

**Investigating synergistic effects of climate and land-use change on the pollination of a
tropical plant, *Heliconia tortuosa***

by
Claire E. Dowd

A THESIS

submitted to

Oregon State University

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(Honors Associate)

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Abstract approved: _____

Matthew G. Betts

Loss of biodiversity due to the effects of climate and land-use change may have implications for pollination services. Disruption to phenological synchronicity or a reduction in the overlap in species distributions of plants and their pollinators may reduce floral resources to pollinators, forcing them to move farther distances. If pollinators that alter their movement based on habitat configuration are forced to move farther distances, then pollinator populations may suffer. Such a reduction in pollinators could lead to a positive feedback loop as the majority of flowering plants are animal pollinated. We tested whether the effects of climate and land-use change synergistically (interact to) influence the hummingbird pollination of a tropical understory herb, *Heliconia tortuosa*. We collected a 9-year dataset from southern Costa Rica comprising regional precipitation and temperature, forest amount and patch size to assess seed set, fruit set and pollen tubes in *H. tortuosa*. We found that while climate and landscape metrics did not act synergistically on *H. tortuosa*, precipitation, forest amount and patch size are strong predictors of the probability of *H. tortuosa* fruit. Reproductive output appeared to be facilitated in dry years, and in locations with large patches in contiguous landscapes, but counterintuitively also small patches in deforested landscapes – perhaps due to constraint on hummingbird movement. In other words, precipitation and forest amount negatively impacted the probability of *H. tortuosa* fruit, while patch size positively influenced the probability of fruit. While we did not detect synergistic effects between climate and land-use change on pollination and reproductive output, that does not mean they do not occur, and further investigations are necessary. We conclude that pollen limitation may be exacerbated by future land-use change as hummingbird habitat and

movement is constrained, or if the regional climate becomes wetter, reducing the flowers available to hummingbirds.

Key Words: climate, land-use, habitat loss, habitat fragmentation, pollination, reproduction, hummingbird, synergistic, tropical forest, *Heliconia*

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I understand that my project will become part of the permanent collection of Oregon State University, Honors College. My signature below authorizes release of my project to any reader upon request.

Claire Dowd, Author

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Introduction

Rates of biodiversity loss are increasing globally (IPBES 2019). There are a multitude of threats contributing to this loss of biodiversity including climate change (Thomas et al. 2004; Brook et al. 2008) and land-use change (Dale et al. 1994; Brooks et al. 2002; Wilson et al. 2016). Loss of biodiversity degrades ecosystem services, such as pollination (Brittain et al. 2013; Garibaldi et al. 2013). The decline of pollinators (Potts et al. 2010) and their associated plants (Biesmeijer et al. 2006) is degrading pollination services. A reduction in pollination could create a positive feedback loop with biodiversity loss because over 85% of flowering plants are animal pollinated (Ollerton et al. 2011) and heterotrophs depend on plant diversity for habitat and food. Therefore, as climate changes, we need to understand how climate and land-use change affect pollination and plant reproduction.

Changes in climate may affect pollination by influencing species distributions and phenology. Broadly, species distributions are expected to shift with changing environmental conditions (Huntley and Webb III 1989). While the overall direction of these shifts is expected to be poleward and into higher elevations (Parmesan 2006), at finer spatial scales there is much more variability in the direction of species distribution shifts (VanDerWal et al. 2013). More variance in the direction of species distribution shifts is expected in the tropics (VanDerWal et al. 2013). This is concerning if plants and their pollinators exhibit distinct shifts in distributions, which could result in reduced overlap in geographic ranges. In addition, climate change can affect the phenology of plants (Parmesan 2006) and animals (Visser and Both 2005), which may contribute to changes in temporal synchronicity that pollination mutualisms depend upon (Schweiger et al. 2010). For example, climate change may amend phenology such as flowering

period (Badeck et al. 2004). Phenological mismatches between plant and pollinator may affect pollinator demography, pollinator population density and distributions, pollen availability, and pollen limitation (Hegland et al. 2009). Based on the expected doubling of atmospheric CO₂, predicted phenological shifts could decrease the floral resources available to 17-50% of pollinator species (Memmott et al. 2007). However, biodiversity acts as a buffer to maintain phenological synchrony between plants and their pollinators despite climate change (Bartomeus et al. 2013).

In this study, we are concerned with how two components of land-use change, habitat loss and habitat fragmentation, influence pollination. Habitat loss negatively affects pollinator diversity (Steffan-Dewenter et al. 2005) and pollinator diversity is associated with higher plant sexual reproduction (Garibaldi et al. 2013). Habitat fragmentation is also known to decrease the sexual reproduction of flowering plants (Aguilar et al. 2006). Habitat configuration can alter animal behavior (Bélisle et al. 2001; Ricketts 2001) – particularly for species for which the matrix increases predation risk or perceived risk (Lima and Zollner 1996). Habitat fragmentation therefore appears to alter pollinator behavior which could, in turn, impact pollination within a system (Hadley and Betts 2012). Therefore, habitat loss and fragmentation have the effect of reducing plant sexual reproduction and fragmentation may alter pollinator behavior.

Although several studies have investigated the interactive impacts of land-use change and climate change on biodiversity (Forister et al. 2010; Oliver et al. 2015; Stangler et al. 2015; Conenna et al. 2017; Northrup et al. 2019), to our knowledge none have focused on how these stressors might synergistically affect pollination (how land-use change and climate change may interact to affect pollination). Several authors have hypothesized that climate change could amplify the well-known hazards of habitat loss and fragmentation (Dale 1997; Brook et al. 2008;

Chazal and Rounsevell 2009; Oliver and Morecroft 2014). Climate change may cause dissimilar shifts in the species distribution of plants and their pollinators or it may disrupt the phenological synchronicity of plants and their pollinators. Such disturbances may lead to fewer floral resources for pollinators, which may force pollinators to move farther distances. The increased movement of pollinators could improve pollination by increasing outcrossing. However, if pollinators, whose behavior is altered by habitat configuration, are forced to move farther in fragmented landscapes, the increased movement may lead to reduced pollinator survival or reproduction. A reduction in pollinators would have implications for pollination within the system, possibly causing a reduction in plant reproduction. This is an example of how the impacts of climate change and fragmentation may synergistically act to exacerbate the stress on pollination mutualisms.

To address the possibility of synergistic effects of climate and land-use change on pollination, we analyzed 9 years of pollination and reproductive output data from a tropical understory herb, *Heliconia tortuosa*, in a fragmented landscape in southern Costa Rica. *H. tortuosa* exhibits pollinator recognition, meaning *H. tortuosa* can differentially accept pollen from distinct pollinators (Betts et al. 2015). *H. tortuosa*'s primary pollinators are *Phaethornis Guy* and *Campylopterus hemileucurus*, which are both forest-associated traplining species that contribute to 80.1% of *H. tortuosa*'s reproductive contributions (Betts et al. 2015). Trapliner hummingbirds routinely visit a sequence of flowers, which greatly increases their daily movement distances compared to territorial hummingbirds. Hummingbirds in our pollination network are known to change their movement in response to habitat configuration; Specifically, *P. guy*, a primary pollinator of *H. tortuosa* will choose longer or more circuitous routes to remain in forested areas (Hadley and Betts 2009) and the likelihood of *P. guy* crossing gaps in forest

declines substantially if gaps are greater than 30m (Volpe et al. 2014; Kormann et al. 2016). We also know that in our system, hummingbird availability is positively correlated to patch size (Hadley et al. 2018). In addition, climate change is predicted to cause montane hummingbirds to alter their distributions to higher elevations in tropical regions (Buermann et al. 2011). Therefore, *H. tortuosa* may be particularly susceptible to population declines and disruptions of pollinator distributions and movement due to its specialized requirements for pollination (Aguilar et al. 2006; Betts et al. 2015).

We formulated a number of non-mutually exclusive hypotheses that reflect potential effects of climate and land-use change on pollination dynamics in a tropical hummingbird system. First, the *landscape composition hypothesis* states that forest amount will positively influence the reproductive success of *H. tortuosa* because reproduction is greatly influenced by broad-scale pollinator and flower availability (Fahrig 2013; Hadley et al. 2014). Next, the *landscape fragmentation hypothesis* asserts that patch size will positively influence the reproductive success of *H. tortuosa*, independent of the effects of forest amount because traplining hummingbirds avoid crossing gaps, and more gaps must be crossed to access flowers when patch size is small (Hadley et al. 2014). The *temperature hypothesis* states that regional temperature will influence the reproductive success of *H. tortuosa* because irregularly hot or cool years may affect *H. tortuosa* and its pollinators' phenology. The *precipitation hypothesis* posits that regional precipitation will positively influence reproductive success of *H. tortuosa* because rain facilitates growth and flowering of tropical species (Dominguez and Dirzo 1995). Alternatively, we hypothesized that reduced rainfall could increase reproductive success because water stress could induce flowering (Opler et al. 1976). Lastly, the *climate and landscape synergy hypothesis* proposes that regional temperature and precipitation will influence effects of

habitat loss and fragmentation on the reproductive success of *H. tortuosa*. Therefore, if annual precipitation or temperature is extreme, then the effects of habitat loss or fragmentation on *H. tortuosa* may be stronger.

