Assessing the effectiveness of honey bee pollinators for cultivated blueberries in South Africa

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Abstract

Globally, agricultural crops are often dependent on insect pollination. Blueberries are an example of such a crop and owing to their proposed health benefits they are grown around the world, including locations where their native bumble bee pollinators do not occur. In the absence of bumble bees, blueberry pollination in South Africa and many other parts of the non-native, commercial range is performed primarily by honey bees. Despite this, the effectiveness of honey bee pollination on blueberries remains understudied. This study determined the effect of honey bee pollination on components of fruit yield (fruit set and mass) of five blueberry varieties that are extensively planted in South Africa. For each variety, two metrics were calculated: 1) the benefit of bees — a comparison of fruit yields after exposure to honey bees and fruit yields after honey bee exclusion, 2) the pollination deficit — the difference in yield between hand pollination (maximum yield potential) and yields after exposure to honey bee pollinators. Honey bee pollination consistently resulted in improved yields, although the magnitude of this improvement (i.e., the benefit of bees) was dependent on the variety considered. Similarly, the pollination deficit also varied considerably across varieties and while some varieties appeared to perform close to maximum potential (small pollination deficit), others yielded well below their maximum potential under honey bee pollination. This study demonstrates that honey bees are functional pollinators of blueberries in areas where native blueberry pollinators are absent. However, in such areas, it is important that special focus be given to selecting blueberry varieties that perform well with honey bees as their sole pollinator. Further research is necessary to determine how the pollination deficit of blueberry varieties can be decreased as well as how to increase the effectiveness of honey bee pollination.

Keywords: Honey bee, blueberries, pollination, agriculture, pollination ecosystem service, yield

1. Introduction

Insect pollination is vital for numerous crops, not only to set fruit but also to increase fruit yield (Klein et al., 2007). Consequently, this ecosystem service has been valued at €153 billion per year (Gallai et al., 2009). Although honey bees are globally the most widely used commercially managed pollinator (Garibaldi et al., 2013; Osterman et al., 2021), they are not always the most efficient pollinators and can be outperformed by wild insects (Garibaldi et al., 2013; Osterman et al., 2021). In a comprehensive study using 41 crops, Garibaldi et al. (2013) found that wild insects were often more effective crop pollinators than honey bees and that on average, fruit set doubled after increasing wild insect visitation compared to equivalent increases in honey bee visitation.

One crop where honey bees may be less effective than other pollinators is blueberries. Wild and cultivated blueberries are extremely reliant on insect pollination (MacKenzie, 1997; Fulton et al., 2015; Reilly et al., 2020; Martin et al., 2021;) and are typically pollinated by large bees. These include blueberry bees (Apidae) (Cane and Payne, 1993; Campbell et al., 2018), bumble bees (Apidae) (Mackenzie and Eickwort, 1996; Stubbs and Drummond, 2001; Javorek et al., 2002; Tuell et al., 2009; Campbell et al., 2017), and mining bees (Andrenidae) (Mackenzie and Eickwort, 1996; Javorek et al., 2002). These bees are thought to be effective pollinators of blueberry flowers due to their ability to buzz pollinate which causes the poricidal anthers to release their pollen (Cane and Payne, 1993). In comparison, honey bees cannot buzz pollinate and are less effective at releasing pollen from these specialised anthers. Consequently, bumble bees deposit about two-thirds more pollen per visit than honey bees (Javorek et al., 2002). However, recently Hoffmann et al. (2018) revealed that honey bees that foraged on blueberries had blueberry pollen on all body parts with the

majority of blueberry pollen being found on their legs and tarsi. These pollen-laden legs and tarsi regularly came into contact with blueberry stigmas during landing, grooming, and foraging and have the ability to effectively pollinate blueberry flowers. Moreover, Martin et al. (2021) showed that honey bees effectively pollinate Ventura, a blueberry variety commonly grown in South Africa, by significantly increasing both blueberry mass and diameter, as well as decreasing ripening time.

Despite these promising results, the perceived inefficiency of honey bees as pollinators has resulted in pressure to import native blueberry pollinators, such as bumble bees. This is extremely problematic as introducing bumble bees into novel areas has the potential to disrupt local ecosystems. For example, introduced bumble bees can outcompete native pollinators, damage flowers, and rob nectar (Morales et al., 2013; Schmid-Hempel et al., 2014; Aizen et al., 2018). Consequently, it is important to quantify the benefits of honey bees for different commercially planted blueberry varieties so that objective decisions can be made about the perceived needs of importing novel pollinators. This may also enable us to farm more intelligently with varieties that do better under honey bee pollination.

We aim to determine the effects of honey bee pollination on the fruit characteristics of five blueberry varieties that are extensively planted in South Africa. Particularly, we compare the benefits in terms of fruit yield (fruit mass, fruit diameter, percentage fruit set, and adjusted fruit mass) after honey bee pollination with fruit yield when pollinators are absent. Although honey bees are often viewed as ineffective pollinators of blueberries, they successfully move pollen between flowers and often increase blueberry fruit production (Aras et al., 1996b; Mackenzie, 1997; Sampson and Cane, 2000; Hoffman et al., 2018; Martin et al., 2021). Accordingly, we hypothesize that honey bees considerably increase fruit yield and

80 decrease fruit developmental period, compared to fruit produced in the absence of
81 pollinators. Additionally, we establish if the pollination environment could be optimized so
82 that fruit yield is improved relative to the present conditions where honey bees are the sole
83 pollinators. Despite honey bees moving pollen between blueberry flowers (Hoffman et al.,
84 2018), we predict considerable room for improvement, with hand pollination producing
85 substantially larger fruit yields than honey bee pollination.

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87

2. Methods

An experimental plot on Backsberg blueberry farm was used as the study site (Western Cape, South Africa, 33°48'30.7"S 18°54'09.8"E). Farmlands surround the experimental plot and there is also a nearby (2.98km) nature reserve consisting of Swartland shale renosterveld and fynbos. Honey bee hives were stocked at 15 hives per hectare, which falls within the typical range of commercial blueberry farm hive densities (4 – 39.5 hives per hectare; Isaacs and Kirk, 2010; Gibbs et al., 2016; Hoffman et al., 2018). Hive densities on blueberries are often much greater than on crops such as apples and pears, where two and four honey bee hives per hectare, respectively, provide sufficient pollination (Allsopp et al., 2008). This experiment comprised three treatments: pollinator exclusion, open honey bee pollination, and hand pollination. We determined the effects of honey bee pollination on blueberry production and also whether there was scope to improve pollination conditions by comparing fruit yield (fruit mass, fruit set, and developmental period) among these three treatments.

Varieties used were Emerald (*Vaccinium corymbosum* hybrid), Eureka (*Vaccinium corymbosum* hybrid), Snowchaser (*Vaccinium sp.* hybrid), Suziblue (*Vaccinium corymbosum* hybrid), and Twilight (*Vaccinium corymbosum* hybrid). Pollination combinations were repeated three times per plant and across nine plants, resulting in 27 pollination combination replicates per variety. Moreover, we minimized the effects of extrinsic factors, which potentially influence fruit development, by conducting our experiments across varieties in an experimental plot of only 50 m X 115 m. To determine pollination deficits and benefits of bees to the five varieties, we followed the methods of Martin et al. (2021). Below we provide a brief description (also see Fig. 1).

