A meta-analytic investigation of the potential for plant volatiles and sex pheromones to enhance detection and management of Lepidopteran pests

Article

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1 **Title Page**

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12   **Abstract**

13   Effective early detection, monitoring and management methods are critical for reducing the

14   impacts of insect pests in agriculture and forestry. Combining host plant volatiles with sex

15   pheromones could enhance trapping methodologies, whilst the use of non-host volatiles could

16   improve the effectiveness of pest management through repellency effects. In this

17   meta-analysis approach, we analysed 51 studies that used electroantennograms (EAG), wind

18   tunnels, and/or field traps, to evaluate the antennal and behavioural responses of Lepidoptera

19   to sex pheromones combined with attractant or repellent plant volatiles. Proposed attractant

20   plant volatiles had a positive association with female Lepidoptera responses to sex

21   pheromone, but effects on males were highly variable, with unexpected repellency reported in

22   some studies. Repellent plant volatiles were significantly or near-significantly negatively

23   associated with male attraction to sex pheromones but were scarcely studied. Sub-group

24   analysis identified that male responses to sex pheromone were reduced when the dose of

25   attractant plant volatile relative to sex pheromone was increased. Green-leaf volatiles were

26   associated with the strongest positive effects for males in field traps. Multiple-compound

27   attractant plant volatile blends were less effective than single compounds in field studies. Our

28   analysis demonstrates, i) the potential value of combining host plant volatiles with sex

29   pheromones to capture females rather than only males, ii) the importance of identifying

30   appropriate host plant volatiles and optimal relative doses, and iii) the potential for non-host

31   plant volatile use in pest management strategies.

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35

Introduction

Insect pests have major economic and environmental impacts within both forestry and agricultural systems worldwide (Culliney, 2014; van Lierop et al., 2015), which is predicted to be exacerbated because of projected climate change scenarios and increased risk of the establishment of non-native invasive species through global trade (Deutsch et al., 2018; Lehmann et al., 2020). The identification of pheromones and plant volatile chemicals which may attract or repel insect pests is a critical research area that could facilitate the development of more effective early detection and monitoring tools and improved or alternative management approaches (Larson et al., 2020; Mafra-Neto et al., 2022). In the Coleoptera for example, successful applications of plant volatiles in insect pest management include the combination of a host plant volatile with a sex pheromone to attract emerald ash borer *Agrilus planipennis* Fairmaire to traps (Ryall et al., 2012; Wittman et al., 2021), and anti-aggregation pheromones combined with non-host volatiles to repel mountain pine beetle *Dendroctonus ponderosae* Hopkins from forestry crops (Fettig & Munson, 2020).

Lepidoptera (butterflies and moths) include many of the most serious pests of plants and have been reported to make up eight of the top 20 most studied arthropod pests, which includes diamondback moth *Plutella xylostella* L., cotton bollworm *Helicoverpa armigera* Hübner, and codling moth *Cydia pomonella* L. (Willis, 2017). Plant volatile lures, typically derived from the insect's favoured host plant species, have previously been shown to be effective in attracting adult Lepidoptera, especially females (Szendrei & Rodriguez-Saona, 2010). Furthermore, the identification of sex pheromones for many Lepidopteran pest species in recent years has led to the development of effective species-specific traps, although these typically only catch males (Witzgall et al., 2010; Rizvi et al., 2021). The combination of host plant volatile lures with sex pheromones therefore has potential to improve capture rates of males whilst also attracting females, on the premise that females are attracted to volatiles associated with favoured host plants, and males are attracted to females located on optimal hosts (Reddy & Guerrero, 2004; Szendrei & Rodriguez-Saona, 2010; Bruce & Pickett, 2011; Xu & Turlings,

63   2018). In addition, the identification of non-host plant volatiles which repel pests could lead to

64   more effective management options, such as 'push-pull' strategies which aim to 'push' pests

65   away from high priority areas using repellent plant volatiles or appropriate non-host plants,

66   whilst simultaneously using attractant volatiles to 'pull' the target pest into traps or to lower-

67   risk areas (Cook et al., 2007; Eigenbrode et al., 2016).

68   Early studies in the 1980s and 1990s found that combining host plant volatiles with sex

69   pheromone lures did improve capture rates of male moths compared with pheromone-only

70   lures (reviewed in Landolt & Phillips, 1997). A number of subsequent studies, however, have

71   found that proposed attractant plant volatiles unexpectedly reduce male capture rates (e.g.

72   Meagher, 2001; Hu et al., 2013; Barros-Parada et al., 2018) or fail to catch females (Tang et

73   al., 2012). Several possible explanations have been suggested to explain the variable

74   effectiveness of candidate attractant plant volatiles. The choice of host plant volatile used

75   within combined lures is an important factor which depends on target species (e.g. Tang et

76   al., 2012; Hu et al., 2013; Mujica et al., 2018), and in some cases effects have been classified

77   according to the type of compound such as green leaf volatiles, floral aromatics or terpenes

78   (Fang et al., 2018). In addition, the dosage of host plant volatiles and their ratio to the sex

79   pheromone has been shown to be an important factor in some cases, with several studies

80   demonstrating that that the dosage of plant volatile can determine whether there is an

81   attractant or repellency effect of a certain plant volatile on male response of a target species

82   to its sex pheromone (e.g. Hu et al., 2013; Yu et al., 2015; Xiang et al., 2019). In the field, trap

83   design can also influence the effectiveness of combined lures (Gregg et al., 2018), because

84   trapping area (i.e. the trap's behaviourally effective plume reach) could depend on trap type,

85   and a plant volatile which is attractive at distance could act as a repellent at close proximity to

86   the insect (Kvedaras et al., 2007). Other factors which might conceivably influence the effects

87   of plant volatiles combined with sex pheromones include; (i) host specialism of the target

88   species, since host-specialists might be more attracted to or repelled by particular volatiles;

89   (ii) blend complexity, given that blends of host volatiles are often more attractive than a single

90   component (Gregg et al., 2018); and (iii) habitat, given that background odour influences the

91   interaction between plant volatiles and pheromones (Cai et al., 2017). However, these factors

92   have yet to be systematically investigated in the context of combining plant volatiles with sex

93   pheromone lures.

