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**Seasonal phenology of Coffee Berry Borer (*Hypothenemus hampei* Ferrari) in Hawaii and
the influence of weather on flight activity**

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24 **Abstract**

25

26 Coffee berry borer (CBB, *Hypothenemus hampei* Ferrari) is the most serious insect pest of coffee
27 worldwide, yet little is known about its seasonal flight behavior or the effect that weather
28 variables have on its activity. We sampled flying female CBB adults bi-weekly over a three-year
29 period using red funnel traps baited with an alcohol lure at 14 commercial coffee farms on
30 Hawaii Island to characterize seasonal phenology and the influence of five weather variables on
31 flight activity. We captured almost 5 million Scolytid beetles during the sampling period, with
32 81-93% of the trap catch comprised of CBB. Of the captured non-target beetles, the majority
33 were tropical nut borer, black twig borer and a species of *Cryphalus*. Two major flight events
34 were consistent across all three years: an initial emergence from January-April that coincided
35 with early fruit development and a second flight during the harvest season from September-
36 December. A linear regression showed a moderate but significant negative relationship between
37 elevation and total trap catch. A generalized additive mixed model (GAMM) revealed that mean
38 daily air temperature has the most significant (positive) effect on CBB flight, with most flight
39 events occurring between 20-26 °C. Mean daily solar radiation also had a significant positive
40 effect, while maximum daily relative humidity negatively influenced flight at values above
41 ~94%. Flight was positively influenced by maximum daily wind speeds up to ~2.5 m/s and
42 cumulative rainfall up to 100 mm, after which activity declined. Our findings provide important
43 insight into CBB flight patterns across a highly variable landscape and will serve as a starting
44 point for the development of flight prediction models.

45

46

47 **Introduction**

48

49 Coffee berry borer, *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae) is the most
50 damaging insect pest of coffee worldwide, causing more than \$5M in annual crop losses [1]. The
51 female coffee berry borer (CBB) initiates infestation when she bores an entrance hole into the
52 coffee fruit (“berry”) and builds galleries for reproduction in the seed (“bean”). The offspring
53 feed on the endosperm tissue, causing further damage to the bean and resulting in reduced
54 quality and yields [1, 2]. Managing CBB is particularly difficult due to the cryptic nature of its
55 life cycle which occurs almost entirely within the coffee berry. Male and female siblings mate
56 within their natal berry, the males die, and mated females leave in search of a new berry to infest.
57 This is the time when CBB are most vulnerable to chemical pesticides.

58

59 Strategies for managing CBB include chemical, biological, and cultural controls. Due to
60 concerns for human and environmental health, chemical controls such as endosulfan and
61 chlorpyrifos are being phased out or banned in many coffee-growing countries [3]. Sprays of the
62 entomopathogenic fungus *Beauveria bassiana* are becoming more widely used as a sustainable
63 replacement for these acutely toxic chemicals [4, 5, 6]. Biological control using parasitoids has
64 also been implemented, particularly in Latin America, but with limited success due to the need
65 for augmentative releases [7]. Cultural controls are typically the most cost-effective methods for
66 managing CBB and include pruning, frequent and efficient harvesting, strip-picking all
67 remaining berries at the end of the season, and sanitation of harvesting equipment and processing
68 facilities [4, 5]. Integrated pest management (IPM) of CBB typically involves multiple
69 components including sprays of *B. bassiana* early in the season, frequent and efficient

70 harvesting, and post-harvest sanitation; these have been shown to be effective for managing CBB
71 in Hawaii [6, 8].

72

73 A critical aspect of most successful IPM programs is monitoring of pest activity with traps
74 and/or infestation assessments. By identifying peaks in flight activity that coincide with berry
75 colonization, coffee growers can maximize the efficiency of *B. bassiana* applications and thereby
76 minimize costs. Traps are used in many countries to monitor CBB activity [9, 10, 11, 12] and
77 mass-trapping using a high density of traps in an area has even been suggested as a possible
78 method of control [13]. In Hawaii, traps were introduced soon after the initial CBB detection in
79 2010 [14] as part of the IPM guidelines for managing this new invasive pest [15]. Traps were
80 adopted by many growers in the early years of the invasion to monitor CBB activity in their
81 fields. However, over time, fewer and fewer growers utilized traps with most transitioning to
82 calendar sprays of *B. bassiana* or relying on casual observation of infestation in their fields to
83 guide the timing of spray applications (A. Kawabata, pers. comm.). This approach has been
84 shown to be inefficient: Hollingsworth et al. [6] reported that 3-5 sprays of *B. bassiana*
85 conducted early in the season were just as effective as 8-12 calendar sprays, highlighting the
86 importance of appropriately timing sprays for cost-effective control of CBB.

87

88 Understanding the seasonal phenology of CBB and the underlying abiotic drivers of flight are
89 essential for predicting periods of high activity. Information on CBB population dynamics for a
90 given coffee-growing region can be used to develop action thresholds and forecasting models for
91 specific locations. This is especially important for Hawaii where the coffee-growing landscape is
92 heterogeneous, and a single set of management recommendations is difficult to apply across the

93 entire region. Coffee is grown commercially on six of the main Hawaiian Islands on volcanic
94 soils that vary in age and nutrient composition and experience a broad range of microclimate
95 conditions from sea level to over 800 m in elevation [16]. On Hawaii Island, more than 800
96 small farms produce coffee, most of which are family-run operations that rely on manual labor to
97 harvest the coffee and implement management practices. Optimizing pest management strategies
98 while minimizing costs are critical to the longevity of these farms as Hawaii has some of the
99 highest labor and production costs of any coffee-growing region.