Methods

Study area

We conducted this study in the area surrounding the Organization for Tropical Studies' Las Cruces Biological Station in the Cotos Brus region of southern Costa Rica. This ~31,000 ha region is composed of premontane tropical forest where most of the matrix is comprised of pasture and shade coffee plantations. As of 1987, only 29% of Costa Rica was forested (Lutz et al. 1993), but as of 2013 forest cover increased to 53% (Costa Rican Ministry of Environment and Energy). We studied forest patches ranging in size from <1 ha to >1200 ha across a gradient of forest amount (% forest within a 1000m radius) from 0.05 to 0.80, and elevation gradient of 500 m to 1600 m above sea level. Over the 9-year study period (2010-2018) mean daily precipitation per year ranged from 7.7 mm to 13.5 mm and the mean daily temperature per year ranged from 19.2 °C to 20.3 °C.

Study organisms

Our study species is *H. tortuosa*, a tropical perennial understory herb that reproduces both clonally and sexually. It is the most common and longest blooming plant in our system (Borgella et al. 2001). *H. tortuosa* is a forest-associated and traplining hummingbird-pollinated species (Stiles 1975). *H. tortuosa* likely serves as a critical source to hummingbirds during the food scarce dry season. However, the majority of *H. tortuosa*'s pollination is accomplished by *P. guy* and *C. hemileucurus* hummingbirds, two forest interior species (Borgella et al. 2001), due to

pollinator recognition (Betts et al. 2015). *P. guy* is the most common hummingbird species in our system (Borgella et al. 2001).

Pollination and Reproduction metrics

We measured *H. tortuosa* pollination and reproductive output using multiple metrics, each of which reflects different components of pollination success (Appendix Table A1). We calculated the pollen tube proportion to provides us with information on the proportion of flowers that are visited by a traplining hummingbird within a patch, as pollen tubes reflect whether or not a plant was visited by a hummingbird (*H. tortuosa* pollination depends on hummingbird visitations; Betts et al. 2015). We measured the proportion of styles collected from a patch with at least one pollen tube. Notably, the pollen tube proportion is a patch scale metric while the other metrics are plant specific. We investigated whether plants produced at least one mature fruit to assess whether the plant is healthy enough to produce a mature fruit or whether traplining hummingbirds visited those plants. As we could not determine whether the lack of fruit was caused by insufficient plant health or lack of traplining hummingbird visitation, we conservatively excluded all the plants that did not produce at least one mature fruit from the analyses for proportion of fruit, proportion of seeds, and number of seeds. This also had the effect of reducing zero inflation in our dataset. Next, we calculated the proportion of successful fruit produced out of the number of flowers that bloomed in order to assess traplining hummingbird visitation and pollen deposit at a flower level. Both the proportion of fruit and the proportion of seeds account for the payoff and plant investment as they represent the fruits or seeds produced per flower. Our last metric is the number of seeds produced per plant, which is important as it represents the per capita contribution to the next generation. We felt it was

important to use multiple metrics of *H. tortuosa* pollination to evaluate how and why pollination is affected by our metrics.

While the pollen tube proportion is an important first step in pollination, we do not have plant-level data regarding the proportion of pollen tubes that translate to viable seeds. To find the pollen tube proportion, styles were collected from day-old flowers, which were inspected for pollen tubes using epifluorescence microscopy (sensu Kress 1983). We observed each style for the presence or absence of pollen tubes. We then summed the presence and divided by the total styles examined in a patch. We examined as many pollen tubes that were available for each patch (ranging from 1 to 61 styles per patch per year). We examined styles from 2010, 2011 and 2013 to 2017 (a total of 7 years) across 34 patches.

For the fruit and seeds, between 2 and 9 focal plants were identified by walking 500m from a randomly selected road access point at each patch's edge. The first 5 *H. tortuosa* plants forming inflorescences were selected for the study. If 5 plants were not quickly located, then searching continued for 3 person-hours to locate as many more as possible. In some cases, there were additional plants marked for other studies, from which we also collected data. After the flowering period, bags were placed over *H. tortuosa* inflorescences to prevent frugivory while fruits ripened. We were able to estimate the number of possible fruits because the pedicels of unsuccessful flowers can be observed long after the flowering event. At the beginning of the observation periods, we placed a thread in each bract to mark which flowers occurred during our observation period to ensure we only counted pedicels from flowers during our study. We later counted and collected the number of mature fruit. This sampling design was repeated between April and October each year from 2010 to 2018 contributing to the sampling of 827 plants from 40 patches.

After collecting the raw fruit and seed data, we summarized it as follows. First, we examined the probability of the *H. tortuosa* plant producing fruit. Then, to reduce zero inflation, we excluded all plants that did not produce any fruit. We calculated the number of mature fruit divided by the number of possible fruit per bract, and then averaged the proportion to a plant level metric. As *H. tortuosa* produces up to 3 seeds per fruit, we calculated the seed proportion by dividing the number of seeds by the number of possible fruit multiplied by 3. We also averaged this measure to the plant level. Finally, we examined the sum of seeds produced by each plant for a measure of per capita reproduction.

Focal-patch metrics

To enhance our ability to separate the effects of habitat loss versus fragmentation, we used a focal-patch design and assessed the neighborhood around the patches. We measured the habitat loss (composition) using the proportion of forest within a 1000 m radius of a focal plant, or focal patch in the case of the pollen tube analysis, because 1000 m is the maximum expected daily movement of hummingbirds in this system (Hadley and Betts 2009). Therefore, 1000 m is an estimate of how far pollen could reasonably be transported by *P. guy* and *C. hemileucurus*. To measure habitat fragmentation (configuration), we used patch size determined by the amount of habitat connected to a focal flower where discontinuity was defined by gaps over 30 m, as hummingbirds in our system avoid crossing forest gaps larger than 30m (Hadley and Betts 2009; Volpe et al. 2014). Patch size is a proxy for configuration in our system because patch size represents the limits of pollen movement by *H. tortuosa*'s pollinators as their movement is restricted to continuous forest. We log-transformed patch size because we expect there to be greater effects of patch size on pollination at low values of patch size (e.g., 1 - 2 ha) than at large values (e.g., 101 to 102 ha). Measures of habitat loss and fragmentation are often highly confounded,

which leads to unreliable modelling. However, this is not a problem in our system: forest amount and patch size have Pearson's correlation coefficients of 0.44 for the count of seeds, proportion of seeds, and proportion of fruit analyses, 0.39 for the probability of fruit analysis, and 0.36 for proportion of pollen tubes analysis (Appendix Tables C1-C3).

Regional Climate metrics

Regional climate data were collected by the Organization for Tropical Studies at the Campbell Meteorological Station at the Las Cruces Biological Station (Organization for Tropical Studies). We utilized data from 2010 to 2018. The average air temperature was taken every 30 minutes with a precision of 0.01°C. We averaged the temperature for each year. The total precipitation was also recorded every 30 minutes by an 8-inch-wide rain gauge with 0.01mm precision. We summed the precipitation over each day and took the mean for each year. We expect our regional climate variables to explain interannual variation, but not between patch variation in reproductive success as our climate metrics are not patch-specific. For this reason, we used elevation as a proxy for microclimate. As our elevation measure was patch-specific or plant-specific, we looked for interactions between elevation and precipitation, and elevation and temperature to see if the effects of climate varied depending on the microclimate (See **Statistical Models**).

Local habitat metrics

Although we are interested in the effects of focal-patch metrics, we also needed to account for local-scale metrics that could also have effects on the successful reproduction of *H. tortuosa*. We expected plant vigor to have a positive association with reproductive success. As age of *H. tortuosa* individuals was unknown and a trend has been shown between height and age for some tropical plants (Horvitz and Schemske 1995), we used height as a proxy for plant vigor.

In addition, there are positive correlations between size and number of inflorescences, and size and fertility (Horvitz and Schemske 1995), so we also used number of bracts as a proxy of plant vigor. We measured height from the ground to the top of the tallest petiole. The height of sampled plants ranged from 0.3 m to 3.2 m and number of bracts per individual from 2 to 13. *H. tortuosa* density and total flower density denote conspecific and heterospecific flower densities. Lower abundance or density of flowers is often thought to lead to smaller pollinator populations. Plant richness supports more diverse pollinator communities (Ghazoul 2005), but it may lead to higher deposition of heterospecific pollen. We measured flowering plant species richness, *H. tortuosa* density, and total flower density within a 20 m radius of each focal plant. As there is a broad range of elevation in our study area, we wanted to account for its effects on temperature, moisture, richness, and phenology. We determined elevation using a 10 m digital elevation layer. Distance to the nearest edge serves as a proxy for any edge effects on *H. tortuosa* or its pollinators, such as increased plant vigor due to more light or reduced pollinator availability of forest-interior hummingbirds. Distance to the nearest stream also affects the moisture of the environment and *H. tortuosa* are often found at higher densities near streams. We measured the distance to the nearest stream and nearest edge using GIS.