94   The current lack of systematic evidence to explain why host plant volatiles can unexpectedly

95   reduce the attraction of male Lepidoptera to sex pheromones and/or fail to attract females,

96   and whether non-host volatiles can repel male Lepidoptera from sex pheromones, is a

97   constraint to ongoing research of pest management strategies for some Lepidoptera species.

98   As such, the aim of this study was to evaluate the effect of proposed attractant or repellent

99   plant volatiles on the antennal and behavioural responses of adult Lepidoptera to sex

100   pheromone in laboratory and field studies. In addition, we considered which factors might be

101   most important in designing effective combined pheromone-plant volatile lures, by evaluating

102   the influence of plant volatile category, plant volatile blend complexity, ratio of the plant volatile

103   to sex pheromone, host specialism of the target insect, habitat type, and trap type, on the

104   attraction of male Lepidoptera to plant volatiles. We also investigated spatial patterns of

105   attraction of males and females to combined pheromone-plant volatile lures in wind tunnels.

106   We then discuss how our findings relate to previous studies which have investigated the

107   effects of plant volatiles alone (e.g., Szendrei & Rodriguez-Saona, 2010).

108

109   **Materials and Methods**

110   *Literature search*

111   A search of the literature was undertaken using Scopus in early 2022. The following search

112   term was used within article title, abstract and keywords: pheromone AND (volatile OR

113   kairomone OR allomone OR semiochemical) AND ("wind tunnel" OR olfactometer OR EAG

114   OR electroantennogram OR trap*). Studies were initially screened by reviewing their titles,

115   abstracts, and main text as appropriate, and included in the meta-analysis if they met all of

116   the following criteria: (i) results presented for a species of Lepidoptera; (ii) the study compared

117   the effects of plant volatile(s) combined with a conspecific sex pheromone simultaneously at

118   the same source, versus a sex pheromone-only control, on the response of the target species.

119   The two treatments otherwise comprised exactly the same specifications (e.g. trap type) and

120   the same sex pheromone constituents; (iii) for field trapping, sites which were not under mating

121   disruption or sterile moth release treatments; (iv) sufficient text in English to decipher the

122   results, and (v) adequate and clearly presented statistical information (e.g. means, standard

123   errors, and sample sizes) for inclusion in the meta-analysis models. Studies which failed the

124   final criterion were included in the Discussion. A non-systematic supplemental search of

125   Google Scholar was also undertaken to identify any additional references including grey

126   literature. Upon completion of the systematic search, references cited in the most recent

127   publications were screened to obtain any additional relevant studies.

128   Volatiles which were tested as both attractants (e.g. host volatiles) and repellents (e.g. non-

129   host volatiles) were included but were evaluated separately. Both male and female adult

130   Lepidoptera were included. The literature search was global with no geographic restrictions.

131   We aimed to include behavioural laboratory studies such as electroantennogram (EAG)

132   responses, choice experiments such as olfactometers, and wind tunnels, in addition to field

133   trapping studies. However, only three choice experiment publications were identified (Xiao et

134   al., 2002; Ma et al., 2016; McCormick et al., 2017), therefore, this method was not included in

135   the meta-analysis.

136   A total of 1699 publications were returned by the search term. The majority of these did not

137   report data for Lepidoptera. Therefore, after screening according to the above criteria, 51

138   studies were selected for inclusion in the meta-analysis (listed in Supplementary Material 1),

139   comprising 9 EAG studies, 23 wind tunnel studies, and 35 field-trapping studies (note that

140   some of the 51 studies included more than one method).

141   *Calculation of effect sizes*

142   Data was extracted from each publication and compiled into separate databases for EAG,

143   wind tunnel, and field-trapping studies. Where necessary, data was extracted from figures

144   using WebPlotDigitizer Version 4.5 (Rohatgi, 2021). The response of Lepidoptera to combined

145   plant volatile-sex pheromone lures versus pheromone-only lures was measured as follows

146   according to each experimental method: for EAG studies, response was measured as

147   electrical antennal signal (which could equally represent an attractant or repellent response);

148   for wind tunnel studies, response was measured as the number of individuals achieving a

149   certain stage in the tunnel (e.g. take-off, half-way, approach to lure; recorded in separate

150   rows); and for field trapping studies, the response was defined as the number of individuals

151   captured in traps. Sex of the target insect was recorded, where stated. Where no female

152   captures were reported, the entire paper was reviewed for any reference to female captures;

153   if the paper stated that no females were captured, this was added into the effect size database

154   for each experiment.

155   All analysis was undertaken using the 'metafor' package (Viechtbauer, 2010) in R version

156   4.0.2 (R Core Team, 2020). Effect sizes were calculated using standardized mean difference

157   (Hedges, 1981) for EAG and field studies, or log odds ratio for wind tunnel studies because of

158   the proportion data. The 'treatment' was insect response to the combined plant volatile and

159   pheromone lure, and the 'control' was response to the pheromone-only lure.

160   *Meta-analysis models*

161   Meta-analysis models were built using the 'rma.mv' function in the 'metafor' package. To

162   account for the non-independence of experiments and studies, a hierarchical random effects

163   structure was specified comprising each effect size nested within experiment number (where

164   specified), nested within study ID. In addition, for wind tunnel data, stage of the wind tunnel

165   (e.g. take-off, halfway, approach to lure) was nested within experiment number. Confidence

166   intervals and significance tests were calculated using the *t*-distribution, which is more
167   conservative than the Z-distribution with less risk of Type I error.

168   Initially, overall meta-analysis models were built to test the effect of attractant or repellent plant
169   volatiles on adult Lepidoptera responses to sex pheromone according to each of the three
170   methods (EAG, wind tunnel, and field-trapping). Subgroup analysis was then used to
171   investigate causes of inconsistent effects among studies (i.e. heterogeneity) for attractant
172   volatiles.

173   *Subgroup analysis*

174   Subgroup analysis was performed to identify any differences in responses to combined versus
175   pheromone-only lures according to sex, host specialism, trap type, habitat, complexity of the
176   volatile blend, ratio of plant volatile to pheromone, and type of volatile chemical. These
177   subgroups were selected based on their expected influence on effect sizes, either
178   hypothetically or from previous evidence (as explained in the Introduction). A separate model
179   was built for each subgroup and method (EAG, wind tunnel, field-trapping), because different
180   data subsets were needed for each subgroup (Table 1). In each model, the subgroup was
181   specified as a moderator in the model.

