

# Independent, But Not Synergistic, Effects of Landscape Structure And Climate Drive Pollination of A Tropical Plant, *Heliconia Tortuosa*

Claire E. Dowd (✉ [cdowd139@gmail.com](mailto:cdowd139@gmail.com))

Oregon State University

Kara G. Leimberger

Oregon State University

Adam S. Hadley

University of Toronto

Sarah J.K. Frey

Oregon State University

Matthew G. Betts

Oregon State University

---

## Research Article

**Keywords:** climate, landscape structure, habitat loss, habitat fragmentation, pollination, interactive effects

**Posted Date:** April 19th, 2021

**DOI:** <https://doi.org/10.21203/rs.3.rs-322197/v1>

**License:**  This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

---

# **Independent, but not synergistic, effects of landscape structure and climate drive pollination of a tropical plant, *Heliconia tortuosa***

Claire E. Dowd<sup>1</sup>, Kara G. Leimberger<sup>2</sup>, Adam S. Hadley<sup>2,3</sup>, Sarah J. K. Frey<sup>2,4</sup>, Matthew G. Betts<sup>2</sup>

Matthew G. Betts  
matthew.betts@oregonstate.edu

<sup>1</sup>Department of Integrative Biology, Oregon State University, Corvallis, OR, USA

<sup>2</sup>Forest Biodiversity Research Network, Department of Forest Ecosystems & Society, Oregon State University, Corvallis, OR 97331, USA

<sup>3</sup>Department of Ecology and Evolutionary Biology, University of Toronto, Mississauga, ON, Canada L5L1C6

<sup>4</sup>College of Earth, Ocean, and Atmospheric Sciences, Oregon State University, Corvallis, OR 97331, USA

## **Acknowledgements**

We appreciate the help of our field assistants Michael Atencio, Esteban Sandi, and Mauricio Paniagua. We thank the Las Cruces Biological Station for logistical support. We are grateful to private landowners who allowed us to work on their property. We also thank Ariel Muldoon and Jonathon Valente for their statistical advice. This work was supported by National Science Foundation (NSF-DEB-1050594 and NSF-DEB-1457837 to MGB and ASH) and associated NSF-Research Experience for Undergraduates grant that supported CED. In addition, we thank the Ernest and Pauline Jaworski Fund and the Deloach Work Scholarship from Oregon State University. This material is based upon work supported by the National Science Foundation Graduate Research Fellowship Program under Grant No. 1840998 to KGL.

1 **Abstract**

2 *Context* Land-cover and climate change are predicted to affect pollination and plant  
3 reproduction but few studies have tested how these stressors interact to drive pollination success.

4 *Objectives* Using a 9-year dataset we tested whether climate interacts synergistically with forest  
5 loss and fragmentation to affect pollination of a tropical understory herb, *Heliconia tortuosa*. We  
6 hypothesized that hot and/or dry conditions might amplify effects of habitat loss and  
7 fragmentation, leading to declines in plant reproduction.

8 *Methods* We collected data on pollen tubes, fruits and seeds of *H. tortuosa* in a mensurative  
9 experiment representing gradients in forest amount and patch size (N=40 focal-patch  
10 landscapes). We modeled these reproductive metrics as a function of landscape composition,  
11 configuration, precipitation, temperature, and statistical interactions among these variables.

12 *Results* We found little support for synergistic landscape and climate effects. However,  
13 probability of fruit production decreased in wet years, and increased in large patches embedded  
14 in more contiguous forest landscapes. Counterintuitively, small patches in heavily deforested  
15 landscapes also exhibited a high probability of fruit – perhaps due to constraints on hummingbird  
16 movement. Amount of *H. tortuosa* fruit decreased in wet years and in deforested landscapes.

17 *Conclusion* Although we did not detect synergistic effects, climate and landscape structure do  
18 have independent impacts on plant reproduction. Unfortunately, the regional climate is predicted  
19 to become wetter and the forest remains fragmented, with potential negative consequences for  
20 *Heliconia* reproduction. Decline in this common species is likely to have cascading  
21 consequences for hummingbird pollinators, and subsequently other hummingbird dependent  
22 plant species.

23

24 **Key Words:** climate, landscape structure, habitat loss, habitat fragmentation, pollination,

25 interactive effects

26

27

## 28 **Introduction**

29 Rates of biodiversity loss are increasing globally (IPBES 2019). There are a multitude of  
30 threats contributing to biodiversity loss including climate change (Thomas et al. 2004; Brook et  
31 al. 2008) and land-cover change (Dale et al. 1994; Brooks et al. 2002; Wilson et al. 2016).  
32 Declines in pollinators (Potts et al. 2010; Winfree et al. 2018; Reilly et al. 2020) and their  
33 associated plants (Biesmeijer et al. 2006) are now well established. A reduction in pollination  
34 could drive further biodiversity losses because over 85% of flowering plants are animal  
35 pollinated (Ollerton et al. 2011). Therefore, as climate changes, it is critical to understand how  
36 climate and land-cover change affect pollination and plant reproduction.

37 Species distributions are expected to shift with changing environmental conditions  
38 (Huntley and Webb 1989). The overall direction of these shifts is expected to be poleward and  
39 into higher elevations (Parmesan 2006). However, the direction of species distribution shifts in  
40 the tropics are expected be less consistent (VanDerWal et al. 2013). If plants and their pollinators  
41 exhibit distinct shifts in distributions, the result could be reduced overlap in geographic ranges.  
42 In addition, climate change can affect the phenology of plants (Parmesan 2006) and animals  
43 (Visser and Both 2005), which may contribute to changes in temporal synchronicity upon which  
44 pollination mutualisms depend (Schweiger et al. 2010). Phenological mismatches between plants  
45 and pollinators may affect pollinator demography, pollinator population density and  
46 distributions, pollen availability, and pollen limitation (Hegland et al. 2009).

47 In this study, we are concerned with how two components of landscape structure –  
48 habitat loss and fragmentation – influence pollination. Habitat loss is the leading driver of  
49 pollinator declines (Brown and Paxton 2009) and has been shown to negatively affect pollinator  
50 diversity (Klein et al. 2003; Spiesman and Inouye 2013) which, in turn, reduces plant sexual

51 reproduction (Garibaldi et al. 2013). Habitat fragmentation – the breaking apart of habitat into  
52 smaller patches – is also known to decrease the sexual reproduction of flowering plants (Aguilar  
53 et al. 2006). This could be due to fragmentation-induced changes to animal behavior (Bélisle et  
54 al. 2001; Ricketts 2001) – particularly for species for which the matrix increases predation risk  
55 or perceived risk (Lima and Zollner 1996). Changes to pollinator movement (Hadley and Betts  
56 2009) could reduce both pollen quality and quantity, thereby reducing plant sexual reproduction  
57 (Hadley and Betts 2012).

58         Although several studies have investigated the interactive impacts of landscape structure  
59 and climate on biodiversity (Forister et al. 2010; Stangler et al. 2015; Oliver et al. 2015; Conenna  
60 et al. 2017; Guo et al. 2018; Northrup et al. 2019), only one study has examined synergistic  
61 climate and landscape structure effects on pollinators (Peters et al. 2019). However, several  
62 authors have hypothesized that climate change could amplify the well-known impacts of habitat  
63 loss and fragmentation (Dale 1997; Brook et al. 2008; de Chazal and Rounsevell 2009; Oliver  
64 and Morecroft 2014). For example, climate change may lead to fewer floral resources for  
65 pollinators due to geographic range shifts, mismatches in phenology, or unpredictable weather  
66 forcing pollinators to move farther distances to acquire resources. However, if fragmentation  
67 reduces pollinator movement, and therefore the capacity to ‘keep up’ with climate change,  
68 pollination will be reduced (Betts et al. 2019). Climate-driven reductions in the abundance of  
69 floral resources (Duchenne et al. 2020) also exacerbate pollinator resource declines driven by  
70 habitat loss. These declines in pollinators could subsequently reduce pollination, potentially  
71 leading to a positive feedback loop.

72         To address the possibility of synergistic effects of climate and land-cover change on  
73 pollination, we analyzed 9 years of pollination and reproductive output data (2010-2018) from a

74 hummingbird-pollinated understory herb, *Heliconia tortuosa*, in southern Costa Rica. In this  
75 region, forest loss has historically been severe, with >70% of forest cover (>22,500 ha) lost  
76 between 1947 and 2014 (Zahawi et al. 2015). This drastic loss of forest cover has produced a  
77 highly fragmented landscape, leading to detrimental effects on the pollination of *H. tortuosa*; in a  
78 previous study analyzing pollination and reproductive output data from the first two years of this  
79 study (2010-2011), forest fragmentation was associated with reduced seed set (Hadley et al.  
80 2014).

81 We formulated five non-mutually exclusive hypotheses that reflect potential effects of  
82 climate and landscape structure on pollination dynamics in a tropical hummingbird system. First,  
83 the *landscape composition hypothesis* states that forest amount will positively influence the  
84 reproductive success of *H. tortuosa* because plant reproduction can be greatly influenced by  
85 pollinator availability (Hadley et al. 2014) and diversity (Klein et al. 2003), which are negatively  
86 impacted by habitat loss (Spiesman and Inouye 2013). The *landscape fragmentation hypothesis*  
87 asserts that patch size will positively influence the reproductive success of *H. tortuosa*,  
88 independent of the effects of forest amount (Hadley et al. 2014), because traplining  
89 hummingbirds avoid crossing non-forested gaps (Kormann et al. 2016; Volpe et al. 2016), and  
90 more gaps must be crossed to access flowers in small patches (leading to lower visitation rates).  
91 The *temperature hypothesis* states that regional temperature will influence the reproductive  
92 success of *H. tortuosa* because irregularly hot or cool years may affect *H. tortuosa* and its  
93 pollinators' phenology resulting in temporal or spatial mismatches (Hegland et al. 2009). The  
94 *precipitation hypothesis* posits that regional precipitation will positively influence reproductive  
95 success of *H. tortuosa* because rain facilitates growth and flowering of many tropical herb  
96 species (Domínguez and Dirzo 1995), and *Heliconia* species are thought to be relatively drought-

97 intolerant (Skillman et al. 1999; Bruna et al. 2002). Alternatively, we hypothesized that reduced  
98 rainfall could increase reproductive success because water stress could induce flowering (Opler  
99 et al. 1976). Lastly, the *landscape and climate synergy hypothesis* proposes that regional  
100 temperature and precipitation will modify the effects of habitat loss and fragmentation on the  
101 reproductive success of *H. tortuosa*. Therefore, if annual precipitation or temperature is extreme,  
102 then the effects of habitat loss or fragmentation on *H. tortuosa* should be stronger.

103

## 104 **Methods**

105

### 106 *Study area and study species*

107 This study was conducted in the area surrounding the Organization for Tropical Studies  
108 Las Cruces Biological Station (8°47'7'' N, 82°57'32'' W). This ~31,000 ha study area, located  
109 in the Cotos Brus region of southern Costa Rica, is primarily composed of premontane tropical  
110 forest and an agricultural matrix of pasture and shade coffee plantations (Hadley et al. 2014). We  
111 studied forest patches ranging in size from <1 ha to >1200 ha across a gradient of forest amount  
112 (5% to 80% forest within a 1000 m radius, Figure 1). Over the 9-year study period (2010-2018),  
113 mean daily precipitation per year ranged from 7.7 mm to 13.5 mm and mean daily temperature  
114 per year ranged from 19.2 °C to 20.3 °C. The region experiences a dry season from January to  
115 March (Borgella et al. 2001).