Statistical Models

We used linear mixed models and generalized linear mixed models to test our hypotheses concerning the effects of landscape composition, landscape configuration, temperature, precipitation and synergistic effects of climate and landscape. All modeling was conducted using R (version 3.6.3, R Core Team 2017) and “glmmTMB” (Brooks et al. 2017). We built global models for each measure of reproductive success to check assumptions of linear models: linearity, constant variance of residuals, and normality of residuals. These models include plant

height, *H. tortuosa* density within 20 m, flower density within 20 m, distance to nearest stream, distance to nearest edge, patch size (we log-transformed the preceding variables), number of bracts, plant richness within 20 m, elevation, proportion of forest within 1000 m, mean precipitation, and mean temperature (Appendix Table B1). We added half of the minimum value for a variable when log-transforming. We included crossed random effects for ‘year’ and ‘patch’ to statistically control for spatial correlation of plants nested within patches and temporal autocorrelation for patches and plants measured in the same place over multiple years. After log transforming the number of seeds and logit transforming the proportion of fruits, we determined that a Gaussian distribution could be used for the fruit proportion, seed proportion, number of seeds, and pollen tube proportion analyses. We used a binomial distribution to model the probability of fruit. We checked the assumptions of the binomial using simulated residuals created by “DHARMA” (Hartig 2020). In addition, we checked for correlations between independent variables, which at maximum had a coefficient of 0.65 (Appendix Tables C1-C3). We also tested for spatial autocorrelation of residuals of global models using correlograms of Moran’s *I* at 1000 m intervals with 1000 permutations; the Moran’s *I* values for the proportion of pollen tubes, proportion of fruit, proportion of seeds and number of seeds global models were lower than 0.20 (Appendix Figures D1-D4). However, one lag for the probability of fruit rose to 0.3 (Appendix Figure D5).

Our sample size did not permit testing the full global model (with 14 parameters). We therefore used a hierarchical variable selection approach to reduce the number of nuisance variables considered for each response variable (after Hadley et al. 2014). First, we tested the importance of each local habitat variable in relation to the null model using bivariate mixed models. These models were ranked using Akaike’s information criterion corrected for small

sample sizes (AIC_c). For each model within two AIC_c of the top-ranked model, we used the secondary criterion that 85% confidence intervals should not overlap zero and removed nuisance variables whose confidence intervals included zero (Appendix Tables E1-E5).

After selecting nuisance variables, we then created a priori models corresponding to our hypotheses for each response variable (Burnham and Anderson 2002). For the *precipitation, temperature, and landscape composition hypotheses*, we fit models with the corresponding variables precipitation, temperature, and proportion of forest, respectively, and included nuisance variables when applicable. In addition to the hypothesis tests for precipitation and temperature, we looked for interactions between elevation and precipitation, and elevation and temperature to investigate if the effects of climate varied based on elevation (a patch or plant-specific metric) when elevation was an important nuisance variable. We did not find support for any interactions between elevation and precipitation or elevation and temperature (Appendix Tables G14-G17). For the *landscape fragmentation hypothesis*, we fit a model with patch size and proportion of forest, as well as a model with the interaction between these variables, including nuisance variables when applicable. This latter model reflects the hypothesis that the effects of patch size could amplify at high or low levels of forest amount. We included proportion of forest because patch size is often confounded with forest amount, so we are statistically accounting for forest amount. To assess our *climate and landscape synergy hypothesis*, we built a model set with a null model, nuisance variable model (if applicable), models representing each hypothesis (precipitation, temperature, composition, and fragmentation), and additive and interaction models for each combination of a climate and landscape metrics (Appendix Table F1). We ranked the models using AIC_c and reported results of models within the top 4 AIC_c of each model set.

Results

Over our 9-year study, we observed at least one pollen tube in $52\% \pm 36\%$ (mean \pm SD) of the *H. tortuosa* styles examined. However, only $19\% \pm 20\%$ of the styles examined had at least 3 pollen tubes, which is the minimum required for a complete seed set. Across our study, the probability that a plant produced fruit was $82\% \pm 38\%$. The average proportion of fruit produced was $63\% \pm 36\%$. Whereas, the proportion of seeds produced was only $43\% \pm 28\%$. The average number of seeds produced by each plant was 12 ± 11 . Variation between the annual averages for pollination and reproductive measures and climate metrics can be seen in Figure 1.

We found that climate and land-use change influence the pollination and subsequent reproduction of *H. tortuosa*. Precipitation, temperature, forest amount, patch size, and the interaction between forest amount and patch size are all associated with *H. tortuosa* reproduction over the 9-year study period. We found the most evidence for the effects of forest amount, patch size, and precipitation on the probability of *H. tortuosa* fruit (Table 1). For every millimeter gained in the average daily precipitation per year, the odds of producing a fruit decreased by a factor of 0.69 (95% CI: 0.58, 0.82). For every percent decrease in the forest amount surrounding the *H. tortuosa* plant, the odds of producing a fruit decreased by a factor of 0.77 (95% CI: 0.62, 0.95). When patch size doubles, then the odds of producing a fruit increase by a factor of 1.15 (95% CI: 1.00, 1.33). The odds of producing a fruit increased by a factor of 1.25 (95% CI: 1.02, 1.53) for every meter increase in the elevation of the *H. tortuosa* plant above sea level (Table 2). We also examined the interaction between forest amount and patch size on the probability of fruit. In large patches, there was a positive relationship between forest amount and probability of fruit. Conversely, in small patches, there is a negative relationship between forest amount and probability of fruit (Table 3, Fig. 2).

We found the most support for the hypothesis that precipitation and forest amount influence the number of seeds produced by *H. tortuosa* after accounting for height (Table 4). Similar to the effect on the probability of fruit, for every millimeter gained in the average daily precipitation per year, the odds of seeds decreased by a factor of 0.90 (95% CI: 0.82, 0.98). The odds of seeds also decreased by a factor of 0.95 (95% CI: 0.89, 1.01) for every percent increase in the forest amount surrounding the *H. tortuosa* plant. The odds of seeds increased by a factor of 1.10 (95% CI: 1.04, 1.17) for every meter in height of a *H. tortuosa* plant (Table 5).

Temperature had a weak positive impact on the proportion of *H. tortuosa* seeds produced; for every degree Celsius increase in the average daily temperature, the odds of the seed production per flower increased by a factor of 1.02 (95% CI: 1.00, 1.04, Appendix Table G12). For every increase in meter above sea level, the odds of pollen tube presence per style decreased by a factor of 0.96 (95% CI: 0.92, 1.00). Elevation was the only predictor with significant impact on the proportion of pollen tubes (Appendix Table G13). We did not detect any significant predictors of the proportion of fruit produced. The null model was within the top 4 AIC_c for the proportion of pollen tubes (Appendix Table G9), proportion of fruit (Appendix Table G12), and proportion of seeds (Appendix Table G11) analyses.

Discussion

To our knowledge, our study is the first to find support for effects of climate and land-use change on pollination success and reproductive output. We found that both climate and land-use influence some measures of fecundity in *H. tortuosa*, but these factors do not tend to act synergistically. In other words, the effects of forest loss and fragmentation were not disproportionately amplified in wetter or hotter years. *H. tortuosa* plants were more likely to

produce fruit at higher elevation and in larger patches, and less likely to in wetter years and when there was more forest in the surrounding landscape.

The majority of support for our hypotheses derive from the probability of fruit analysis and was not observed in the analyses for the proportion of pollen tubes, proportion of fruit, proportion of seeds and number of seeds. The proportion of pollen tubes analysis may differ as it was patch-specific not plant-specific like the other dependent variables. The probability of fruit analysis utilized a slightly different dataset than the other plant-specific response variables as it included plants that did not produce at least one successful fruit. These plants were excluded from those analyses because the lack of successful fruit could be due to insufficient plant vigor or lack of traplining hummingbird visitations. Therefore, we attribute the inconsistency of our results between metrics of pollination and reproductive output to the difference in scale for the proportion of pollen tubes analysis and the exclusion of plants for the proportion of fruit, proportion of seeds, and number of seeds analyses.

H. tortuosa plants that did not produce at least one successful fruit, may have failed due to insufficient vigor or lack of visitations from traplining hummingbirds. However, both of our measures of plant vigor (height and number of bracts) did not satisfy our nuisance variable selection and therefore are poor predictors of the probability of fruit. Alternatively, as only 53% of the styles examined had at least one pollen tube, visitations from *P. guy* and *C. hemileucurus* are likely limiting pollen deposition. Previous findings in this system are mixed; Kormann et al. suggests that pollen is limiting to *H. tortuosa* as approximately 25% of the *H. tortuosa* styles examined had at least one pollen tube (2016). However, Hadley et al. found pollen tubes were present in 79% of *H. tortuosa* plants and on average there were 2.43 pollen tubes per style, so the quantity of pollen was not considered limiting (2014).

