35 days before emerged adult flies were counted and
257 identified. All flies were identified as *C. cosyra*, and dead larvae/pupae
258 were assumed to be *C. cosyra* and added to the total fly count per fruit.

259 2.4.2 Pheromone trapping

260 We used pheromone traps (SensusTM traps, River Bioscience, Port
261 Elizabeth, South Africa) to determine where *C. cosyra* accumulate after
262 mango and marula fruiting has ended. Trapping was conducted in both
263 mango fields and natural vegetation on Bavaria Fruit Estate, along four
264 parallel transects (~100 m) at 0, 10, 50, 100, 200 m from the field-natural
265 vegetation margin in four 2-week periods (early April, late April, early

266 May, late May 2014, i.e. 160 traps in total) when fruits were no longer
267 available in either habitat. Traps were equipped with Questlure bait for
268 female *Ceratitis* flies (Insect Science Ltd, Tzaneen, South Africa) and a
269 Dichlorovos tablet, which was replaced after 4 weeks to maintain trapping
270 efficiency. Flies were counted and identified after 11 – 14 days in each
271 sample period.

272 2.4.3 Data analysis

273 For fly emergence data, we used binomial and negative binomial GLMMs
274 to compare *C. cosyra* presence/absence and abundance per fruit,
275 respectively, between mango and marula. The negative binomial model
276 included a parameter to account for zero-inflation of the count data. Both
277 models included fruit type and distance from the habitat margin as fixed
278 effects, and tree nested within transect as random effects to account for
279 pseudoreplication and non-independence of fruits from the same tree.

280 For pheromone trap data, we used a negative binomial GLMM to
281 compare *C. cosyra* abundance between habitats and over several periods
282 after mango/marula fruiting has ended. We used fly abundance per trap as
283 the response variable, and habitat, distance from the habitat margin and
284 sample period as fixed effects. Trap nested within transect were random
285 effects to account for pseudoreplication and repeat trapping at the same
286 locations between sample periods (Bates, 2016).

287 2.5 Model selection

288 All analyses were performed using R (R Core Team, 2014), with GLMMs
289 fitted for random intercept analyses using packages lme4 (Bates, 2016)
290 and glmmADMB. Before fitting the models, we checked for outliers and
291 collinearity using pairwise scatterplots of explanatory variables (Dormann
292 et al., 2013). For each count model, we considered Poisson and negative
293 binomial error structure and compared model fit using Akaike
294 Information Criteria (AIC). We also compared GLMMs structured for
295 random intercept and random slopes using AIC (Zuur et al., 2009). In all
296 cases, negative binomial models and random intercept GLMMs had the
297 lowest AIC values and were considered better models. For model
298 validation, residuals were plotted against fitted values and explanatory
299 variables to check for overdispersion. Log-likelihood ratio tests and AIC
300 were used to identify optimal models in backward model simplification.
301 For each GLMM, we determined the proportion of variance explained by
302 fixed and random effects (conditional R^2) and fixed effects only (marginal
303 R^2) using (Nakagawa and Schielzeth, 2013).

304 **3. Results**

305 **3.1 How is marula fruit infestation in natural vegetation** 306 **associated with distance to nearby mango fields?**

307 At the field scale, distance from mango had no effect on the likelihood of
308 infestation per marula ($\chi^2_1 = 2.46$, $p = 0.12$), regardless of sample period
309 ($\chi^2_1 = 1.03$, $p = 0.60$). However, intensity of infestation decreased with
310 distance from mango ($\chi^2_1 = 5.00$, $p = 0.025$, Fig. 1), with average fly

311 abundance per fruit declining by ~37% (~2 flies) from 4 m to 275 m into
312 the natural vegetation.

313 Marula were ~2-3 times more likely to be infested when early marula
314 fruiting coincided with peak mango fruiting than at the end of mango
315 fruiting or when mango had been cleared ($\chi^2_1 = 32.21$, $p < 0.001$, Fig. 2)
316 (R^2 marginal = 0.34; R^2 conditional = 0.46). Approximately twice as
317 many flies emerged per marula fruit on average in early marula/peak
318 mango (1.45 ± 0.20) and late marula/post-mango fruiting periods ($5.46 \pm$
319 0.49) than when late marula and mango fruiting coincided (3.12 ± 0.27)
320 ($\chi^2_1 = 48.82$, $p < 0.001$) (R^2 marginal = 0.47; R^2 conditional = 0.86).