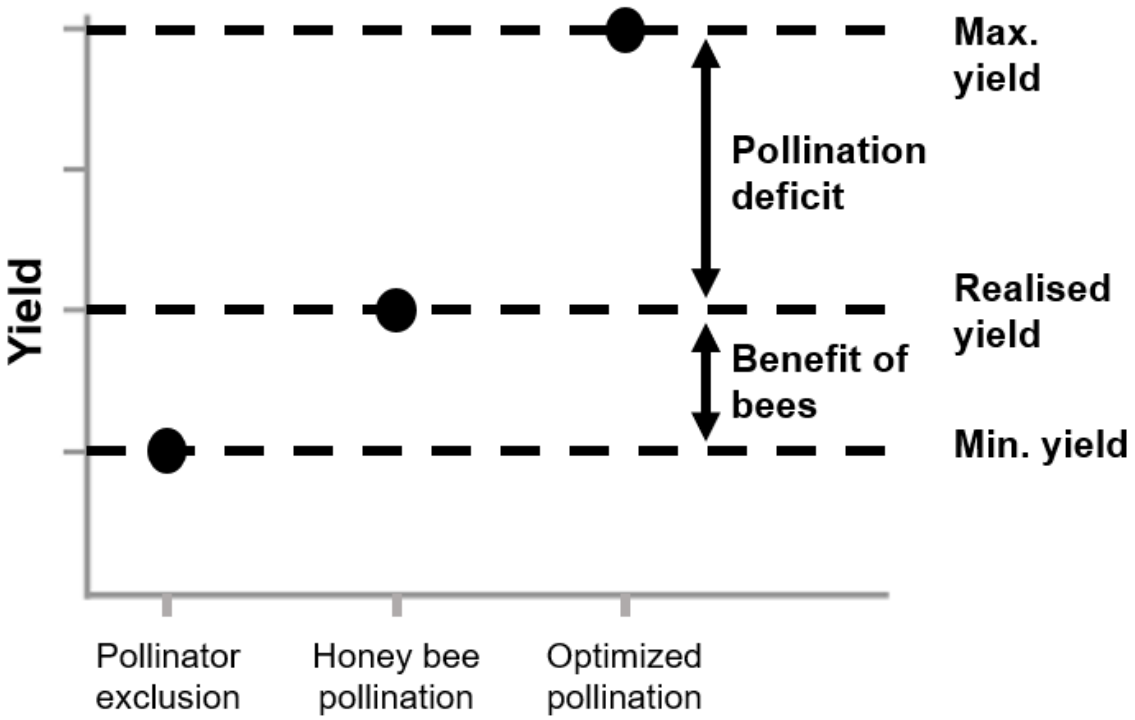

Fig 1: Hypothetical figure showing how three treatments can be used to determine the benefits of honey bee pollination as well as how realised yields may potentially be improved (originally produced by Martin et al. 2021).

2.1 Benefit of bees

We determined the benefit of bees by comparing blueberry fruit production under honey bee pollination to blueberry fruit production in the absence of honey bees (pollinator exclusion). Pollinators were denied access to flowers by covering 27 individual virgin flowers with fine mesh bags. Once flowers had wilted, these bags were removed to allow for normal fruit maturation. We estimated the fruit yield through honey bee pollination by exposing (unbagging) 27 flowers to bee pollinators. For the duration of the time spent at the

experimental plot (approximately 280 hours), honey bees were the only pollinator seen visiting blueberry flowers, which is typical for South African blueberry farms.

2.2 Pollination deficit

We calculated the pollination deficit for each variety by comparing the honey bee treatment to the optimized hand pollination treatment. Hand pollination is thought to result in the best fruit quality as it enhances both pollen deposition and quality of pollen. Data from the optimized hand-pollination treatment were gathered at the same time as other treatments but was previously published in Martin et al. (2019). The aims of Martin et al. (2019) were exclusively to determine which varieties were most compatible, whereas the aims of this paper were to calculate the benefit of bees and pollination deficit which require data sets in addition to the ones collected by Martin et al. (2019). For the current manuscript, we used data from the best pollen donator (i.e., the cross-combination resulting in the highest yield) for each variety from Martin et al. (2019), to represent the optimized hand-pollination treatment. We followed hand pollination protocols as set out by Martin et al. (2021).

2.3 Measurements of fruit quality

Following pollination treatments, fruit development was examined weekly to determine whether fruit were ready to be picked. Fruits were considered ready for picking when the entire berry had transformed to a uniform dark blue. Fruit were then harvested and the weight, diameter, and developmental period (weeks from pollination to harvesting) were determined on the harvest day. We also calculated the percentage fruit set per treatment. Fruit mass and percentage fruit set were combined to calculate the adjusted fruit mass for each treatment as follows:

$$Adjusted\ fruit\ mass = \text{Proportion fruit set X mean fruit mass} \qquad (\textit{Equation 1})$$

147 **2.4 Statistical analyses**

148 Linear mixed-effects models were used with fruit mass, developmental period, and adjusted
149 fruit mass as functions of pollination treatment (fixed effect). To account for variation
150 between individual plants, plant ID was used as a random effect. This increased the
151 sensitivity of the model in identifying differences in fruit yield measures as a consequence of
152 treatment alone. Linear contrasts (Tukey) were used to detect treatment differences.
153 Nakagawa R^2 values (Nakagawa and Schielzeth, 2013) were used to assess model fit,
154 providing conditional variance (R^2c) and marginal variance (R^2m) estimates for linear mixed-
155 effects models, which can be equated to traditional R^2 values. The conditional R^2 values (R^2c)
156 explain the variance of the entire model (fixed effects and random effects), whereas
157 marginal R^2 values (R^2m) explain the variance of the fixed effects alone.

158 All statistical analyses were conducted in R (version 3.3.2) (R Core Team, 2017) using
159 the packages nlme (Pinheiro et al., 2017), multcomp (Hothorn et al., 2008), ggplot2
160 (Wickham, 2009), sjPlot (Lüdecke, 2017), car (Fox and Weisberg, 2011), lme4 (Bates et al.,
161 2015), grid (R Core Team, 2017), gridExtra (Auguie, 2017), lattice (Deepayan, 2008), MuMIn
162 (Barton, 2017), plyr (Wickham, 2011), and plotrix (Lemon, 2006).

163

3. Results

3.1 Emerald

3.1.1 Benefit of bees

We found strong statistical support indicating that honey bees increased blueberry production in Emerald compared to fruits produced in the absence of pollinators for three-quarters of the metrics measured. We provide further details on the four metrics below.

The conditional variance for the developmental period model was R^2c=0.471 and the marginal variance was R^2m=0.062. This shows that variation was mostly explained by the random effect (plant ID). The presence of honey bee pollinators appeared to decrease (statistically borderline) the developmental period of blueberry fruits by about 2 weeks (z=-2.085, p=0.089, Fig 2) compared to when they were absent.