Given that pollinator movement is restricted in our system (Hadley and Betts 2009; Volpe et al. 2014; Kormann et al. 2016), we posit that the higher probability of fruit found in small patches in deforested landscapes (small patches surrounded by a low forest amount) is due to restricted pollinator movement preventing pollinator dispersal – a “fence effect” – resulting in a pollinator saturated system. Large patches in forested landscapes support more pollinators of *H. tortuosa*, resulting in a higher probability of fruit. When pollinator availability to *H. tortuosa* is high, we expect reduced pollen limitation by trapliner visitations. The positive effects of patch size on the probability of *H. tortuosa* fruit are consistent with previous findings in our study system that fragmentation per se is associated with an increase in the successful reproduction of *H. tortuosa* (Hadley et al. 2014).

The lower probability of fruit we find in small patches in forested landscapes and in large patches in deforested landscapes is likely due to poor habitat quality for *H. tortuosa*'s pollinators. Small patches in forested landscapes likely provides insufficient habitat for *H. tortuosa*'s pollinators, which may vacate the small patch for the surrounding forest. We attribute the negative effect of forest amount on the probability of fruit to hummingbirds vacating small patches when surrounding forest amount is high. We also found that large patches in deforested landscapes had a lower probability of fruit. The majority of large patches in deforested landscapes are isolated in the East part of our study area, while the small patches in forested landscapes are closer to a large expanse of continuous forest in the West part of our study area (Figure 1). We attribute the low probability of fruit found in large patches in deforested landscapes to a lack of connectivity to a larger expanse of forest that is idiosyncratic to our study area. Thus, pollen limitation in our system may be caused by a lack of habitat quality for *H.*

tortuosa's pollinators when patch size is small and forest amount is high, and a lack of broad habitat quality when patch size is large and forest amount is low.

The negative effect of precipitation on the probability of *H. tortuosa* fruit and number of seeds may be due to reduced light received by *H. tortuosa* when precipitation is high as high precipitation is accompanied with increased cloud cover. Light can be limiting to trees in tropical forests, leading to reduced growth and fruit production (Graham et al. 2002). As *H. tortuosa* is an understory herb, the light limitation may be more pronounced than for trees. If light is limiting to *H. tortuosa*, then increased precipitation may reduce the floral resources available to *H. tortuosa*'s pollinators. Another explanation of the negative effect of precipitation is water stress during the dry season may induce *H. tortuosa* flowering (Opler et al. 1976). If lack of water in the dry season induces *H. tortuosa* flowering, then altered precipitation patterns due to climate change could alter the phenological synchronicity between *H. tortuosa* and its pollinators. Alternatively, the increased probability of fruit and number of seeds in dry years could be the results of less flowering causing increased outcrossing between *H. tortuosa* plants as pollinators are forced to move farther due to fewer floral resources. Temperature did not appear to influence *H. tortuosa* pollination and reproductive output.

The effects of habitat loss and fragmentation resulting in pollen limitation of *H. tortuosa* has implication for future resources for pollinators. We know that habitat loss and habitat fragmentation are associated with declines in plant sexual reproduction (Garibaldi et al. 2013; Aguilar et al. 2016). Reduced sexual reproduction may lead to decreased floral resources, forcing pollinators to travel further to obtain resources. An increase in the distance that pollinators travel may increase plant reproduction by increasing outcrossing. However, when pollinators that alter their movement in response to habitat configuration are forced to move further, the increased

exertion may lead to declines in pollinators through increased mortality or decreased reproduction. A reduction in pollinators will likely have implications for plant pollination and reproduction. This positive feedback loop is one explanation for the associated decline of plants and their pollinators (Biesmeijer et al. 2006). The limitation of *H. tortuosa* pollination is of concern because as land-use change and climate change progress, biodiversity loss will continue, which may decrease pollination and dispersal.

A limitation of this study was not recording plant specific data for pollen tubes. As pollen tubes are a proxy for the presence of traplining hummingbirds, comparisons between the proportion of pollen tubes and the probability of fruit would have helped us determine whether our plants were limited by traplining hummingbird visitations or their health. In addition, this study would have been improved by more knowledge about the species distribution and phenology of *H. tortuosa* and its pollinators. This study would have also been enhanced by patch-specific climate data. Recent afforestation in Costa Rica has nearly doubled forest cover since 1985 to 53% in 2013 (Costa Rican Ministry of Environment and Energy). Our study area is particularly dynamic as there has been a net loss of forest since 1980, however both deforestation and reforestation have occurred (Zahawi et al. 2015). As our measures for patch size and forest amount were static throughout the experiment, we are unable to detect the benefits of afforestation. In addition, most larger patches surrounded by less forest are distant and unconnected from large amounts of continuous habitat in our study system. This idiosyncratic trend may explain the spatial autocorrelation we found in our probability of fruit analysis. However, spatial autocorrelation is an additional limitation of our study (Appendix Figures D5-D7).

While we do not find evidence of synergistic effects of climate and land-use change, we find that climate and land-use change do independently affect *H. tortuosa* reproduction. Pollen limitation appears to be due to a lack of habitat quality in small patches in forested landscapes and an idiosyncratic lack of broad-scale habitat quality in large patches in deforested landscapes. The pollen limitation expected in small patches in deforested landscapes may be masked by constraint of pollinator movement causing pollinator saturation. Pollen limitation may be exacerbated by future habitat loss, habitat fragmentation, and climate change as reductions in floral resources could lead to a positive feedback loop of biodiversity loss. Our lack of evidence for synergistic effects of climate and land-use change on pollination do not prove that such synergistic effects do not occur. Further studies should investigate how habitat fragmentation may interact with the effects of climate in different systems. Conservation of *H. tortuosa* and its pollinators is dependent on maintaining sufficient habitat, habitat connectivity, overlapping species distributions and their phenological synchronicity.

Literature Cited

- Aguilar R, Ashworth L, Galetto L and Aizen MA (2006) Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. *Ecology letters*, 9(8), pp.968-980.
- Badeck FW, Bondeau A, Böttcher K, Doktor D, Lucht W, Schaber J, Sitch S (2004) Responses of spring phenology to climate change. *New Phytologist* 162(2):295-309.
- Bartomeus I, Park MG, Gibbs J, Danforth BN, Lakso AN, Winfree R (2013) Biodiversity ensures plant–pollinator phenological synchrony against climate change. *Ecology letters*, 16(11):1331-1338.
- Bélisle MA, Descrochers A, Fortin MJ (2001) Influence of forest cover on the movement of forest birds: a homing experiment. *Ecology* 82:1893-1904.
- Betts MG, Hadley AS, Kress WJ (2015) Pollinator recognition by a keystone tropical plant. *PNAS* 112(11):3433-3438.
- Biesmeijer JC, Roberts SP, Reemer M, Ohlemüller R, Edwards M, Peeters T, Schaffers AP, Potts SG, Kleukers R, Thomas CD, Settele J (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* 313(5785):351-4.
- Borgella R Jr, Snow AA, Gavin TA (2001) Species Richness and Pollen Loads of Hummingbirds using Forest Fragments in Southern Costa Rica. *Biotropica* 33(1):90-109.
- Brittain C, Kremen C, Klein AM (2013) Biodiversity buffers pollination from changes in environmental conditions. *Global change biology*, 19(2), pp.540-547.
- Brook BW, Sodhi NS, Bradshaw CJA (2008) Synergies among extinction drivers under global change. *Trends in Ecology and Evolution* 23(8): 453-460.
- Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielson A, Skaug HJ, Maechler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9(2):378-400.
- Brooks TM, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Rylands AB, Konstant WR, Flick P, Pilgrim J, Oldfield S, Magin G, Hilton-Taylor C (2002) Habitat loss and extinction in the hotspots of biodiversity. *Conservation biology* 16(4):909-23.
- Buermann W, Chaves JA, Dudley R, McGuire JA, Smith TB, Altshuler DL (2011) Projected changes in elevational distribution and flight performance of montane Neotropical hummingbirds in response to climate change. *Global Change Biology*. 17(4):1671-80.
- Burnham KP, Anderson DR (2002) *Model selection and multimodel inference: a practical information-theoretic approach* Second., New York: Springer.
- Chazal JD, Rounsevell MDA (2009) Land-use and climate change within assessments of biodiversity change: A review. *Global Environmental Change* 19:306-315.
- Conenna I, Valkama J, Chamberlain D (2017) Interactive effects of climate and forest canopy cover on Goshawk productivity. *Journal of Ornithology* 158:799–809.
- Costa Rican Ministry of Environment and Energy (2018) Report on the State of the Environment 2017 [In Spanish]
- Dale VH (1997) The relationship between land-use change and climate change. *Ecological applications*, 7(3): 753-769.
- 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(4): 1027-1036.