116 Our study species is *H. tortuosa* (Zingiberales: Heliconiaceae), a tropical perennial  
117 understory herb that is one of the most common and longest blooming plants in the study area  
118 (Borgella et al. 2001). *H. tortuosa* reproduces both clonally and sexually and is partially self-  
119 compatible, but hummingbird visitation is required for pollination (Kress 1983). Flowers of *H.*

120 *tortuosa* last for a single day (Kress 1983) and are contained within brightly colored protective  
121 bracts that gradually open—and begin producing flowers—as the flowering season progresses.

122 *H. tortuosa* may be particularly susceptible to reproductive declines due to its specialized  
123 requirements for pollination. Specifically, two hummingbird species—the green hermit  
124 (*Phaethornis guy*) and violet sabrewing (*Campylopterus hemileucurus*)—are responsible for  
125 80% of *H. tortuosa* pollination (Betts et al. 2015). These forest-associated species travel  
126 relatively long distances each day (Volpe et al. 2014) while visiting a routine sequence of  
127 flowers (‘trapline’) and alter their movements in response to habitat configuration; specifically,  
128 *P. guy* will choose longer or more circuitous routes to remain in forested areas (Hadley and Betts  
129 2009), and the likelihood of *P. guy* crossing gaps in forest declines substantially if gaps are  
130 greater than 30 m (Kormann et al. 2016; Volpe et al. 2016). Moreover, large forest patches in  
131 this study system are associated with increased availability of large, traplining hummingbirds  
132 such as *P. guy* and *C. hemileucurus* (Hadley et al. 2018). In addition to these landscape structure  
133 impacts, climate change is predicted to cause montane hummingbirds to alter their distributions  
134 to higher elevations in tropical regions (Buermann et al. 2011). Hence, *H. tortuosa* may be  
135 particularly susceptible to population declines and disruptions of pollinator movement due to its  
136 specialized requirements for pollination (Aguilar et al. 2006; Betts et al. 2015).

137

### 138 ***Pollination and reproduction metrics***

139

140 We measured *H. tortuosa* pollination and reproductive output using multiple metrics,  
141 each of which reflects different components of pollination/reproductive success: pollen tubes,

142 fruit probability, fruit set, seed set, and total number of seeds (See *Supplemental Information*  
143 Table A1).

#### 144 *Pollen tubes*

145         Pollen tubes provide information about whether a plant was visited by a hummingbird  
146 carrying conspecific pollen grains. We collected all the abscised flowers from *H. tortuosa* plants  
147 during the flowering period (February to September) once a year. This sampling represents the  
148 last 4 days of flowers produced in the patch as older flowers would have degraded. Styles were  
149 extracted from flowers, fixed in formalin-acetic acid-alcohol, and subsequently inspected for the  
150 presence or absence of pollen tubes using epifluorescence microscopy (sensu Kress 1983). We  
151 then calculated, per patch and year, the proportion of styles with at least one pollen tube,  
152 dividing by the total styles examined. We examined as many styles as were available for each  
153 patch (ranging from 1 to 61 styles per patch per year). We repeated this sampling from 2010,  
154 2011 and 2013 to 2017 (a total of 7 years) across 34 patches.

#### 155 *Fruit and seed set*

156         Focal plants were identified by searching from a randomly selected road access point at  
157 the edge of each patch (after Hadley et al. 2014). We selected the first 5 *H. tortuosa* plants we  
158 found with developing inflorescences. If 5 plants were not quickly located, then searching  
159 continued for 3 person-hours to locate as many more as possible. In some cases, there were  
160 additional plants marked for other studies, from which we also collected data. After the  
161 flowering period, mesh bags were placed over *H. tortuosa* inflorescences to prevent frugivory  
162 while fruits ripened. We randomly selected two bracts per inflorescence from which we counted  
163 and collected the number of mature fruits. Later, we counted the number of seeds within each  
164 mature fruit. We also counted the pedicels of unsuccessful flowers, which can be observed long

165 after the flowering event as a measure of flowering attempts (i.e., number of possible fruits).  
166 This sampling design was repeated between April and October each year from 2010 to 2018  
167 contributing to the sampling of 827 plants from 40 patches.

168 In addition to the proportion of pollen tubes metric outlined above, we developed four  
169 fruit or seed-related metrics of plant fitness. After collecting the raw fruit and seed data, we  
170 summarized it as follows. To create our second metric (the first of the fruit or seed metrics), we  
171 quantified the probability of each *H. tortuosa* plant producing fruit. The presence of fruit reflects  
172 sufficient plant vigor and conspecific pollen deposition by a hummingbird. Then, to reduce zero  
173 inflation, we excluded all plants that did not produce any fruit. Third, we calculated the number  
174 of mature fruits divided by the number of possible fruits per bract, and then averaged to obtain a  
175 plant-level metric. This proportion of fruit indicates hummingbird visitation and pollen deposit  
176 while accounting for the individual plant-level reproductive investment. Fourth, as *H. tortuosa*  
177 produces up to 3 seeds per fruit, we calculated seed set by dividing the number of seeds produced  
178 per bract by the number of possible seeds (number of possible fruits multiplied by 3), then  
179 averaged to the plant level. This proportion of seeds again accounts for the individual plant-level  
180 investment. Fifth, we examined the number of seeds produced by each plant for a measure of per  
181 capita reproduction.

182

### 183 ***Focal-patch metrics***

184

185 Following Hadley *et al.* (2014), we used a focal-patch design (Fletcher *et al. In Review*;  
186 Betts *et al.* 2006b) which combines patch size with the surrounding landscape context of each  
187 patch (Halstead *et al.* 2019). We measured habitat loss (landscape composition) using the

188 proportion of forest within a 1000 m radius of a focal plant, or the centroid of each focal patch in  
189 the case of the pollen tube analysis. We selected the 1000 m spatial extent because it is the  
190 maximum expected daily movement of hummingbirds in this system (Volpe et al. 2014) and is  
191 therefore our best estimate of how far pollen could reasonably be transported. To measure habitat  
192 fragmentation (landscape configuration), we quantified the size of focal patches. Patch  
193 boundaries were delineated by gaps >30 m, as hummingbirds in this system avoid crossing forest  
194 gaps larger than this size (Hadley and Betts 2009; Volpe et al. 2016). We log-transformed patch  
195 size because we expected there to be greater effects of patch size on pollination at low values of  
196 patch size (e.g., 1 - 2 ha) than at large values (e.g., 101 to 102 ha). Measures of habitat loss and  
197 fragmentation are often highly confounded, which results in model collinearity (Dormann et al.  
198 2013). However, we deliberately designed our experiment to reduce such intercorrelation  
199 (Hadley et al. 2014); Pearson's correlation coefficients between forest amount and patch size  
200 range from 0.36-0.44 depending on the metric of pollination/reproduction examined (See  
201 *Supplemental Information Tables C1-C3*).

202

### 203 *Climate metrics*

204

205 Regional climate data were collected by the Organization for Tropical Studies  
206 (Organization for Tropical Studies). We utilized data from 2010 to 2018. The average air  
207 temperature was taken every 30 minutes with a precision of 0.01 °C. We averaged the  
208 temperature for each year. The total precipitation was also recorded every 30 minutes by an 8-  
209 inch-wide rain gauge with 0.01 mm precision. We summed precipitation over each day and took  
210 the mean for each year.

211 Our regional climate variables vary interannually, but do not reflect among-patch  
212 variation (no downscaled data are yet available for this region). For this reason, we used  
213 elevation as a proxy for local climate. Elevation was calculated at the patch level for the pollen  
214 tube analysis and at the plant level for all other reproduction metrics. We determined elevation  
215 using a 10-m digital elevation layer.

216

### 217 ***Plant-level metrics***

218

219 Although we are primarily interested in the effects of climate and land-cover change on  
220 pollination, we sought to statistically account for potential confounding effects of inter-patch  
221 variability in plant vigor and plant communities that could affect reproduction of *H. tortuosa*  
222 ('nuisance variables'). Plant vigor tends to have a positive association with reproductive success  
223 (Horvitz and Schemske 1995). Age of *H. tortuosa* individuals was unknown, but height tends to  
224 reflect age for some tropical plants (Horvitz and Schemske 1995) so we used height as a proxy  
225 for vigor. We measured height from the ground to the top of the tallest petiole. In addition, there  
226 can be positive correlations between plant size and number of inflorescences, and size and  
227 fertility (Horvitz and Schemske 1995), so we also used number of flower-producing bracts as a  
228 second proxy for plant vigor. The height of sampled plants ranged from 0.3 m to 3.2 m and  
229 number of bracts per individual from 2 to 13.

230 Within a 20 m radius of each focal plant, we measured flowering plant species richness,  
231 *H. tortuosa* density, and flowering plant density. Plant richness often supports more diverse  
232 pollinator communities (Ebeling et al. 2008), but it may lead to higher deposition of

233 heterospecific pollen, while lower density of flower resources should lead to reduced pollinator  
234 availability.

235         Finally, we measured distance to the nearest edge and distance to the nearest stream.  
236 Edge distance serves as a proxy for any edge effects on *H. tortuosa* or its pollinators, such as  
237 increased plant vigor due to more light or reduced pollinator availability of forest-interior  
238 hummingbirds (Jackson et al. *In Review*). Proximity to streams also affects moisture availability,  
239 as *H. tortuosa* are often found at higher densities near streams. We measured the distance to the  
240 nearest stream and nearest edge using GIS.

241

#### 242 ***Statistical models***

243

244         We used linear mixed models and generalized linear mixed models to test our hypotheses  
245 concerning the additive and synergistic effects of landscape and climate on pollination and plant  
246 reproduction. All models included crossed random effects for ‘year’ and ‘patch’ to statistically  
247 control for spatial correlation of plants nested within patches, temporal autocorrelation for  
248 patches measured across multiple years, and plants measured in the same location over multiple  
249 years. In addition, all predictor variables were standardized to mean of 0 and standard deviation  
250 of 1.

251         First, we used a hierarchical variable selection approach to reduce the number of nuisance  
252 variables considered per response variable (after Hadley et al. 2014). This was necessary because  
253 our sample size did not permit testing the full global model with 14 parameters: focal-patch  
254 variables, climate variables, plant-level nuisance variables, and the crossed random effects for  
255 ‘year’ and ‘patch’ (See *Supplemental Information* Table B1). Because this many variables

256 resulted in parameter estimates with poor precision, we tested the importance of each local  
257 habitat variable in relation to the null model using bivariate mixed models (e.g., pollen tubes ~  
258 elevation). These models were ranked using Akaike's information criterion corrected for small  
259 sample sizes (AIC<sub>c</sub>). For each model within two AIC<sub>c</sub> of the top-ranked model, we used a  
260 secondary criterion that 85% confidence intervals should not overlap zero and removed nuisance  
261 variables whose confidence intervals included zero (See *Supplemental Information Tables E1-*  
262 *E5*).

