Contrasting patterns of fig wasp communities along Mt. Wilhelm, Papua New Guinea.

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5   **Contrasting patterns of fig wasp communities along Mt. Wilhelm, Papua New Guinea.**

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1

19   **Abstract**

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21   The fig (Moraceae) and pollinating fig wasp (Agaonidae) mutualism is best known as a

22   model system for the study of coevolution in plant-pollinator interactions and its central role

23   in shaping vertebrate communities in tropical forests. Figs also host myriad antagonistic

24   parasitic fig wasps which impose costs on both partners threatening mutualism stability.

25   Spatio-temporal variation in parasitic wasp abundance is a key factor in mitigating these

26   effects. Because fig wasps are temperature sensitive and likely vary in their ability to traverse

27   environmental gradients, we expect community assemblages and abundance of both

28   pollinating and non-pollinating fig wasps to respond to changes along an elevational gradient.

29   In the present study, we compare the fig wasp communities and abundance of three fig

30   species growing along the slopes of the Mount Wilhelm altitudinal gradient in Papua New

31   Guinea. We quantified wasps from over 100 male fig trees and calculated seed set for 55

32   female trees along each of the species' distribution on the transect. Our results show that the

33   abundance of both pollinating and non-pollinating fig wasps follow a mid-elevation peak,

34   consistent with fig species richness found in the same transect. The patterns, however, are

35   different according to the host's species distribution. Seed set remained relatively constant

36   along the gradient for all species with some decrease along higher elevations, potentially

37   affecting connectivity along the gradient. As suggested for insects in general, temperature and

38   habitat diversity appear to play a fundamental role in the species richness and abundance of

39   fig wasps.

40   **Key words:** *Ficus*; pollination; non-pollinating fig wasps; seed set; altitudinal gradient.

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41 INSECT SPECIES RICHNESS AND COMPOSITION ALONG ALTITUDINAL GRADIENTS IS KNOWN TO

42 VARY WITH ELEVATION. These patterns, however, are different among different taxonomic

43 groups (Warren *et al.* 1988, McCoy 1990, Peck *et al.* 2008, Maunsell *et al.* 2015). As insects

44 are ectothermic, they are particularly sensitive to temperature (Arroyo *et al.* 1982, García-

45 Robledo *et al.* 2016) and correspondingly less diverse at higher elevations and lower

46 latitudes. The vast majority of angiosperms are pollinated by insects which inextricably links

47 plant and insect fitness (Lowry *et al.* 2008, Ollerton *et al.* 2011, Ellstrand 2014). The

48 abundance of wasps and beetles tends to decrease with increasing elevation and instead, more

49 abundant dipteran communities pollinate flowers at higher elevations, implying a shift in

50 pollinator composition which influences plant reproductive strategies and success (Warren *et*

51 *al.* 1988). Also affected by elevation is parasitoid wasp abundance and species richness. Both

52 are highest at mid-elevations, due in part to the abundance of potential hosts. This distribution

53 likely influences structure and function of food webs by affecting plant herbivore and/or

54 pollinator interactions (Peck *et al.* 2008, Maunsell *et al.* 2015).

55   Obligate pollination mutualisms offer a tractable and relatively simple model for

56 measuring fitness related traits along environmental gradients (Souto-Vilarós *et al.* 2018)

57 because species specificity is high and traits can be easily quantified. Parasites and

58 parasitoids of mutualisms add an extra layer of complexity because direct and indirect costs

59 on mutualistic partners can influence the stability of such mutualisms (Bronstein 2001), and

60 in some cases, abiotic factors may even shift mutualists into parasites and vice versa

61 (Kawakita *et al.* 2015). Studies focusing on the response of trophic interactions with

62 increasing elevation have found that while there is a general trend for insect predation and

63 parasitism rates to decline, the predators and parasitoids involved do not necessarily respond

64 in the same manner and in many cases depend on host distribution, as well as their density

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65 and temporal overlap during key life stages (Péré *et al.* 2013, Maunsell *et al.* 2015, Corcos *et*

66 *al.* 2018).

67   For this study, we focus on the fig (Moraceae) and fig-wasp (Agaonidae) mutualism,

68 one of the most specialized nursery pollination systems (Cook & Rasplus 2003), where the

69 reproductive success of both parties depends on species-specific encounters. Briefly

70 summarizing, female wasps emerge from the figs (called syconia) and are guided by volatile

71 signals as they search for a receptive fig of the same host species. Upon landing, mated and

72 pollen-loaded wasps enter the floral cavity through a narrow passage (ostiole) and pollinate

73 the flowers within. While approximately half of described fig species are monecious, having

74 both male and female flowers within the same fig, the remainder are functionally dioecious

75 meaning that sexual function are segregated between trees (though they are anatomically

76 gynodioecious; Bronstein 1988, Corlett *et al.* 1990). Monoecious figs contain both long-

77 styled flowers (which frequently develop as seeds) and short-styled flowers that are more

78 accessible for wasps to oviposit, thus housing the next generation of wasps. In dioecious

79 species, male figs contain flowers suitable for oviposition and produce only wasps becoming

80 nurseries while female fig trees deceive the wasps to enter and pollinate, but wasps are unable

81 to oviposit in the long-styled flowers inside and so female fig trees produce only seeds (Galil

82 & Eisikowitch 1968, Kjellberg *et al.* 2005). Some fig-wasps are known for long distance

83 pollen dispersal as these minute insects (1-2 mm) appear to be transported by wind over wide

84 distances of up to 160km (Ahmed *et al.* 2009, Kobmoo *et al.* 2010, Liu *et al.* 2015). Thus far,

85 these findings have been restricted mostly to large monoecious trees which occur at naturally

86 low densities. In contrast there is evidence that dioecious and under-canopy fig trees are

87 clustered into dense local populations and so pollinating fig-wasps do not disperse over such

88 long distances (Dev *et al.* 2011). Figs house a large number of non-pollinating fig wasps

89 (NPFW) which parasitize pollinator larvae or compete for seed resources thus significantly

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affecting pollinator populations and consequentially, fig pollen dispersal (Kerdelhué &

Rasplus 1996, Weiblen *et al.* 2001, Weiblen 2002). NPFW have a fascinating ecology of their

own: ranging from gallers which enter the syconia alongside pollinators to kleptoparasites

which oviposit into pre-existing galls or parasitoids. Many parasitoids oviposit from the

outside of the fig, the ovipositor length correlated with the fig developmental stage at which

these wasps oviposit (Weiblen 2002, Cook & Segar 2010, Borges 2015).