- Dominguez CA, Dirzo R (1995) Rainfall and flowering synchrony in a tropical shrub: Variable selection on the flowering time of *Erythroxylum havanense*. *Evolutionary Ecology*, 9(2): 204-216.
- Fahrig L (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography*, 40(9): 1649-1663.
- Forister, M.L., McCall, A.C., Sanders, N.J., Fordyce, J.A., Thorne, J.H., O'Brien, J., Waetjen, D.P. and Shapiro, A.M., 2010. Compounded effects of climate change and habitat alteration shift patterns of butterfly diversity. *Proceedings of the National Academy of Sciences*, 107(5): 2088-2092.
- Garibaldi LA, Steffan-Dewenter I, Winfree R, Aizen MA, Bommarco R, Cunningham SA, Kremen C, Carvalheiro LG, Harder LD, Afik O, Bartomeus I (2013) Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *science*, 339(6127): 1608-1611.
- Ghazoul J (2005) Pollen and seed dispersal among dispersed plants. *Biol. Rev.* 80:413-443.
- Graham EA, Mulkey SS, Kitajima K, Phillips NG, Wright SJ (2002) Cloud cover limits net CO₂ uptake and growth of a rainforest tree during tropical rainy seasons. *PNAS* 200(2):572-576.
- Hadley AS, Betts MG (2009) Tropical Deforestation alters hummingbird movement patterns. *Biology Letters* 5(2):207-210.
- Hadley AS, Betts MG (2012) The effects of landscape fragmentation on pollination dynamics: absence of evidence not evidence of absence. *Biological Reviews*, 87(3): 526-544.
- Hadley AS, Frey SJ, Robinson WD, Betts MG (2018) Forest fragmentation and loss reduce richness, availability, and specialization in tropical hummingbird communities. *Biotropica* 50(1):74-83.
- Hadley AS, Frey SJ, Robinson WD, Kress, WJ. Betts MG (2014) Tropical forest fragmentation limits pollination of a keystone understory herb. *Ecology* 95(8): 2202-2212.
- Hartig F (2020) DHARMA: Residual diagnostics for hierarchical (multi-level / mixed) regression models. R package version 0.2.7. <https://CRAN.R-project.org/package=DHARMA>
- Hegland SJ, Nielsen A, Lázaro A, Bjercknes AL, Totland Ø (2009) How does climate warming affect plant-pollinator interactions?. *Ecology letters* 12(2):184-95.
- Horvitz CC, Schemske DW (1995) Spatiotemporal variation in demographic transitions of a tropical understory herb: Projection matrix analysis. *Ecological Monographs* 65(2):155-192.
- Huntley B, Webb III T (1989) Migration: species' response to climatic variations caused by changes in the earth's orbit. *Journal of Biogeography* 16(1): 5-19.
- IPBES (2019) Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. E. S. Brondizio, J. Settele, S. Díaz, and H. T. Ngo (editors). IPBES secretariat, Bonn, Germany.
- Kormann U, Scherber C, Tschardt T, Klein N, Larbig M, Valente JJ, Hadley AS, Betts MG (2016) Corridors restore animal-mediated pollination in fragmented tropical forest landscapes. *Proceedings of the Royal Society B: Biological Sciences*. 283(1823):20152347.
- Kress WJ (1983) Self-incompatibility in Central American *Heliconia*. *Evolution* 37:735-744.
- Lima SL, Zollner PA (1996) Towards a behavioral ecology of ecological landscapes. *Trends in Ecology & Evolution* 11(3):131-5.

- Lutz E, Vedova WM, Martinez H, San Roman I, Vazquez L. R, Alvarado A, Merino I, Celis R, and Husing J (1993) Interdisciplinary fact-finding on current deforestation in Costa Rica. The World Bank Sector Policy and Research Staff Report Environment Working Paper No. 61. World Bank, Environment Dept., Washington, D.C.
- Memmott J, Craze PG, Waser NM, Price MV (2007) Global warming and the disruption of plant-pollinator interactions. *Ecology Letter* 10(8):710-7.
- 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(5): 1561-1575.
- Oliver TH, Marshall HH, Morecroft MD, Brereton T, Prudhomme C, Huntingford C (2015) Interacting effects of climate change and habitat fragmentation on drought-sensitive butterflies. *Nature Climate Change* 5:941–945.
- Oliver TH, Morecroft MD (2014) Interactions between climate change and land use change on biodiversity: attribution problems, risks, and opportunities. *Wiley Interdisciplinary Reviews: Climate Change*, 5(3): 317-335.
- Ollerton J, Winfree R, Tarrant S (2011) How many flowering plants are pollinated by animals? *Oikos* 120(3):321-6.
- 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(3):231-236.
- 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.
- Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE (2010) Global pollinator declines: trends, impacts and drivers. *Trends in ecology & evolution*, 25(6): 345-353.
- R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Ricketts T (2001) The matrix matters: effective isolation in fragmented landscapes. *American Naturalist* 158: 87-99.
- Schweiger O, Biesmeijer JC, Bommarco R, Hickler T, Hulme PE, Klotz S, Kühn I, Moora M, Nielsen A, Ohlemüller R, Petanidou T (2010) Multiple stressors on biotic interactions: how climate change and alien species interact to affect pollination. *Biological Reviews*. 85(4): 777-95.
- Stangler, E. S., P. E. Hanson, and I. Steffan-Dewenter. 2015. Interactive effects of habitat fragmentation and microclimate on trap-nesting Hymenoptera and their trophic interactions in small secondary rainforest remnants. *Biodiversity and Conservation* 24:563–577.
- Steffan-Dewenter I, Potts SG, Packer L (2005) Pollinator diversity and crop pollination services are at risk. *Trends in ecology & evolution*. 20(12):651-2.
- Stiles FG (1975) Ecology, Flowering Phenology, and Hummingbird Pollination of Some Costa Rican Heliconia Species. *Ecology* 56(2):285-301.
- Thomas C, Cameron A, Green R, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, Ferreira de Siqueira M, Grainger A, Hannah L, Hughes L, Huntley B, van Jaarsveld AS,

- Midgley GF, Miles L, Ortega-Huerta MA, Peterson AT, Phillips OL, Williams SE (2004) Extinction risk from climate change. *Nature* 427: 145–148.
- VanDerWal J, Murphy HT, Kutt AS, Perkins GC, Bateman BL, Perry JJ, Reside AE (2013) Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change. *Nature Climate Change*, 3(3):239-243.
- Visser ME, Both C (2005) Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B: Biological Sciences* 272(1581):2561-9.
- Volpe NL, Hadley AS, Robinson WD, Betts MG (2014) Functional connectivity experiments reflect routine movement behavior of a tropical hummingbird species. *Ecological Applications*, 24(8): 2122-2131.
- Wilson MC, Chen XY, Corlett RT, Didham RK, Ding P, Holt RD, Holyoak M, Hu G, Hughes AC, Jiang L, Laurance WF (2016) Habitat fragmentation and biodiversity conservation: key findings and future challenges. *Landscape Ecology* 31:219-227
- Zahawi RA, Duran G, Kormann U (2015) Sixty-seven years of land-use change in southern Costa Rica. *PloS one*, 10(11).

Tables

Table 1. Ranking of models predicting the probability of fruit within the top 4 AIC_c and the null model. Nuisance variables were included in these models. Precipitation, patch size and forest amount appear to exert influence over the probability of *H. tortuosa* fruit.

Model	DF	Log Likelihood	Δ Log Likelihood	AIC _c	Δ AIC _c	Weight
Patch size + precipitation	10	-366.5	15.0	753.3	0.0	0.385
Patch size x precipitation	11	-365.9	15.7	754.1	0.8	0.262
Forest amount + precipitation	9	-368.3	13.3	754.8	1.5	0.184
Precipitation	8	-370.0	11.5	756.2	2.9	0.091
Forest amount x precipitation	10	-368.2	13.4	756.6	3.3	0.074
Null	3	-381.6	0.0	769.1	15.8	<0.001

Table 2. Coefficients for the top AIC_c-ranked model predicting the probability of fruit as a function of local-scale nuisance variables (distance to the nearest edge, flower richness, flower density, and elevation), land-use change (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. After accounting for these variables, patch size had a positive influence.

Independent Variable	Estimate	95% CI	P-value
Forest amount	-0.268	-0.482, -0.053	0.0145*
Patch size	0.206	0.001, 0.412	0.0488*
Precipitation	-0.369	-0.539, -0.199	0.0000212*
Distance to edge	0.082	-0.108, 0.272	0.3980
Richness	0.076	-0.184, 0.335	0.5682
Flower density	0.058	-0.216, 0.332	0.6763
Elevation	0.222	-0.021, 0.423	0.0306*

Table 3. Coefficients for the top AIC_c-ranked model predicting the probability of fruit as a function of local-scale nuisance variables (distance to the nearest edge, flower richness, flower density, and elevation) and land-use change (forest amount, patch size, and the interaction between forest amount and patch size). While the effect of forest amount on the probability of fruit is negative, the interaction between forest amount and patch size exerts a large positive impact on the probability of fruit.