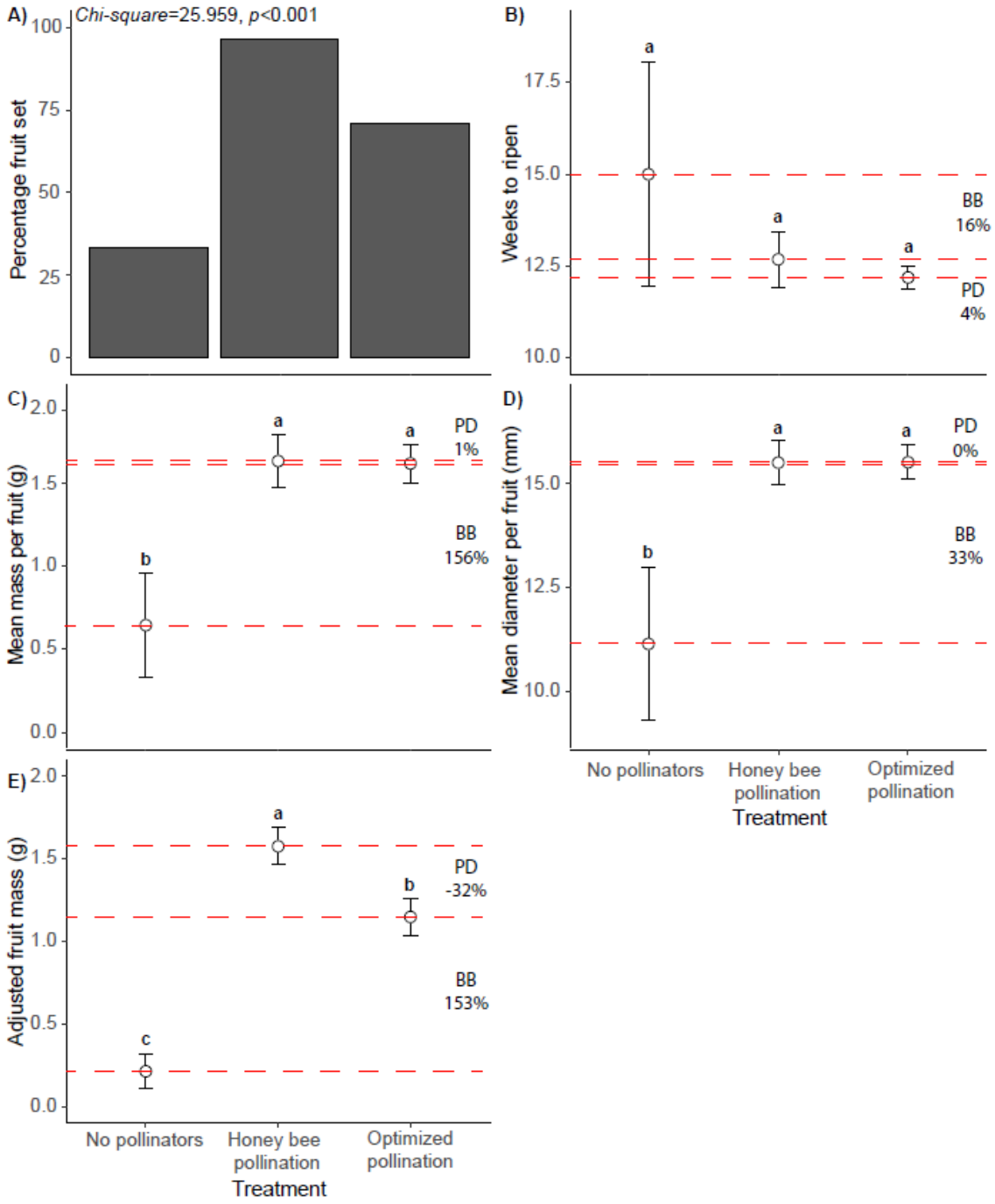

Fig 2: Pollination deficit and the benefit of bees for Emerald fruit. A) Percentage fruit set. B) Developmental period. C) Mean fruit mass. D) Mean fruit diameter. E) Adjusted fruit mass. Significance ($p<0.05$) of linear contrasts (Tukey HSD) are indicated by letters. Error bars indicate standard error. BB = benefit of bees, the difference (in percentage) between fruit produced in the absence of pollinators compared (n=27) to fruits

180 produced by honey bees (n=27). PD = pollination deficit, the difference (in percentage) between fruits
181 produced after honey bee exposure compared to fruits produced after hand pollination (n=27).

182 The conditional variance for the Emerald fruit mass model was R^2c=0.238 while the
183 marginal variance was R^2m=0.151. The conditional variance for the fruit diameter model
184 was R^2c=0.303 and the marginal variance was R^2m=0.210. This suggests that for both fruit
185 mass and diameter, variation is primarily explained by treatment. Fruit mass was
186 significantly increased by the presence of honey bees (mean ± SE fruit mass = 1.64g ± 0.12g,
187 z=2.799, p=0.013), resulting in a 156% mass increase compared to fruit produced in the
188 absence of pollinators (mean ± SE fruit mass = 0.64g ± 0.32g, Fig 2C). Likewise, honey bees
189 increased the fruit diameter by 4mm (33%) per fruit (mean ± SE = 15.51mm ± 0.41mm)
190 compared to treatments produced in the absence of pollinators (mean ± SE = 11.12mm ±
191 1.86mm, Fig 2D, z=3.412, p=0.002). There were significant differences in fruit set following
192 the three treatments (*Chi-square*=25.959, df=2, p<0.001, Fig 2A). Honey bees increased fruit
193 set by 63% relative to bagged plants. Similarly, honey bee pollination outperformed the
194 hand pollination treatment by 25%.

195 The conditional variance for the adjusted Emerald fruit mass model was R^2c=0.478
196 and marginal variance was R^2m=0.347. This suggests that adjusted fruit mass variation was
197 primarily explained by treatment. Honey bees led to a significant increase of adjusted fruit
198 mass (mean ± SE = 1.58g ± 0.11g, Fig 2E) of 153% compared to bagged treatments (mean ±
199 SE = 0.21g ± 0.11g, Fig 2E, z=4.639, p<0.001).

200 ***3.1.2 Pollination deficit***

201 The pollination deficit metric indicated that for Emerald, honey bee pollinators performed
202 equally or better than hand pollinations. Below we present those results.

203 Hand pollination resulted in a statistically non-significant (z=-0.073, p=0.997)
204 decrease in the developmental period of blueberry fruit, from 12.68 ± 0.32 weeks (mean ±
205 SE) when open to honey bee pollination to 12.19 ± 0.76 weeks (mean ± SE) when hand-
206 pollinated (Fig 2B). Mass of fruit produced from hand pollination (1.62g ± 0.16g, mean ± SE),
207 and fruit produced from honey bee pollination (1.64g ± 0.12g, mean ± SE, Fig 2C) did not
208 differ significantly (z=-0.110, p=0.993). The diameter of hand-pollinated fruit (mean ± SE =
209 15.52mm ± 0.54mm) and fruit pollinated by honey bees (mean ± SE = 15.51mm ± 0.41mm),
210 also did not differ significantly (z=-0.026, p=0.999). Honey bees outperformed hand
211 pollination with regards to fruit set by 25%.

212 The adjusted fruit mass decreased by 32% (z=-2.471, p=0.034) when hand-pollinated
213 (mean ± SE = 1.15g ± 0.11g, Fig 2E) in comparison to fruit produced from honey bee
214 pollination (mean ± SE = 1.58g ± 0.11g, Fig 2E).

215

3.2 Eureka

3.2.1 Benefit of bees

For all four metrics measured we found no statistical evidence suggesting that honey bees improved Eureka fruit quality compared to fruits produced in the absence of pollinators. We provide further details on each metric below.

For the developmental period model, the conditional variance was R^2c=0.405 and the marginal variance was R^2m=0.370. The variation is therefore explained mostly by the fixed effect (treatment). Honey bees did not change the developmental period (z=-0.042, p=0.999, Fig 3B).