321 **3.2 How is marula infestation associated with proximity to** 322 **mango fields at the landscape scale?**

323 Marula were ~30 times more likely on average to be infested alongside
324 mango fields than in the distant vegetation ($\chi^2_1 = 13.20$, $p < 0.001$). The
325 distance effect did not vary with sample period ($\chi^2_1 = 0.07$, $p = 0.79$),
326 although marula were almost twice as likely to be infested before than
327 after mango harvesting ($\chi^2_1 = 6.67$, $p < 0.01$) (R^2 marginal = 0.72; R^2
328 conditional = 0.78). Although the likelihood of being infested was
329 markedly different between near and distant sites, once infested, fruit fly
330 abundance per fruit did not differ alongside mango fields (11.78 ± 0.25)
331 or in distant vegetation (8.00 ± 0.25 ; $\chi^2_1 = 1.15$, $p = 0.56$), regardless of
332 sample period ($\chi^2_1 = 1.54$, $p = 0.46$). However, marula infestation was
333 affected by fruit ripeness and fruit abundance in the tree canopy and on
334 the ground surrounding the tree (Fig. A.1).

335 **3.3 Does *C. cosyra* accumulate in mango fields or natural**
336 **vegetation at the end of the fruiting season?**

337 Fly emergence from fruit

338 Adult flies reared from mango were *Ceratitis cosyra* (92%), *C. rosa* (5%)
339 and *C. capitata* (3%). Dead larvae/pupae comprised 70% and 10% of the
340 total emerged individuals from mango and marula, respectively. The
341 proportion of emerged individuals that failed to develop was not
342 associated with distance from the margin in both fruit types ($\chi^2_1 = 1.11$, p
343 = 0.29; Table A.1).

344 Since we cannot distinguish the three *Ceratitis* species among
345 larvae/pupae emerging from mango, we first ran GLMMs with data
346 including only adult *C. cosyra* flies from mango (and total *C. cosyra*
347 abundance from marula). Fruit infestation was not associated with
348 distance from the margin in either mango or marula (infestation
349 likelihood: $\chi^2_1 > 0.01$, $p = 0.99$; infestation intensity: $\chi^2_1 = 0.231$, $p =$
350 0.64). However, marula were ~4 times more likely to be infested (χ^2_1
351 = 14.28, $p < 0.001$) and had ~3 times more flies emerging per fruit than
352 mango ($\chi^2_1 = 7.46$, $p < 0.01$).

353 We also ran GLMMs with data including both adult *C. cosyra* flies and a
354 proportion of dead larvae/pupae emerging from mango (and total *C.*
355 *cosyra* abundance from marula). This was based on the assumption that
356 there was equal likelihood of mortality for all three *Ceratitis* species, so
357 we included 92% of larvae/pupae from mango as *C. cosyra* in the total fly
358 count per fruit.

359 Plotted residuals of these GLMMs indicated an outlying data point (51
360 flies from mango at 50 m from margin) in the fruit infestation data
361 containing a proportion of larvae/pupae from mango. This point exerted
362 excessive influence on the model parameter estimation (function
363 `influencePlot.car`, Fox 2015). We excluded it from the data ($n = 506$) and
364 re-analysed the data. Results including the outlier are presented in Table
365 A.2.

366 With the outlier removed, the likelihood of infestation was equal between
367 mango and marula ($\chi^2_1 = 1.55$, $p = 0.46$) and was not associated with
368 distance from the habitat margin ($\chi^2_1 = 0.09$, $p = 0.76$). However, marula
369 had twice as many flies on average emerging per gram of marula ($0.08 \pm$
370 0.009 flies/g) than mango (0.002 ± 0.0005 flies/g) ($z = 2.57$, $df = 2$, $p =$
371 0.01).

372 Fly abundance per mango increased with distance from natural vegetation
373 and decreased with distance from mango fields in marula ($\chi^2_2 = 3.95$, $p =$
374 0.047 , Fig. 3) (R^2 marginal = 0.51; R^2 conditional = 0.59). The increase in
375 infestation intensity with distance in mango fields (slope = $0.0027x$) was
376 twice as strong as the decrease with distance in natural vegetation ($-$
377 $0.0012x$).

378 Pheromone traps

379 For two months after mango and marula fruiting, *C. cosyra* abundance in
380 pheromone traps was not associated with distance in either habitat ($\chi^2_1 =$
381 2.81 , $p = 0.42$).