100

101 In the present study we monitored the flight activity of CBB using funnel traps at 14 commercial
102 coffee farms in the two main coffee-growing regions of Hawaii Island, Kona and Ka‘u, over a
103 three-year period. Five weather variables thought to be important for insect flight (temperature,
104 relative humidity, solar radiation, wind speed and rainfall) were tracked at each site. Our
105 objective was to provide insights into the seasonal phenology of CBB across a highly variable
106 landscape, as well as to characterize the abiotic factors that trigger CBB flight, which will aid in
107 the development of models for predicting future flight events. These models can serve as
108 decision support tools to guide the timing of pesticide applications. While this study is focused
109 on Hawaii, we expect that the information gained on CBB flight and associated weather
110 variables will be useful for developing IPM strategies in other coffee-growing regions.

111

112 **Materials and Methods**

113

114 *Study Sites*

115

116 Fourteen commercial coffee farms were selected for the study on Hawaii Island. Eight farms
117 were located on the West side of the island in the Kona district and six farms were on the
118 Southeast side of the island in the Ka‘u district (Fig. 1). While coffee is grown throughout the
119 Hawaiian Islands, Kona and Ka‘u are the two primary coffee-growing regions, both of which are
120 world-renowned for the high quality of their coffee. Farms were selected to encompass the broad
121 range of elevations and climatic conditions under which coffee is grown on Hawaii Island. In
122 Kona, farms ranged in elevation from 204 m – 607 m and in Ka‘u farms ranged from 279 m –
123 778 m in elevation. All farms were actively managed for coffee production throughout the study,
124 although the timing and number of interventions varied. Management practices included regular
125 pruning, weed management, fertilizer, pesticide application, cherry harvesting and end of season
126 strip-picking. Farms were largely characterized as sun-grown although some farms had scattered
127 fruit, nut or ornamental shade trees planted as well. All farms had *Coffea arabica* var. *typica*
128 planted with the exception of one farm in Ka‘u which had primarily var. *catuai* planted.

129

130 **Figure 1.** Map of Hawaii Island showing 14 study sites (eight in the Kona district and 6 in the
131 Ka‘u district). Inset map shows the main Hawaiian Islands and the location of Hawaii Island
132 within the archipelago.

133

134 *Flight Activity*

135

136 Red funnel traps (CIRAD, Montpellier, France) baited with an alcohol lure (3:1
137 methanol:ethanol) were randomly distributed throughout each farm. Trap density was based on
138 farm size, with 3-5 traps used for small farms (1-1.4 ha) and 6-9 traps used for large farms (1.5-2

139 ha). Traps were hung on stakes at ~1 m in height and were equipped with a collection cup
140 containing propylene glycol. Trap contents were collected in 70% ethanol on a bi-weekly
141 schedule from 2016-2018. Lures were refilled as needed and propylene glycol was replaced bi-
142 weekly. In the laboratory, trap contents were passed through a sieve (1.5 mm mesh size) to
143 separate out all large insects, which were discarded (see [17] for additional details on trap setup,
144 collection and processing). The remaining insects from each trap collection were placed under a
145 stereomicroscope (Leica microsystems GmbH, Wetzlar, Germany). All Scolytine beetles were
146 counted and CBB were separated from these other beetles to estimate trap specificity. If >500
147 beetles were caught in a single trap, we used a volumetric method to estimate count (see [17] for
148 details). For each site, the number of CBB per trap per day (CBB/trap/day) was estimated by
149 dividing the total number of CBB caught by the number of traps in the farm and then dividing
150 this by the number of days in the sampling period (14 days on average, although this varied
151 occasionally). This calculation was also done to estimate the number of other Scolytid beetles
152 caught per trap per day.

153

154 *Weather Variables*

155

156 Manual or cell-service weather stations were set up at each farm to measure the following
157 variables: air temperature, relative humidity (RH), rainfall, wind speed and solar radiation.
158 Manual stations consisted of a Hobo Pro v2 temperature/RH data logger (U23-002, Onset
159 Computer Corporation, Bourne MA) housed in a solar shield (RS3, Onset Computer
160 Corporation, Bourne MA), a solar pendant (UA-002-64, Onset Computer Corporation, Bourne
161 MA) and a rain gauge equipped with a manual data logger (RainLog 2.0, RainWise Inc.). Cell-

162 service weather stations were comprised of a 4G remote monitoring station (RX3004-00-01,
163 Onset Computer Corporation, Bourne MA) equipped with a temperature/RH sensor (S-THB-
164 M002), solar panel (SOLAR-5W), solar radiation sensor (S-LIB-M003) placed within a solar
165 shield (RS3-B) and rain gauge (S-RGB-M002). Wind speed sensors (S-WSET-B) were added to
166 each cell-service station in 2018. For each site, the daily maximum, mean, and minimum were
167 estimated for air temperature and RH in R v. 3.5.0 using the ‘aggregate’ function in the *stats*
168 package [18]. We used the same method to estimate the daily mean and maximum wind speed
169 and solar radiation, as well as daily cumulative rainfall. We then used these daily values to
170 calculate the average air temperature ($^{\circ}\text{C}$), RH (%), wind speed (m/s) and solar radiation (W m^{-2}),
171 as well as the cumulative rainfall (mm) for each ~bi-weekly sampling period.

172

173 *Data Analysis*

174

175 All statistical analyses were conducted in R v.3.5.0 [18]. The assumption of normality for each
176 variable was validated using quantile-quantile plots and a Shapiro-Wilks test; an *F* test was
177 conducted to assess for equal variances using the *stats* package. A Pearson correlation test was
178 conducted using the *stats* package to examine the relationship between total CBB capture for
179 each year/site and elevation. The mean number of CBB caught per trap per day was log-
180 transformed ($\log + 1$) prior to analysis. Linearity of the relationship between CBB/trap/day and
181 each weather variable was also checked prior to analysis using two-dimensional scatterplots.
182 Given the non-linear nature of the relationship between weather variables and CBB flight, the
183 influence of weather on CBB flight activity was evaluated with a generalized additive mixed
184 model (GAMM) in the *mgcv* package v. 1.8-23 [19].