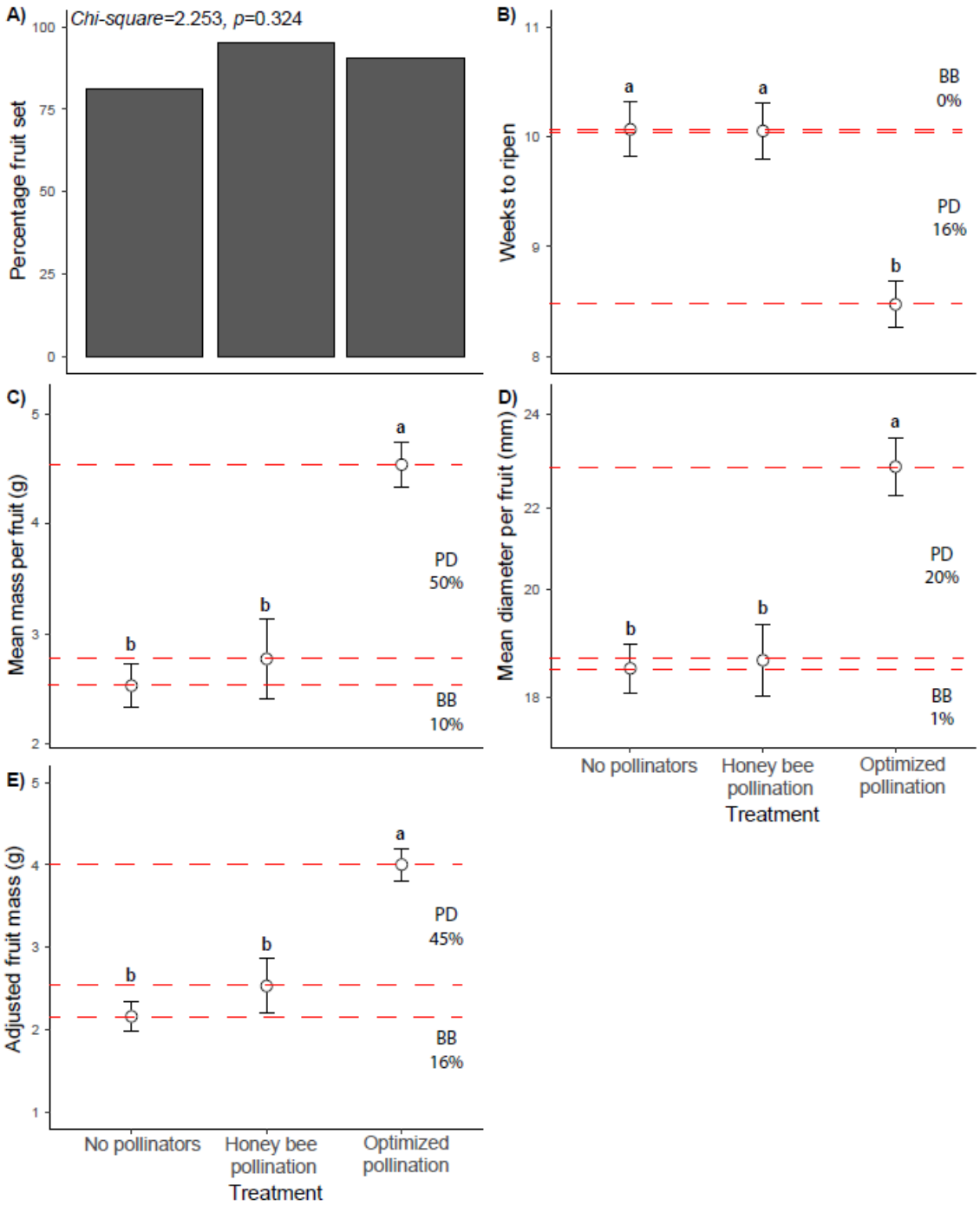

Fig 3: Pollination deficit and the benefit of bees for Eureka fruit. A) Percentage fruit set. B) Developmental period. C) Mean fruit mass. D) Mean fruit diameter. E) Adjusted fruit mass. Significance ($p<0.05$) of linear contrasts (Tukey HSD) are indicated by letters. Error bars indicate standard error. BB = benefit of bees, the difference (in percentage) between fruit produced in the absence of pollinators compared (n=27) to fruits

230 produced by honey bees (n=27). PD = pollination deficit, the difference (in percentage) between fruits
231 produced after honey bee exposure compared to fruits produced after hand pollination (n=27).

232 The fruit mass model resulted in a conditional variance of R^2c=0.693 and a marginal
233 variance of R^2m=0.398. The conditional variance was R^2c=0.569 for the fruit diameter
234 model, while the marginal variance was R^2m=0.371. This indicated that variance is primarily
235 explained by treatment for fruit mass and diameter. Honey bee presence did not increase
236 fruit mass (mean ± SE fruit mass = 2.66g ± 0.21g) significantly (z=0.815, p=0.684), compared
237 to when pollinators were absent (mean ± SE fruit mass = 2.41g ± 0.20g, Fig 3C). Likewise,
238 honey bees did not significantly increase (z=0.232, p=0.970) fruit diameter (mean ± SE =
239 18.50mm ± 0.61mm) compared to when they were absent (mean ± SE = 18.33mm ±
240 0.52mm, Fig 3D,). Honey bee pollination appeared to increase fruit set by 14%, however, the
241 differences between the three treatments were not significantly different (*Chi-*
242 *square*=2.253, *df*=2, p=0.324, Fig 3A).

243 The conditional variance for Eureka adjusted fruit mass was R^2c=0.678 and the
244 marginal variance was R^2m=0.383. This indicated that for the adjusted fruit mass model,
245 most of the variance was explained by pollination treatment. The adjusted fruit mass of
246 honey bee pollination (mean ± SE = 2.53g ± 0.20g, Fig 3E), did not differ significantly
247 (z=1.334, p=0.363) from the adjusted fruit mass of fruit produced in the absence of honey
248 bees (mean ± SE = 2.16g ± 0.18g, Fig 3E).

249

250 ***3.2.2 Pollination deficit***

251 For all pollination deficit metrics measured for Eureka, hand pollinations outperformed
252 honey bee pollination. We provide further details on each metric below.

253 The developmental period of fruit produced by hand pollination was significantly
254 decreased by approximately one week (z=-4.521, p<0.001), from 10.05 ± 0.26 weeks (mean
255 ± SE) when honey bee pollinated to 8.47 ± 0.26 weeks (mean ± SE) when hand-pollinated
256 (Fig 3B). Hand pollination significantly increased (z=3.239, p=0.003) the mass of fruit by 50%
257 (4.42g ± 0.36g, mean ± SE), compared to the fruit produced by flowers exposed to honey
258 bees (2.66g ± 0.21g, mean ± SE, Fig 3C). Furthermore, hand pollination also significantly
259 increased (z=3.657, p<0.001) fruit diameter (mean ± SE = 22.61mm ± 0.76mm) by 20% in
260 comparison to honey bee pollinated flowers (mean ± SE = 18.50mm ± 0.61mm, Fig 3D).
261 Hand pollination did not increase fruit set compared to honey bee pollination and in fact,
262 led to a 4% decrease in fruit set.

263 The adjusted fruit mass increased significantly (z=3.008, p<0.007) by 45% after being
264 hand-pollinated (mean ± SE = 4.00g ± 0.33g, Fig 2E), compared to the adjusted fruit mass
265 after honey bee exposure (mean ± SE = 2.53g ± 0.20g, Fig 3E).

266

267 **3.3 Snowchaser**

268 ***3.3.1 Benefit of bees***

269 For all four metrics, access by honey bees substantially improved Snowchaser fruit
270 production compared to when they were excluded. We provide further details on each
271 metric below.

272 The conditional variance of the Snowchaser developmental period model was
273 R^2c=0.482, while the marginal variance was R^2m=0.460, suggesting that the variance in the
274 developmental period was explained primarily by treatment (fixed effect). Honey bee
275 pollinators significantly shortened the developmental period of blueberry fruits (mean ± SE
276 fruit weeks = 11.48 weeks ± 0.20 weeks, z=-3.533, p=0.001, Fig 4B) by approximately two
277 weeks compared to fruits produced in the absence of honey bees (mean ± SE fruit weeks =
278 13.14 weeks ± 0.80 weeks, Fig 4B).