382 Differences in *C. cosyra* abundance trapped in mango fields and natural
383 vegetation varied with time since mango and marula fruiting ended ($\chi^2_4 =$
384 12.8, $p < 0.01$, Fig. 4). Immediately after fruiting had ended (early April),
385 ~25 times as many *C. cosyra* flies on average were collected per trap in
386 mango fields (5.60 ± 1.96) than in natural vegetation (0.20 ± 0.09). The
387 abundance of flies trapped in both habitats increased significantly in late
388 April, with only 3 times as many flies on average collected per trap in
389 mango fields (6.95 ± 2.16) than in natural vegetation (2.10 ± 0.57). In
390 early and late May, 6.5 and 20 times more flies were collected per trap on
391 average in mango fields (1.85 ± 0.46 ; 0.9 ± 0.30) than in natural
392 vegetation (0.35 ± 0.13 ; 0.05 ± 0.05), respectively (R^2 marginal = 0.80;
393 R^2 conditional = 0.87).

394 **4. Discussion**

395 We found that a polyphagous pest, *Ceratitis cosyra*, spills-over from crop
396 fields into natural vegetation in search of alternate wild hosts at the end of
397 crop fruiting. The pest remained in crop fields for two months after crop
398 and wild host fruiting has ended, suggesting that mango fields are more
399 likely to be a pest reservoir than natural vegetation at the end of mango
400 fruiting. Our results also point to the importance of differences in peak
401 fruit timing between crop and natural hosts, which influenced both the
402 likelihood and intensity of pest infestation. Below, we discuss the
403 implications of these findings for management of pests using both crop
404 and wild hosts in a mixed landscape.

405

406

407 **4.1 How is marula fruit infestation in natural vegetation**

408 **associated with distance to nearby mango fields?**

409 Decreasing abundance of *C. cosyra* per marula fruit with distance from
410 mango fields suggests that the pest spills-over from crop fields into
411 nearby natural vegetation. This occurred both when mango fruiting had
412 ended or continued over marula season. Gradients in resource availability
413 at the landscape scale drive pest dispersal between habitats differing in
414 resource concentration in mixed landscapes (Tscharntke et al., 2005).
415 Considering that monoculture crops provide a concentrated resource that
416 frequently support high pest abundance (Marques et al., 2000),
417 contrasting with the low-density and randomly-distributed resources
418 available in natural vegetation, dispersal of *C. cosyra* from crop fields
419 into natural vegetation may be expected.

420 Flies may also be driven out into nearby natural vegetation when
421 pesticides are applied in crop fields before and during the harvest. The
422 farms practice conventional pest control using insecticides, such as
423 neonicotinoids or organophosphates, which they spray in low
424 concentration throughout the year, including during the mango fruiting
425 season (November – March). In sampled fields on Bavaria Fruit Estates,
426 pesticides are sprayed every month except for a period at the end of and
427 after mango fruiting season (March – May). Absence of pesticide during
428 these months may account for the accumulation of *C. cosyra* in crop

429 fields for two months after mango/marula fruiting season (See section
430 4.3).

431 Adult female flies may not only disperse out of crop fields in search of
432 alternate hosts, but also for resources like food and shelter, which are
433 removed from crop fields by mowing in-crop weeds in corridors between
434 rows of mango trees. Mowing occurs after mango harvesting (April –
435 June) as another form of pest control on the farms.

436 **4.2 How is marula infestation associated with proximity to** 437 **mango fields at the landscape scale?**

438 Although *Ceratitis* adults can disperse up to 50 km in some instances
439 (Israely et al., 2005), they are generally poor dispersers, remaining within
440 tens of metres but up to 400-700 m from the point of emergence from
441 hosts (Meats and Smallridge, 2007). This would explain the marked
442 difference in infestation probability of marula (30 times greater) near
443 mango fields than in distant vegetation, both when mango was available
444 or had been cleared from crop fields, and provides further evidence of
445 spillover from crop to natural vegetation. Accumulation of *C. cosyra*
446 alongside mango fields may suggest that the pest encounters substantial
447 alternate host resources here without having to disperse over large
448 distances into distant vegetation.

449 By acting as an alternate host for *C. cosyra* when mango is fruiting,
450 marula may act as a “decoy” that retains the pest (Holmes and Barrett,
451 1997) and provides the crop with “associational resistance” to infestation.
452 Previous research in our study area showed higher predation rates of

453 *Ceratitis* larvae in natural vegetation than in mango fields (Henri et al.,
454 2015). Therefore, marula removal may actually drive pests into crop
455 fields but this requires further research. Nevertheless, the success of area-
456 wide pest management programs that target wild hosts has not been
457 widely documented to date (Norris and Kogan, 2009).