185
186 The response variable for the model was the log-transformed mean number of CBB/trap/day,
187 with year and site included as random effects and the weather variables included as fixed effects
188 with cubic regression splines. We assumed a gaussian error distribution and an identity link
189 function for the model. We used the generalized cross-validation (GCV) score to measure model
190 smoothness with respect to the smoothing parameters as well as the estimate prediction error. A
191 lower GCV score indicates a smoother model and is somewhat comparable to an Akaike
192 Information Criterion (AIC) value, in that a lower score equates to a better fitting model.
193 Pairwise Pearson correlation tests of continuous explanatory variables were conducted to assess
194 multicollinearity at a correlation coefficient threshold of 0.7; maximum temperature, mean RH
195 and maximum solar radiation were subsequently dropped from the model due strong correlations
196 with mean temperature, maximum RH and mean solar radiation, respectively.

197

198 **Results**

199

200 In total, just under 5 million Scolytid beetles were captured over a period of 143 weeks. Across
201 all 14 sites, CBB made up an average of 81% of the total trap catch in 2016, 91% in 2017, and
202 93% in 2018 (Fig. 2). The most trapped non-CBB beetles were *Hypothenemus obscurus* F.
203 (tropical nut borer), *Xylosandrus compactus* Eich. (black twig borer) and a species of bark beetle
204 tentatively identified to the genus *Cryphalus* Erichson. Peak activity for non-CBB beetles was in
205 the summer months of June and July. Farms observed to have higher percentages of non-CBB
206 beetles in traps were located next to macadamia nut orchards or forests or had other fruit and nut
207 trees interplanted with the coffee. The combined CBB catch across all sites was similar for 2017

208 (~1.98M CBB) and 2018 (~2.05M CBB), but considerably lower for 2016 (~600K CBB) given
209 that data collection did not start until March (Kona) and May (Ka‘u), thereby missing the initial
210 emergence for that year.

211

212 **Figure 2.** Total trap catch across three years on Hawaii Island. Study sites are in order of
213 increasing elevation from left to right. Black bars represent coffee berry borer (CBB) while gray
214 bars represent other Scolytid beetles.

215

216 Although variation was observed among years and farms in terms of the average number of
217 CBB/trap/day, the general pattern of flight was consistent (Fig. 3). Seasonal phenology was
218 observed in two stages: an initial emergence from January-April which coincides with early fruit
219 development, and a secondary flight which occurs from September-December and coincides with
220 the harvest season (Fig. 3). This secondary flight corresponds to the emergence of new
221 generations of CBB that were the offspring of the initial colonizing females. Although we did not
222 observe any consistent differences in trap capture patterns among farms in the Kona vs. Ka‘u
223 regions, a linear regression revealed a moderate but significant negative correlation between
224 elevation and total trap catch ($R = -0.48$, $t = -3.39$, $p = 0.002$) (Fig. 4).

225

226 **Figure 3.** Seasonal flight phenology of coffee berry borer (CBB) on Hawaii Island over a three-
227 year period. Sampling began in March 2016 and ended in December 2018. Error bars show the
228 variation across 14 study sites.

229

230 **Figure 4.** Linear regression showing a moderate but significant negative relationship between
231 the log-transformed total CBB capture for each site/year and elevation ($R = -0.48$, $p = 0.002$).
232
233 The final GAMM explained 75.7% of the deviance (adjusted $R^2 = 0.66$, $GCV = 0.29$), with the
234 following weather variables having a significant effect on CBB flight at an $\alpha < 0.05$: mean
235 temperature, maximum RH, cumulative rainfall, maximum wind, and mean solar radiation
236 (Table 1). Mean daily temperature had the greatest positive effect on CBB flight (Table 1) with
237 three peaks observed between 20-26 °C (Fig. 5A). Mean daily solar radiation also had a positive
238 effect on CBB flight, with peaks observed at 200-300 W/m^2 and 400-500 W/m^2 (Fig. 5A).
239 Flight levels were generally high at maximum daily RH values between 80-94%, after which
240 they fell sharply (Fig. 5B). Cumulative rainfall had a positive effect on CBB flight up to 100
241 mm, after which flight decreased (Fig. 5B). Flight increased up to maximum daily wind speeds
242 of ~2.5 m/s and subsequently dropped off (Fig. 5C). Both the random effects of site ($p < 0.001$)
243 and year ($p = 0.003$) also had significant effects on CBB flight (Table 1).

244

245 **Figure 5.** Results from a generalized additive mixed model (GAMM) exploring the effects of
246 mean daily temperature (A, C), mean solar radiation (A), maximum relative humidity (B),
247 cumulative rainfall (B) and maximum wind speed (C) on coffee berry borer flight activity.
248 Three-dimensional contour plots show peaks in CBB flight activity in yellow and decreased
249 activity in cooler colors (green and blue).

250

251 **Table 1.** Results from the generalized additive mixed model (GAMM) analyzing the influence of
252 five independent weather variables (fixed effects) and site and year (random effects) on CBB
253 flight.