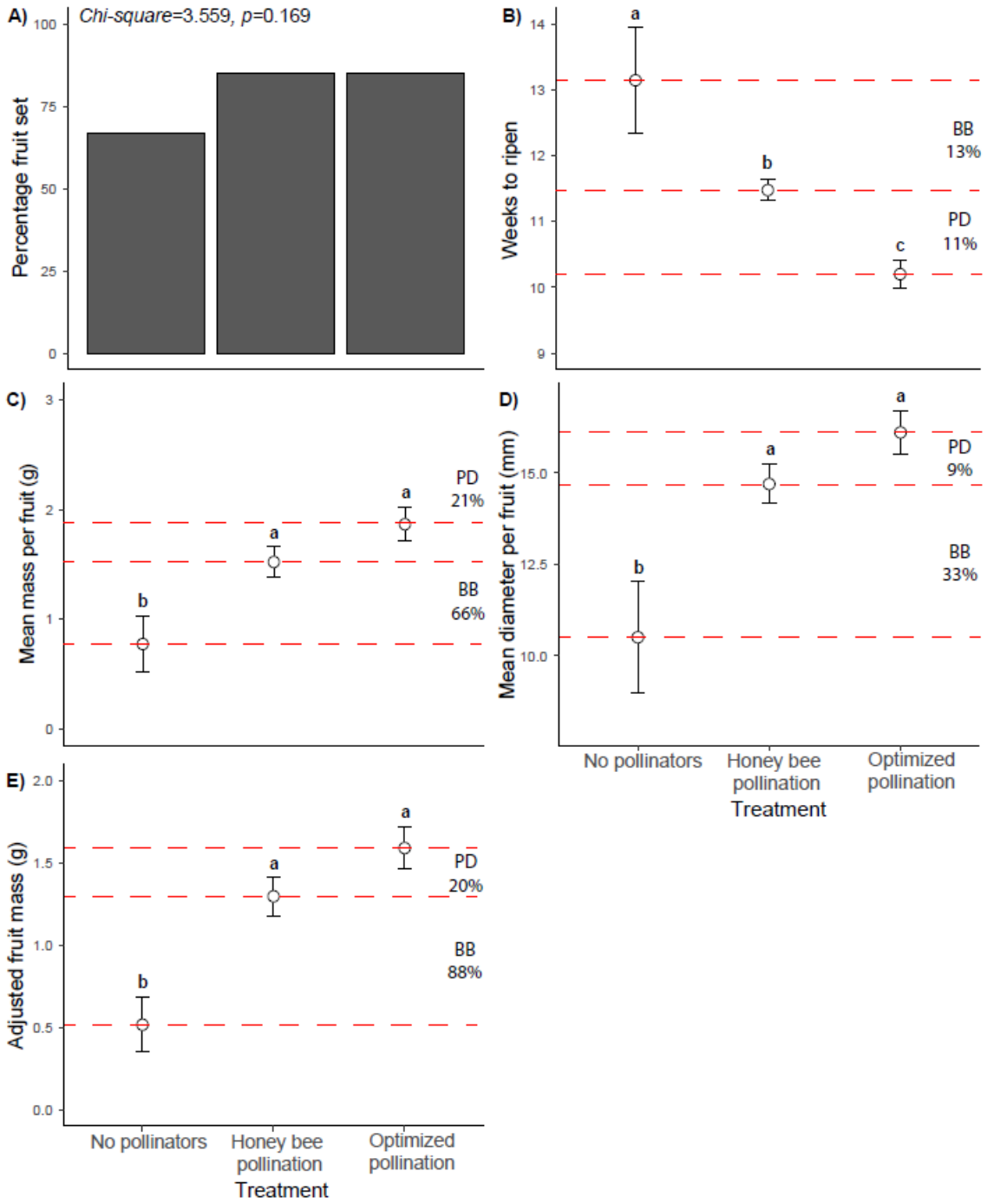

Fig 4: Pollination deficit and the benefit of bees for Snowchaser fruit. A) Percentage fruit set. B) Developmental period. C) Mean fruit mass. D) Mean fruit diameter. E) Adjusted fruit mass. Significance ($p<0.05$) of linear contrasts (Tukey HSD) are indicated by letters. Error bars indicate standard error. BB = benefit of bees, the difference (in percentage) between fruit produced in the absence of pollinators compared (n=27) to fruits

284 produced by honey bees (n=27). PD = pollination deficit, the difference (in percentage) between fruits
285 produced after honey bee exposure compared to fruits produced after hand pollination (n=27).

286 The conditional variance of the fruit mass model was R^2c=0.520 and the marginal
287 variance was R^2m=0.203. Similarly, the conditional variance of the fruit diameter model was
288 R^2c=0.469, while the marginal variance was R^2m=0.284. This suggests that variance in
289 Snowchaser fruit mass and diameter was primarily explained by treatment. Here, honey bee
290 presence significantly increased fruit mass (mean ± SE fruit mass = 1.52g ± 0.15g, z=2.362,
291 p=0.047), by 66% compared to treatments where honey bees were excluded (mean ± SE
292 fruit mass = 0.77g ± 0.25g, Fig 4C). Likewise, honey bee exposure resulted in a 4mm (33%)
293 mean increase in fruit diameter per fruit (mean ± SE = 14.70mm ± 0.59mm) in comparison
294 to fruit produced in the absence of honey bees (mean ± SE = 10.51mm ± 0.81mm, Fig 4D,
295 z=3.229, p=0.003). Honey bee pollination appeared to increase fruit set by 18%, however,
296 the differences between the three treatments were not significantly different (*Chi-*
297 *square*=3.559, *df*=2, p=0.169, Fig 4A).

298 The adjusted fruit mass model resulted in a conditional variance of R^2c=0.576 and a
299 marginal variance of R^2m=0.273, suggesting that most of the variance in adjusted fruit mass
300 is explained by treatment. Honey bee pollination significantly (z=3.062, p=0.006) increased
301 adjusted fruit mass (mean ± SE = 1.30g ± 0.13g, Fig 4E), by 86% compared to the adjusted
302 fruit mass of treatments where pollinators were excluded (mean ± SE = 0.52g ± 0.17g, Fig
303 4E).

304

305 ***3.3.2 Pollination deficit***

306 Statistics indicated that honey bee pollinators and hand pollinations performed similarly for
307 Snowchaser in three of the four metrics measured. We provide further details below.

308 Hand pollination resulted in a one week or 11% decrease in the developmental
309 period (z=-3.788, p<0.001), from 11.48 ± 0.20 weeks (mean ± SE) after honey bee exposure
310 to 10.20 ± 0.16 weeks (mean ± SE) after hand pollination (Fig 4B). Hand-pollinated fruits had
311 similar fruit mass (mean ± SE fruit mass = 1.87g ± 0.14g, z=1.469, p=0.303) to fruit produced
312 after exposure to honey bees (1.52g ± 0.15g, mean ± SE, Fig 4C). Hand pollination slightly,
313 but not significantly (z=1.425, p=0.325) increased fruit diameter (mean ± SE = 16.10mm ±
314 0.54mm) by 9% in comparison to flowers exposed to honey bees (mean ± SE = 14.70mm ±
315 0.59mm, Fig 4D). Hand pollination did not lead to an increase in fruit set compared to honey
316 bee pollination.

317 The adjusted fruit mass appeared to increase by 20% for hand-pollinated flowers
318 (mean ± SE = 1.59g ± 0.12g, Fig 2E) compared to the adjusted fruit mass after honey bee
319 exposure (mean ± SE = 1.30g ± 0.13g, Fig 4E), however, this difference was not statistically
320 significant (z=1.486, p=0.295).

321

3.4 Suziblue

3.4.1 Benefit of bees

We found evidence suggesting that for Suziblue, honey bees do not improve blueberry fruit quality compared to when pollinators were excluded. We provide further details on each metric below.

Conditional variance for the developmental period model was R^2c=0.235 and the marginal variance was R^2m=0.235, suggesting that the variation was mostly explained by the fixed effect (treatment). Exposure to honey bees did not significantly affect the developmental period of Suziblue fruits (z=-0.957, p=0.604, Fig 5B).