263         After selecting nuisance variables, we then created models corresponding to each of our  
264 five *a priori* hypotheses (Burnham and Anderson 2002). For the *landscape composition*,  
265 *temperature*, and *precipitation hypotheses*, we fit models with the corresponding variables  
266 (proportion of forest, temperature, and precipitation respectively) and included nuisance  
267 variables when applicable. When elevation was an important variable, we tested for interactions  
268 between elevation and precipitation, and elevation and temperature to investigate if the effects of  
269 climate were mediated by elevation.

270         For the *landscape fragmentation hypothesis*, we fit models with patch size and proportion  
271 of forest, and additional models that also included the interaction between these variables. This  
272 latter model reflects the hypothesis that the effects of patch size could be mediated by forest  
273 amount; for instance, theory predicts that small patches should be particularly problematic if they  
274 are isolated (i.e., forest amount is low; Hadley and Betts 2012). To test for the independent  
275 effects of configuration (patch size), we statistically controlled for forest amount in all patch-size  
276 models.

277         To assess our *landscape and climate synergy hypothesis*, we built model sets that tested  
278 for additive and synergistic effects between each combination of landscape and climate metrics

279 (e.g., fruit set ~ precipitation + forest amount, fruit set ~ precipitation x forest amount), a model  
280 with each landscape and climate metric, a model with just the nuisance variables, and a null  
281 model (See *Supplemental Information* Table F1). We ranked models using AIC<sub>c</sub> and report  
282 results of models within the top 4 AIC<sub>c</sub> of each model set. To make the interpretation of effects  
283 more practical, the coefficient interpretations are determined using unstandardized coefficients.

284 To check the assumptions of linear models, we built separate global models for each of  
285 our five measures of reproductive success and assessed linearity, constant variance of residuals,  
286 and normality of residuals. We log-transformed variables, where necessary, to improve normality  
287 in residuals. We added half of the 2<sup>nd</sup> lowest value for a variable when log-transforming to avoid  
288 minimum values of zero (Birks et al. 2012, p. 127). After log-transforming number of seeds and  
289 logit-transforming the proportion of fruits, we determined that a Gaussian distribution could be  
290 used for the fruit proportion, seed proportion, number of seeds, and pollen tube proportion  
291 analyses. We used a binomial distribution to model the probability of fruit. All modeling was  
292 conducted using R (version 4.0.4, R Core Team 2017) and “glmmTMB” (Brooks et al. 2017).  
293 We checked the assumptions of the binomial using simulated residuals created by “DHARMA”  
294 (Hartig 2020).

295 In addition, we checked for correlations between independent variables; if correlations  
296 between independent variables were high ( $r > 0.65$ ) we did not include both variables in the same  
297 model (See *Supplemental Information* Tables C1-C3). We also tested for spatial autocorrelation  
298 of residuals of global models using correlograms. We established spatial lags of 1000 m intervals  
299 and tested for statistical significance of Moran’s *I* values at each spatial lag using permutation  
300 tests (1000 iterations; Betts et al. 2006a); Moran’s *I* values for the proportion of pollen tubes,  
301 proportion of fruit, proportion of seeds and number of seeds global models were  $< 0.20$  (See

302 *Supplemental Information* Figures D1-D4) indicating very weak spatial autocorrelation.  
303 However, one lag (0 m) for the probability was 0.3, which might slightly increase the likelihood  
304 of type I error in these models (See *Supplemental Information* Figures D5-D6).

305 Finally, there is evidence to suggest phenological responses to climate change may  
306 exhibit time lags (Sherry et al. 2011; Bedford et al. 2012). While we are concerned such lags in  
307 this system, testing the full suite of models described above, but with time lags may create  
308 extraneous models. Therefore, as an exploratory step, we tested for time lags, only for models  
309 within the top 4 AIC<sub>c</sub> of the top models (if the null model was not within the top 4 AIC<sub>c</sub>). We did  
310 this by using the previous year's measures of precipitation and temperature in the updated  
311 models. Ultimately, lagged climatic effects were not important for explaining reproduction in *H.*  
312 *tortuosa* (See *Supplemental Information* Tables H1-2).

313

## 314 **Results**

315

316 Over our 9-year study, we observed at least one pollen tube in  $52\% \pm 36\%$  (mean  $\pm$  SD)  
317 of the *H. tortuosa* styles examined. However, only  $19\% \pm 20\%$  of the styles examined had at  
318 least 3 pollen tubes, which is the minimum required for a complete seed set. Across our study,  
319 the probability that a plant produced at least one successful fruit was  $82\% \pm 38\%$ . The average  
320 proportion of fruit produced was  $63\% \pm 36\%$ , whereas the proportion of seeds produced was  
321 only  $43\% \pm 28\%$ . The average number of seeds produced by each plant (from the two focal  
322 bracts) was  $12 \pm 11$ . Variation between the annual averages for pollination and reproductive  
323 measures and climate metrics can be seen in Figure 2.

324 Overall, we found that landscape structure and climate and influenced the pollination and  
325 subsequent reproduction of *H. tortuosa*. Forest amount, patch size, the interaction between forest  
326 amount and patch size, precipitation, and temperature were all associated with at least one  
327 element of *H. tortuosa* reproduction over the 9-year study period.

328

### 329 *Fruit production*

330 We found the most evidence for the effects of forest amount, patch size, and precipitation  
331 on the probability of *H. tortuosa* fruit (See *Supplemental Information Table G1*). For every  
332 percent decrease in the forest amount surrounding the *H. tortuosa* plant, the estimated odds of  
333 producing a fruit decreased by a factor of 0.20 (95% CI: 0.05, 0.72, Table 1, Figure 4). When  
334 patch size doubled, the estimated odds of producing a fruit increased by a factor of 1.07 (95%  
335 CI: 1.00, 1.16). For every millimeter increase of average daily precipitation per year, the  
336 estimated odds of producing a fruit decreased by a factor of 0.75 (95% CI: 0.66, 0.86). The  
337 estimated odds of producing a fruit increased by a factor of 1.001 (95% CI: 1.0001, 1.002) for  
338 every meter increase in the elevation of the *H. tortuosa* plant above sea level. We also examined  
339 the interaction between forest amount and patch size on the probability of fruit. In large patches,  
340 there was a positive relationship between forest amount and probability of fruit. Conversely, in  
341 small patches, there is a negative relationship between forest amount and probability of fruit  
342 (Figure 3). We did not detect any significant predictors of the proportion of fruit produced. The  
343 null model was within the top 4 AIC<sub>c</sub> of the model set for the proportion of fruit (See  
344 *Supplemental Information Table G2*).

345 We only detected lagged climate effects in our model testing the synergistic effects of  
346 patch size and lagged precipitation on probability of fruit (See *Supplemental Information Tables*

347 H1-H2). While neither patch size or past precipitation had significant additive effects, the  
348 interaction between patch size and past precipitation was marginally statistically significant (See  
349 *Supplemental Information Table H2*). In large patches, the relationship between past  
350 precipitation and probability of fruit was positive (i.e., wetter years yielded higher probability of  
351 fruit). However, in small patches, the impact of past precipitation on the probability of fruit was  
352 negative (wetter years resulted in lower probability of fruit). These trends for the probability of  
353 fruit in different patch size classes are consistent with our other findings.

354

#### 355 *Seed set*

356 After statistically accounting for plant height, we found strongest support for the  
357 hypothesis that forest amount and precipitation influence the number of seeds produced by *H.*  
358 *tortuosa* (Table 1, Figure 5). The estimated median number of seeds decreased by 27% (95% CI:  
359 51% decrease, 9% increase) for every percent increase in the forest amount surrounding the *H.*  
360 *tortuosa* plant. Similar to the effect on the probability of fruit, for every millimeter gained in  
361 average daily precipitation per year, the estimated median number of seeds decreased by 8%  
362 (95% CI: 15%, 1%). The median number of seeds increased by a factor of 1.27 (95% CI: 1.09,  
363 1.47) for every doubling of the height of a *H. tortuosa* plant (Table 1).

364 Temperature had a weak positive impact on the proportion of *H. tortuosa* seeds produced;  
365 for every degree Celsius increase in average daily temperature, the mean seeds produced per  
366 flower increased approximately 0.05 (95% CI: -0.01, 0.12, See *Supplemental Information Table*  
367 *G4*). The null model was within the top 4 AIC<sub>c</sub> of the proportion of seeds model set (See  
368 *Supplemental Information Table G3*).

369

370 *Pollen tubes*

371           For each meter increase in elevation, the mean pollen tube presence per style decreased  
372 by approximately 0.0002 (95% CI: -0.0005, 0). Interestingly, elevation was the only predictor  
373 with significant impact on the proportion of pollen tubes (See *Supplemental Information Table*  
374 G6). However, the null model was within the top 4 AIC<sub>c</sub> of the model set for the proportion of  
375 pollen tubes (See *Supplemental Information Table G5*), and confidence intervals bounded zero,  
376 so this variable did not have strong support.

377

## 378 **Discussion**

379           To our knowledge, this is the first study to test for combined long-term effects of  
380 landscape structure and climate on pollination success and plant reproductive output. We found  
381 that both landscape structure and climate influence measures of fecundity in *H. tortuosa*, but  
382 these factors do not tend to act synergistically; we did not find support for the *landscape and*  
383 *climate synergy hypothesis*. In other words, the effects of forest loss and fragmentation were not  
384 disproportionately amplified in wetter or hotter years.

385           *H. tortuosa* plants were more likely to produce fruit at higher elevations and in larger  
386 patches, and less likely to produce fruit when there was more forest in the surrounding  
387 landscape. Consistent with previous work in this system, we found support for the *landscape*  
388 *fragmentation hypothesis*, but less so for the *landscape composition hypothesis*. *H. tortuosa*  
389 plants were also less likely to produce fruit in wetter years, which supports the *precipitation*  
390 *hypothesis*. We could not substantiate the *temperature hypothesis*, perhaps due to the regional  
391 scale of the climate data.

392 Fruit probability appeared to be the most responsive to both landscape structure and  
393 climate, but seed output also responded to these drivers. Why was the probability of fruit  
394 variable seemingly the most sensitive to the combined effects of climate and land cover? This  
395 response variable differed from other measures of reproductive success in that it included plants  
396 that did not produce at least one successful fruit (i.e., those that failed entirely to reproduce). We  
397 conservatively excluded these plants from additional measures of plant reproduction because  
398 plants could lack fruit for several reasons in addition to low rates of pollination. In particular,  
399 these plants may have lacked the vigor to grow fruit (perhaps due to lack of resources). On the  
400 other hand, to be included in our analyses, proportion of fruit and seed set variables needed to  
401 have produced at least one fruit, indicating that plants had at least some minimum level of vigor,  
402 and pollinators occurred in the vicinity. Plant-specific data for pollen tubes would have enabled a  
403 comparison with the probability of fruit to ascertain whether *H. tortuosa* plants were limited by  
404 vigor or by hummingbird visitation, but unfortunately, we did not collect these data.