254

Variable	edf	ref.df	F	p-value
Mean Temperature	8.432	8.870	5.868	5.07e ⁻⁰⁷ ***
Minimum Temperature	2.138	2.824	1.081	0.282
Maximum RH	8.062	8.580	3.504	0.001**
Minimum RH	4.075	4.960	1.991	0.096
Mean Solar	5.064	5.898	3.234	0.005**
Cumulative Rain	7.737	8.355	2.815	0.006**
Maximum Wind	8.695	8.948	2.277	0.015*
Mean Wind	2.648	3.439	1.693	0.184
Site	7.237	8.000	8.520	1.21e ⁻¹⁰ ***
Year	0.849	1.000	8.834	0.003**

255 Legend: edf – effective degrees of freedom; ref.df – reference degrees of freedom; F – *F*-

256 statistic; p-values were considered significant at the following levels: < 0.001 ‘***’, < 0.01 ‘**’,

257 < 0.05 ‘*’.

258

259 Discussion

260

261 Determining the seasonal phenology and abiotic factors involved in flight activity is a critical
262 step in developing an integrated pest management plan for invasive insects. In the present study
263 we examined 14 commercial coffee farms in two coffee-growing districts on Hawaii Island to
264 elucidate seasonal flight patterns and the influence of five weather variables on CBB flight. Our
265 findings suggest that although there are differences from farm to farm, general patterns of CBB
266 flight activity can be described across this highly variable landscape. We observed two major
267 flight events that were consistent across all three years: an initial emergence from January-April
268 that coincides with early fruit development and a secondary flight that occurs during the harvest

269 season from September-December. We also found that despite not having a species-specific lure,
270 trap specificity was generally high with CBB making up 81-93% of the total trap catch across all
271 farms.

272

273 These results correspond to findings from two earlier studies that examined CBB flight patterns
274 on Hawaii Island. Messing [20] reported CBB flight from November-March at two farms in
275 Kona. That study also found that 1:1 and 3:1 ratios of methanol:ethanol captured similar
276 numbers of beetles, and that non-target beetles made up an insignificant proportion of trap catch
277 relative to CBB (3-7 non-target beetles/trap/day compared to 100-400 CBB/trap/day). Our
278 findings are also in line with those of Aristizábal et al. [21], who examined flight activity at 15
279 farms in Kona and Ka'u using 3:1 methanol:ethanol baited funnel traps. That study reported a
280 small peak in flight from May-July and a larger peak from December-February. The authors
281 suggested that peaks appeared to coincide with increased levels of rainfall following a dry
282 period, although weather data was not available for each farm, excluding statistical analyses.
283 Aristizábal et al. [21] also estimated that non-target insects made up < 5% of all trap catch based
284 on subsampling from a few farms. While these earlier studies provided initial insights into
285 seasonal flight trends in Hawaii, sampling was limited to a one-year period and did not include
286 site-specific data on weather. In the present study we were able to expand on these initial
287 findings by collecting data over multiple years and correlating flight activity to five individual
288 weather variables at each farm. Below we summarize our main findings with respect to the
289 influence of weather variables on trap catch, our proxy for flight activity.

290

291 Mean daily air temperature was observed to be the single weather variable with the strongest
292 (positive) relationship to CBB flight activity across all sites. This is relatively unsurprising since
293 insects are poikilotherms, meaning their body temperature depends on ambient environmental
294 temperature. Many aspects of insect biology are driven by temperature including generation
295 length, rate of development, mating activity and dispersal [22]. It is widely reported that insects
296 actively regulate body temperature before and during flight by behavioral or physiological means
297 [23; 24; 25; 26; 27; 28; 29], and that there is a lower and upper temperature threshold for flight
298 [30]. Insects need warm temperatures to initiate and maintain flight as it becomes difficult at
299 lower temperatures to generate heat [27, 31, 32, 33]. As air temperatures increase, the
300 aerodynamic force and mechanical power output of insects is also increased along with wing
301 beat frequency [34, 35].

302
303 Chen and Seybold [36] reported a lower threshold of 11 °C, an optimum of 27 °C and an upper
304 threshold of 39 °C for the walnut twig beetle (*Pityophthorus juglandis* Blackman). In a
305 controlled laboratory setting with RH held at 90% and 100%, Baker et al. [37] reported low CBB
306 emergence from dried berries at temperatures below 20 °C, a marked increase in emergence from
307 20-25 °C, and no significant increase above 25 °C. In the present study under highly variable
308 field conditions, we observed that most flight events took place when mean daily temperatures
309 were between 20-26 °C, with very few events below 16 °C or above 32 °C.

310
311 Along with a positive effect of increasing temperature, we found a positive significant
312 relationship between CBB flight and mean daily solar radiation. This is line with the findings of
313 several studies that reported temperature and solar radiation as the main abiotic factors positively

314 influencing beetle flight [36, 38, 39, 40]. Related to this, we also observed a significant negative
315 correlation between elevation and total CBB capture. Hamilton et al. [41] showed that CBB
316 development on Hawaii Island is faster at low elevations primarily due to higher temperatures at
317 these locations. The authors estimated 4-5 generations per season at low elevations (200-300 m),
318 compared to 2-3 generations per season at high elevations (600-800 m). Thus, the higher
319 abundance of CBB caught at lower elevations is directly related to the shorter development times
320 at these sites.

321
322 In accordance with numerous studies on insect flight, we observed a significant negative effect
323 of maximum daily relative humidity above ~94%. CBB may be reluctant to leave the berries
324 during periods of very high RH as this may indicate rain (along with an associated drop in
325 barometric pressure, not measured in the current study), causing them to shelter. In addition,
326 greater CBB mortality can occur during periods of high RH due to proliferation of *B. bassiana*
327 under moist, humid conditions. Lastly, at very high RH there is a higher requirement of wing-
328 beat frequency, which is metabolically costly [23, 29]. Farnworth [42] showed that *Periplaneta*
329 *americana* Linnaeus had a higher wing beat frequency at 95% RH compared to 50% RH at
330 temperatures between 27-35 °C, which could reflect greater effort to dissipate heat at high vs.
331 low humidity. In contrast to our findings, under laboratory conditions with temperature held at
332 25 °C, Baker et al. [37] described high CBB emergence from infested two-month-old berries at
333 RH values of 20% and 55%, minimum emergence at 78% and 90%, and a steady increase in
334 emergence from 94-100%. It is likely that differences between this study and our findings are
335 related to the setting under which emergence was estimated. We did not observe a minimum RH
336 lower than 52%, and mean RH values ranged from 80-90% for most sites/years. Maximum RH

337 values were typically >94% through spring and summer and dropped during the winter months
338 (November-March), which coincided with peak CBB flight.