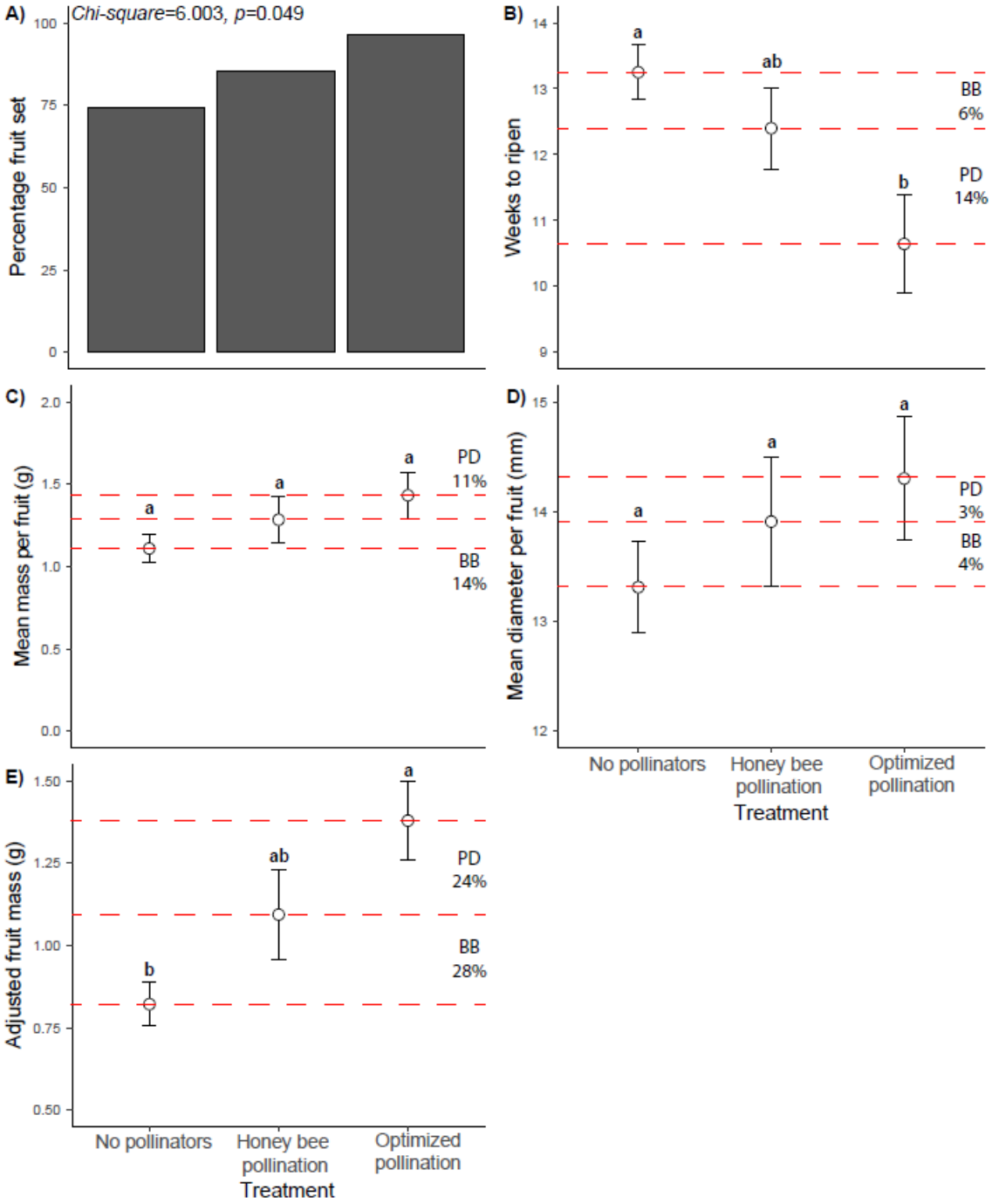

Fig 5: Pollination deficit and the benefit of bees for Suziblue fruit. A) Percentage fruit set. B) Developmental period. C) Mean fruit mass. D) Mean fruit diameter. E) Adjusted fruit mass. Significance ($p<0.05$) of linear contrasts (Tukey HSD) are indicated by letters. Error bars indicate standard error. BB = benefit of bees, the difference (in percentage) between fruit produced in the absence of pollinators compared (n=27) to fruits

336 produced by honey bees (n=27). PD = pollination deficit, the difference (in percentage) between fruits
337 produced after honey bee exposure compared to fruits produced after hand pollination (n=27).

338 The conditional variance of the fruit mass model was R^2c=0.645 and the marginal
339 variance was R^2m=0.144. For the fruit diameter model, the conditional variance was
340 R^2c=0.492 and the marginal variance was R^2m=0.088. Plant ID explained most of the
341 variance for fruit mass and diameter. Honey bee pollination had a minimal effect on fruit
342 mass (mean ± SE fruit mass = 1.28g ± 0.14g, z=1.137, p=0.485), in comparison to bagged
343 treatments (mean ± SE fruit mass = 1.11g ± 0.09g, Fig 5C). Honey bees also had a minimal
344 effect on fruit diameter (mean ± SE = 13.91mm ± 0.56mm) in comparison to bagged
345 treatments (mean ± SE = 13.31mm ± 0.42mm, Fig 5D, z=1.018, p=0.562). Significant
346 differences were found in fruit set following the three treatments (*Chi-square*=6.003, *df*=2,
347 p=0.049, Fig 5A). Honey bees increased fruit set by 11% relative to bagged plants, however,
348 this still left a pollination deficit of 11% (honey bee treatment compared to hand
349 pollination).

350 The adjusted fruit mass model resulted in a conditional variance of R^2c=0.757 and a
351 marginal variance of R^2m=0.330. The variance in the adjusted fruit mass model was
352 explained mostly by treatment (fixed effect). Flowers open to honey bee pollination resulted
353 in similar adjusted fruit masses (mean ± SE fruit mass = 1.09g ± 0.12g, z=1.816, p=0.160),
354 compared to honey bee exclusion treatments (mean ± SE = 0.82g ± 0.07g, Fig 5E).

355

356 ***3.4.2 Pollination deficit***

357 Below, we provide details showing that for all metrics measured, hand pollinations of
358 Suziblue flowers did not outperform honey bee pollination.

359 The developmental period of hand-pollinated fruit was similar (mean ± SE weeks =
360 10.64 ± 0.62 weeks, z=-2.047, p=0.101) to that of fruit produced from honey bee pollination
361 (12.40 ± 0.75, mean ± SE, Fig 5B). The fruit mass of hand-pollinated fruits was also similar
362 (mean ± SE fruit mass = 1.43g ± 0.14g, z=0.786, p=0.707), to fruit produced from honey bee
363 pollinated flowers (1.28g ± 0.14g, mean ± SE, Fig 5C). Hand pollination did not increase
364 (z=0.579, p=0.830) fruit diameter (mean ± SE = 14.30mm ± 0.59mm) in comparison to the
365 diameter of fruit produced by honey bee pollination (mean ± SE = 13.91mm ± 0.71mm, Fig
366 5D).

367 Adjusted fruit mass was similar and not significantly different (z=1.48, p=0.290) for
368 hand-pollinated flowers (mean ± SE = 1.38g ± 0.14g, Fig 5E) and for flowers exposed to
369 honey bees (mean ± SE = 1.09g ± 0.12g, Fig 5E).

370

371 **3.5 Twilight**

372 ***3.5.1 Benefit of bees***

373 For three out of the four metrics measures, honey bee presence enhanced blueberry
374 production compared to when pollinators were excluded. We provide further details on
375 each metric below.

376 The developmental period model had a conditional variance of R^2c=0.360 and a
377 marginal variance of R^2m=0.320. The fixed effect (treatment) explained most of the
378 variation. Honey bee pollination decreased the developmental period (mean ± SE weeks =
379 11.29 weeks ± 0.43 weeks, Fig 6B) of blueberry fruits by approximately one week or 10%
380 compared to fruits produced in the absence of honey bees (mean ± SE fruit weeks = 12.55
381 weeks ± 0.49 weeks, Fig 2C). This was borderline-significant (z=-2.170, p=0.076, Fig 6B).