405 Only 52% of the styles examined had at least one pollen tube, likely indicating that visits  
406 from specialized pollinators (*P. guy* and *C. hemileucus*) are limiting pollen deposition. This  
407 finding is consistent with previous work from this study system showing severe limitation in *H.*  
408 *tortuosa* in small, fragmented patches (25% pollen tube prevalence; Kormann et al. 2016) and up  
409 to 79% when sampling occurred across a gradient in fragmentation – including large, connected  
410 patches (Hadley et al. 2014).

411 Our finding that forest amount had a negative effect on the probability of fruit is  
412 inconsistent with our previous findings that deforestation detracts from hummingbird movement  
413 (Hadley and Betts 2009), hummingbird community structure (Hadley et al. 2018) and plant  
414 reproduction (Hadley et al. 2014). We found that the effect of forest amount on the probability of

415 fruit was only negative when patch size was small; in contrast, when patches were large and in a  
416 forested landscape, the effect of forest amount was positive as anticipated. We hypothesize that  
417 this counterintuitive positive effect on pollination of small patches embedded within deforested  
418 landscapes could be due to a ‘fence effect’.

419 Pollinator movement is strongly restricted by forest fragmentation in this system (Hadley  
420 and Betts 2009; Kormann et al. 2016; Volpe et al. 2016); The higher probability of fruit in  
421 fragmented landscapes could therefore be due to restricted pollinator movement preventing  
422 pollinator dispersal. Movement barriers may prevent inter-patch movement by hummingbirds,  
423 resulting in frequent visitation of the plants remaining in small patches. Although, this  
424 hypothesized mechanism may enable reproduction in the short term, it is possible that repeated  
425 mating among spatially proximate plants will restrict gene flow; indeed, higher rates of  
426 inbreeding are already apparent in small patches (Torres-Vanegas et al. 2021).

427 The negative effect of precipitation on the probability of *H. tortuosa* fruit and number of  
428 seeds may be an indirect result of reduced light received by *H. tortuosa* when precipitation is  
429 high; high precipitation is accompanied with increased cloud cover. Light is often limiting for  
430 trees in tropical forests (Graham et al. 2003) and as *H. tortuosa* is a tropical understory herb, the  
431 light limitation may be particularly pronounced. Alternatively, reduced precipitation could result  
432 in water stress, that may induce increased *H. tortuosa* flowering (Opler et al. 1976). Regardless  
433 of the mechanism, if lack of water in the dry season induces *H. tortuosa* flowering, a continued  
434 tendency toward wetter dry seasons could alter the phenological synchrony between *H. tortuosa*  
435 and its pollinators.

436 In 1987, only 29% of Costa Rica was forested (Lutz et al. 1993), but as of 2013 forest  
437 cover increased to 53% (Costa Rican Ministry of Environment and Energy 2018). The study area

438 is particularly dynamic as there has been a net loss of forest since 1980, however both  
439 deforestation and reforestation have occurred (Zahawi et al. 2015). As our measures for patch  
440 size and forest amount were static throughout the experiment, we are unable to detect the effects  
441 of afforestation or further deforestation. Indeed, the matrix surrounding several of the small,  
442 isolated patches that was formerly pasture is beginning regenerate to scrub forest, thereby  
443 reducing isolation and enhancing hummingbird movement (Jackson et al. *In Review*). Such  
444 patterns may explain the contrast between the current findings and previous findings from the  
445 same study system, in which effects of forest loss and fragmentation on plant reproduction were  
446 stronger (Hadley et al. 2014; Kormann et al. 2016). This is certainly a hypothesis in need of  
447 future investigation.

448         The effects of habitat loss and fragmentation resulting in pollen limitation of *H. tortuosa*  
449 has implications for future resources for pollinators. Habitat loss and fragmentation tend to be  
450 associated with declines in plant sexual reproduction (Aguilar et al. 2006; Garibaldi et al. 2013).  
451 Reduced sexual reproduction may lead to decreased floral resources, forcing pollinators to travel  
452 further to obtain resources. When pollinators that alter their movement in response to habitat  
453 configuration are forced to move further, the increased exertion may lead to declines in  
454 pollinators through increased mortality or decreased reproduction. A reduction in pollinators will  
455 likely have consequences for plant pollination and reproduction. This positive feedback loop is  
456 one explanation for the associated decline of plants and their pollinators (Biesmeijer et al. 2006).  
457 If landscapes continue to be fragmented, and the climate in the Neotropics becomes wetter  
458 (Trenberth 2011), this sort of feedback loop could be a concern for *H. tortuosa* and the  
459 pollinators that depend upon it.

460           While we did not find evidence of synergistic effects of landscape structure and climate,  
461 we emphasize that additive effects of these stresses did occur. Reproductive output increased in  
462 large patches in forested landscapes and in small patches in deforested landscapes during dry  
463 years. Reduced reproductive output is likely due to pollen limitation caused by a lack of habitat  
464 quality in small patches surrounded by forested landscapes and a lack of connectivity in large  
465 patches in deforested landscapes influencing hummingbird movement. The pollen limitation  
466 expected in small patches in deforested landscapes may be obscured by a “fence effect” causing  
467 pollinator saturation. We conclude that pollen limitation and reduced reproduction may be  
468 exacerbated by future land-cover and climate changes.

## Declarations

*Funding* This work was funded by the National Science Foundation (NSF-DEB-1050594 and NSF-DEB-1457837 to MGB and ASH) and associated NSF-Research Experience for Undergraduates grant that supported CED. In addition, we thank the Ernest and Pauline Jaworski Fund and the Deloach Work Scholarship from Oregon State University. This material is based upon work supported by the National Science Foundation Graduate Research Fellowship Program under Grant No. 1840998 to KGL.

*Conflicts of interest/Competing interests* The authors have no conflicts of interests to declare.

*Ethics approval* Not applicable.

*Consent to participate* Not applicable.

*Consent for publication* The authors give consent to the publication of this study.

*Availability of data and material* The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

*Code availability* The code created during the study is available from the corresponding author on reasonable request.

*Authors' contributions* **Claire E. Dowd**: Formal analysis (lead), Data visualization (lead), Writing-original draft (lead), reviewing & editing (lead). **Kara G. Leimberger**: Formal analysis (equal), Writing-review & editing (supporting). **Adam S. Hadley**: Conceptualization (equal), Data Collection (equal), Writing-review & editing (supporting), Funding Acquisition (equal). **Sarah J.K. Frey**: Data Collection (equal), Data visualization (equal), Writing-review & editing (supporting). **Matthew G. Betts**: Conceptualization (equal), Formal analysis (equal), Data visualization (equal), Writing-review & editing (equal), Funding Acquisition (equal).

## Literature Cited

- Aguilar R, Ashworth L, Galetto L, Aizen MA (2006) Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. *Ecology Letters* 9:968–980. <https://doi.org/10.1111/j.1461-0248.2006.00927.x>
- Bedford FE, Whittaker RJ, Kerr JT (2012) Systemic range shift lags among a pollinator species assemblage following rapid climate change <sup>1</sup> This article is part of a Special Issue entitled “Pollination biology research in Canada: Perspectives on a mutualism at different scales”. *Botany* 90:587–597. <https://doi.org/10.1139/b2012-052>
- Bélisle M, Desrochers A, Fortin M-J (2001) Influence of Forest Cover on the Movements of Forest Birds: A Homing Experiment. *Ecology* 82:1893–1904. [https://doi.org/10.1890/0012-9658\(2001\)082\[1893:IOFCOT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[1893:IOFCOT]2.0.CO;2)
- Betts MG, Diamond AW, Forbes GJ, et al (2006a) The importance of spatial autocorrelation, extent and resolution in predicting forest bird occurrence. *Ecological Modelling* 191:197–224. <https://doi.org/10.1016/j.ecolmodel.2005.04.027>
- Betts MG, Forbes GJ, Diamond AW, Taylor PD (2006b) Independent Effects Of Fragmentation On Forest Songbirds: An Organism-Based Approach. *Ecological Applications* 16:1076–1089. [https://doi.org/10.1890/1051-0761\(2006\)016\[1076:IEOFOF\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[1076:IEOFOF]2.0.CO;2)
- Betts MG, Hadley AS, Kormann U (2019) The landscape ecology of pollination. *Landscape Ecol* 34:961–966. <https://doi.org/10.1007/s10980-019-00845-4>
- Betts MG, Hadley AS, Kress WJ (2015) Pollinator recognition by a keystone tropical plant. *Proc Natl Acad Sci USA* 112:3433–3438. <https://doi.org/10.1073/pnas.1419522112>
- Biesmeijer JC, Roberts SPM, Reemer M, et al (2006) Parallel Declines in Pollinators and Insect-Pollinated Plants in Britain and the Netherlands. 313:5
- Birks HJB, Lotter AF, Juggins S, Smol JP (2012) *Tracking Environmental Change Using Lake Sediments: Data Handling and Numerical Techniques*. Springer Science & Business Media
- Borgella R, Snow AA, Gavin TA (2001) Species Richness and Pollen Loads of Hummingbirds Using Forest Fragments in Southern Costa Rica. *Biotropica* 33:90–109. <https://doi.org/10.1111/j.1744-7429.2001.tb00160.x>
- Brook B, Sodhi N, Bradshaw C (2008) Synergies among extinction drivers under global change. *Trends in Ecology & Evolution* 23:453–460. <https://doi.org/10.1016/j.tree.2008.03.011>
- Brooks M E, Kristensen K, Benthem K J ,van, et al (2017) glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal* 9:378. <https://doi.org/10.32614/RJ-2017-066>

- Brooks TM, Mittermeier RA, Mittermeier CG, et al (2002) Habitat Loss and Extinction in the Hotspots of Biodiversity. *Conservation Biology* 16:909–923. <https://doi.org/10.1046/j.1523-1739.2002.00530.x>
- Brown MJF, Paxton RJ (2009) The conservation of bees: a global perspective. *Apidologie* 40:410–416. <https://doi.org/10.1051/apido/2009019>
- Bruna EM, Nardy O, Strauss SY, Harrison S (2002) Experimental Assessment of *Heliconia acuminata* Growth in a Fragmented Amazonian Landscape. *Journal of Ecology* 90:639–649
- Buermann W, Chaves JA, Dudley R, et al (2011) Projected changes in elevational distribution and flight performance of montane Neotropical hummingbirds in response to climate change. *Global Change Biology* 17:1671–1680. <https://doi.org/10.1111/j.1365-2486.2010.02330.x>
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, Second. Springer
- Conenna I, Valkama J, Chamberlain D (2017) Interactive effects of climate and forest canopy cover on Goshawk productivity. *J Ornithol* 158:799–809. <https://doi.org/10.1007/s10336-017-1432-0>
- Costa Rican Ministry of Environment and Energy (2018) Report on the State of the Environment 2017
- Dale VH (1997) The Relationship Between Land-Use Change and Climate Change. *Ecological Applications* 7:753–769. [https://doi.org/10.1890/1051-0761\(1997\)007\[0753:TRBLUC\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1997)007[0753:TRBLUC]2.0.CO;2)
- Dale VH, Pearson SM, Offerman HL, O’Neill RV (1994) Relating Patterns of Land-Use Change to Faunal Biodiversity in the Central Amazon. *Conservation Biology* 8:1027–1036
- de Chazal J, Rounsevell MDA (2009) Land-use and climate change within assessments of biodiversity change: A review. *Global Environmental Change* 19:306–315. <https://doi.org/10.1016/j.gloenvcha.2008.09.007>
- Díaz S, Settele J, Brondízio ES, et al (2019) Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science Policy Platform on Biodiversity and Ecosystem Services
- Domínguez CA, Dirzo R (1995) Rainfall and flowering synchrony in a tropical shrub: Variable selection on the flowering time of *Erythroxylum havanense*. *Evol Ecol* 9:204–216. <https://doi.org/10.1007/BF01237757>
- Dormann CF, Elith J, Bacher S, et al (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36:27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>