339

340 We observed a similar trend for maximum wind speed, with flight increasing at wind speeds up
341 to ~2.5 m/s and then decreasing at speeds above that value. Chen and Seybold [36] reported that
342 *P. juglandis* flight was limited at very low wind speeds and peaked when temperature was ~30
343 °C and wind speed was 2 km/h. Pawson et al. [43] reported low flight activity of the bark beetle
344 *Hylurgus ligniperda* Fabricius at very low wind speeds, an increase with rising wind speeds, and
345 a peak at 2 m/s. Thus, some wind may help to initiate flight as well as provide olfactory cues to
346 allow detection of resources, but at very high wind speeds flight appears to be inhibited. The
347 long-distance dispersal of many weak-flying smaller insects is dictated mostly by wind [44, 45,
348 46], which may explain the tendency of CBB to fly near the ground (M. Johnson, unpub. data)
349 where ambient wind speeds are generally low [47]. Lastly, cumulative rainfall had a positive
350 effect on CBB flight up to a point; flight appeared to be inhibited during periods of heavy rainfall
351 (>100 mm). Other studies have reported negative effects of heavy rainfall on bark beetle flight
352 [48, 49, 50]; the very small size of CBB likely precludes its movement during periods of
353 inundation.

354

355 By considering the phenology of the coffee crop and the CBB together with the trap catches
356 reported here, the pattern of CBB movement in Hawaii coffee plantations comes into focus. At
357 the very beginning of the year the new coffee crop must become mature enough (>20% dry
358 matter content [51, 52, 53]) to be infested by the previous season's beetles. These CBB are
359 mostly in raisins (dried berries) on the ground under the coffee trees or on the raisins remaining

360 on the branches- the latter being the most heavily infested repositories on a per-bean basis [54].
361 The first flight suggests movement from these refugia into developing green berries in the first
362 quarter of the calendar year. Given that few berries may be available early in the season, CBB
363 will have to travel more extensively to find suitable hosts. Once a suitable berry is located, the
364 female CBB will penetrate the exocarp and wait to complete entry into the coffee bean until
365 conditions are suitable, or may begin boring immediately into the seed depending on fruit stage
366 [1].

367
368 After the first flight, CBB begin reproducing within the beans and berry development continues.
369 During this middle part of the year, there is very little baseline movement of CBB and trap
370 catches are low since the host berries are abundant. The second major flight, observed here in the
371 last quarter of the calendar year, is likely driven by waning food supplies in the original berries
372 (as the numbers of CBB increase in the individual beans, food is reduced and movement again
373 becomes necessary) in combination with physical disturbance during harvesting, strip-picking
374 and tree pruning. Based on observations of lower flight activity in this second part of the year in
375 feral and unmanaged sites vs. well-managed sites on Hawaii Island [55], physical disturbance via
376 management practices are a larger stimulus for this second flight relative to the need to locate
377 food, which is the primary stimulus for the first flight of the season.

378

379 **Conclusions**

380

381 Our investigation into CBB seasonal phenology and the influence of weather on CBB flight
382 activity revealed important insights that will be useful for the development of future flight

383 prediction models. Seven of the 10 variables included in the GAMM were found to have a
384 significant influence on CBB flight activity. Of the eight fixed effects, mean daily temperature,
385 mean solar radiation, maximum RH, maximum wind speed and cumulative rainfall were
386 significant, while both the random effects of site and year also had a significant effect on flight.
387 Variation among years was likely due to a combination of weather events and the timing of study
388 initiation, while variation among farms likely involved differences in management style, timing,
389 and the number of interventions, as well as differences in CBB development times across
390 elevations. That the best model explained only 75.7% of the observed variance likely reflects the
391 absence of additional weather variables that were not measured such as barometric pressure, as
392 well as variation that was missed due to sampling frequency. Given the large travel distance
393 between sites, all traps were sampled on a bi-weekly schedule, such that correlating weather
394 events to trap catch at finer scales was not possible. The timing of daily CBB flight and the
395 weather events correlated with flight activity on an hourly basis are currently being examined at
396 several sites on Hawaii Island to further elucidate flight patterns in this global pest of coffee.