Independent Variable	Estimate	95% CI	P-value
Forest amount	-0.260	-0.478, -0.043	0.0190*
Patch size	0.055	-0.206, 0.316	0.6798
Patch size \times forest amount	0.229	-0.035, 0.493	0.0897
Distance to edge	0.018	-0.182, 0.218	0.8617
Richness	0.130	-0.134, 0.394	0.3349
Flower density	0.046	-0.231, 0.324	0.7446
Elevation	0.155	-0.050, 0.360	0.1386

Table 4. Ranking of models predicting the number of *H. tortuosa* seeds within the top 4 AIC_c and the null model. Nuisance variables were included in these models. Precipitation, forest amount and patch size appear to influence the number of seeds produced.

Model	DF	Log Likelihood	Δ Log Likelihood	AIC _c	Δ AIC _c	Weight
Forest amount + precipitation	7	-823.5	8.1	1661.1	0.0	0.284
Precipitation	6	-824.7	6.8	1661.6	0.4	0.230
Patch size + precipitation	8	-823.3	8.2	1662.8	1.7	0.123
Forest amount \times precipitation	8	-823.4	8.2	1662.9	1.8	0.115
Forest amount	6	-826.1	5.4	1664.3	3.2	0.058
Patch size \times precipitation	9	-823.2	8.3	1664.7	3.6	0.048
Height	5	-827.4	4.1	1664.9	3.8	0.043
Null	4	-831.5	0.0	1671.1	10.0	0.002

Table 5. Coefficients for the top AIC_c-ranked model predicting the number of seeds as a function of local-scale nuisance variables (plant height) and land-use change (forest amount), and precipitation. After accounting for height, precipitation has a negative impact on the number of *H. tortuosa* seeds produced.

Independent Variable	Estimate	95% CI	P-value
Forest amount	-0.051	-0.114, 0.011	0.10600
Precipitation	-0.107	-0.196, -0.018	0.01887*
Height	0.098	0.037, 0.159	0.00158*

Figures

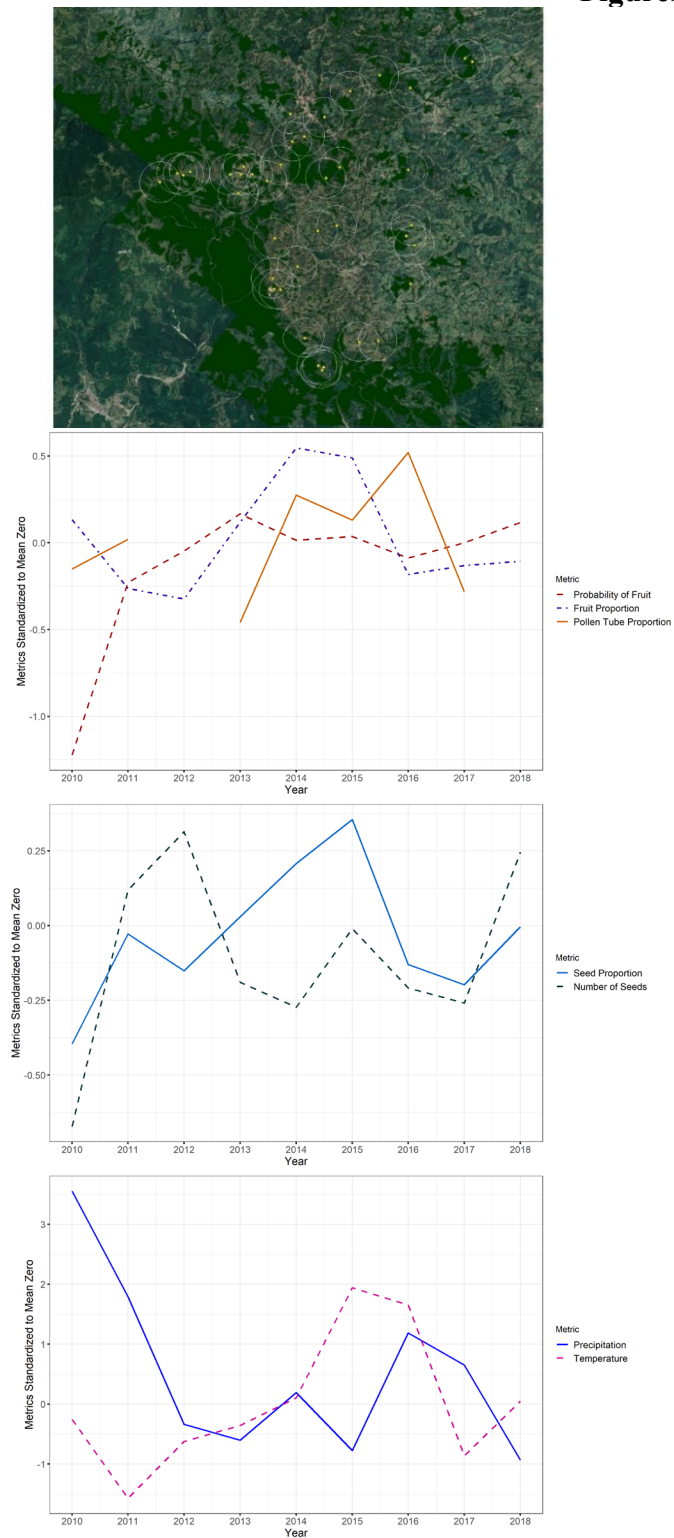


Figure 1. Our study area, showing forest cover, forest patch locations, and 1000m radii around the patches. Standardized and averaged pollination, reproductive output, and climate metrics over the 9-year study period. Landscape metrics are not included in the figure as we did not have year specific landscape data.

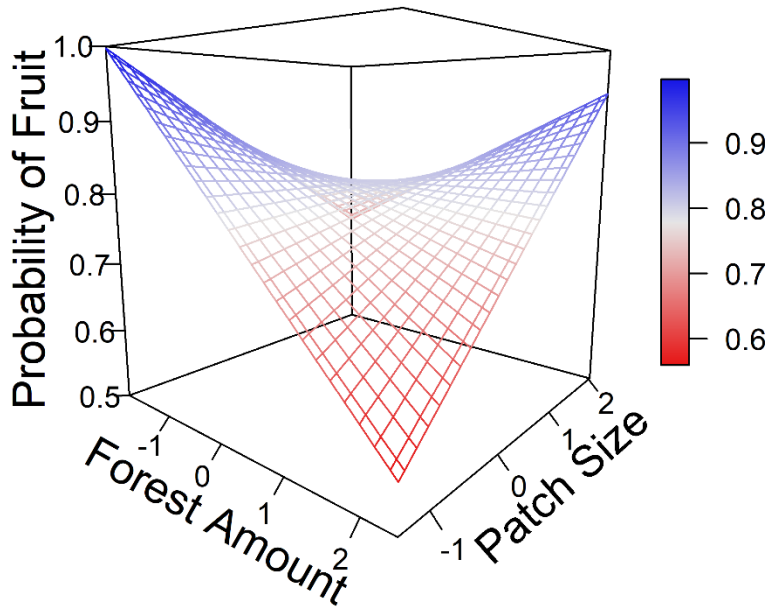


Figure 2. Fitted results of a generalized linear mixed model that predicts the probability of *H. tortuosa* fruit as a function of the interaction between patch size and forest amount (standardized to mean zero). Although patch size had a strong positive effect on the probability of fruit, larger patches appeared to be detrimental to fruit in landscapes with high forest cover.

Appendix

Pollination and Reproductive Output Metric Descriptions

Table A1. Descriptions, explanations, and ranges of response variables.

Response Variable	Description	Explanation	Range
Pollen tube proportion	The proportion of styles within a patch that had at least one pollen tube.	As <i>H. tortuosa</i> pollination depends on traplining hummingbird visitations, the pollen tube proportion provides us with a proportion of flowers within a patch that were visited by a traplining hummingbird.	0 - 1
Probability of fruit	The presence of absence of successful fruits per plant.	The probability of <i>H. tortuosa</i> fruit indicates that either the plant has insufficient vigor to produce fruits or it did not receive traplining hummingbird visitations.	0 , 1
Proportion of fruit	The proportion of successful fruits out of the number of flowers that bloomed per plant.	The proportion of fruit is a measure of the amount of fruit produced after accounting for the plant's investment into flowering.	0.1 - 1
Proportion of seeds	The proportion of seeds produced out of the number of flowers that bloomed per plant.	The proportion of seeds is a measure of the amount of seeds produced after accounting for the plant's investment into flowering.	0 - 1
Number of seeds	The number of seeds produced per plant.	The number of seeds produced represents the per capita contribution to the next generation.	0 – 57 seeds

Independent Variables Descriptions

Table B1. Descriptions, sampling frequency, and ranges of our independent variables.