Some authors have suggested that the negative effect of parasitism is stabilized

through temporal and spatial heterogeneity in non-pollinator occurrence and abundance, as

well as variation in the availability of figs at the right developmental stage for them to invade.

So far, the distribution and abundance of NPFW along environmental gradients has

not been well studied, despite the knowledge that parasitism varies with both phenotypic and

environmental variation (Maunsell *et al.* 2015, Yu *et al.* 2018). We suggest that elevational

gradients, which to some extent control for species pool effects, make excellent systems to

study environmentally mediated variation in fitness traits and parasite loads. Such gradients

provide natural spatial structure and environmental clines which mimic more wide scale

variation across the range of a given resource species.

Specifically, we test the hypotheses that (1) pollinating wasp abundance decreases

with elevation, (2) non-pollinator diversity and abundance have a mid-elevation peak due to

mixing between lowland and highland communities, (3) seed set is highly dependent on

pollinator abundance and so will follow the same trend as (1); finally, (4) because fig size

limits the amount of seeds or developing wasps that can fit within them, we also test whether

or not fig size (volume) varies along the gradient.

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METHODS

The study was conducted along an elevational gradient in the central range of New Guinea. The continuously forested Mount Wilhelm (5.7800ºS, 145.0297ºE) gradient ranges from lowland alluvial forest up to lower montane forest and has been previously described in detail elsewhere (Toussaint *et al.* 2014, Marki *et al.* 2016, Robillard *et al.* 2016). Our study was conducted at six sites each with approximately 500 meters elevational intervals from 200m to 2,700m (all elevations stated as above sea level; table 1). Approximately half of the 150 *Ficus* (Moraceae) species recorded for the island occur there along the transect (Berg & Corner 2005) and previous fig species surveys along the transect reveal that some of these species have wide elevational ranges (Novotny *et al.* 2005, Segar *et al.* 2017). For the present study, we focused on three dioecious species endemic to New Guinea and adjacent islands selected on the basis of their distribution along the transect: *Ficus wassa* Roxb., is a botanically recognized species abundant throughout the gradient with a wide distributional range occurring between 200m and 2,700m pollinated by the fig-wasp *Kradibia wassae*; *Ficus arfakensis* King, distributed between 200m and 700m and pollinated by *Ceratosolen solitarius*; *Ficus trichocerasa* Diels is represented by lowland and a highland subspecies with the nominate *F.t. trichocerasa* distributed between 700 and 1,200m and the highland *F.t. pleioclada* distributed between 1,200 and 2,600m, these subspecies appear to be pollinated by undescribed species of *Ceratosolen* wasps. Recent genomic analyses have revealed that these species are pollinated by three, four and two species complexes, respectively (Souto-Vilarós *et al.* 2019), distributed in parapatry along the gradient.

Sampling was conducted between August 2015 and November 2016. At each of six sites along the transect, we tagged several male and female trees of each locally available

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136   focal species and monitored them during the duration of the sampling. For each of the focal

137   trees, we collected up to five ripe figs for each female tagged tree, stored them in plastic pots

138   in a 70% ethanol solution and exported to the University of South Bohemia, Czech Republic

139   for later dissection. Using a microscope, up to two figs selected haphazardly from each pot

140   were dissected (n=112) and all fully developed seeds and all available ovules were counted,

141   seed set was calculated as the number of seeds divided by the number of ovules.

142   For each male tree, figs were sampled either through emergence or dissection

143   methods (Segar *et al.* 2014). For the emergence method, we collected up to five D-stage figs

144   (Galil & Eisikowitch 1968), the stage when wasps are already hatched from the galls and are

145   clustered within the fig cavity, and stored them in individual plastic pots covered with fine

146   mesh. Wasps were allowed to emerge naturally from the figs (n=113) and were immediately

147   collected and stored in 100% ethanol. Wasp individuals were sorted to at least genus and

148   morpho-species level. For the dissection method, a second set of D-stage figs were directly

149   stored in 70% ethanol solution. All collections were sent to the University of South Bohemia

150   for later dissection of figs and sorting and identification of wasps. Up to two figs per tree

151   (n=110) were selected haphazardly and dissected under a microscope and the total number of

152   wasps recorded. Width and height were measured to the nearest 0.01mm using Vernier

153   callipers to calculate fig volume following the standard cone volume formula (as per Segar *et*

154   *al.* 2017):

155   $V = \pi r^2 \, \frac{h}{3}$

156   To test the influence of elevation and fig species on fig volume, seed set and total

157   number of wasps produced, we performed generalized linear models (GLMs) separately

158   using collection site (as elevation) and fig species as explanatory variables. Minimal models

159   were retained using standard backward selection by removing non-significant higher-level

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160 interactions. We used Welch Two Sample t-test to compare fig volume between male and

161 female figs, as there was no significant difference according to sex (see results), volume

162 analyses combined both sexes. Analyses on seed set and wasp numbers were conducted

163 separately for female and male figs. The full models run were: i) fig volume as a response to

164 elevation and species, ii) seed set as a response to elevation and species, iii) total wasps

165 number per fig as a response to elevation and species; further, we separated analyses on

166 wasps to include iv) number of pollinating wasps as a response to elevation and species and

167 v) number of non-pollinating wasps as a response to elevation and species. For all models we

168 fitted a quasipoisson error structure, except for seed set for which we used a Gaussian

169 distribution. Finally, multiple comparisons between elevations were tested for significance

170 using Tukey's test of main effects as implemented in the General Linear Hypothesis function

171 *glht* in the R package 'multcomp' v.1.10 (Hothorn *et al.* 2008). All analyses were conducted

172 in R version 3.5.1 (R Core team 2015).