458 **4.3 Does *C. cosyra* accumulate in mango fields or natural** 459 **vegetation at the end of the fruiting season?**

460 We consider it more reasonable to consider a proportion of larvae/pupae
461 in the total *C. cosyra* count from mango than to include only *C. cosyra*
462 adults in the analyses. Firstly, we reared adults from only 9 mango, while
463 34 mangos had *Ceratitis* larvae, pupae and adults emerge. This high
464 larval/pupal mortality is likely due individuals drowning in large volumes
465 of liquid as the mangos (~600 g) rotted. Owing to the low emergence
466 success of adult *Ceratitis* for mango, the results from the adult model
467 alone are an underestimate of mango infestation. Secondly, population
468 dynamics among *Ceratitis* species appear to cyclical, with *C. cosyra* able
469 to sustain its populations for longer at the end of the fruit season than the
470 other two species (W. Lammers, unpublished data). Since *C. cosyra* was
471 the dominant adult emerging from mango, it is reasonable to assume that
472 the same proportion of larvae/pupae would also be *C. cosyra*. Below, we
473 discuss results from the analyses including these individuals.

474 Marula is an important alternate host for *C. cosyra* when the mango
475 resource becomes less abundant, given that marula were more severely
476 infested than mango in the late mango/marula fruiting season. During this

477 season, the pest appears to spillover from crop fields and disperse evenly
478 through both habitats in search of hosts, as suggested by equal infestation
479 likelihood between fruit types and the absence of distance effects in either
480 habitat.

481 Greater infestation intensity per marula may have resulted from easier
482 host detection in the natural vegetation, where fallen fruits remain on the
483 ground surrounding trees (Fig. A.1), compared to crop fields, where fallen
484 fruits are removed as part of sanitation practices. Alternatively, higher
485 pest loads on marula may be linked to harsh conditions in crop fields,
486 including the use of chemical pesticides and mowing in-crop weeds,
487 which might drive *C. cosyra* into nearby natural vegetation in search of
488 alternate hosts, shelter and food (See Section 4.1).

489 Host abundance in the landscape also influences pest spill-over between
490 habitats (Tscharntke et al. 2005). Using 2013 mango production data from
491 Bavaria Fruit Estates and recorded marula fruit abundance from this
492 study, we extrapolated the total number of flies/g of fruit to a hectare of
493 Kent mango fields and adjacent natural vegetation. A hectare of mango
494 containing 1200 ± 1100 kg of fruit (mean \pm SD) (~500 trees) would yield
495 2400 ± 2150 flies, while a hectare of natural vegetation containing 180 kg
496 marula (15 trees, randomly dispersed) would yield 980 ± 700 flies. This
497 estimate is based on average flies emerging per fruit from a single season
498 (late mango/marula fruiting, March 2014) but the infestation rate between
499 the fruits may change as the relative availability of the fruits changes (See
500 Section 4.5 below).

501 The estimate should be considered in context of an agricultural landscape,
502 with isolated patches of natural vegetation interspersed amongst hundreds
503 of hectares of crop fields. In this context, the crop fields on large farming
504 estates provide a larger, more concentrated host resource for *C. cosyra*,
505 despite higher infestation per fruit among marula observed in this study,
506 resulting in large-scale spillover and higher infestation of the dispersed
507 marula trees in nearby natural vegetation.

508 Indeed, this is supported by consistently greater fly abundance trapped in
509 mango fields over two months after mango and marula fruiting has ended.

510 This also provides further evidence against natural vegetation as a
511 reservoir for *C. cosyra* outside of mango fruiting. Around this time (May
512 – July), winter crops that are known to host *C. cosyra*, such as several
513 *Citrus* spp., avocado (*Persea americana*) and passion fruit (*Passiflora*
514 *edulis*) (De Meyer et al., 2002) begin fruiting on farms sampled here.

515 Unlike other climate-sensitive *Ceratitis* species that are dormant over the
516 winter in South Africa (e.g. *Ceratitis capitata*; *C. rosa*), *C. cosyra* persists
517 on available hosts throughout the year (De Villiers et al., 2013).

518 Therefore, by harbouring higher relative *C. cosyra* abundance long after
519 marula/mango season, mango fields themselves may provide an important
520 source of pests for winter crops. Thus, crops may be more important for
521 *C. cosyra* population cycling throughout the year than wild hosts such as
522 marula in the natural vegetation.

523 Despite its polyphagous nature, *C. cosyra* was not reared from fruit
524 samples from 121 species of non-crop plants in natural vegetation,
525 including known hosts of the species (e.g. *Cucurbita*, *Ficus*, *Opuntia*,

526 *Solanum* and *Strychnos* spp., (De Meyer et al., 2002), throughout winter
527 (April – July 2014; C. Moxley, unpublished data), suggesting that the pest
528 is not hosted at significant densities in the natural vegetation. Further
529 research into landscape-scale population cycling could benefit
530 conservationists and advocates of natural vegetation in agricultural
531 landscapes by elucidating the relative importance of other wild hosts and
532 crops in harbouring pests.