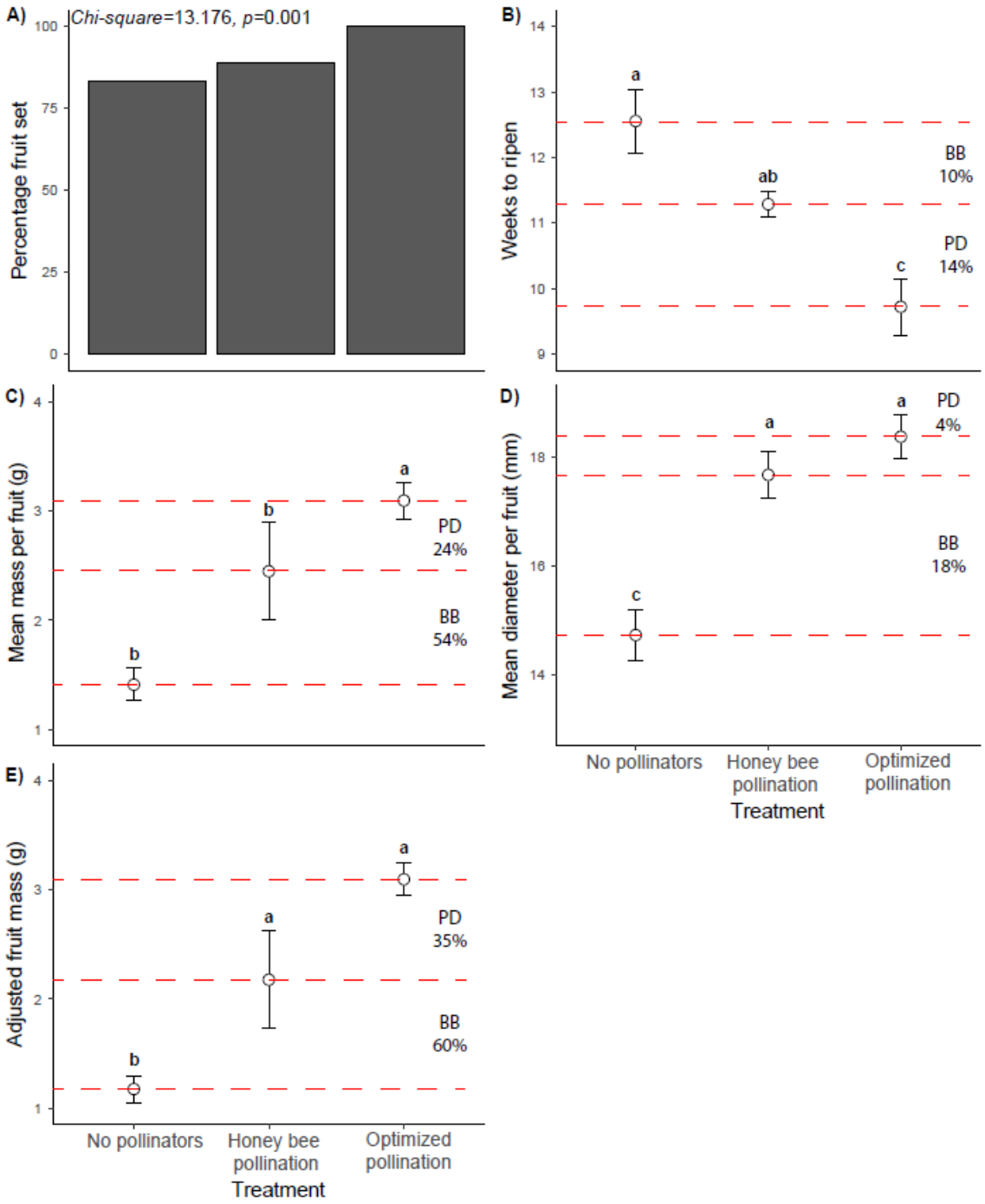

Fig 6: Pollination deficit and benefit of bees for Twilight fruit. A) Percentage fruit set. B) Developmental period. C) Mean fruit mass. D) Mean fruit diameter. E) Adjusted fruit mass. Significance ($p<0.05$) of linear contrasts (Tukey HSD) are indicated by letters. Error bars indicate standard error. BB = benefit of bees, the difference (in percentage) between fruit produced in the absence of pollinators compared (n=27) to fruits produced by

honey bees (n=27). PD = pollination deficit, the difference (in percentage) between fruits produced after honey bee exposure compared to fruits produced after hand pollination (n=27).

The conditional variance for the Twilight fruit mass model was R^2c=0.337 and the marginal variance was R^2m=0.170. For the fruit diameter model, the conditional variance was R^2c=0.392, while the marginal variance was R^2m=0.369. This suggests that for both fruit mass and diameter, the majority of the variance was explained by treatment. Fruit mass was significantly increased after honey bee exposure (mean ± SE fruit mass = 2.45g ± 0.17g, z=2.397, p=0.043), resulting in a 54% increase compared to bagged treatments (mean ± SE fruit mass = 1.41g ± 0.17g, Fig 6C). Honey bee exposure similarly increased the mean fruit diameter by 3mm (18%) per fruit (mean ± SE = 17.66mm ± 0.39mm) in comparison to bagged treatments (mean ± SE = 14.73mm ± 0.47mm, Fig 6D, z=4.643, p<0.001). There were significant differences in fruit set following the three treatments (*Chi-square*=13.176, df=2, p=0.001, Fig 6A). Honey bees increased fruit set by 6% relative to bagged plants, however, this still left a pollination deficit of 11% (honey bee treatment compared to hand pollination).

The adjusted fruit mass model resulted in a conditional variance of R^2c=0.383 with the marginal variance of R^2m=0.216 suggesting that fruit mass variance was primarily explained by treatment. Honey bee presence significantly (z=2.368, p=0.046) increased adjusted fruit mass (mean ± SE = 2.18g ± 0.15g, Fig 6E), resulting in a 60% increase compared to pollinator exclusion treatments (mean ± SE = 1.18g ± 0.12g, Fig 6E).

408 ***3.5.2 Pollination deficit***

409 Hand pollinations resulted in improved Twilight fruit quality compared to honey bee
410 pollinations. However, these were only statistically supported for developmental period.
411 Below, we explain the details relating to each of the metrics measured.

412 The developmental period of blueberry fruit was significantly decreased by approximately
413 one week or 14% (z=-2.824, p=0.0132), from 11.29 ± 0.43 weeks (mean ± SE) when flowers
414 were open to honey bee pollination to 9.72 ± 0.22 weeks (mean ± SE) when flowers were
415 pollinated by hand (Fig 6B). Hand-pollinated fruits appeared to be about 10% heavier (2.69g
416 ± 0.13g, mean ± SE), than fruit produced from flowers exposed to honey bees (2.45g ±
417 0.17g, mean ± SE, Fig 6C), however, this relationship was non-significant (z=1.134, p=0.493).
418 Hand pollination did not significantly increase (z=1.134, p=0.493) the fruit diameter (mean ±
419 SE = 18.36mm ± 0.43mm) when compared to fruit produced by honey bee pollinated
420 flowers (mean ± SE = 17.66mm ± 0.39mm, Fig 6D).

421 Hand pollination appeared to improve the adjusted fruit mass by 23% (mean ± SE =
422 2.69g ± 0.13g, Fig 2E) when compared to flowers exposed to honey bees (mean ± SE = 2.18g
423 ± 0.15g, Fig 2E), although this difference was not statistically significant (z=1.694, p=0.205).

424 For discussion purposes, we have included a summary table which enables visual
425 comparisons of bee benefit and pollen deficits to be made between different varieties. We
426 have chosen to use adjusted fruit mass as a summary metric (Table 1) because it
427 incorporates arguably the two most important yield metrics (fruit mass and fruit set). It also
428 indirectly incorporates fruit diameter, which is highly correlated with fruit mass (Jorquera-
429 fontena et al., 2017). Similarly, we also summarize treatment effects (figure 7) for all
430 blueberry varieties, using adjusted fruit mass as a metric.

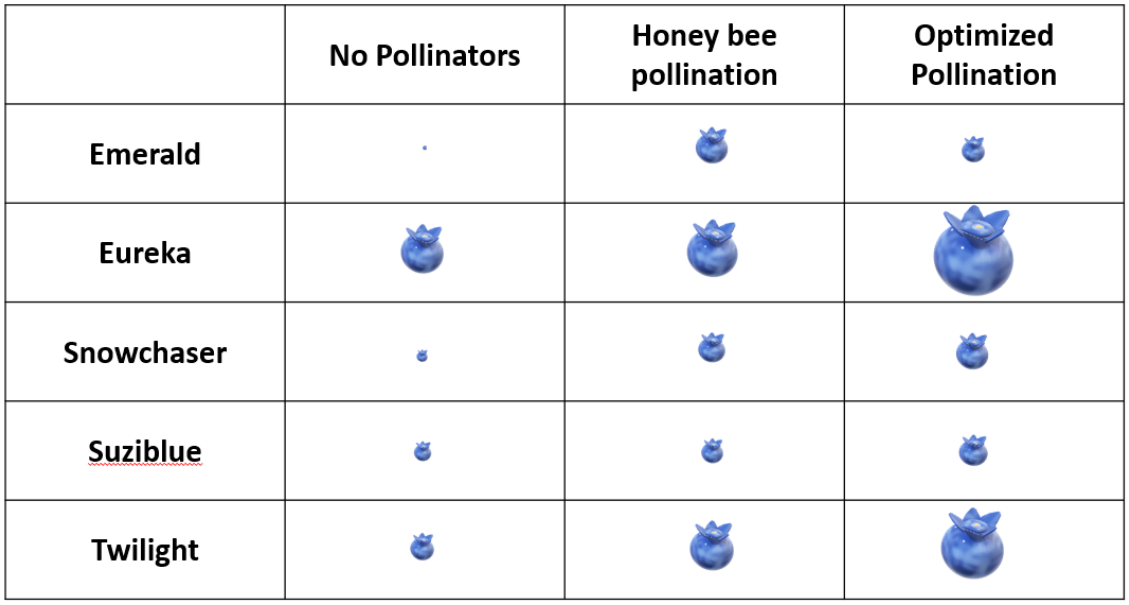

Fig 7: Relative size comparisons (linear scale) of treatment effects for adjusted fruit mass in the five blueberry varieties. The largest blueberry has an equivalent adjusted fruit mass of 4g while the smallest has an equivalent adjusted fruit mass of 0.21g.

Table 1: Summary table comparing the benefit of bees and the pollination deficit for adjusted fruit mass in the five blueberry varieties from this study and Ventura, which was published by Martin et al. (2021). Positive benefit of bees implies that the addition of honey bees increases fruit yields compared to when pollinators are absent. Positive pollination deficit indicates that plants pollinated by honey bees produce lower yields than plants pollinated by hand. Statistical significance ($p < 0.05$) is indicated by bold fonts, while colour differences (red vs black) suggest differences in trend direction.