173 **RESULTS**

174 Fɪɢ Vᴏʟᴜᴍᴇ Vᴀʀɪᴀᴛɪᴏɴ Bᴇᴛᴡᴇᴇɴ Sᴘᴇᴄɪᴇs Aɴᴅ Eʟᴇᴠᴀᴛɪᴏɴ. - We measured volume for a

175 total of 222 figs (female n = 112, male n=110) for each species separately (details

176 summarized in table 1). We initially tested fig volume separately according to tree sex but

177 found no significant difference between them (t = -1.048, df = 266.7, p = 0.295) and so we

178 analyzed the effect elevation has on fig volume for both sexes combined. Elevation affected

179 fig volume, however, the strength and direction varied according to species (Fig. 1): there

180 was a positive effect of altitude for *F. arfakensis* while fig volume remains almost constant

181 for *F. wassa* with declines at the 1,700m and the 2,700m sites. In the case of *F. trichocerasa*,

182 volume increased with elevation for both subspecies.

183 Sᴇᴇᴅ Sᴇᴛ Vᴀʀɪᴀᴛɪᴏɴ Bᴇᴛᴡᴇᴇɴ Fɪɢ Sᴘᴇᴄɪᴇs Aɴᴅ Eʟᴇᴠᴀᴛɪᴏɴ - The effect of fig volume and

184 seed set were analyzed for female figs only using a total of 112 dissected figs and shows that

185 in general, larger figs have higher seed set. Overall, seed production remains constant for all

186 species along the transect (Fig. 2B) with the exception of a significant decrease of seed set for

187 *F. wassa* at the 1,700m site (Tukey HSD test shows significant difference between this site

188 and all other $p.$ < 0.04 except at 200m) . Important to note is that for this species, all mature

189 female figs found at the highest elevation (2,700m) were infested by maggots or decaying on

190 the tree and so we were unable to calculate seed set.

191 Wᴀsᴘ Aʙᴜɴᴅᴀɴᴄᴇ Aɴᴅ Vᴀʀɪᴀᴛɪᴏɴ Bᴇᴛᴡᴇᴇɴ Fɪɢ Sᴘᴇᴄɪᴇs Aᴄʀᴏss Eʟᴇᴠᴀᴛɪᴏɴs - All

192 analyses pertaining to wasp numbers (both pollinators and parasites) were conducted on data

193 from male figs only. Elevation played a significant role on the total number of wasps

194 produced per fig with a distinct mid-elevation peak; however, the effect varies according to

195 fig species (Fig 3). Wasp numbers steadily increased with elevation in *F. arfakensis* and *F.*

196 *wassa* up to the 1,200m site where the former appears to plateau at its range limit (1,700m)

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197 and the latter sharply decreases beyond this point (Fig 3). In the case of *F. trichocerasa*, there

198 is a significant decrease of total number of wasps per fig in subsp. *trichocerasa* while the

199 total number of wasps for *F. t. pleioclada* remains constant between both elevations (Fig 3).

200 Separating the data into pollinator and non-pollinator numbers reveals a similar

201 pattern. Pollinator numbers vary in response to elevation with a sharp increase at the mid-

202 elevation peak (between 1,200m and 1,700m) followed by a decrease in pollinator numbers

203 in the highlands (Fig 4). In the case of NPFWs, the total number of wasps was affected by

204 elevation but the effect varied among species (Fig 5). For both pollinating and non-

205 pollinating wasps associated with *F. arfakensis* elevation had a positive effect on the total

206 number of wasps, however in the case of NPFWs, there is a sharp decline at the species range

207 limit (1,700m) where very few NPFWs were found (mean = 0.75 ± 0.49; Table 1), however,

208 inter-sample variation was high. The effect of elevation for both pollinating and non-

209 pollinating wasps from *F. trichocerasa* was similar for both subspecies. There was a general

210 decline of wasp numbers in *F. t. trichocerasa* and no significant changes in wasp numbers

211 from *F. t. pleioclada.* For *F. wassa* elevation played a significant role on the total number of

212 pollinators per fig with an increase up to the 1,200m site followed by a sharp decline

213 increasing again at the highest elevation site. NPFW numbers remained relatively constant

214 with significant differences between the 700m and 1,200m sites. Notably, the increase of

215 parasitic wasp loads at the 700m site is due to a considerable increase in non-pollinating wasp

216 species richness, rather than exclusively numbers, as at this site we found most figs to host up

217 to six different morphospecies of NPFW (Table 3).

218 In terms of community composition (Table 3), the most diverse community was found

219 in the figs of *F. wassa* with up to eight different genera at the 700m site. Overall, the

220 diversity of NPFW of *F. wassa* remains between one and two genera at each site, with

221 *Philotrypesis* and an Otitesellinae being the most abundant NPFWs found in these figs

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222   commonly found throughout *F. wassa*'s range. In the case of *F. arfakensis*, we found two

223   very abundant species from the genus *Apocrypta*, and *Sycophaga*, in nearly all of the figs

224   sampled. The lowland populations (200m and 700m) supported up to three genera while in

225   the highest elevation of this species (1,700m) we only found five individuals of *Apocrypta*.

226   The NPFW community of *F. trichocerasa* is similar in both subspecies with up to six

227   different genera with, individuals from *Sycophaga* being the most abundant in both

228   subspecies. Nevertheless, the genera between subspecies varied; for instance, in *F. t.*

229   *trichocerasa* we found one species of *Apocrypta* while in *F t. pleioclada* we found wasps

230   from the subfamily Otitesellinae (possibly *Micranisa*) and *Megastigmus*, the latter only

231   known from figs in the section *Malvanthera* (Cook & Segar 2010).

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DISCUSSION

The present study is, to our knowledge, the first to offer insight on fig seed set and wasp load variation along an elevational gradient. We found that elevation substantially affected the variables studied here (fig size, seed set and wasp production). However, the direction of the effect varies between species. As with other taxa (García-Robledo *et al.* 2016, Peters *et al.* 2016, Robillard *et al.* 2016), altitude plays an important role in abundance of both pollinating and NPFWs as well as species richness of the latter. Climatic changes that occur with increasing elevation have been shown to be some of the major factors affecting the distribution and survival of insect species (Jevanandam *et al.* 2013, García-Robledo *et al.* 2016). Temperature decreases with elevation while precipitation tends to increase at higher altitudes directly affecting insect development and survival while the same factors influence the surrounding vegetation, similarly affecting links along the trophic chain (i.e. herbivores and parasitoids). The results presented herein follow the *Ficus*-wide species trends presented by Segar *et al.* (2017) where fig species richness decreases with increasing elevation after a mid-elevation peak. We find wasp production follows this trend with a clear increase with elevation up to between 1,200m and 1,700m followed by a sharp decrease at higher elevations.