182   In each subgroup model, the intercept term was removed to provide effect sizes for each level.
183   Data was filtered to only include males (apart from the sex subgroup), because males and
184   females responded differently, and males were much better represented in the data than
185   females. The significance of levels within each subgroup was tested using the omnibus
186   moderator test in the metafor package for models with the intercept term included, to test the
187   null hypothesis that the subgroup has no influence on effect sizes.

188   In addition, sex-specific differences in responses to combined attractant lures versus
189   pheromone-only lures at varying stages in wind tunnels was analysed by including the
190   interaction between sex and wind tunnel stage as a moderator, with the intercept removed.

191   Subgroup data was extracted from each publication where provided. Specialism was classified

192   according to the main host range of the study species according to CABI's Invasive Species

193   Compendium (CABI, 2022), with other sources used where necessary (Supplementary

194   Material 2). Specialists were defined as having main host plants within one taxonomic family,

195   while generalists had main hosts within more than one taxonomic family. Plant volatile types

196   were classified into seven categories (Table 1) based on their chemical composition. Values

197   for ratio of plant volatile to sex pheromone were quantified by standardising the amount of

198   plant volatile per one equivalent unit of sex pheromone. This quantity varied enormously

199   among studies, therefore, the amount of plant volatile relative to sex pheromone was further

200   standardised within each study using the 'scale' function in R.

201   *Sex ratios*

202   Ratios of female to male Lepidoptera were calculated for each field trapping study which

203   reported data for both sexes. The effect of combined attractant lures versus pheromone-only

204   lures on sex ratio was tested using a mixed model in the 'lme4' package (Bates et al., 2015),

205   where the sex ratio was log(x+1) transformed to account for positive skew. Random effects

206   comprised experiment number nested within study ID. Marginal means were calculated using

207   the 'emmeans' package (Lenth, 2021) and back-transformed.

208   *Publication bias*

209   Publication bias was assessed by visual inspection of funnel plots, and via a multilevel

210   meta-regression model with the square-root of the inverse effective sample size as a

211   moderator. This model tests whether larger effect sizes are associated with larger standard

212   errors, which would indicate publication bias (Nakagawa et al., 2022). Evidence of publication

213   bias was found for the EAG models according to both funnel plots and the standard error

214   moderator models, although given that only nine studies were available for this method, the

215   apparent publication bias could be a chance effect. Therefore, the findings for the EAG models

216   are presented as preliminary results, which require further research.

217 *Influential cases*

218 The influence of individual effect sizes on the model outputs was tested by calculating

219 DFBETAS values in the 'metafor' package. In accordance with the guidance for this function,

220 DFBETAS values greater than 1 were considered to be influential effect sizes. This was

221 detected in one model, the sex subgroup model for EAG studies. Omitting the five influential

222 effect sizes from this model did not substantially alter the results; the moderator and each sex

223 was still significant and the contrast between the sexes was greater. Therefore, the full model

224 is presented.

225

226 **Results**

227 A total of 1561 effect sizes were extracted from 51 studies, comprising 126 from 9

228 electroantennogram (EAG) studies, 993 from 23 wind-tunnel studies, and 442 from 35 field-

229 trapping studies (note that some papers fell into more than one category). The majority of

230 these studies reported effects for plant volatiles tested as attractants, while only 3 wind tunnel

231 studies and 4 field trapping studies tested proposed repellents. The number of publications

232 rose sharply after 2010 (Figure 1). The publications reported data from a total of 27

233 Lepidopteran species, comprising 6 in EAG studies, 15 in wind tunnel studies, and 21 in field-

234 trapping studies. The most frequently studied species were oriental fruit moth *Grapholita*

235 *molesta* Busck (included in 11 of 57 studies) and codling moth *Cydia pomonella* L. (10 of 57

236 studies). The field-trapping data originated from 11 countries across Asia (14 studies), North

237 America (14 studies), Europe (4 studies), Australia/New Zealand (2 studies), and South

238 America (1 study).

239 Attractant plant volatiles had a significant positive association with Lepidoptera responses

240 (both sexes) to sex pheromones in field-trapping studies (0.210 ± 0.069 SE, t = 3.028, p-value

241 = 0.003) and in the more limited number of EAG studies (effect size 1.347 ± 0.395 SE, t =

242 3.413, p-value < 0.001), but the effect was not significant in wind tunnel studies (0.241 ± 0.149

243 SE, t = 1.619, p-value = 0.106). Repellents had a significant negative association with male

244 Lepidoptera responses to sex pheromone lures in wind tunnels (effect size -1.120 ± 0.177 SE,

245 t = -6.338, p-value < 0.001), and a near-significant negative association with male capture

246 rates in pheromone traps in the field (-1.243 ± 0.646 SE, t = -1.924, p-value = 0.062). No data

247 on combining repellents with sex pheromones was available for EAG studies or for females.

248 There was significant heterogeneity in the effect of combined attractant lures (i.e. plant volatile

249 and pheromone) versus pheromone-only lures on adult Lepidoptera responses, for all three

250 methods (EAG: Q = 609 (df = 125), p-value < 0.001; wind tunnel: Q = 3702 (df = 935), p-value

251 <0.001; field-trapping: Q = 669 (df = 352), p-value < 0.001), indicating that variation in effect

252 sizes was greater than expected based on sampling error alone. Subgroup analysis explained

253 some of this variability, demonstrated by the significant moderator tests for five of the seven

254 subgroups, according to at least one method (Figure 2). The five significant effects comprised;

255 (1) females responded more strongly than males to the combined lures compared with sex

256 pheromone lures alone, which was consistent across all three methods (EAG, wind tunnel,

257 and field trapping) but only significant for field trapping; (2) significant differences among plant

258 volatile categories on male responses to sex pheromone in wind tunnels, where fruit volatiles

259 were associated with the strongest attraction effects. In field traps, effect sizes were

260 significantly higher for green leaf volatiles, although plant volatile category was not significant

261 overall; (3) significantly stronger effects of male responses to combined host plant volatiles

262 with pheromone lures versus pheromone-only lures in agricultural rather than orchard

263 habitats; (4) significant effects of blend complexity on male responses to combined lures in

264 the field, with stronger attractant effects associated with single-component plant volatile

265 blends; and (5) significantly stronger associations of male responses to sex pheromone when

266 combined with lower doses of plant volatiles across all three methods (EAG, wind tunnel, and

267 field trapping). Trap type and host specialism were not significant sub-groups for any method,

268 although consistently stronger associations of male responses to combined lures were

269 observed in specialist rather than generalist species across methods.