- Duchenne F, Thébault E, Michez D, et al (2020) Phenological shifts alter the seasonal structure of pollinator assemblages in Europe. *Nature Ecology & Evolution* 4:115–121. <https://doi.org/10.1038/s41559-019-1062-4>
- Ebeling A, Klein A-M, Schumacher J, et al (2008) How does plant richness affect pollinator richness and temporal stability of flower visits? *Oikos* 117:1808–1815. <https://doi.org/10.1111/j.1600-0706.2008.16819.x>
- Forister ML, McCall AC, Sanders NJ, et al (2010) Compounded effects of climate change and habitat alteration shift patterns of butterfly diversity. *Proc Natl Acad Sci USA* 107:2088–2092. <https://doi.org/10.1073/pnas.0909686107>
- Garibaldi LA, Steffan-Dewenter I, Winfree R, et al (2013) Wild Pollinators Enhance Fruit Set of Crops Regardless of Honey Bee Abundance. *Science* 339:1608–1611. <https://doi.org/10.1126/science.1230200>
- Graham EA, Mulkey SS, Kitajima K, et al (2003) Cloud cover limits net CO<sub>2</sub> uptake and growth of a rainforest tree during tropical rainy seasons. *PNAS* 100:572–576. <https://doi.org/10.1073/pnas.0133045100>
- Guo F, Lenoir J, Bonebrake TC (2018) Land-use change interacts with climate to determine elevational species redistribution. *Nature Communications* 9:1315. <https://doi.org/10.1038/s41467-018-03786-9>
- Hadley AS, Betts MG (2012) The effects of landscape fragmentation on pollination dynamics: absence of evidence not evidence of absence. *Biological Reviews* 87:526–544. <https://doi.org/10.1111/j.1469-185X.2011.00205.x>
- Hadley AS, Betts MG (2009) Tropical deforestation alters hummingbird movement patterns. *Biol Lett* 5:207–210. <https://doi.org/10.1098/rsbl.2008.0691>
- Hadley AS, Frey SJK, Robinson WD, et al (2014) Tropical forest fragmentation limits pollination of a keystone understory herb. *Ecology* 95:2202–2212. <https://doi.org/10.1890/13-0929.1>
- Hadley AS, Frey SJK, Robinson WD, Betts MG (2018) Forest fragmentation and loss reduce richness, availability, and specialization in tropical hummingbird communities. *Biotropica* 50:74–83. <https://doi.org/10.1111/btp.12487>
- Halstead KE, Alexander JD, Hadley AS, et al (2019) Using a species-centered approach to predict bird community responses to habitat fragmentation. *Landscape Ecol* 34:1919–1935. <https://doi.org/10.1007/s10980-019-00860-5>
- Hartig F (2020) DHARMA: Residual diagnostics for heirarchical (multi-level / mixed) regression models.

- Hegland SJ, Nielsen A, Lázaro A, et al (2009) How does climate warming affect plant-pollinator interactions? *Ecology Letters* 12:184–195. <https://doi.org/10.1111/j.1461-0248.2008.01269.x>
- Horvitz CC, Schemske DW (1995) Spatiotemporal Variation in Demographic Transitions of a Tropical Understory Herb: Projection Matrix Analysis. *Ecological Monographs* 65:155–192. <https://doi.org/10.2307/2937136>
- Huntley B, Webb T (1989) Migration: Species' Response to Climatic Variations Caused by Changes in the Earth's Orbit. *Journal of Biogeography* 16:5–19. <https://doi.org/10.2307/2845307>
- Klein A, Steffan-Dewenter I, Tscharntke T (2003) Fruit set of highland coffee increases with the diversity of pollinating bees. *Proc R Soc Lond B* 270:955–961. <https://doi.org/10.1098/rspb.2002.2306>
- Kormann U, Scherber C, Tscharntke T, et al (2016) Corridors restore animal-mediated pollination in fragmented tropical forest landscapes. *Proc R Soc B* 283:20152347. <https://doi.org/10.1098/rspb.2015.2347>
- Kress WJ (1983) Self-Incompatibility in Central American Heliconia. *Evolution* 37:735–744. <https://doi.org/10.2307/2407915>
- Lima SL, Zollner PA (1996) Towards a behavioral ecology of ecological landscapes. *Trends in Ecology & Evolution* 11:131–135. [https://doi.org/10.1016/0169-5347\(96\)81094-9](https://doi.org/10.1016/0169-5347(96)81094-9)
- Lutz E, Vedova W. M, Martínez H, et al (1993) Interdisciplinary fact-finding on current deforestation in Costa Rica. The World Bank Environment Department
- Northrup JM, Rivers JW, Yang Z, Betts MG (2019) Synergistic effects of climate and land-use change influence broad-scale avian population declines. *Global Change Biology* 25:1561–1575. <https://doi.org/10.1111/gcb.14571>
- Oliver TH, Marshall HH, Morecroft MD, et al (2015) Interacting effects of climate change and habitat fragmentation on drought-sensitive butterflies. *Nature Climate Change* 5:941–945. <https://doi.org/10.1038/nclimate2746>
- Oliver TH, Morecroft MD (2014) Interactions between climate change and land use change on biodiversity: attribution problems, risks, and opportunities. *WIREs Climate Change* 5:317–335. <https://doi.org/10.1002/wcc.271>
- Ollerton J, Winfree R, Tarrant S (2011) How many flowering plants are pollinated by animals? *Oikos* 120:321–326. <https://doi.org/10.1111/j.1600-0706.2010.18644.x>
- Opler PA, Frankie GW, Baker HG (1976) Rainfall as a Factor in the Release, Timing, and Synchronization of Anthesis by Tropical Trees and Shrubs. *Journal of Biogeography* 3:231–236. <https://doi.org/10.2307/3038013>

- Organization for Tropical Studies Las Cruces Biological Station and Wilson Botanical Garden, Meteorological Station. San Vito de Coto Brus, Costa Rica
- Parmesan C (2006) Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology, Evolution, and Systematics* 37:637–669.  
<https://doi.org/10.1146/annurev.ecolsys.37.091305.110100>
- Peters MK, Hemp A, Appelhans T, et al (2019) Climate-land-use interactions shape tropical mountain biodiversity and ecosystem functions. *Nature* 568:88–88.  
<https://doi.org/10.1038/s41586-019-1048-z>
- Potts SG, Biesmeijer JC, Kremen C, et al (2010) Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution* 25:345–353.  
<https://doi.org/10.1016/j.tree.2010.01.007>
- R Core Team (2017) R: A language and environment for statistical computing
- Reilly JR, Artz DR, Biddinger D, et al (2020) Crop production in the USA is frequently limited by a lack of pollinators. *Proc R Soc B* 287:20200922.  
<https://doi.org/10.1098/rspb.2020.0922>
- Ricketts TH (2001) The Matrix Matters: Effective Isolation in Fragmented Landscapes. *The American Naturalist* 158:87–99. <https://doi.org/10.1086/320863>
- Schweiger O, Biesmeijer JC, Bommarco R, et al (2010) Multiple stressors on biotic interactions: how climate change and alien species interact to affect pollination. *Biological Reviews* 85:777–795. <https://doi.org/10.1111/j.1469-185X.2010.00125.x>
- Sherry RA, Zhou X, Gu S, et al (2011) Changes in duration of reproductive phases and lagged phenological response to experimental climate warming. *Plant Ecology & Diversity* 4:23–35. <https://doi.org/10.1080/17550874.2011.557669>
- Skillman JB, Garcia M, Winter K (1999) Whole-Plant Consequences of Crassulacean Acid Metabolism for a Tropical Forest Understory Plant. *Ecology* 80:1584–1593.  
[https://doi.org/10.1890/0012-9658\(1999\)080\[1584:WPCOCA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[1584:WPCOCA]2.0.CO;2)
- Spiesman BJ, Inouye BD (2013) Habitat loss alters the architecture of plant–pollinator interaction networks. *Ecology* 94:2688–2696. <https://doi.org/10.1890/13-0977.1>
- Stangler ES, Hanson PE, Steffan-Dewenter I (2015) Interactive effects of habitat fragmentation and microclimate on trap-nesting Hymenoptera and their trophic interactions in small secondary rainforest remnants. *Biodivers Conserv* 24:563–577.  
<https://doi.org/10.1007/s10531-014-0836-x>
- Thomas CD, Cameron A, Green RE, et al (2004) Extinction risk from climate change. *Nature* 427:145–148. <https://doi.org/10.1038/nature02121>