Fig female fitness, measured as seed set, remains relatively stable for all species (Fig 2) throughout the transect, similar to findings from Weiblen, Flick & Spencer (1995) in *F. variegata* (69% seed set), a dioecious species distributed through most of South East Asia; however, there is seed set variation between the different sites (Table 1). It is known that reduced seed set in figs is explained by the number wasps entering figs at receptivity (Corlett *et al.* 1990), but is also limited by the amount of pollen they carry, which is often related to

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257 emergence times (with early emerging wasps generally carrying more pollen than late

258 emerging ones; Kjellberg *et al.* 2014). Our results show that even at the range limits of *F.t.*

259 *pleioclada* (2,200m), nearly every available ovule in female figs produced a seed suggesting

260 little pollen limitation occurring when a fig is entered. There is evidence suggesting that seed

261 set increases with foundress wasps entering receptive figs (Nefdt & Compton 1996, Moore &

262 Greeff 2003), as well as more wasps entering bigger figs (Anstett *et al.* 1996). We did find

263 variation in the size of figs along the gradient for some species. However, although the size of

264 figs of *F. arfakensis* steadily increased with increasing elevation, seed set remained constant

265 throughout the elevational range occupied by this species. We did not record the number of

266 foundress wasps entering figs. It was hard to assess the occurrence of multiple foundress

267 wasps in the dissected figs and so we were unable to relate seed set to the number of wasps

268 entering receptive figs. Contrastingly, at the range limits of *F. wassa* (2,700m), we were

269 unable to find figs with seeds. It is known that fig trees abort figs if there are no available

270 pollinators or if there is a mismatch between receptivity of figs and pollinator arrival

271 (Suleman *et al.* 2011). The variation in seed set of *F. wassa* could be attributed to the lack of

272 pollinators available at the highland sites (above 1,700m), where fig trees can survive the

273 colder temperatures, but wasp survival may be limited (Chen *et al.* 2018).

274   We found variation in the total number of wasps in the studied species with increasing

275 elevation having a significant effect (Fig 3). Studies on the monoecious *F. petiolaris* in

276 northern Mexico concluded that foundress wasp distribution likely affects pollinator and non-

277 pollinator abundances as well as overall seed production on the landscape (Duthie & Nason

278 2016). Duthie & Nason (2016) suggest that seed set and non-pollinator production are

279 negatively affected by pollinator abundance which is in turn positively affected by the

280 number of foundress wasps. Foundress arrival appears to be associated with tree aggregation

281 suggesting that habitat connectivity plays an important role in the overall mutualism. Studies

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282 on *F. racemosa* along a disturbance gradient also found that production of non-pollinating fig

283 wasps was higher in highly fragmented habitat (Wang *et al.* 2005). The Mount Wilhelm

284 elevational gradient is continuously forested from the lowland up to the treeline. Souto-

285 Vilarós *et al.* (2019) found that these fig species do form highland and lowland populations

286 often with a distinct mid-elevation 'contact-zone,' however, connectivity between these

287 populations is high (Souto-Vilarós *et al.* 2019) suggesting that variation in wasp abundances

288 may be related to varying conditions along the gradient instead of tree connectivity.

289   The ecology and life history strategies of these NPFWs is beyond the scope of this

290 study, however, placing these wasps along the various trophic levels would greatly contribute

291 to our as of yet limited understanding of NPFW communities. Species richness and

292 abundance of galling wasps influences the diversity of parasitoids and hyperparasitoids.

293 Larger figs have greater number of flowers, which in turn offer more opportunities for wasp

294 colonization (Borges 2015). Indeed, the largest figs in this study, *F. arfakensis,* supported the

295 largest number of pollinating and non-pollinating fig wasps, but not the most diverse

296 communities. Due to our limited taxonomic identification, we cannot rule out the ability of

297 some of these NPFWs to use multiple host species. Although host specificity for NPFW may

298 be less constrained than that of pollinators, it has been suggested that some degree of

299 specificity is still frequent (Jousselin *et al.* 2008, McLeish *et al.* 2012, Duthie & Nason 2016).

300 Ecological and/or morphological requirements for NPFW development such as synchrony

301 with fig development, volatile cues for host recognition, fig wall thickness and/or the

302 presence of other wasps either as hosts, competitors or parasitoids may promote species

303 specificity and/or invasion (Weiblen *et al.* 2001, Marussich & Machado 2007, McLeish *et al.*

304 2012, Borges 2015, Farache *et al.* 2018). The co-occurrence of specific genera in different fig

305 species at the same elevation may be of great interest from a community network perspective.

306 Similarly, under-sampling individual trees may be a constraint in our results. It is known that

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307   NPFWs do not colonize all available figs within a patch due to asynchrony of developing fig.

308   Furthermore, the available species pool is likely to vary over time and space, and hence wasp

309   communities in a given fig crop depend on a multitude of factors (McLeish *et al.* 2012).

310   Molecular approaches would help greatly in determining species turnover and population

311   connectivity between the NPFW groups identified herein. Of particular interest are some of

312   the uncommon associations reported, particularly the occurrence of Otitesellinae wasps and

313   *Megastigmus* in *F. t.pleioclada* figs: both occur alongside *Sycophaga* in the same figs on the

314   same tree. One of the main challenges of describing NPFW assemblages is the variability in

315   their abundance and distribution across fig sections. *Megastigmus* species, for instance, are

316   only known from fig species in subsection *Malvanthera* (Cook & Segar 2010), however, this

317   genus is known to be associated with a wide range of host plants both as seed feeders and

318   parasitoids of gall-makers (Auger-Rozenberg *et al.* 2006). Otitesellinae on the other hand, are

319   well known to parasitize sympatric figs from section *Urostigma* (Jousselin *et al.* 2006).

320   Within our sampling, we found at least two instances of *Megastigmus* and Otitesellinae wasps

321   within reared figs of *F. t. pleioclada* both coming from different elevations. Wider sampling

322   at both inter- and intraspecific level would help reveal if these associations were frequent or a

323   mistake on our part, or by the wasps themselves. Indeed unusual associations in communities

324   at the range edge of figs are more common.