397

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409

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20° N

Kona

Ka'u

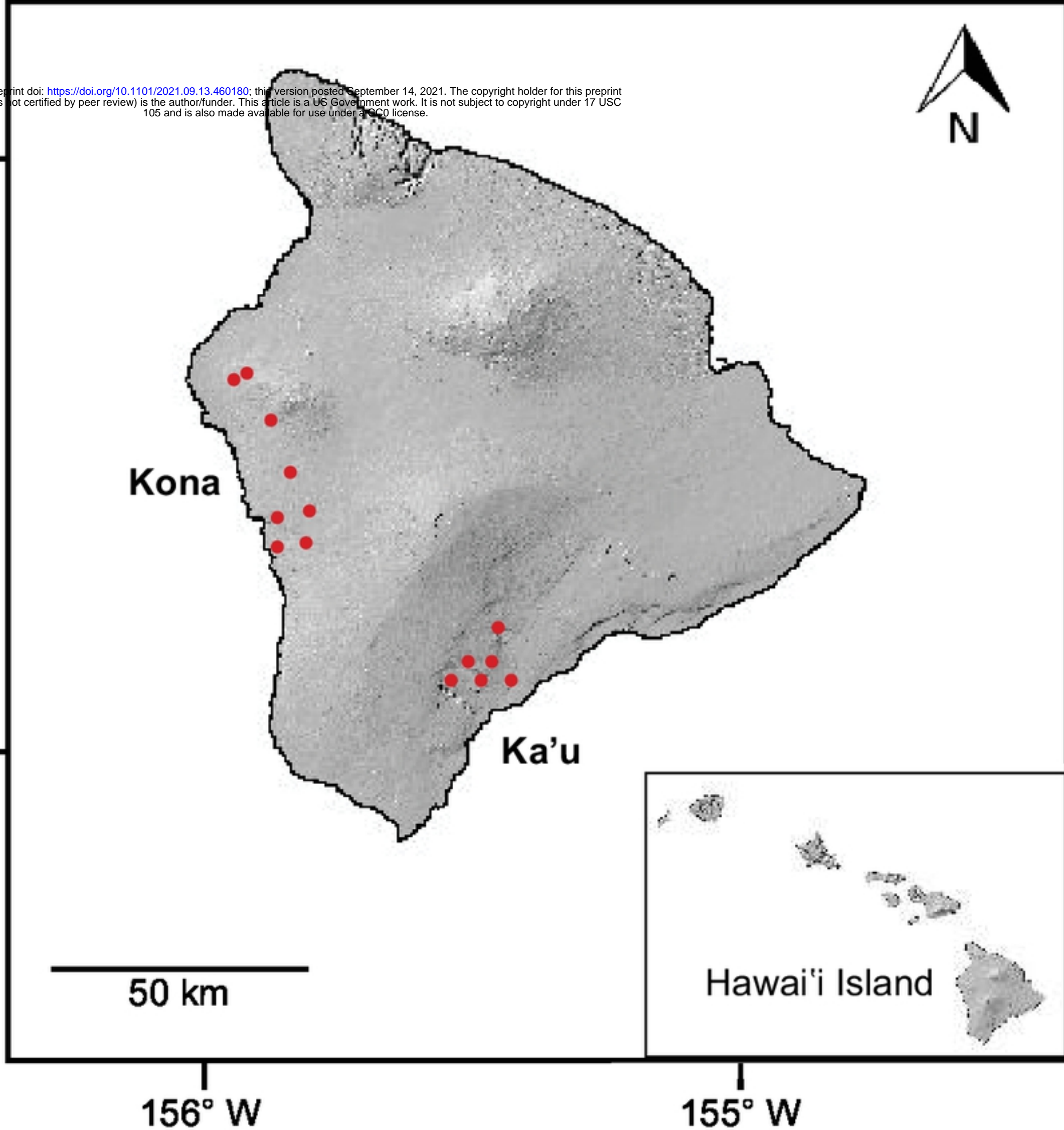
19° N