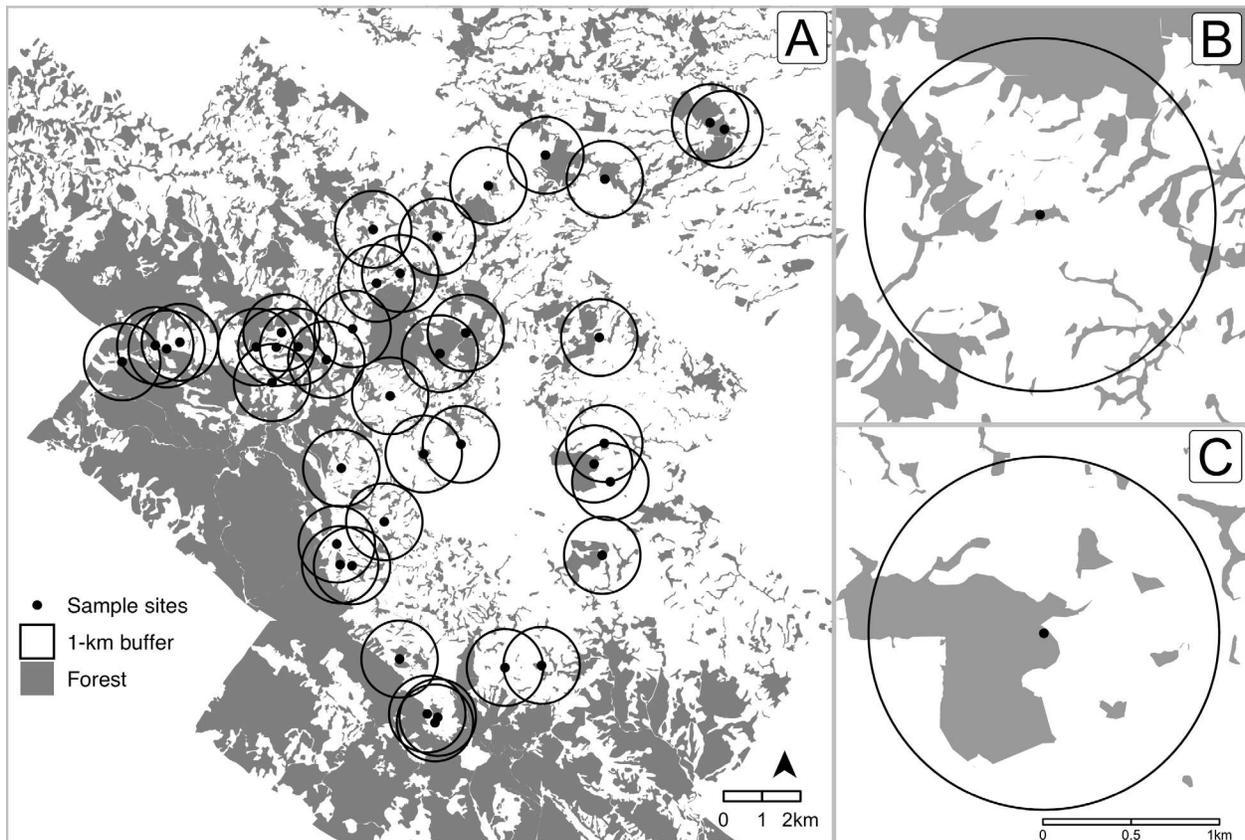
- Torres-Vanegas F, Hadley AS, Kormann UG, et al (2021) Tropical deforestation reduces plant mating quality by shifting the functional composition of pollinator communities. *Journal of Ecology* 0:1–17. <https://doi.org/10.1111/1365-2745.13594>
- Trenberth K (2011) Changes in precipitation with climate change. *Clim Res* 47:123–138. <https://doi.org/10.3354/cr00953>
- VanDerWal J, Murphy HT, Kutt AS, et al (2013) Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change. *Nature Climate Change* 3:239–243. <https://doi.org/10.1038/nclimate1688>
- Visser ME, Both C (2005) Shifts in phenology due to global climate change: the need for a yardstick. *Proc R Soc B* 272:2561–2569. <https://doi.org/10.1098/rspb.2005.3356>
- Volpe NL, Hadley AS, Robinson WD, Betts MG (2014) Functional connectivity experiments reflect routine movement behavior of a tropical hummingbird species. *Ecological Applications* 24:2122–2131. <https://doi.org/10.1890/13-2168.1>
- Volpe NL, Robinson WD, Frey SJK, et al (2016) Tropical Forest Fragmentation Limits Movements, but Not Occurrence of a Generalist Pollinator Species. *PLOS ONE* 11:e0167513. <https://doi.org/10.1371/journal.pone.0167513>
- Wilson MC, Chen X-Y, Corlett RT, et al (2016) Habitat fragmentation and biodiversity conservation: key findings and future challenges. *Landscape Ecol* 31:219–227. <https://doi.org/10.1007/s10980-015-0312-3>
- Winfrey R, Reilly JR, Bartomeus I, et al (2018) Species turnover promotes the importance of bee diversity for crop pollination at regional scales. *Science* 359:791–793. <https://doi.org/10.1126/science.aao2117>
- Zahawi RA, Duran G, Kormann U (2015) Sixty-Seven Years of Land-Use Change in Southern Costa Rica. *PLoS ONE* 10:e0143554. <https://doi.org/10.1371/journal.pone.0143554>

## Tables

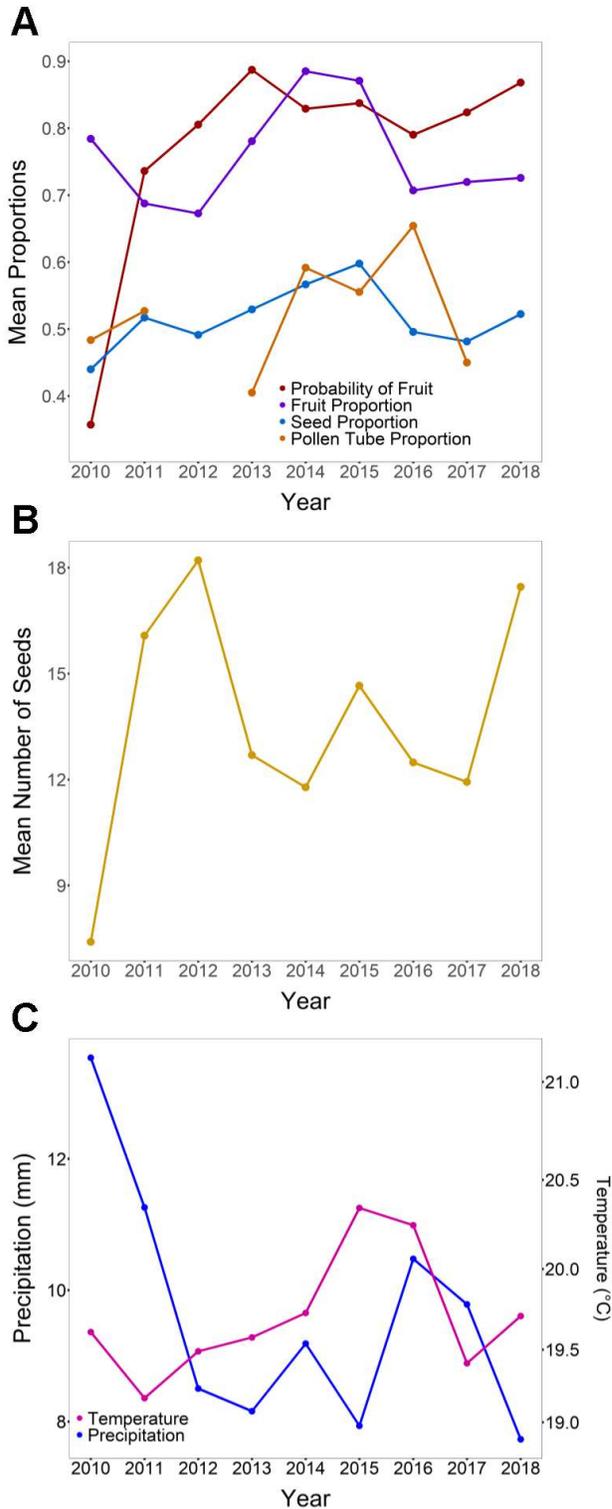
**Table 1.** Coefficients for the top AIC<sub>c</sub>-ranked models predicting the probability of fruit and the number of seeds as a function of local-scale nuisance variables (e.g., flower richness, elevation, height), landscape structure (forest amount and patch size), and precipitation. The probability of fruit at the scale of individual plants decreased with increased rainfall, and as a function of the amount of forest in the landscape. Patch size and elevation had positive influences on the probability of fruit. After accounting for height, precipitation also has a negative impact on the number of *H. tortuosa* seeds produced.

<b>Response variable</b>	Variable	Estimate	95% CI	P-value
<b>Probability of fruit</b>				
Patch size + precipitation	Forest amount	<b>-0.268</b>	<b>-0.482, -0.053</b>	<b>0.0145*</b>
	Patch size	<b>0.206</b>	<b>0.001, 0.412</b>	<b>0.0488*</b>
	Precipitation	<b>-0.369</b>	<b>-0.539, -0.199</b>	<b>0.0000212*</b>
	Distance to edge	0.082	-0.108, 0.272	0.3980
	Plant richness	0.076	-0.184, 0.335	0.5682
	Flowering plant density	0.058	-0.216, 0.332	0.6763
	Elevation	<b>0.222</b>	<b>-0.021, 0.423</b>	<b>0.0306*</b>
<b>Probability of fruit</b>				
Patch size x precipitation	Forest amount	<b>-0.271</b>	<b>-0.490, -0.052</b>	<b>0.0152*</b>
	Patch size	<b>0.190</b>	<b>-0.021, 0.400</b>	<b>0.0770</b>
	Precipitation	<b>-0.368</b>	<b>-0.539, -0.198</b>	<b>0.0000234*</b>
	Patch size x precipitation	0.109	-0.081, 0.300	0.2601
	Distance to edge	0.080	-0.112, 0.272	0.4126
	Plant richness	0.074	-0.187, 0.336	0.5776
	Flowering plant density	0.052	-0.224, 0.328	0.7134
	Elevation	<b>0.226</b>	<b>0.022, 0.431</b>	<b>0.0302*</b>
<b>Logged number of seeds</b>				
Forest amount + precipitation	Forest amount	-0.051	-0.114, 0.011	0.10600
	Precipitation	<b>-0.107</b>	<b>-0.196, -0.018</b>	<b>0.01887*</b>
	Height	<b>0.098</b>	<b>0.037, 0.159</b>	<b>0.00158*</b>