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336 **AUTHORS'CONTRIBUTIONS**

337 V.N., S.T.S., and D.S.V. planned the research and provided input at all stages. G.D.W. and B.I.

338 suggested suitable species for the study. D.S.V., M.S and T.K. conducted and managed all fieldwork

339 aspects with initial assistance of S.T.S. J.M. assisted with data analysis and management of fig

340 dissections. D.S.V. and M.H. analysed the data and interpreted the results. D.S.V. wrote the

341 manuscript with substantial help from all authors. All authors contributed and approved the final

342 version of the manuscript.

343 **DATA ACCESSIBILITY**

344 Data used for this study will be made available through public repositories such as Dryad upon

345 acceptance of the manuscript.

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495 TABLE 1. Summary of collections per species including name of collection sites (female figs only)

Ficus species	Collection Site	Elevation (m)	Female figs (dissected) (Total trees = 55)	Fig volume (±SE)	Seed set (±SE)
F. arfakensis	Kausi	200	6	1.13 ± 0.049	0.739 ± 0.058
	Numba	700	6	1.565 ± 0.063	0.758 ± 0.028
	Memeku	1200	4	2.599 ± 0.311	0.91 ± 0.031
	Degenumbu	1700	6	3.408 ± 0.114	0.794 ± 0.039
F. trichocerasa	Numba	700	9	0.781 ± 0.051	0.98 ± 0.008
	Memeku	1200	10	1.5 ± 0.219	0.975 ± 0.007
F. pleioclada	Degenumbu	1700	9	0.479 ± 0.017	0.7 ± 0.087
	Snowpass	2200	8	0.627 ± 0.064	0.796 ± 0.092
F. wassa	Kausi	200	12	0.599 ± 0.059	0.748 ± 0.053
	Numba	700	12	0.569 ± 0.03	0.786 ± 0.035
	Memeku	1200	10	0.653 ± 0.054	0.79 ± 0.047
	Degenumbu	1700	12	0.464 ± 0.037	0.546 ± 0.071
	Snowpass	2200	8	0.512 ± 0.05	0.795 ± 0.112
	Bruno Sawmill	2700	na	0.351 ± 0.026	na

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TABLE 1 cont. Summary of collections per species including name of collection sites of collections (male figs only)

Ficus species	Collection Site	Elevation (m)	Male figs[b] (Trees = 103)	Infested figs (%)	Number of pollinators (±SE)	Number of NPFW (±SE)	Percentage parasitism (±SE)
F. arfakensis	Kausi	200	35(8)	96	116.571 ± 8.152	22.677 ± 3.489	0.173 ± 0.031
	Numba	700	9(7)	88	247.222 ± 34.29	23.222 ± 9.212	0.098 ± 0.037
	Memeku	1200	12(8)	100	475.833 ± 63.768	98.833 ± 16.692	0.172 ± 0.036
	Degenumbu	1700	9(7)	25	526.556 ± 82.802	0.75 ± 0.496	0.002 ± 0.001
F. trichocerasa	Numba	700	8(8)	100	136.875 ± 23.394	33.125 ± 9.48	0.225 ± 0.074
	Memeku	1200	10(10)	100	89 ± 5.55	14.889 ± 2.939	0.138 ± 0.027
F. pleioclada	Degenumbu	1700	27(13)	95	65.296 ± 8.552	14.792 ± 1.689	0.245 ± 0.018
	Snowpass	2200	12(11)	91	64.667 ± 18.915	20.917 ± 3.487	0.377 ± 0.074
F. wassa	Kausi	200	15(6)	75	126.2 ± 20.018	10.417 ± 3.306	0.082 ± 0.03
	Numba	700	27(10)	95	176.556 ± 36.166	29.792 ± 5.08	0.31 ± 0.071
	Memeku	1200	15(4)	73	344.467 ± 42.177	8.8 ± 4.018	0.037 ± 0.022
	Degenumbu	1700	10(6)	75	77.9 ± 17.805	7.625 ± 2.656	0.073 ± 0.026
	Snowpass	2200	27(13)	75	31.074 ± 6.403	17.826 ± 3.258	0.323 ± 0.059

Bruno Sawmill	2700	7(2)	50	63.571 ± 31.742	3.333 ± 1.846	0.083 ± 0.039

497   [a]Numbers within parenthesis indicate the number of figs which were sorted from emerged wasps. Total numbers include sorted and dissected fig samples

498   TABLE 2. Summary of generalized linear model results and Analysis of Variance for each model

499   tested. Values in bold indicate significant effect of the predictive term on the response variable.

Response	Interaction	χ^2	df	p
Volume				
	Elevation	253.01	5	**<0.001**
	species	941.88	3	**<0.001**
	species:Elevation	104.90	5	**<0.001**
Seed Set				
	Elevation	9.393	4	**0.051**
	species	24.580	3	**<0.001**
Total Wasps				
	Elevation	185.835	5	**<0.001**
	species	128.351	3	**<0.001**
	Elevation: species	66.865	5	**<0.001**
Total Pollinators				
	Elevation	163.735	5	**<0.001**
	species	105.359	3	**<0.001**
	Elevation: species	59.101	5	**<0.001**
Total NPFW				
	Elevation	66.61	5	**<0.001**
	species	41.273	3	**<0.001**
	Elevation: species	60.474	5	**<0.001**

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TABLE 3. Summary of non-pollinating fig wasp community found at each elevation and *Ficus* species. Individuals were reared from individual

syconia and sorted to family and morphospecies when possible.