270   Captures in field traps were dominated by males in both the pheromone-only and combined

271   lures, although the latter captured significantly higher proportions of females (t = 3.767 (df =

272   205.7), p-value < 0.001). Estimated marginal mean sex ratios were 0.051 females per male in

273   pheromone-only traps, increasing to 0.100 females per male in the combined lure traps.

274   A comparison of sex-specific responses within wind tunnels revealed a strong differentiation

275   in female responses to combined plant volatile and sex pheromone versus pheromone-only

276   sources at the activation and take-off stages (Figure 3). By contrast, significant differences in

277   male responses to combined versus pheromone-only lures were only seen at the final

278   approach stage (Figure 3).

279

280   **Discussion**

281   The indications from our meta-analysis study highlighted that proposed attractant plant

282   volatiles had a significant positive association with adult Lepidoptera responses to sex

283   pheromones in EAG and field-trapping studies. Similarly, proposed repellents, such as non-

284   host volatiles, had a significant negative association with male responses to sex pheromones

285   in wind-tunnel trials, and a near-significant negative association in field trapping studies,

286   although only 3 and 4 studies were available, respectively.

287   A number of sub-group factors significantly influenced the effect of combined plant volatile-

288   sex pheromone versus pheromone-only lures across EAG, wind tunnel and field-trapping

289   studies (Figure 2): (i) responses of females to the combined versus pheromone-only lures

290   were consistently stronger than males (but only significantly so in field-trapping studies), (ii)

291   lower ratios of plant volatile to sex pheromone were associated with a stronger response to

292   combined lures in males, and (iii) there was an indication that host-specialist male Lepidoptera

293   responded more strongly to the combined lures than generalists. The properties of the plant

294   volatile, in terms of blend complexity and chemical category, were significant factors for certain

295   methods. Attractant volatiles had a stronger effect on male responses to sex pheromones in

296   agricultural than in orchard habitats. Analysis of wind tunnel studies revealed that the

297   combination of plant volatiles with sex pheromones increased female attraction at an early

298   stage, but aided male attraction at the final approach stage (Figure 3).

299   *Interactions between attractant plant volatiles and sex pheromones*

300   A previous meta-analysis reported that attractant plant volatiles alone have a significant effect

301   on insect herbivore captures, particularly in Lepidoptera, with stronger effects on females than

302   males (Szendrei & Rodriguez-Saona, 2010). This is supported by a more recent study

303   included in our meta-analysis (Judd et al., 2017a), albeit other studies reported similar

304   responses of both sexes to attractant plant volatiles alone (Li et al., 2018; Kong et al., 2020).

305   In contrast, sex pheromone lures are designed to be highly effective for males, but are typically

306   ineffective for females. Our meta-analysis indicates that combined sex pheromone-plant

307   volatile lures are more effective than pheromone-only lures at attracting both sexes, although

308   captures continue to be dominated by males due to the potency of sex pheromones. However,

309   our findings support those of individual studies which reported highly variable success in

310   combining proposed attractant plant volatiles with sex pheromones to attract males (e.g.

311   Meagher, 2001; Hu et al., 2013; Barros-Parada et al., 2018).

312   *Attractant vs repellent plant volatiles*

313   Repellent plant volatiles were far less studied than attractants, with only 4 field-trapping

314   studies included in our meta-analysis, compared with 27 studies on proposed attractants.

315   Despite the limited research in this area, plant volatiles tested as repellents relatively

316   consistently deterred males from sex pheromones, particularly in wind tunnel studies, in

317   contrast to proposed attractants which had highly variable outcomes. A similar pattern has

318   been reported for studies of the effects of plant volatiles alone on herbivorous insects

319   (Szendrei & Rodriguez-Saona, 2010). Non-host plant volatiles can interfere with male

320   attraction to females, and suppress female egg-laying (McNair et al., 2000; Jactel et al., 2011),

321   demonstrating their potential application in push-pull strategies (McNair et al., 2000; Cook et

322   al., 2007) or mating disruption (Wang et al., 2016). However, more field studies are needed,

323   given the lack of overall significant effect (p-value = 0.062) in our meta-analysis.

324   *Sex-specific differences*

325   Females consistently responded more strongly than males to combined lures compared with

326   sex pheromone-only lures, especially in field studies. This is perhaps unsurprising given the

327   low effectiveness of sex pheromone lures on female attraction; the addition of plant volatiles

328   to sex pheromone traps increased the proportion of females from ca. 5% to 10% relative to

329   male captures. As such, a key advantage of combined plant volatile and sex pheromone lures

330   is the potential to attract both female and male Lepidoptera, albeit males typically remain

331   dominant. This could have applications in mass trapping or monitoring programmes where

332   detecting females is advantageous. However, the number of field studies reporting data for

333   female captures was limited (16, compared to 27 for males), and only 4 of these 16 specified

334   that no females were captured. As such, the significant positive effect of combined attractant

335   lures on female capture rates could be affected by reporting bias. Where combined lures do

336   not capture females, this could be explained by the limited mobility of females in some species

337   (Li et al., 2012a; Miluch et al., 2014) and the repellent effect of conspecific sex pheromone

338   (Barnes et al., 1992; Weissling & Knight, 1996; Judd et al., 2017b), although this appears to

339   vary among species (Jósvai et al., 2016; Judd et al., 2017a).