533 **4.4 Natural pest control in natural vegetation**

534 Flies trapped after mango and marula fruiting had likely emerged after
535 pupating in the soil over the two months since dropping from fruit. Lower
536 abundance per trap in natural vegetation may be explained by greater
537 predation of *Ceratitis* pupae in natural vegetation compared to mango
538 fields (Henri et al., 2015).

539 During our rearing experiment, nine Opiinae parasitoid wasps emerged
540 from marula, while none emerged from mango. This is likely an under-
541 estimate of parasitoid density because we limited further parasitism by
542 removing fruit from the field and parasitoids take longer to emerge,
543 beyond the time we allowed for *C. cosyra* (C. Moxley, unpublished data).
544 While higher larval/pupal mortality in mango (70%) than marula (10%)
545 may suggest that parasitism by natural enemies is greater in crop fields,
546 we observed no association between the proportion of eclosed individuals
547 in both mango and marula and the distance from the margin (Table A.1).
548 Causes for the high larval/pupal mortality outlined above may also
549 explain the lack of parasitoid wasps emerging from mango.

550 Distance effects detected here provide additional evidence for stronger
551 pest control in natural vegetation than mango fields. In mango fields, flies
552 may encounter more natural enemies along margins nearest natural
553 vegetation where pesticides are less concentrated, and weedy borders
554 provide habitats and complementary resources for natural enemies. Our
555 findings are consistent with those of Henri et al., 2015, where adult
556 *Ceratitis* abundance increased and pupal predation decreased in mango
557 fields with distance from natural vegetation, suggesting that natural
558 enemies are favoured over pest populations in natural vegetation, as
559 predicted elsewhere (Chaplin-Kramer et al., 2011).

560 Data in this section were collected on a single estate (~2 km) and in one
561 fruiting season (March 2014). At present, we cannot determine whether
562 the weak distance effects are driven by other gradients along the sampled
563 edge. To test the generality of our findings, mango/marula infestation
564 should be considered across multiple, spatially independent edges on
565 several farms in the future.

566 **4.5 Effects of seasonal differences in relative marula-mango** 567 **resource availability**

568 Spatiotemporal shifts in resource availability drive spillover of consumer
569 species, including insect pests, between habitats in mixed agricultural
570 landscapes (Gavriel et al., 2012). Here, marula infestation by *C. cosyra*
571 seemed to change with relative availability of the mango crop. Marula
572 had the greatest infestation when early marula fruiting coincided with
573 peak crop fruiting, suggesting spillover of *C. cosyra* from crop fields.

574 Interestingly, when marula was the only host resource available for *C.*
575 *cosyra* in the landscape (after mango fruiting), marula had lower
576 infestation than when mango was in peak fruiting, providing further
577 evidence against natural vegetation as a population reservoir for *C. cosyra*
578 at the end of crop fruiting. Rather, *C. cosyra* appeared to shift to marula
579 as a secondary resource, in contrast to the concentrated resource provided
580 by the crop.

581 These conclusions are derived from data collected in only two seasons.
582 Further long-term studies are needed to establish how infestation of the
583 wild host, and its role in harbouring the pest depends on timing of crop
584 fruiting relative to the wild host, as well as availability of other crops in
585 the landscape. This could inform optimal spatial configuration of crop
586 fields in the landscape.

587 **4.6 Implications for conservation**

588 While negative impacts of pest spill-over from natural vegetation into
589 crop fields can be quantified economically as declines in crop production,
590 it is less straightforward to assess impacts of pest spillover in the reverse
591 direction. Effects may be indirect, such as decreased ecosystem
592 functioning, resulting from competition for shared resources (e.g. food
593 and shelter) and consequent displacement of pollinators and natural
594 enemies by the pest (e.g. Pearce, 2001). The pest may also associate with
595 other wild plants besides marula in the natural vegetation (See Section
596 4.3) and displace native herbivores from their hosts. This may also impact
597 the reproductive success of these plants (e.g. Kaiser et al. 2008) by

598 affecting seed health or the likelihood of fruits being eaten and dispersed.
599 Such effects may be of particular concern at close proximity to crop fields
600 at the field scale, rather than the landscape scale, if the pest is generally a
601 weak disperser like *Ceratitis* (Meats & Smallridge 2007). Future
602 extensions of this work to consider such impacts on marula would benefit
603 conservation, given that marula is a keystone species in the lowveld
604 savanna (Shackleton et al. 2002).