Variety	Benefit of bees	Pollination deficit
Emerald	**153%**	**-32%**
Eureka	16%	**45%**
Snowchaser	**86%**	20%
Suziblue	28%	24%
Twilight	**60%**	35%
Ventura (Martin et al. 2021)	**134%**	**37%**

4. Discussion

We provide a comprehensive comparison of honey bee effectiveness as pollinators of common commercial blueberry varieties in South Africa. Evidence suggests that the fruit quality of these southern highbush blueberry varieties is affected considerably by the pollination environment. Overall, we show that the absence of pollinators in highbush blueberries typically leads to reductions in fruit yield. This shows that honey bees are usually extremely beneficial and can act as reliable blueberry pollinators, even in areas without access to native blueberry pollinators. Importantly, the study also highlights differences in the effectiveness of honey bees across different blueberry varieties. Finally, it also suggests that pollination conditions could be improved for certain varieties which appear not to be producing at their full production potential under honey bee pollination.

In all cases, honey bees increase yields (usually statistically significant) compared to when pollinators were absent (Table 1). Martin et al. (2021) also demonstrated this for Ventura, another southern highbush variety used in South Africa. In this study, honey bees led to a 134% increase of adjusted fruit mass compared to fruits formed in the absence of honey bees, demonstrating that honey bees can effectively pollinate highbush blueberry varieties.

The addition of honey bees can result in very impressive yield increases for some varieties (i.e. Emerald, Snowchaser, Twilight, and Ventura), but for two varieties (Eureka and Suziblue), honey bee exposure had relatively small effects on fruit production (Fig 7). This may occur if a variety is good at autonomous self-pollination and does not need pollinators. Excellent autonomous self-pollinators should also have low pollination deficits because pollinators are not needed for good fruit production. Consequently, fruit yields without

460 pollinators should be similar to fruit yields under optimized pollination conditions. However,
461 none of the varieties appear to be excellent autonomous selfers and Emerald appears to be
462 a particularly poor selfer and had minute adjusted fruit mass when pollinators were
463 excluded. However, the pollination deficit for Emerald was remarkable because it was so
464 small (less than zero), suggesting that honey bee pollination was more effective than hand
465 pollinations. The presence of honey bees also had an enormous (153%) positive impact on
466 yield, suggesting that this variety is exceptionally well suited to honey bee pollination. While
467 the low pollination deficit of Emerald may potentially make it a good variety to use in areas
468 with honey bee pollinators, the inherently small fruit sizes of this variety, even under
469 optimal pollination conditions may make it less attractive than other varieties with larger
470 pollination deficits.

471 Eureka, for example, had a large pollination deficit (45%), suggesting that the
472 pollination environment was far from optimal and that improvements in pollination
473 conditions can markedly increase yields. However, this variety has two redeeming features
474 which make it a potentially good commercial variety, even under very poor pollination
475 conditions. Eureka appears to be a reasonably good autonomous selfer and can set fruit in
476 the absence of pollinators. In fact, fruit yields without pollinators are only marginally smaller
477 (16%) than fruit yield after honey bee exposure, suggesting that honey bees do not currently
478 add much benefit to this crop. Despite this, its adjusted fruit mass without pollinators is still
479 larger than most other varieties when they are under optimized pollination conditions
480 (except Twilight) (Fig 7).

481 Snowchaser appears to be a poor autonomous self-pollinator and had a very small
482 adjusted fruit mass in the absence of honey bees. However, honey bee presence had a

483 significantly positive impact on Snowchaser yields and this, in combination with small (20%)
484 pollination deficits, suggests that this variety is also quite well suited to honey bee
485 pollination. Unfortunately, this advantage may be outweighed by its small fruit size (even
486 under optimized pollination conditions) which is likely to reduce its attractiveness as a
487 commercial crop.

488 Suziblue appears to be a good autonomous self-pollinator because it is able to
489 produce yields without pollinators, which are similar to the yields after honey bee exposure.
490 This suggests that autonomous self-pollination does a reasonable job of ensuring fruit
491 production and that yields are not strongly increased by the presence of honey bees.
492 Furthermore, it had one of the smaller (non-significant) pollination deficits measured (24%).
493 Although it may appear as though Suziblue is potentially a good variety to plant in
494 conditions with unpredictable pollinator variability, its generally small fruit size, even under
495 optimal pollination conditions leads to low adjusted fruit mass.

496 Twilight does not appear to produce its best fruit in the absence of pollinators,
497 although the fruits are nevertheless still large compared to several of the other varieties.
498 The presence of honey bees made a significant increase in Twilight yields although there still
499 appeared to be a large (but not significant) pollination deficit. While the large pollination
500 deficit suggests that Twilight is not well suited to the honey bee pollination environment, its
501 inherently large fruit size enables it to produce large fruit under honey bee pollination, with
502 plenty of potential to improve pollination. The large fruit size compared to other varieties
503 under honey bee pollination may make this variety a good commercial candidate despite
504 the relatively large pollination deficit.

Importantly, our interpretations of yield data in this manuscript do not consider potential differences in the number of buds produced by different varieties of blueberry plants as we were not able to access these data. Also, we did not attempt to determine the temporal value of yield produced by each variety. For example, early or late season varieties may demand higher export prices than mid-season varieties when the export market is saturated. These market-level considerations are beyond the scope of the manuscript.

It is not always clear exactly why some varieties differ so markedly in the size of their pollination deficits. However, in some cases, varieties (e.g. Suziblue) that are good at autonomous selfing can reduce the pollination deficit. In others, the pollination deficit can be reduced if varieties are well suited to honey bee pollination (e.g. Emerald). While we did not study the mechanics of "suitability to honey bee pollination," this may depend on how well blueberry and honey bee morphology are matched. Blueberry flowers can differ significantly in terms of their morphological characters and certain floral traits may make it difficult for honey bees to access rewards. This may reduce pollinator visitation rates to those varieties or possibly make it hard for pollen grains to be extracted. Studies on wild pollinators have often found that traits such as floral tube length and diameter can have a profound influence on the effectiveness of pollen transfer and also on whether pollinators are able to access nectar or not (Campbell et al., 1996; Aigner, 2004; Fenster et al., 2006; Martins and Johnson, 2013; Lázaro et al., 2015; Minnaar et al., 2019). It is possible that varieties with long tubes can exclude pollinators from accessing nectar, especially if the tubes are also narrow and do not allow the bees to enter very deeply into the flowers. Varieties with narrow entrances may also exclude pollinators from accessing both nectar and pollen, even if the tube lengths are short. Evidence that some varieties have inaccessible or poor rewards for pollinators can be seen in studies that show strong

529 pollinator preferences for one blueberry variety over another (Dorr and Matin, 1966;
530 Courcelles et al., 2013).

531 Honey bees are often thought to be poor pollinators of blueberries because of their
532 reluctance to forage in cold weather conditions (Tuell and Isaacs, 2010), slower foraging
533 times (Javorek et al., 2002), and decreased pollen deposition per visit (Javorek et al., 2002)
534 when compared to pollinators such as bumble bees. Despite this, we show that honey bees
535 are likely to be reliable pollinators of several blueberry varieties in regions that do not have
536 access to bumble bees. This is especially true for Emerald, where honey bee pollination is so
537 effective that it can potentially negate the need for other pollinators. While the small fruits
538 of this variety may make it less attractive for commercial use, its suitability to honey bee
539 pollination suggests that its floral characteristics may hold the key to improving fruit quality
540 of varieties still to be developed in the future. Inherent differences in fruit size among
541 blueberry varieties may be a very important factor guiding the choice of variety. However,
542 considerable variation in autonomous selfing ability, benefit of bees, and pollination deficits
543 across varieties suggest that it may be possible to identify the plant traits responsible for
544 these differences and actively select for those traits in the development of new varieties.

545 Considerable research is needed to identify which blueberry varieties do best under
546 honey bee pollination under commercial conditions, what makes varieties successful or
547 unsuccessful, which varieties can be effectively pollinated by honey bees, and which
548 varieties need other effective means to increase fruit quality. Future research should
549 therefore aim to determine how to decrease the pollination deficit of blueberry varieties
550 either by increasing the effectiveness of autonomous selfing or by increasing the
551 effectiveness of honey bees.

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