340   *Relative dosage: less is more?*

341   Our findings strongly corroborate previous reports from individual studies that higher

342   concentrations of host plant volatile relative to sex pheromone can inhibit male Lepidopteran

343   responses to sex pheromones (e.g. Hu et al., 2013; Yu et al., 2015; Xiang et al., 2019). This

344   effect was significant even for the limited number of EAG studies, suggesting that the addition

345   of host plant volatiles at high relative doses do not repel males, given that EAG responses do

346   not differentiate between attractant and repellent effects, but instead interfere with the

347   attraction effect of sex pheromones (Deisig et al., 2014). This response could potentially help

348   males avoid heavily defoliated host plants. If the relative concentration of plant volatile is too

349   low however, it might not have any observable effect (Varela et al., 2011; Barros-Parada et

350   al., 2018). As such, there is likely to be an optimal ratio of plant volatile to sex pheromone,

351   which will depend on the component chemicals and target species. Although ratio of repellent

352   plant volatile to sex pheromone was not included in this meta-analysis due to limited previous

353   research, some evidence suggests that the effect could be simpler, with stronger repellent

354   effects at higher relative doses of plant volatile (Jactel et al., 2011; Wang et al., 2016).

355   Similarly, the effect of relative plant volatile dose on female attraction could be simpler, for

356   example, higher doses of pear ester can increase female capture rates (Knight et al., 2005;

357   Mitchell et al., 2008).

358   *Blend complexity: keep it simple?*

359   Unexpectedly, the use of single plant volatiles with sex pheromones outperformed more

360   complex plant volatile blends in terms of male capture rates in the field. Although a previous

361   meta-analysis of plant volatile effects without sex pheromones found that blend complexity

362   increased effectiveness (Szendrei & Rodriguez-Saona, 2010), our findings suggest that using

363   complex blends with sex pheromones could increase the risk of plant volatiles interfering with

364   male responses to sex pheromones, as discussed above. For instance, in the case of

365   *Grapholita molesta*, the lowest doses of (Z)-3-hexenyl acetate and 1-undecanol increased

366   male capture rates by approximately 4.8 and 3.1 times, respectively, compared with

367   pheromone-only traps (Yu et al., 2015). However, when these two plant volatiles were

368   combined, capture rates were only 2.4 times higher than the pheromone-only controls. The

369   authors hypothesise that this decrease in effectiveness was due to interference among the

370   plant volatile compounds.

371   *Plant volatile categories*

372   There were no consistent differences in the effect of plant volatile compound type on male

373   responses to pheromones across laboratory and field studies. Our findings indicated that

374 green leaf volatiles were associated with the strongest responses of males to sex pheromones

375 in the field, and were the most commonly studied chemical category. In contrast, fruit volatiles

376 (limited to pear ester) were associated with the strongest attractant effects in wind tunnel

377 studies.

378 A wide variety of plant volatiles were reported in the literature. For example, 37 individual

379 compounds were included in our meta-analysis of field trapping studies, in addition to blends

380 of multiple compounds. These were typically selected based on their identified presence in

381 host plants or previous success in attracting the same or similar species. (*Z*)-3-hexenyl acetate

382 was the most frequently studied plant volatile, appearing in 9 of the 35 field trapping studies,

383 while pear ester and phenylacetaldehyde were tested in 7 and 6 field studies, respectively.

384 Other alcohols and aldehydes were also frequently studied, such as (*Z*)-3-hexen-1-ol and (*E*)-

385 2-hexenal which were each tested as unblended volatiles in three field studies. The

386 relationship between plant volatile and growth stage or condition of the host plant (defoliated

387 or undefoliated) could also be relevant in determining their interactive effects with sex

388 pheromones on Lepidoptera (Tang et al., 2012).

389 The variable effects of plant volatile categories are unsurprising given the diversity of

390 compounds within each category, while their effects also depend on target species and

391 background odour. For example, linalool enhanced the attraction of codling moth *Cydia*

392 *pomonella*, but inhibited the attraction of tobacco cutworm *Spodoptera litura* Fabricius, to their

393 respective sex pheromones (Yang et al., 2004; Fang et al., 2018). In addition, the effects of

394 herbivore-induced plant volatiles on phytophagous insect behaviour may depend on their

395 survival strategy, e.g. gregarious versus solitary species (Guo & Wang, 2019). Therefore,

396 understanding the host plant volatile profiles of the target insect species, and their attraction

397 to damaged versus healthy plants, may be important to assemble informed hypotheses for

398 potential future lure development.

399   *Influence of habitat and host specialism*

400   The positive effects (either synergistic or additive) of adding plant volatiles to pheromone traps

401   on male capture rates were higher in herbaceous-crop agriculture than in orchard habitats,

402   despite a similar number of studies in the meta-analysis. This could be because in herbaceous

403   crops, combined traps are often used to increase male captures (e.g. Li et al., 2012b; Miluch

404   et al., 2014; Fang et al., 2018), while in orchard pest management, the aim is often to attract

405   both sexes (e.g. Light, 2016; Knight et al., 2017; Mujica et al., 2018). Only 4 studies were

406   available in forestry contexts, and whilst results were generally positive overall, but non-

407   significant, only one of the studies reported female capture rates (Jósvai et al., 2016).

408   Pheromone traps positioned within host plant tree species have been shown to capture

409   significantly more males of a specialist Lepidoptera than those in suboptimal congeneric hosts

410   (Williams & Jonusas, 2019), while single-species forest stands tend to be more susceptible to

411   specialist pests than generalists (Jactel et al., 2021), indicating potential applications for

412   attractant and repellent plant volatiles for host-specialist Lepidopteran tree pests.

413   Our hypothesis that males of host-specialist Lepidoptera species would exhibit stronger

414   responses to plant volatiles than generalist species was tentatively supported across all three

415   methods but was not statistically significant. As such, the use of plant volatiles to increase

416   male capture rates in pheromone traps might be easier to achieve for host specialist species.

417   *Other potential causes of heterogeneity*

418   Although our analysis provides some insights into the lack of effect or unexpected repellent

419   effects of proposed attractant plant volatiles on male Lepidoptera responses to sex

420   pheromones, other potentially important variables could not be investigated due to insufficient

421   data. Mating experience is one such variable that can influence Lepidopteran responses to

422   sex pheromones and plant volatiles, because newly-mated males can stop responding to sex

423   pheromone and may also change their response to plant volatiles (Deisig et al., 2014). For

424   example, green leaf volatiles of host plants increased the response of unmated but not mated

425 diamondback moth *Plutella xylostella* males to sex pheromone in a wind tunnel experiment
426 (Reddy & Guerrero, 2000). This factor could potentially confound field studies where mating
427 experience is uncontrolled.