Independent Variable	Description	Sampling frequency	Included in the pollen tube analysis (Yes / No)	Log-transformed (Yes / No)	Range
Precipitation	A regional measure of daily precipitation averaged over each year.	The regional average for precipitation was remeasured each year.	Y	N	7.7 – 13.5 mm
Temperature	A regional measure of daily temperature averaged over each year.	The regional average for temperature was remeasured each year.	Y	N	19.2 - 20.3 °C
Forest amount	Proportion of forest within a 1000 m radius of the focal plant (or focal patch for the pollen tube analysis).	Forest amount was remeasured for each focal plant (and patch for the pollen tube analysis).	Y	N	0.05 – 0.80
Patch size	Size of the forest patch in hectares.	Patch size was measured once for each patch.	Y	Y	<1 - >1200 ha
Height	Height of <i>H. tortuosa</i> plants measured from the ground to the top of the tallest petiole. This is a proxy for plant vigor.	Height was remeasured for each focal plant.	N	N	0.3 – 3.2 m
Number of bracts	Number of bracts in the <i>H. tortuosa</i> inflorescence, which is another proxy for plant vigor.	Number of bracts was remeasured for each focal plant.	N	N	2 – 13 bracts

<i>H. tortuosa</i> density	Number of <i>H. tortuosa</i> plants within a 20 m radius of the focal plant divided by the area within that 20 m radius.	<i>H. tortuosa</i> density was remeasured for each focal plant.	N	Y	0.0 – 0.13
Total flower density	Number of flowering plants within a 20 m radius of the focal plant divided by the area within the 20 m radius.	Total flower density was remeasured for each focal plant.	N	Y	0.0 – 0.48
Flowering plant richness	Number of unique flowering plant species within a 20 m radius of the focal plant.	Flowering plant richness was remeasured for each focal plant.	N	N	1 – 8 flowering plant species
Elevation	Elevation above sea level for each focal plant, or an estimate of the elevation for the patch for the pollen tube analysis.	Elevation was remeasured for each focal plant (and each patch in the pollen tube analysis).	Y	N	500 – 1600 m
Distance to edge	Distance from the focal <i>H. tortuosa</i> plant to the nearest edge of the forest patch. This measure is a proxy for edge effects.	Distance to edge was remeasured for each focal plant.	N	Y	0 – 101 m
Distance to stream	Distance from the focal <i>H. tortuosa</i> plant to the nearest stream.	Distance to stream was remeasured for each focal plant.	N	Y	0 – 100 m

Spatial Autocorrelation

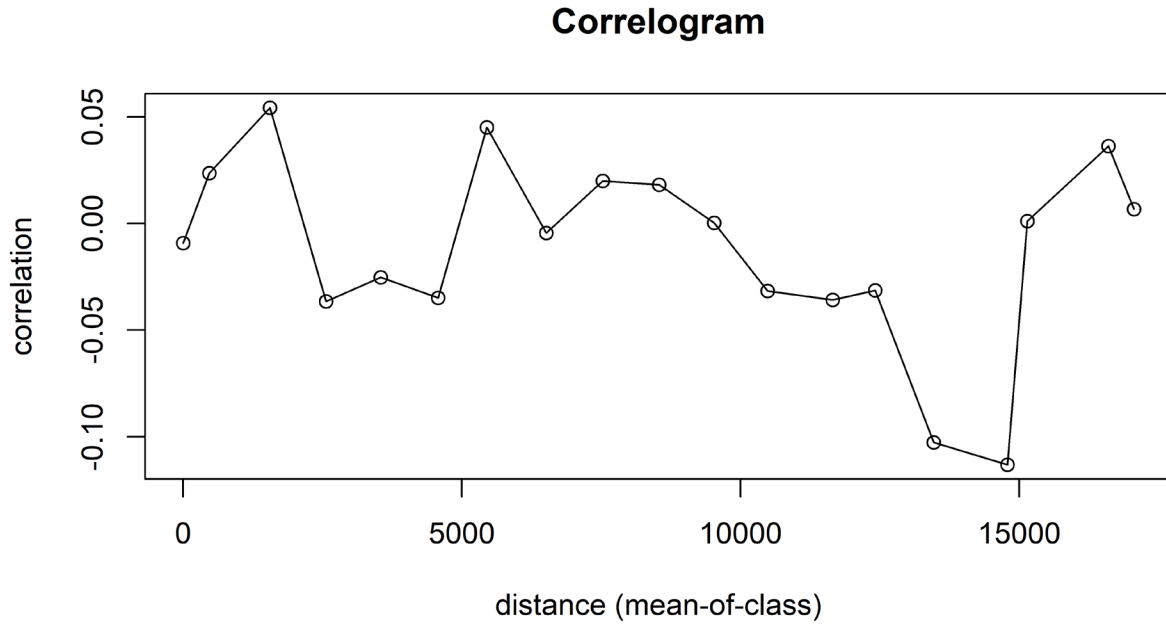


Figure D1. Correlogram of residuals from the global model for the proportion of pollen tubes at 1000 m lags with 1000 permutations.

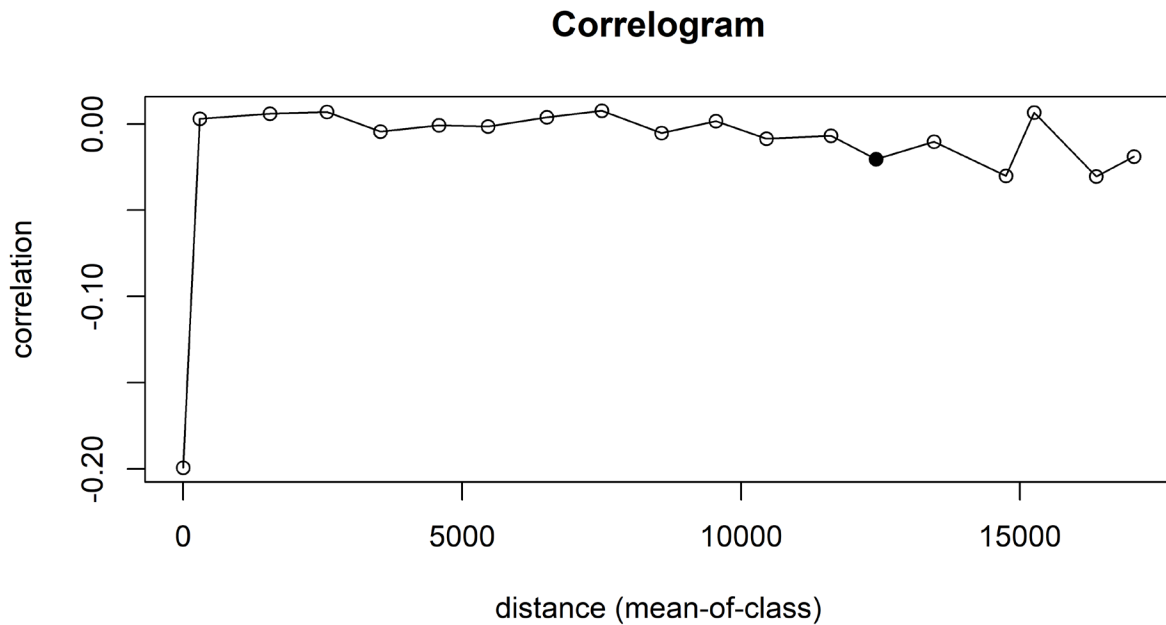


Figure D2. Correlogram of residuals from the global model for the number of seeds at 1000 m lags with 1000 permutations.

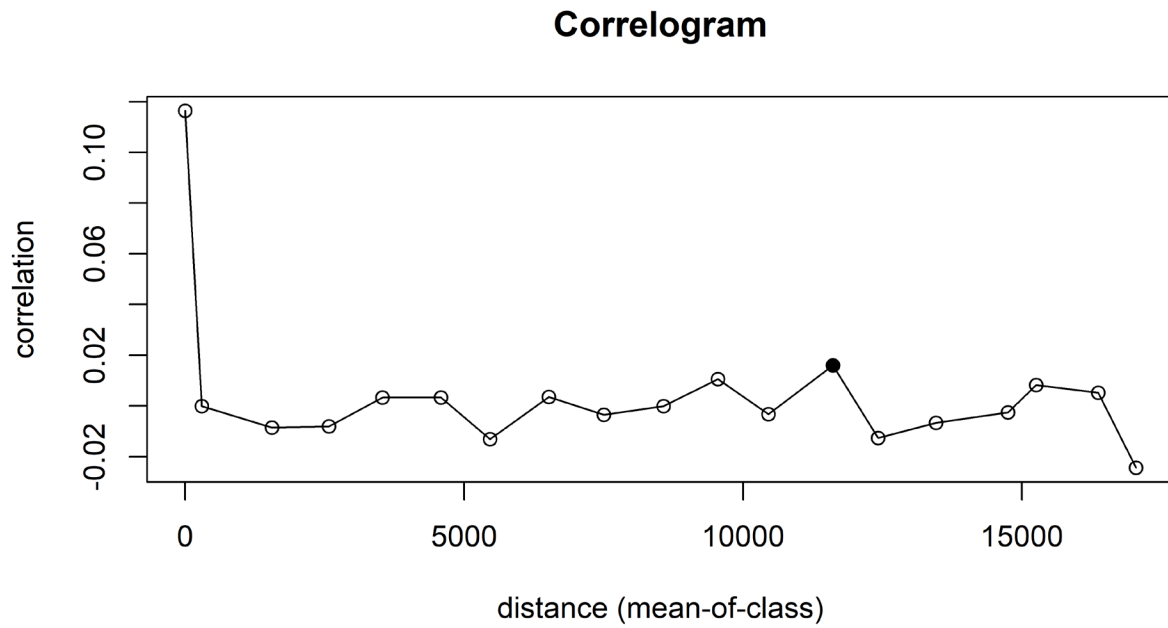


Figure D3. Correlogram of residuals from the global model for the proportion of seeds at 1000 m lags with 1000 permutations.