Ficus species	Collection Site	Elevation (m asl)	Philotripesis black 1	Philotrypesis black 2	Philotrypesis black 3	Philotrypesis O1	Philotrypesis O 2	Otitesellinae 1	Otitesellinae 2	Apocrypta 1	Apocrypta 2	Sycophaga 1	Sycophaga 2	Arachonia 1	Arachonia 2	Arachonia 3	Sycoscapter 1	Megastigmus 1	Ficobracon 1	Epichrysomallinae 1	Epichrysomallinae 2	Eurytomidae1	Eurytomidae 2
F. arfakensis	Kausi	200	1							62	21												
	Numba	700	19							86	27			2									
	Memeku	1200								534	214												
	Degenumbu	1700								5													
F. t. trichocerasa	Numba	700				3							171					11				2	
	Memeku	1200									2		129		2								
F .t. pleioclada	Degenumbu	1700											109						10				
	Snowpass	2200		1					7				182		1				2			2	
F. wassa	Kausi	200						48															
	Numba	700			6		19	38									34	3	34			44	2
	Memeku	1200			7																		
	Degenumbu	1700			22			7															
	Snowpass	2200			89			62															
	Bruno Sawmill	2700			11																		

504   FIGURE 1. Effect of elevation on fig volume for all (sub)species. Effect was calculated using

505   generalized linear model with volume as the response variable to elevation and (sub)species

506   interaction. The interaction of elevation and (sub)species identity is highly significant ($\chi^2 = 104.90$, df

507   = 5, $p <0.001$). Pairwise differences between elevations were tested using Tukey HSD post-hoc test.

508   Different letters indicate significant differences between comparisons ($P < 0.05$).

509   FIGURE 2. Boxplots showing seed set per (sub)species and elevation. Effect was calculated

510   using generalized linear model with seed set as the response variable to elevation and

511   (sub)species interaction. The interaction of elevation and (sub)species identity was not

512   significant and so removed from the model through backwards elimination. The effect of

513   elevation and (sub)species are significant (Elevation $\chi^2 = 9.393$, df = 4, $p <0.051$;

514   (sub)species $\chi^2 = 24.580$, df = 3, $p <0.001$). Pairwise differences between elevations were tested

515   using Tukey HSD post-hoc test. Different letters indicate significant difference between comparisons

516   ($P < 0.05$).

517   FIGURE 3. Effect of elevation on total wasp production for all (sub)species. Effect was

518   calculated using generalized linear model with total wasp as the response variable to

519   elevation and (sub)species interaction. The interaction of elevation and (sub)species identity

520   is highly significant ($\chi^2 = 66.865$, df = 5, $p <0.001$). Pairwise differences between elevations were

521   tested using Tukey HSD post-hoc test. Different letters indicate significant difference between

522   comparisons ($P < 0.05$).

523   FIGURE 4. Effect of elevation on pollinating wasp production for all (sub)species. Effect

524   was calculated using generalized linear model with total pollinating wasps as the response

525   variable to elevation and (sub)species interaction. The interaction of elevation and

526   (sub)species identity is highly significant ($\chi^2 = 59.101$, df = 5, $p <0.001$). Pairwise differences

527   between elevations were tested using Tukey HSD post-hoc test. Different letters indicate significant
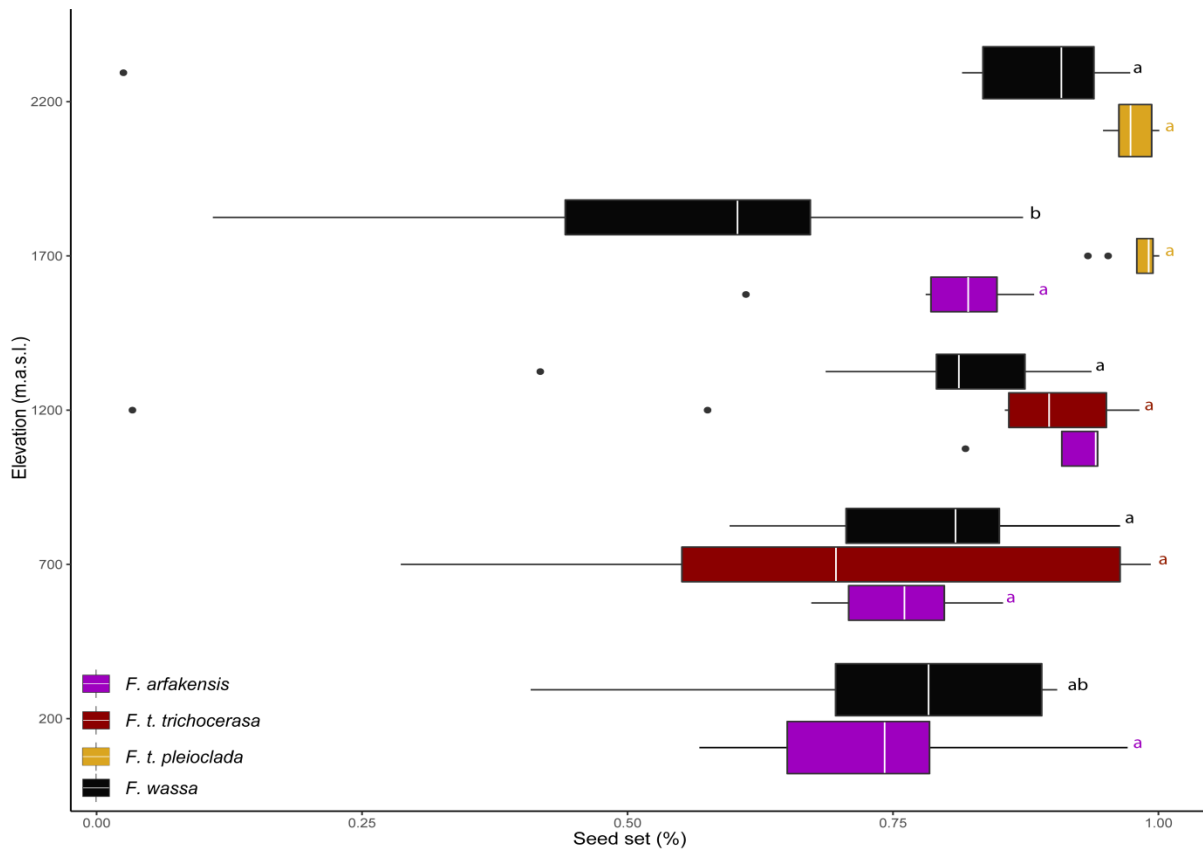
528   difference between comparisons ($P < 0.05$).