428 Weather conditions such as temperature, humidity, and wind speed are also likely to affect
429 success of combining plant volatiles with sex pheromones, and could explain some of the
430 discrepancy between wind tunnel and field trapping results. For example, flight activity of
431 moths is dependent on suitable temperatures and wind speeds, while wind speed also affects
432 trapping area (Elkinton & Cardé, 1988; Schouest Jnr & Miller, 1994; Reardon et al., 2006).

433 The choice and dosage of sex pheromone can also be relevant, although studies have found
434 conflicting evidence of how these factors interact with plant volatiles. Stronger attractant
435 effects have been demonstrated for plant volatiles combined with less effective pheromones
436 (Knight et al., 2014; Miluch et al., 2014; Sans et al., 2016; Borrero-Echeverry et al., 2018), and
437 with pheromones at underdosed or overdosed concentrations (Schmidt-Büsser et al., 2009).
438 However, other studies have found the reverse pattern, where host plant volatiles reduce male
439 attraction to incomplete synthetic pheromones, but increase attraction to optimal pheromones
440 (Sans et al., 2016; Borrero-Echeverry et al., 2018). It is likely that this interaction depends on
441 the combination of pheromone and plant volatile and whether the plant volatile stimulates
442 receptors for missing pheromone components or interferes with pheromone detection (Deisig
443 et al., 2014; Miluch et al., 2014). Clearly initial dosage and release rates of both sex
444 pheromones and plant volatiles are likely to be important factors influencing trap efficacy.

445 Finally, the effect of plant volatiles on Lepidopteran responses to sex pheromone appears to
446 depend on background odour, which can interfere with plant volatile lures when their
447 components overlap (Cai et al., 2017). This perhaps might explain the contrasting results from
448 field studies in different crop types, while findings from laboratory studies in controlled
449 environments are often not corroborated by field studies (Deng et al., 2004; Li et al., 2012b;
450 Tang et al., 2012; Miluch et al., 2014).

451   *Conclusion*

452   This meta-analytic review provides evidence that the addition of attractant plant volatiles to

453   sex pheromone traps leads to higher captures rates of adult Lepidoptera. A key advantage of

454   combined plant volatile-sex pheromone lures is the potential to develop trapping approaches

455   that attract both sexes, which could improve early detection, monitoring, and mass trapping

456   programmes. Although research on proposed repellent plant volatiles is limited, we found

457   preliminary evidence of repellent effects on males towards sex pheromones, which presents

458   opportunities to develop natural pest management strategies such as push-pull and mating

459   disruption approaches.

460   However, effects of attractant plant volatiles on male responses to sex pheromones were

461   highly variable, and in some cases resulted in unexpected repellent effects. We found

462   evidence that this effect depends on factors such as relative concentrations of plant volatile to

463   sex pheromone, category of plant volatile tested, and blend complexity. Hence, our findings

464   demonstrate the potential applications of both attractant and repellent plant volatiles in

465   Lepidoptera pest management, but that careful consideration of attractant lures is critical to

466   minimise interference of plant volatiles on male attraction to sex pheromones. In addition,

467   further research, particularly field trials, is urgently needed to investigate repellent volatiles.

468

474

475 **Competing Interests**

476 Competing interests: The authors declare none.

477

478 **Supplementary Materials**

479 Supplementary Material 1: List of studies included in the meta-analysis, according to the three

480 methodological categories: electroantennograms (EAG), wind tunnels, and field trapping.

481 Supplementary Material 2: List of Lepidoptera species included in the meta-analysis and their

482 host specialism.

483

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706 **Tables**

707 **Table 1** Subgroup analysis for attractant plant volatiles, showing the subsets of data applied to each

708 subgroup and level of replication.

Subgroup	Levels	Data subset	Number of data points (and studies)		
			EAG	**Wind tunnel**	**Field trapping**
Sex	Male Female	Excludes unsexed data	87 (9) 39 (2)	807 (21) 129 (3)	213 (27) 134 (20)
Plant volatile blend	Single Multiple	Males	78 (8) 9 (4)	572 (17) 235 (13)	143 (23) 70 (15)
Habitat	Agriculture (herbaceous crops) Forest Orchard		N/A	N/A	108 (12) 19 (4) 86 (13)
Specialism	Generalist Specialist		30 (4) 57 (5)	352 (10) 455 (11)	86 (14) 127 (13)
Trap type	Delta Inverted cone Panel Unitrap Water trap		N/A	N/A	73 (14) 10 (2) 2 (1) 22 (3) 100 (6)
Plant volatile category	Fruit volatile GLV Homoterpene Monoterpene/oid Organosulfur Phenylpropanoid Sesquiterpene	Males, excludes blends of >1 type	0 34 (5) 0 16 (5) 0 22 (4) 7 (2)	13 (2) 256 (14) 14 (3) 100 (11) 0 125 (9) 68 (7)	18 (5) 83 (12) 1 (1) 18 (6) 3 (1) 28 (7) 7 (2)
Ratio (standardised amount of plant volatile (PV) per unit of sex pheromone (SP))	PV:SP > mean* PV:SP < mean*	Males, experiments where >1 ratio tested	18 (2) 56 (2)	123 (10) 370 (10)	50 (13) 73 (13)

709 * mean ratio calculated separately for each study

710

711

712   **Figure Captions**

713   **Figure 1.** Cumulative number of studies included in the meta-analysis by publication date, for the three

714   different methods (electroantennogram, wind tunnel, and field trapping). Each study reported the effects

715   of combined sex pheromone and plant volatile lures versus pheromone-only lures on antennal or

716   behavioural responses of Lepidopteran pests.

717   **Fig. 2** Effect (with 95% confidence intervals) of combined plant volatile and sex pheromone lures,

718   versus pheromone only, on the responses of adult Lepidoptera according to six subgroups (rows) and

719   three methods (columns). Positive effects represent higher responses to the combined lures compared

720   with pheromone-only lures. One subgroup, trap type in field-trapping studies, is not shown because

721   none of the levels were significant and the results were not informative. Data was filtered according to

722   each subgroup, as shown in Table 1. Asterisks denote where there was a significant difference between

723   levels of the subgroup (F test, with intercepts), where *** = $p<0.001$, ** = $p<0.01$, and * = $p<0.05$.