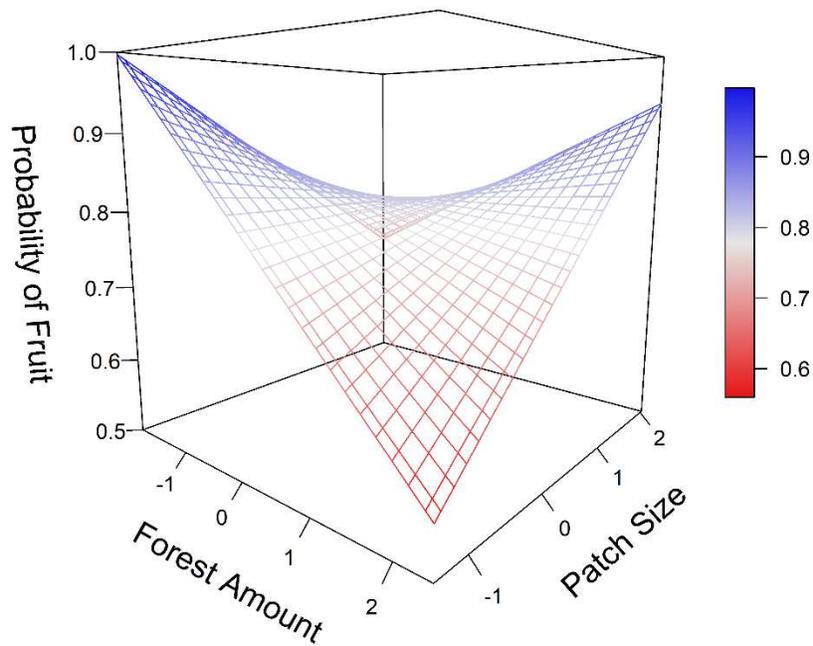
## Figures



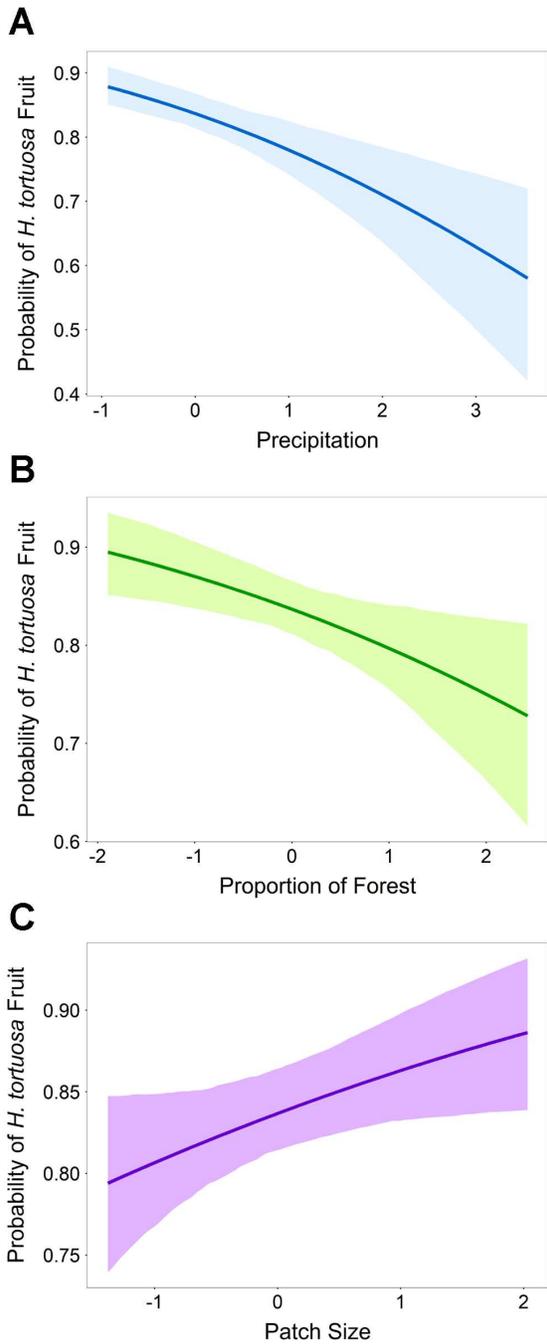
**Figure 1.** A) The study area, showing forest cover in a gray layer, forest patch location in black dots, and 1000m radii around the patches in black outline. Patches were sampled along a gradient in size and surrounding forest amount. Featured are two examples: B) a small patch with in a relatively forested landscape and C) a large patch in a deforested landscape.



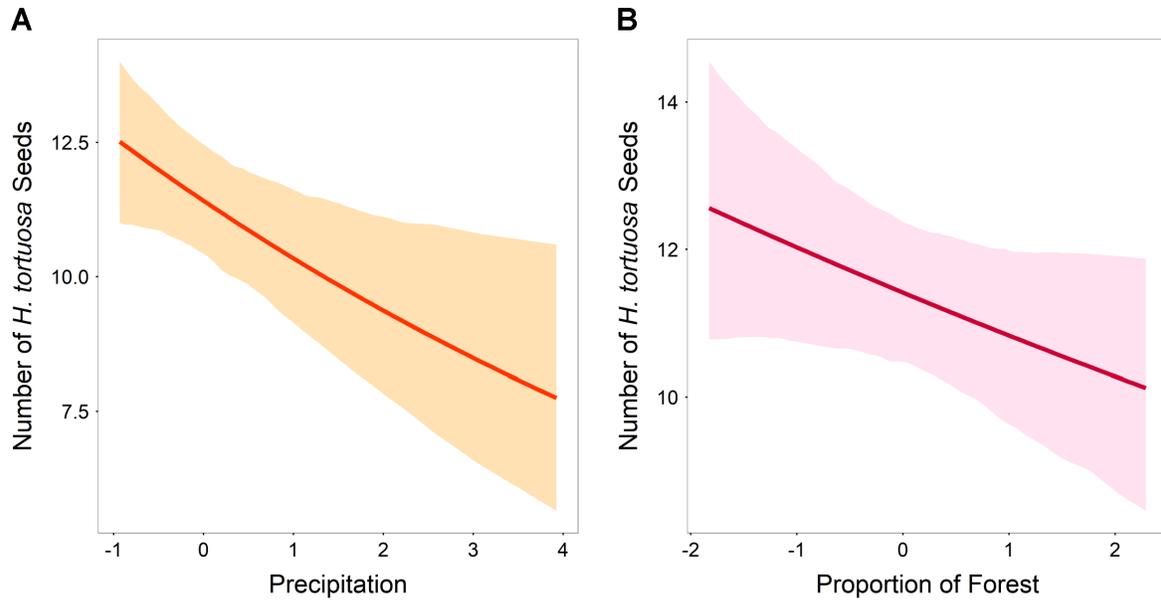
**Figure 2.** A) The proportional and binary pollination and reproductive output of *H. tortuosa* over the 9-year study period. Data was not collected for the pollen tube proportion in 2012 and 2018. B) The mean number of seeds produce per plant per year over our 9-year study period. C) The average daily precipitation and average daily temperature over our 9-year study period.



**Figure 3.** Fitted values from a generalized linear mixed model that predicts the probability of *H. tortuosa* fruit as a function of the interaction between patch size and forest amount (standardized to mean zero). Although patch size had a strong positive effect on the probability of fruit, larger patches appeared to be detrimental to fruit in landscapes with high forest cover.

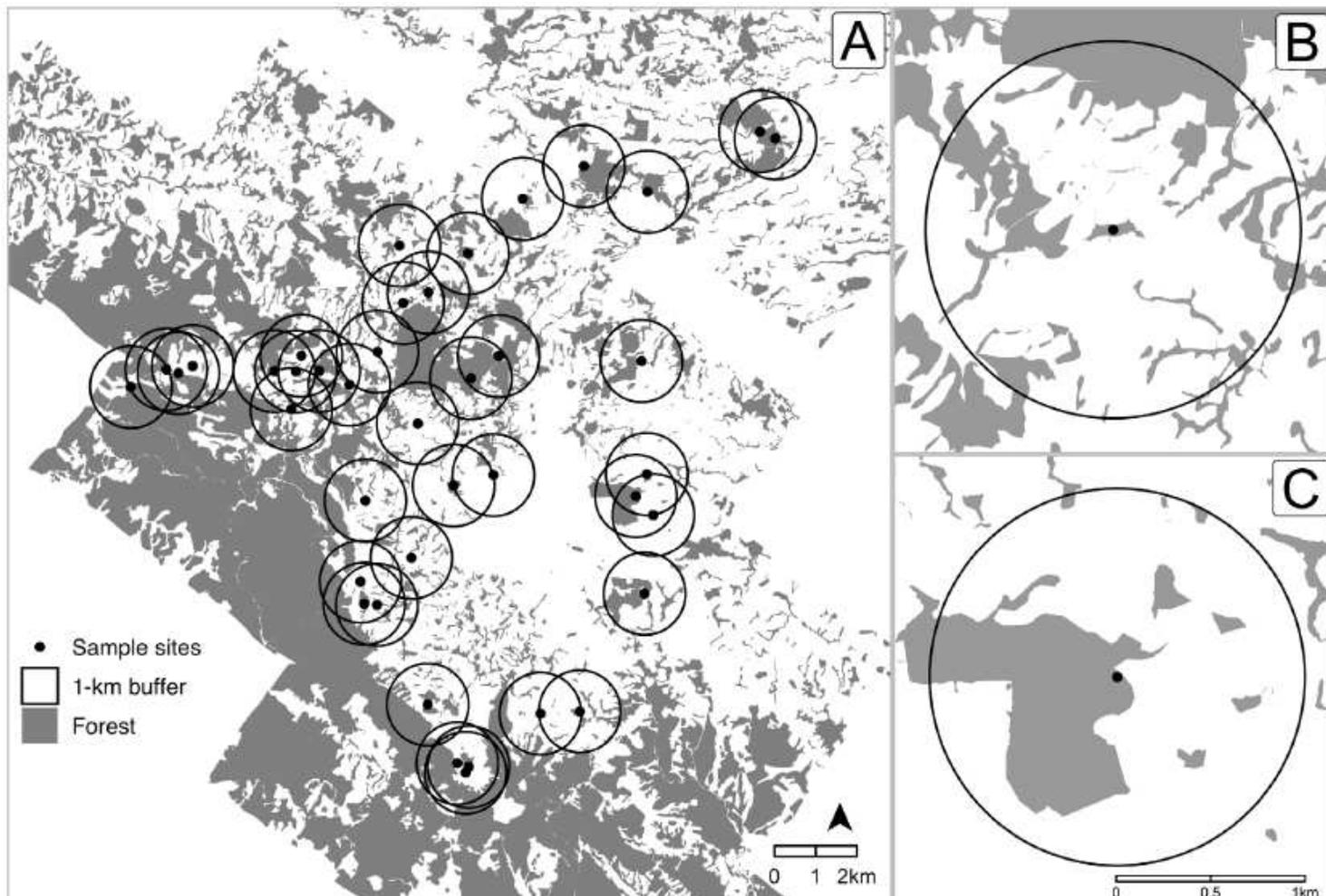


**Figure 4.** Fitted values from the top AIC<sub>c</sub>-ranked model predicting the probability of *H. tortuosa* fruit as a function of A) precipitation B) proportion of forest, and C) a patch size. All fitted values statistically account for other terms in the model (probability of fruit ~ precipitation + patch size + proportion of forest + nuisance variables). Shaded areas show bootstrapped 95% confidence intervals.



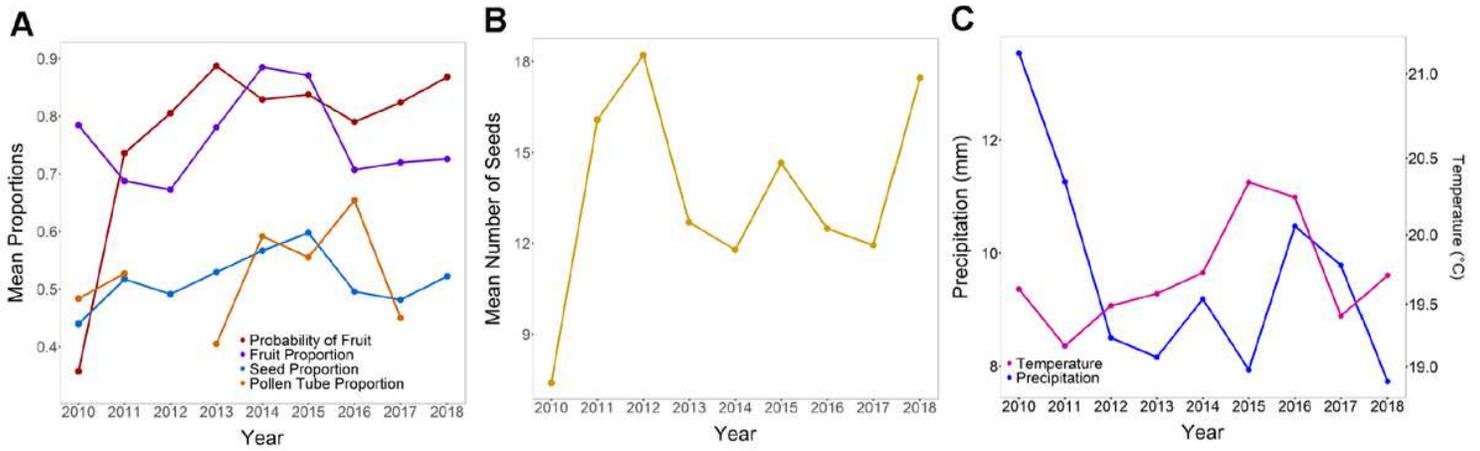
**Figure 5.** Fitted values from the top AIC<sub>c</sub>-ranked model predicting the number of *H. tortuosa* seeds as a function of A) precipitation B) proportion of forest. All fitted values statistically account for other terms in the model (number of seeds ~ precipitation + proportion of forest + nuisance variables). Shaded areas show bootstrapped 95% confidence intervals.