29

529   FIGURE 5. Effect of elevation on parasitic wasp production for all (sub)species. Effect was

530   calculated using generalized linear model with total parasitic wasps as the response variable

531   to elevation and (sub)species interaction. The interaction of elevation and (sub)species

532   identity is highly significant ($\chi^2 = 60.474$, df = 5, p <0.001). Pairwise differences between

533   elevations were tested using Tukey HSD post-hoc test. Different letters indicate significant

534   differences between comparisons ($P < 0.05$).
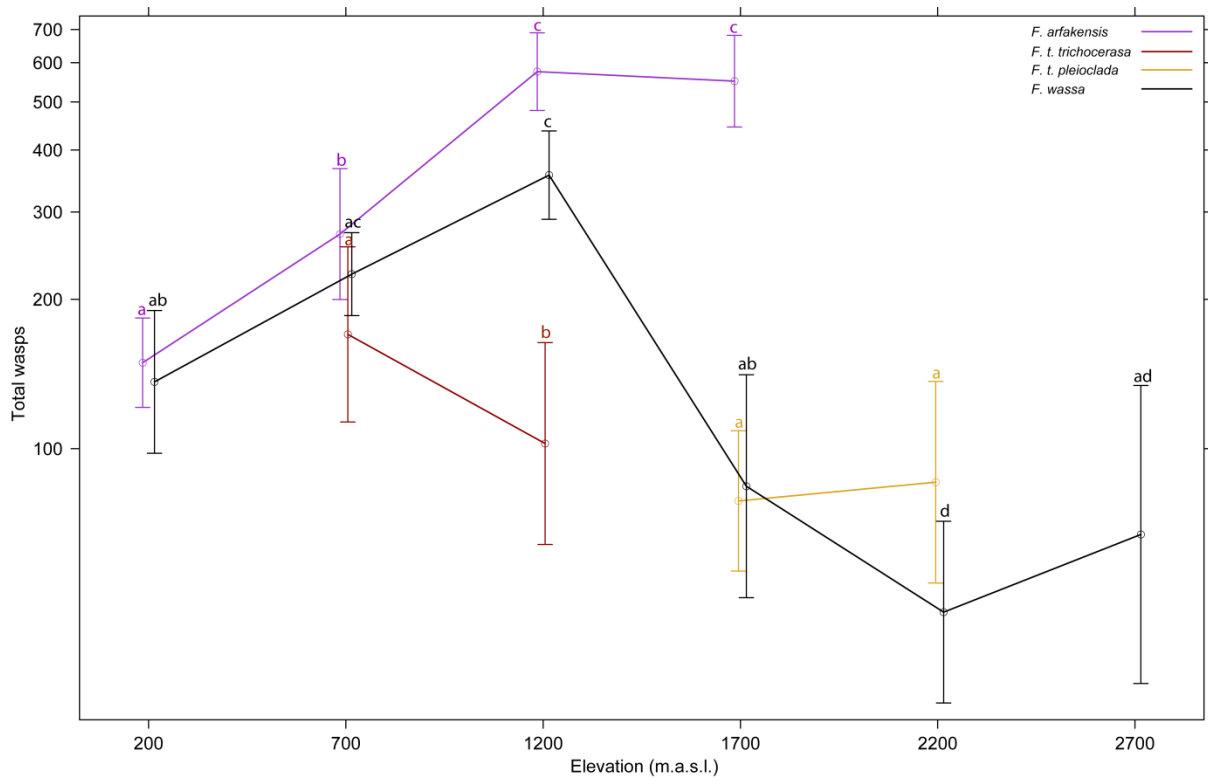