724   Abbreviations: PV = plant volatile, SP = sex pheromone.

725   **Fig. 3** Effect (with 95% confidence intervals) of combined attractant plant volatile and sex pheromone

726   lures, versus pheromone-only lures, on male and female Lepidoptera according to wind tunnel stage.

727   Positive values are associated with stronger effects of the combined lure versus the pheromone.
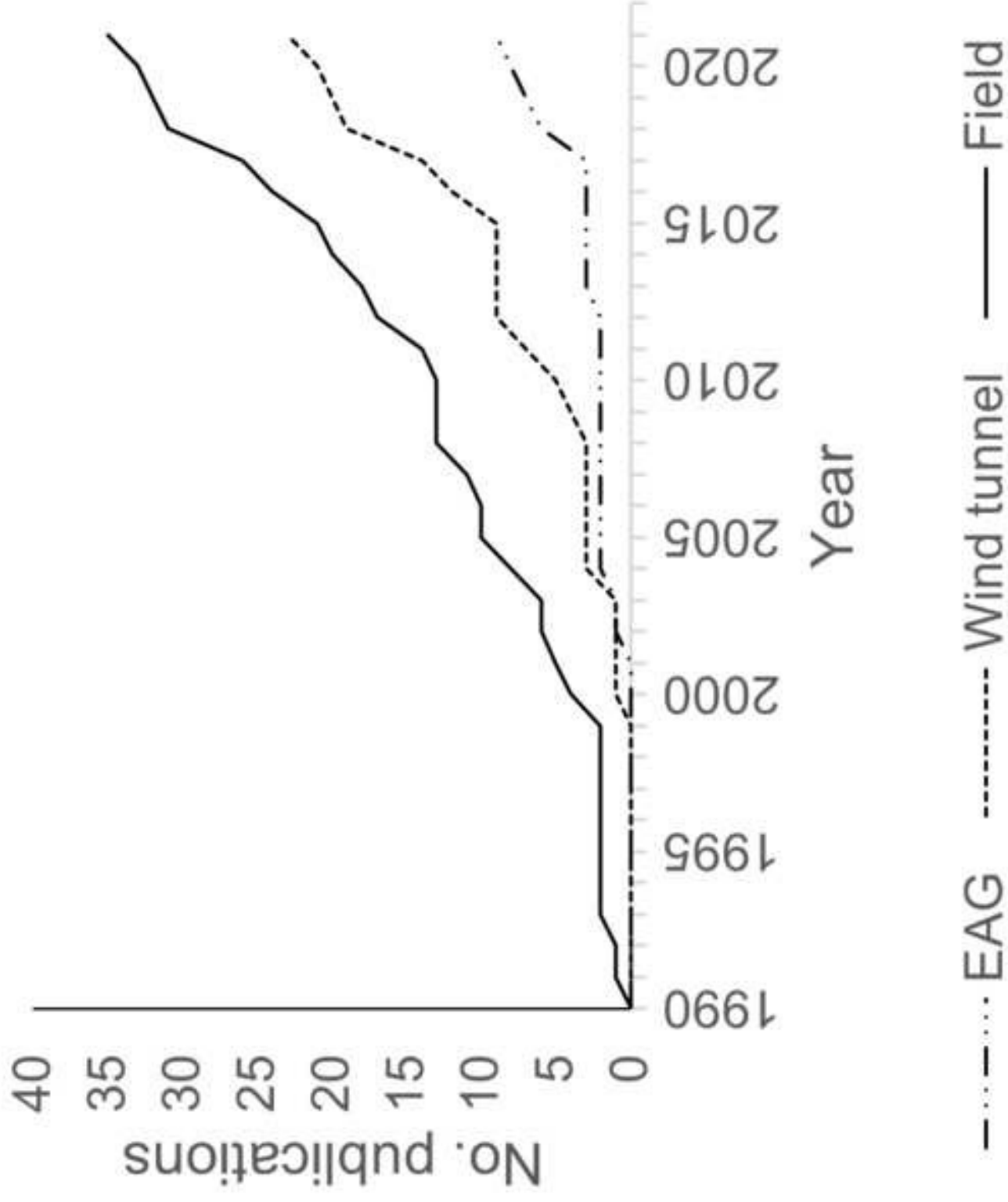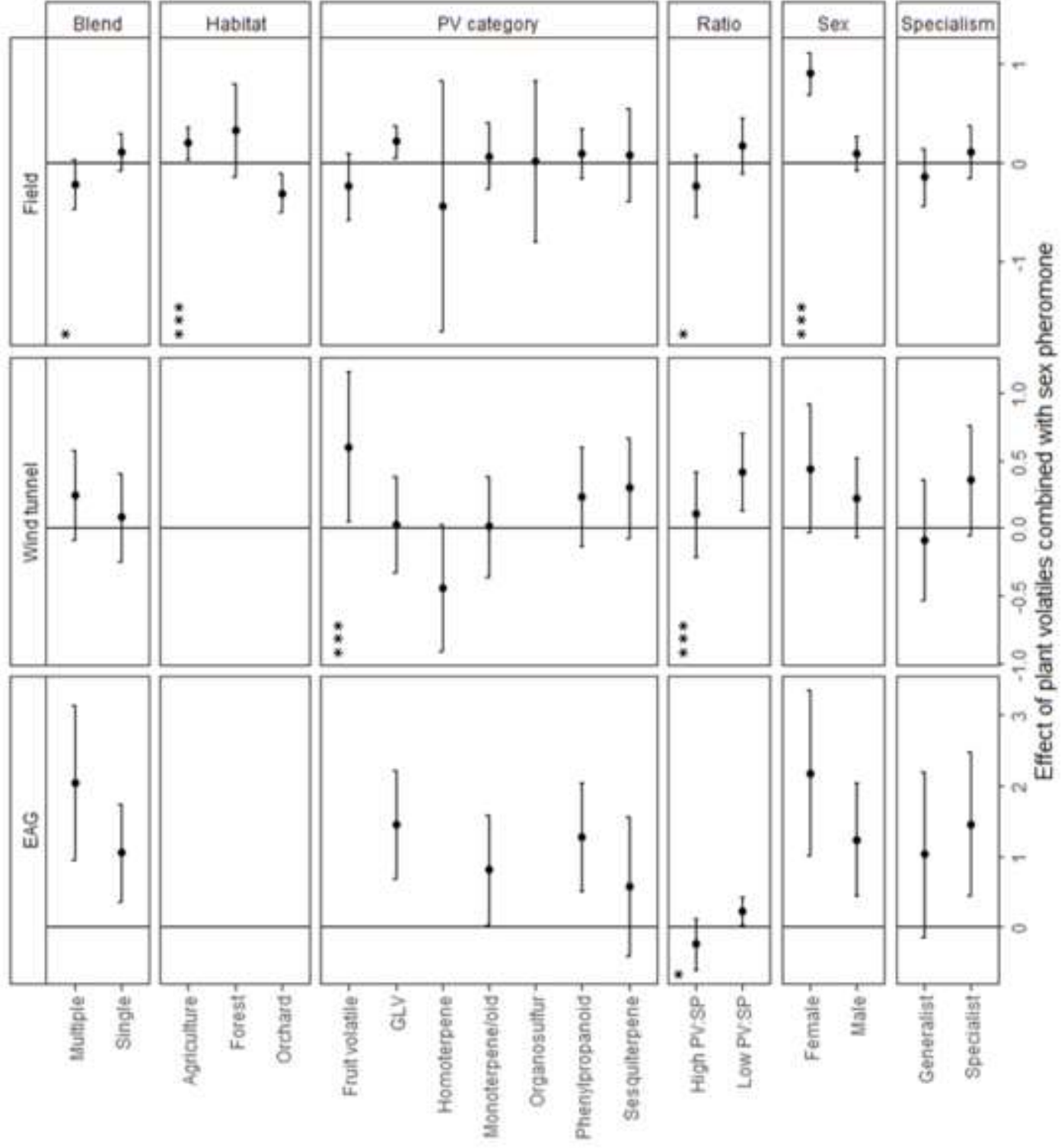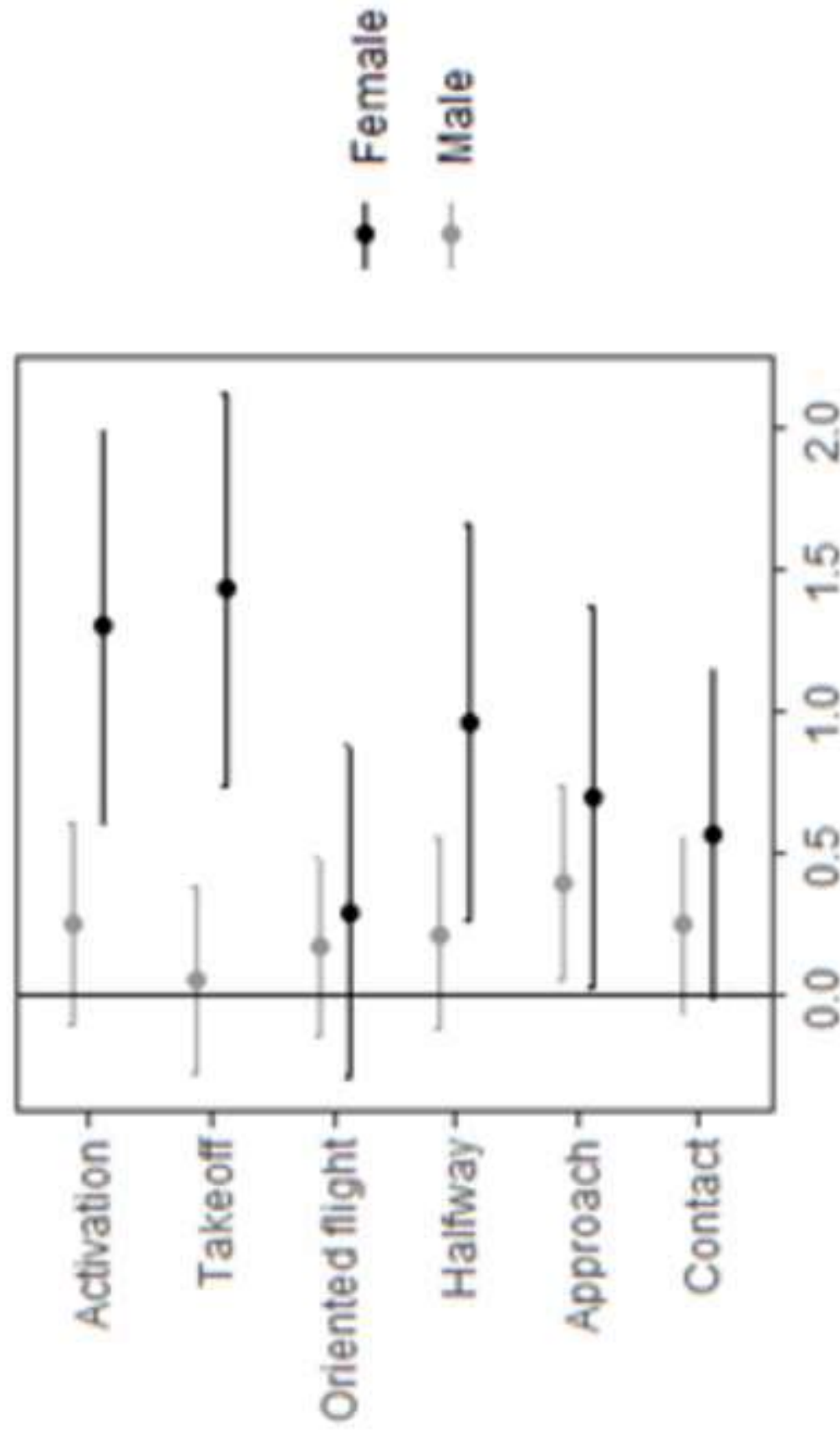
Figure 1

Figure 2

Figure 3

Effect of plant volatiles combined with sex pheromone

Female
Male

Activation
Takeoff
Oriented flight
Halfway
Approach
Contact