605 **6. Conclusions**

606 Our data suggest that the primary direction of pest spillover is from crop
607 fields into nearby natural vegetation. Wild hosts in distant vegetation (1.3
608 – 6.2 km away from crop fields) are less likely to support the pests than
609 natural vegetation in close proximity to the crop host. Natural vegetation
610 does not necessarily harbour the pest outside the crop season, even if the
611 pest accumulates on the wild host at the end of fruiting, possibly because
612 of biological pest control in natural vegetation. It is likely that the nature
613 of *C. cosyra*'s lifecycle, in which it pupates in the soil over two months,
614 facilitates its transition to other crops that begin to fruit one to two months
615 after mango fruiting has ended. Thus, the wild host may only act as a
616 temporary alternate host at the end of mango fruiting, and greater
617 likelihood of predation in natural vegetation may reduce pest numbers.

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768

769 **Figure Legends**

770 **Fig. 1.** Fly abundance per marula fruit with distance from the margin into natural
771 vegetation (data from N = 3 farms). Lines and equations represent negative
772 binomial glm fits of mean values \pm 1 SE. Point size is weighted by frequency
773 of fruit with the same number of flies emerging per distance point. The y-axis
774 is truncated to exclude five data points for visual clarity (40, 46 and 54 flies
775 per fruit at 8 m from the margin, 36 at 40 m and 55 flies at 275 m) but all data
776 were included in analyses.

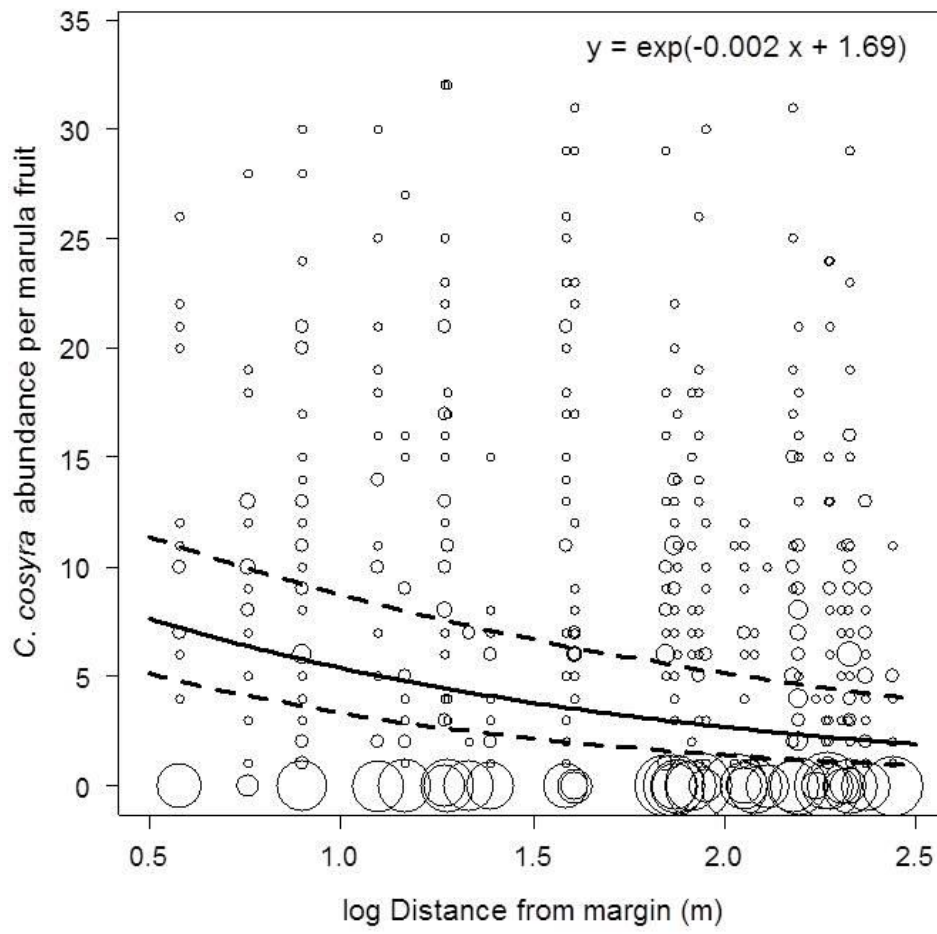
777 **Fig. 2.** Fly abundance per marula fruit in three periods differing in relative
778 marula/mango resource availability (data from N = 3 farms): 1) Late/Late
779 '14: late marula fruiting coincides with late mango (2014), 2) Early/Peak '15:
780 early marula fruiting coincides with peak mango fruiting (2015) and 3)
781 Late/Post '15: late marula fruiting coincides with post mango fruiting (2015).
782 Letters denote differences in infestation intensity per fruit between sample
783 periods, with significance at $\alpha = 0.05$. The y-axis is truncated to exclude five
784 data points for visual clarity (46 and 54 flies per fruit in early season 2015,
785 and 36, 40 and 55 in late season 2015) but all data were included in analyses.