50 km

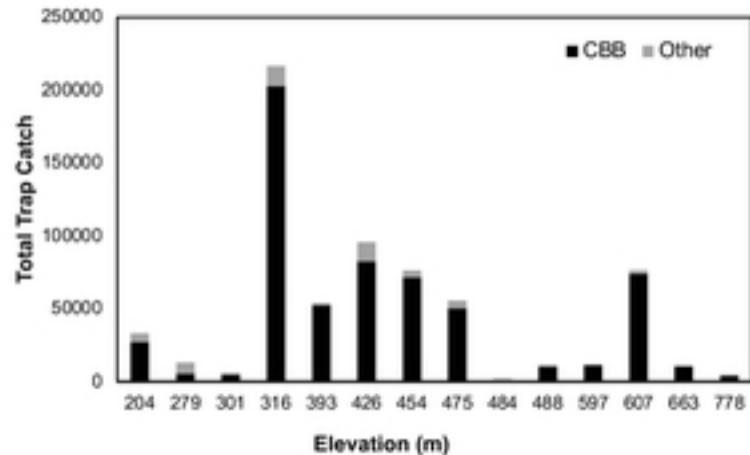
156° W

155° W

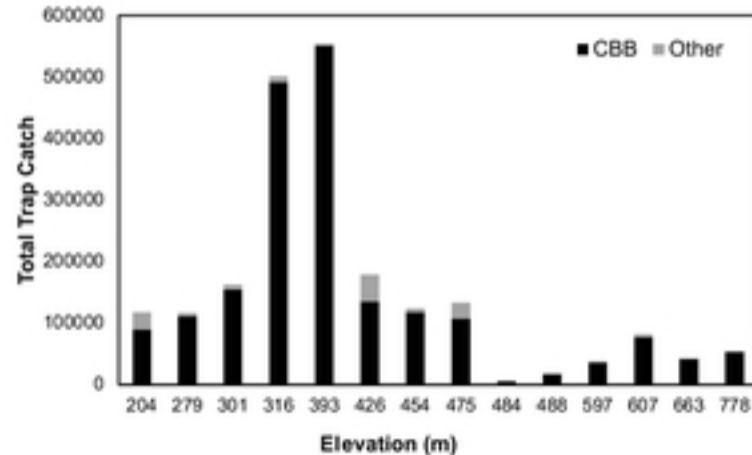
Hawai'i Island



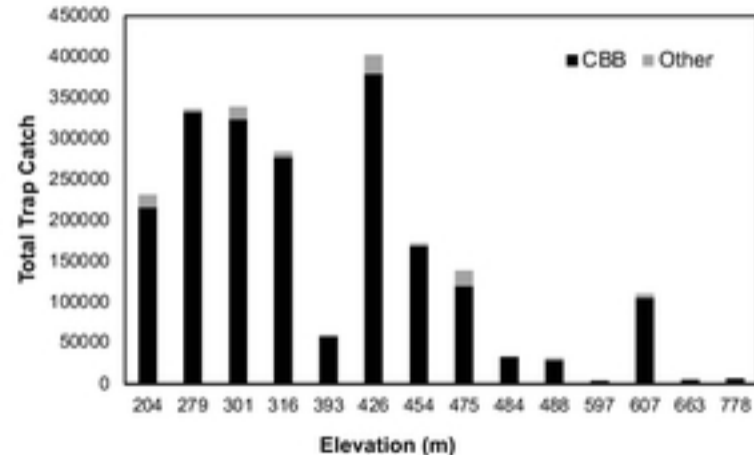
2016