## Figures



**Figure 1**

A) The study area, showing forest cover in a gray layer, forest patch location in black dots, and 1000m radii around the patches in black outline. Patches were sampled along a gradient in size and surrounding forest amount. Featured are two examples: B) a small patch with in a relatively forested landscape and C) a large patch in a deforested landscape. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.



**Figure 2**

A) The proportional and binary pollination and reproductive output of *H. tortuosa* over the 9-year study period. Data was not collected for the pollen tube proportion in 2012 and 2018. B) The mean number of seeds produce per plant per year over our 9-year study period. C) The average daily precipitation and average daily temperature over our 9-year study period.

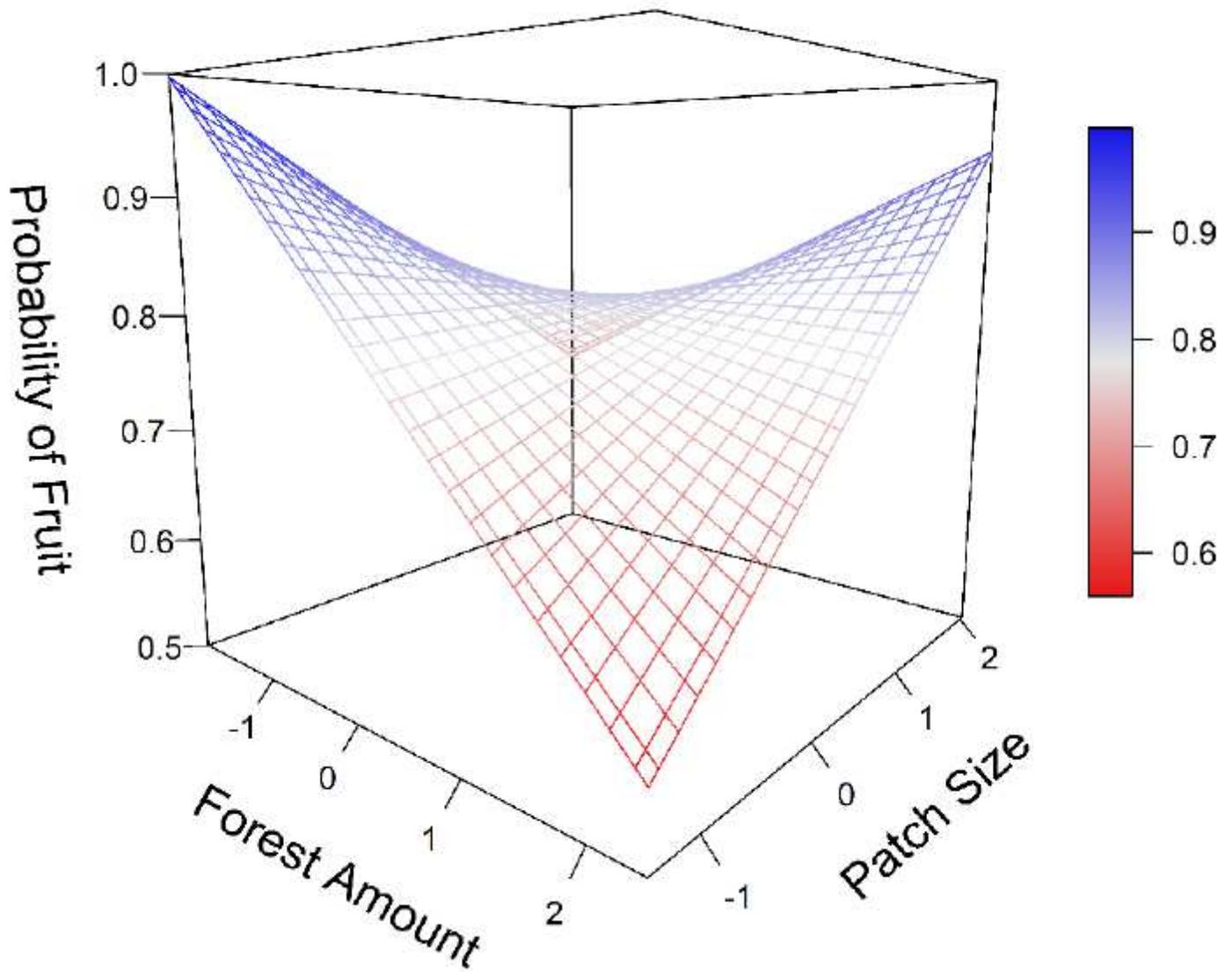
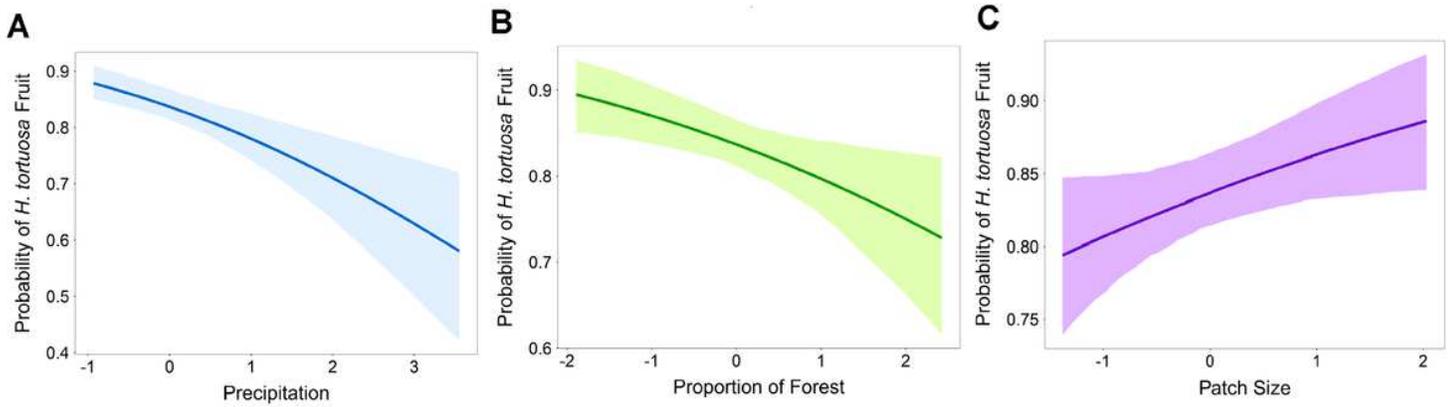


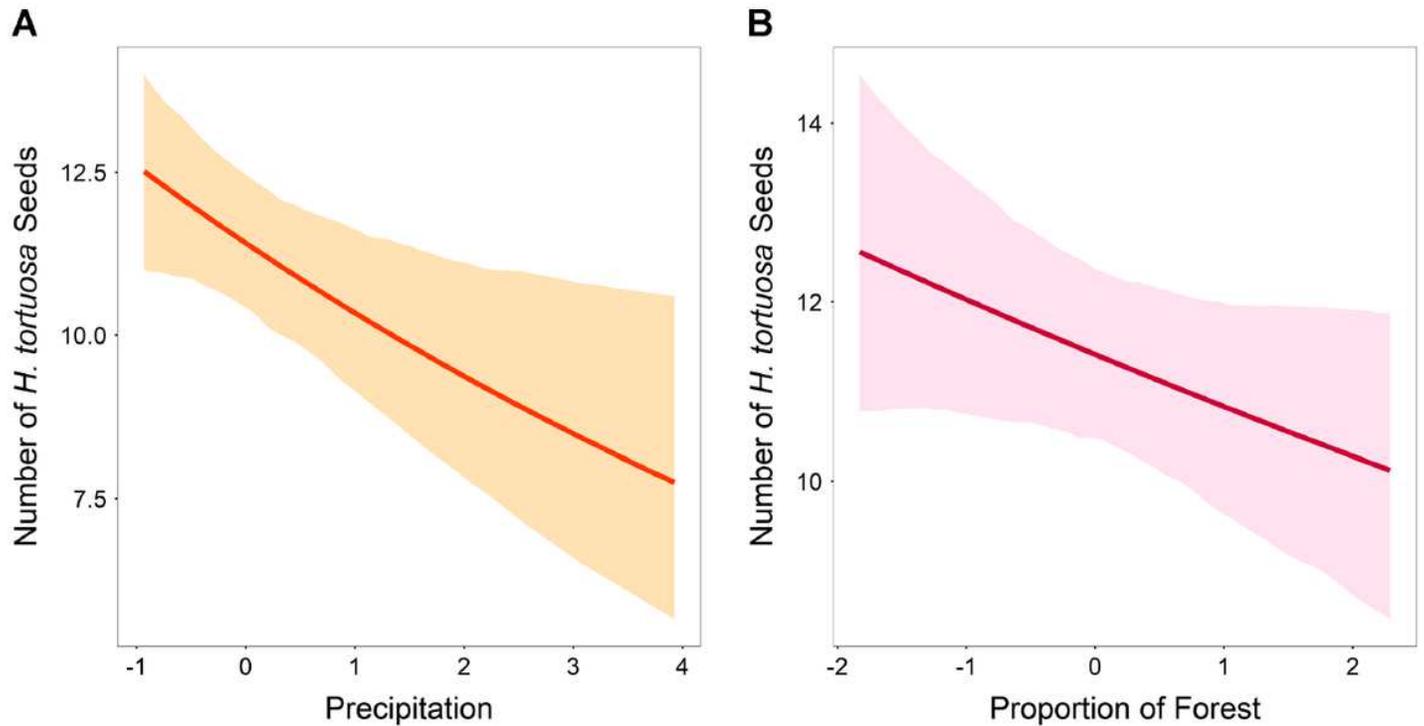
Figure 3

Fitted values from a generalized linear mixed model that predicts the probability of *H. tortuosa* fruit as a function of the interaction between patch size and forest amount (standardized to mean zero). Although patch size had a strong positive effect on the probability of fruit, larger patches appeared to be detrimental to fruit in landscapes with high forest cover.



**Figure 4**

Fitted values from the top AICc-ranked model predicting the probability of *H. tortuosa* fruit as a function of A) precipitation B) proportion of forest, and C) a patch size. All fitted values statistically account for other terms in the model (probability of fruit  $\sim$  precipitation + patch size + proportion of forest + nuisance variables). Shaded areas show bootstrapped 95% confidence intervals.



**Figure 5**

Fitted values from the top AICc-ranked model predicting the number of *H. tortuosa* seeds as a function of A) precipitation B) proportion of forest. All fitted values statistically account for other terms in the model (number of seeds  $\sim$  precipitation + proportion of forest + nuisance variables). Shaded areas show bootstrapped 95% confidence intervals.

## Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [DowdetaSupplementMarch112021.pdf](#)