786 **Fig. 3.** Fly abundance per fruit at increasing distance from the habitat margin
787 into (a) natural vegetation and (b) mango fields (data from N = 1 farm). Lines
788 and equation represent model of best fit \pm 1 SE. Point size is weighted by
789 frequency of fruit with the same number of flies emerging per distance point.
790 Figure does not include an outlier (51 flies emerging at 50 m from margin)
791 from mango fields and trends are derived from model that excluded the
792 outlier.

793 **Fig. 4.** Fly abundance per SensusTM trap in mango fields and natural vegetation
794 in early and late April and May 2014 (data from N = 1 farm). Letters denote
795 differences in abundance between habitats and periods, with significance at α

796 = 0.05 determined from negative binomial GLMM. The y-axis is truncated to
797 exclude three outliers >20 flies per trap for visual clarity.
798

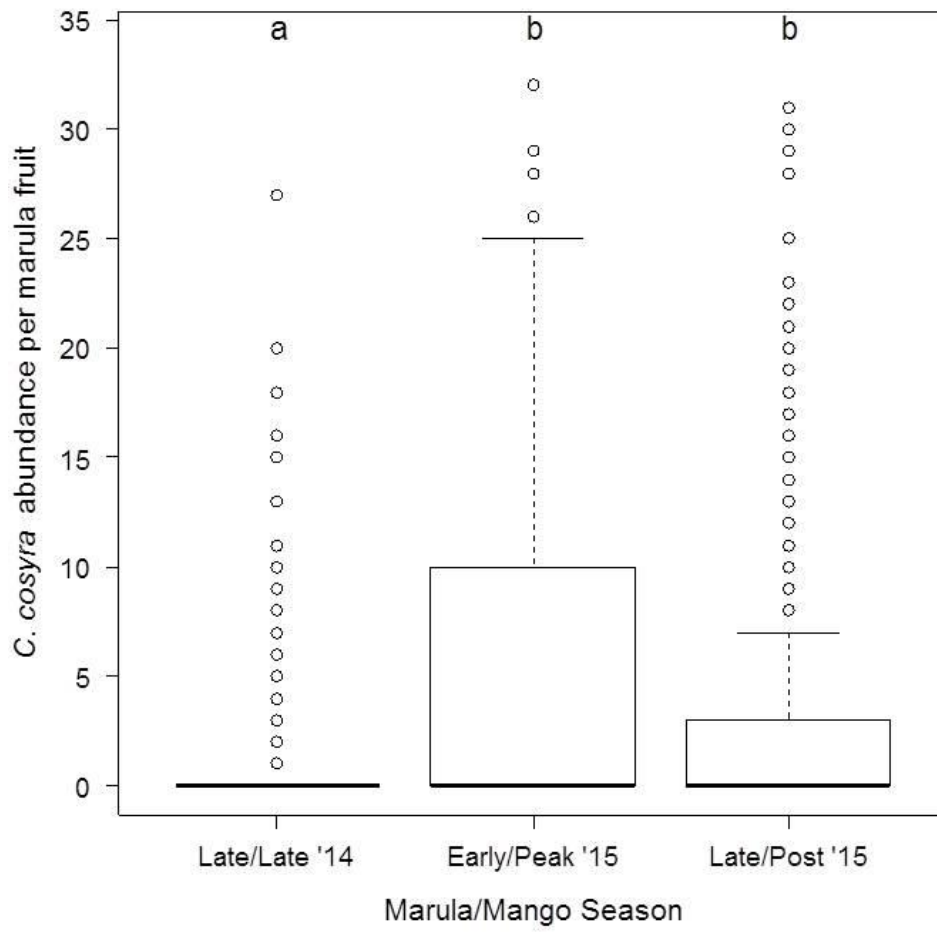
799 **Figure 1**



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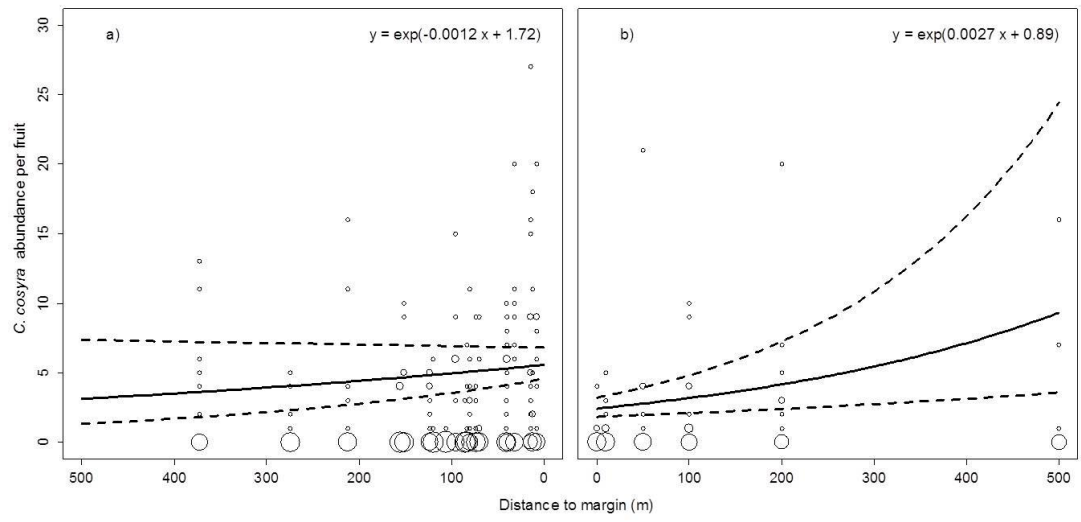
802 **Figure 2**



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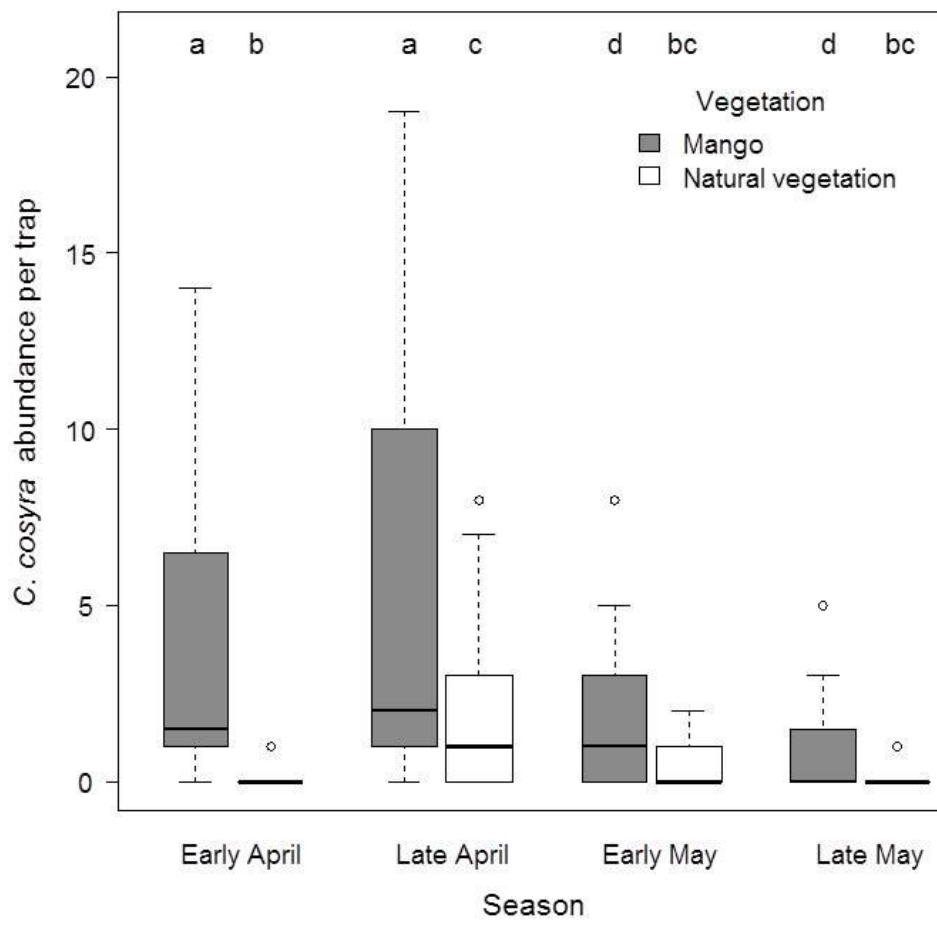
805 **Figure 3**



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808 **Figure 4**



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