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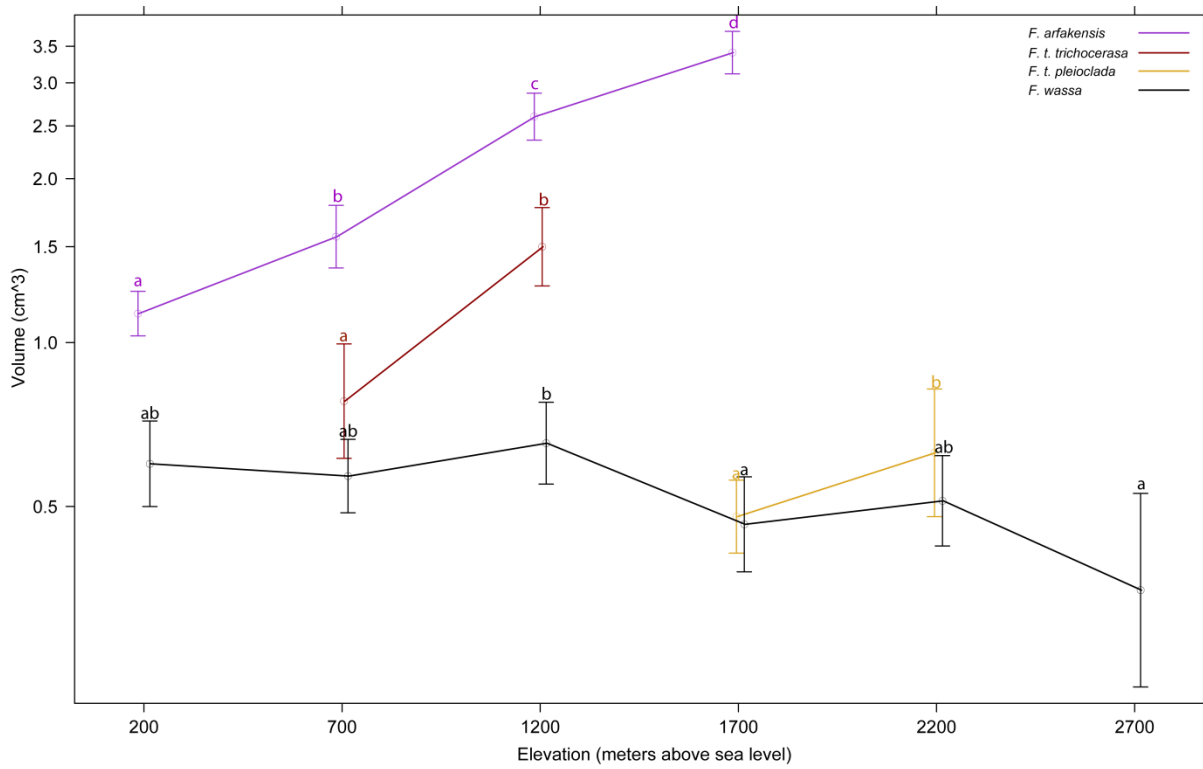
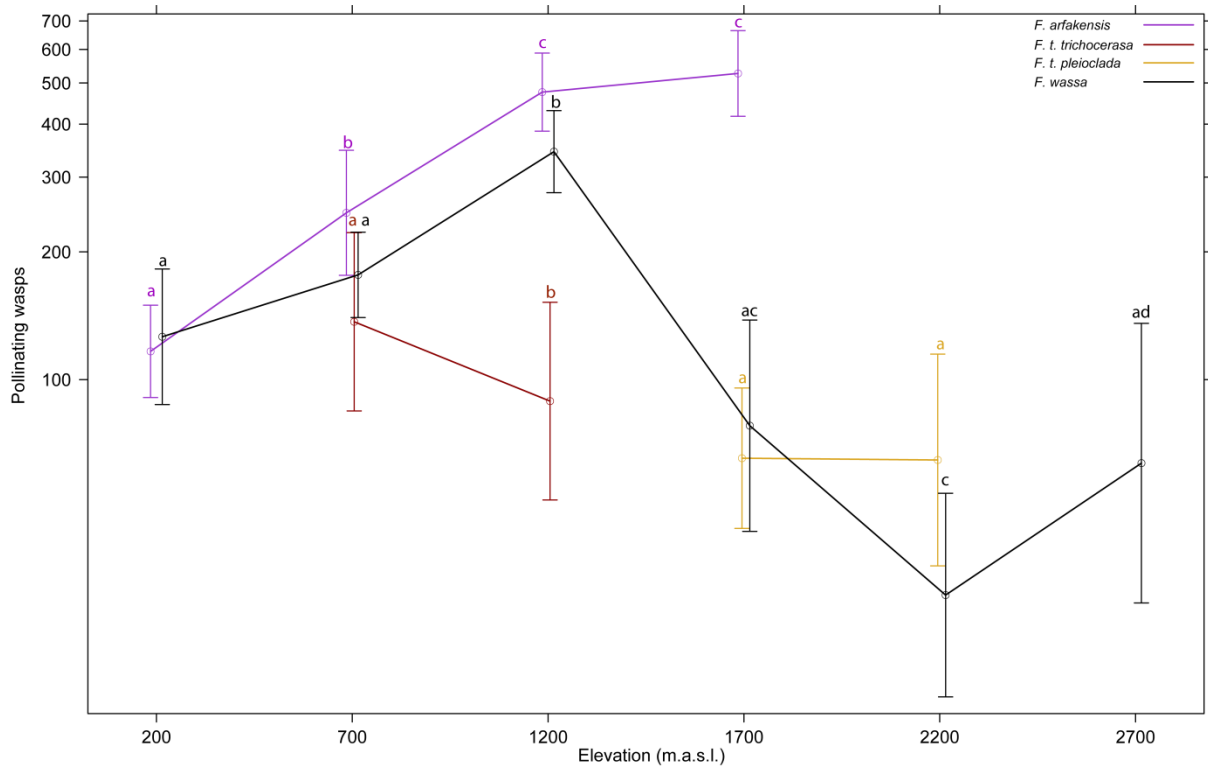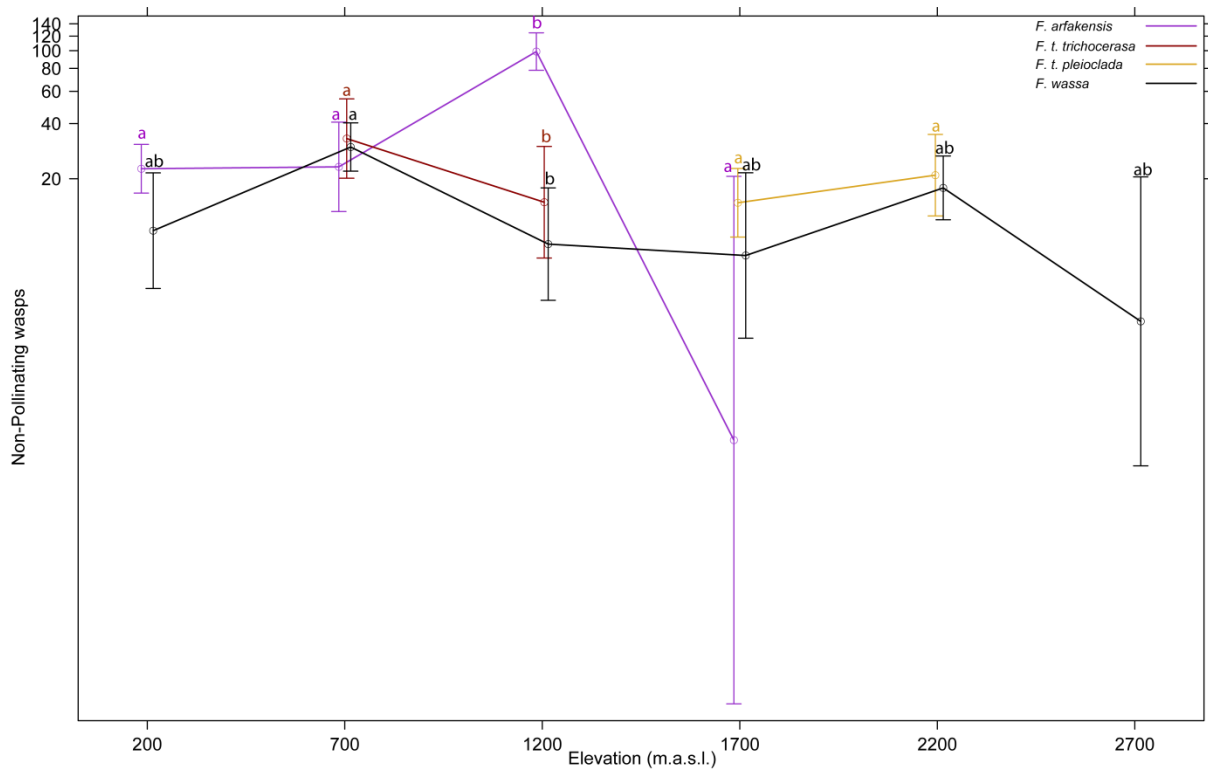
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538 **FIGURE 1**

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541 **FIGURE 2**

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FIGURE 3

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FIGURE 4

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550 **FIGURE 5**

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