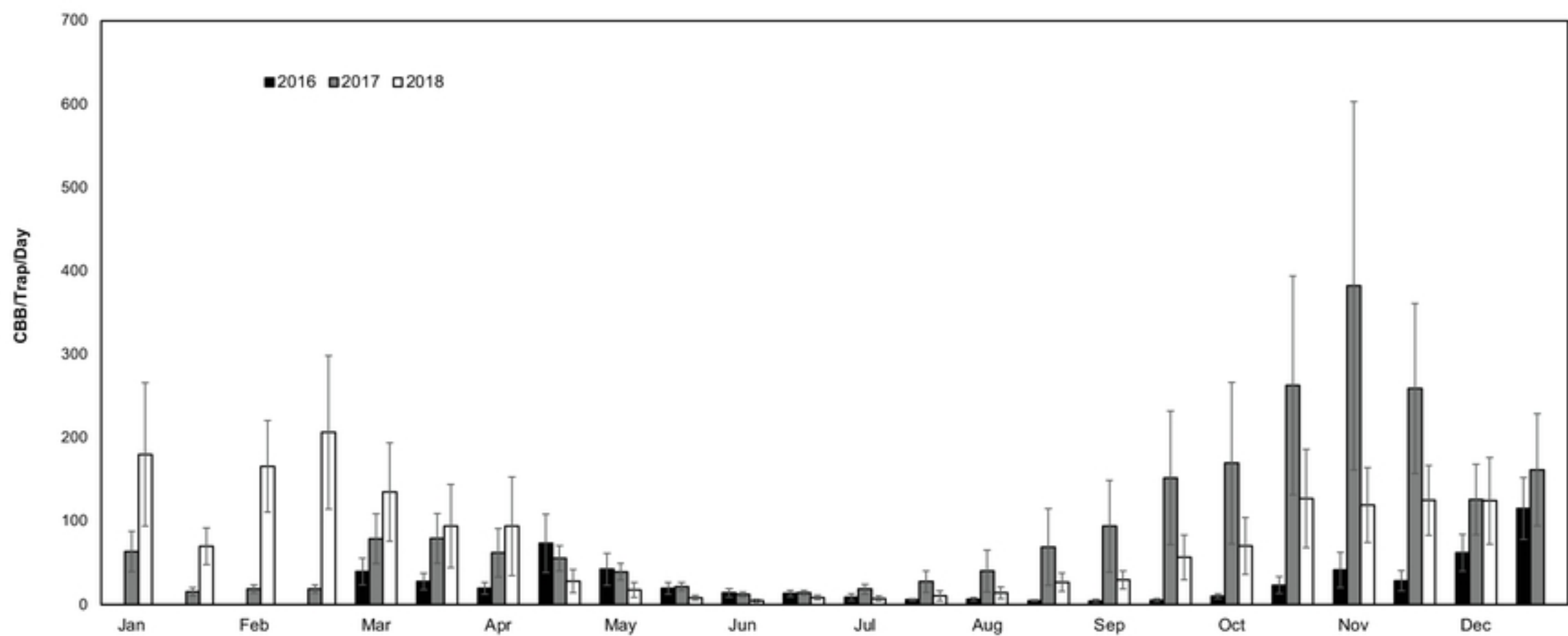


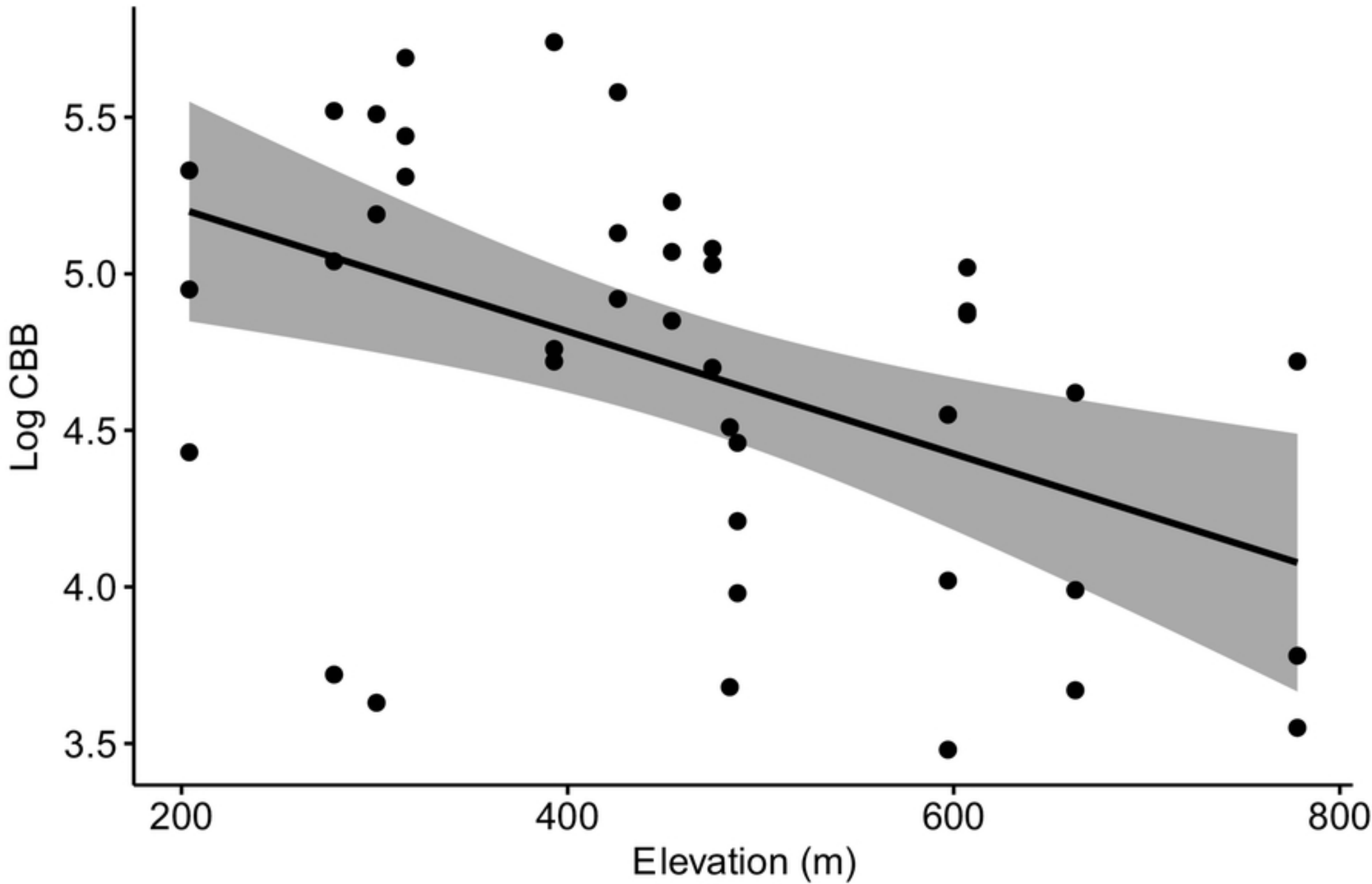
2017



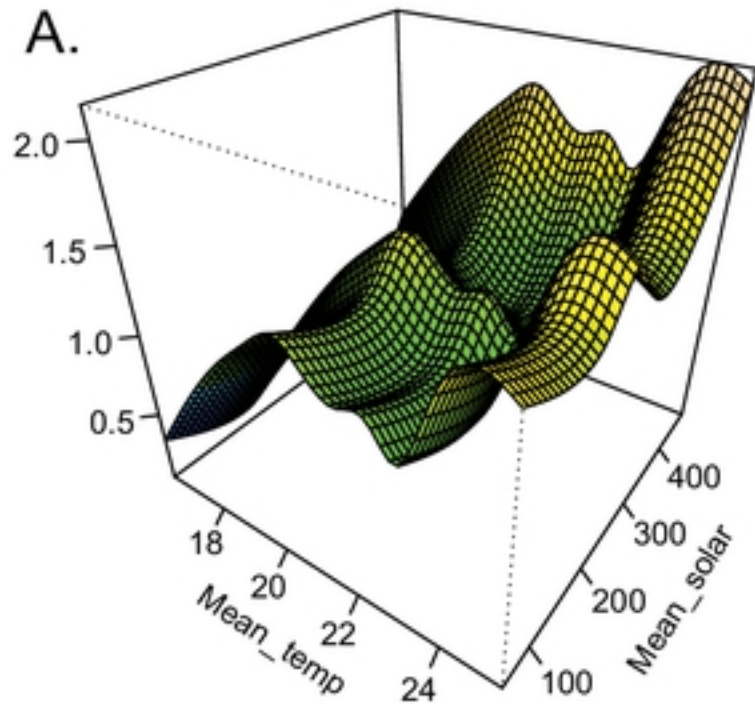
2018



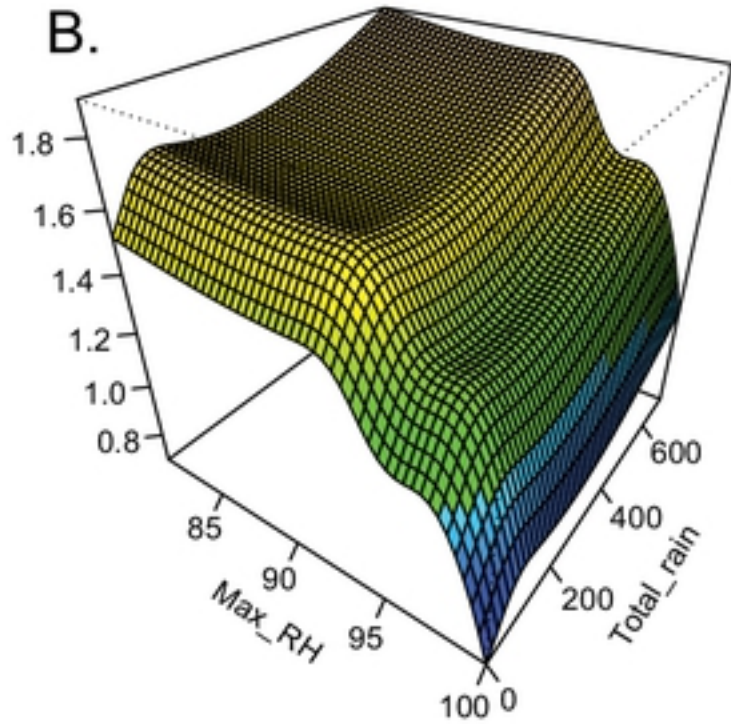




A.



B.



C.