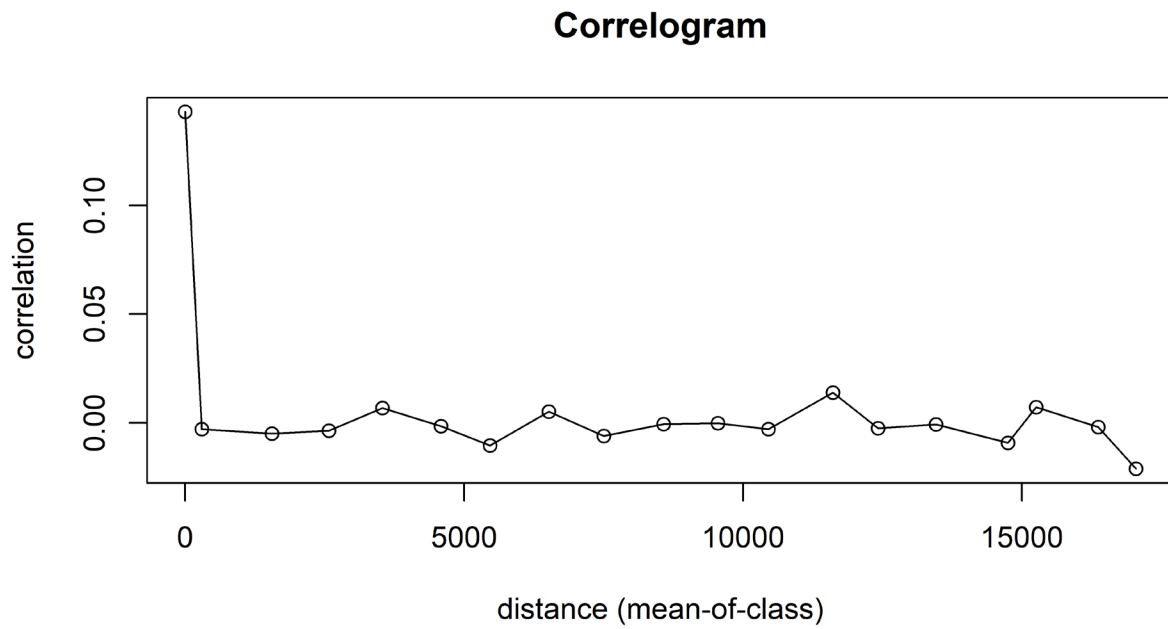


Figure D4. Correlogram of residuals from the global model for the proportion of fruit at 1000 m lags with 1000 permutations.

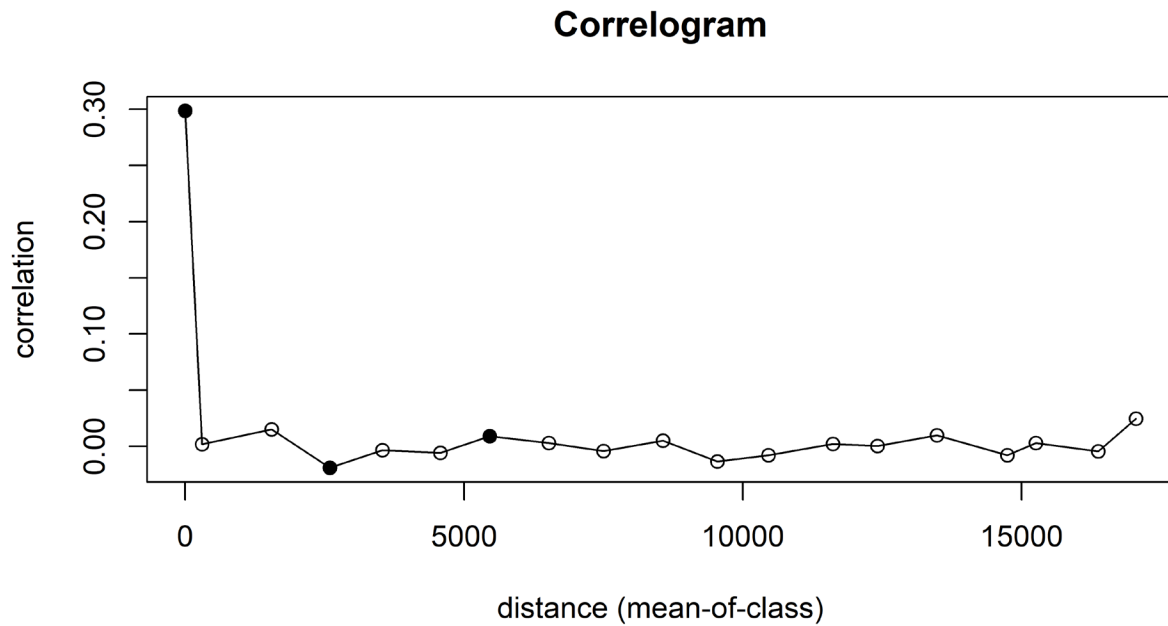


Figure D5. Correlogram of residuals from the global model for the probability of fruit at 1000 m lags with 1000 permutations. The highest correlation value is 0.299 with a p-value of 0.0170.

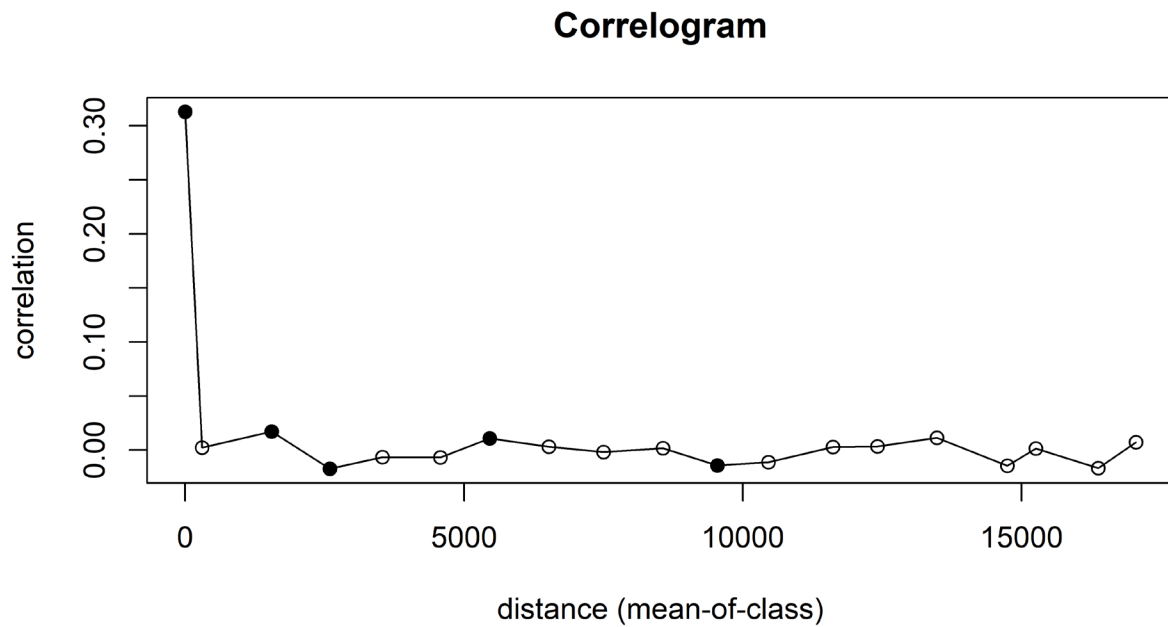


Figure D6. Correlogram of residuals from the interaction model between patch size and forest amount for the probability of fruit at 1000 m lags with 1000 permutations. The highest correlation value is 0.313 with a p-value of 0.013.

Correlogram

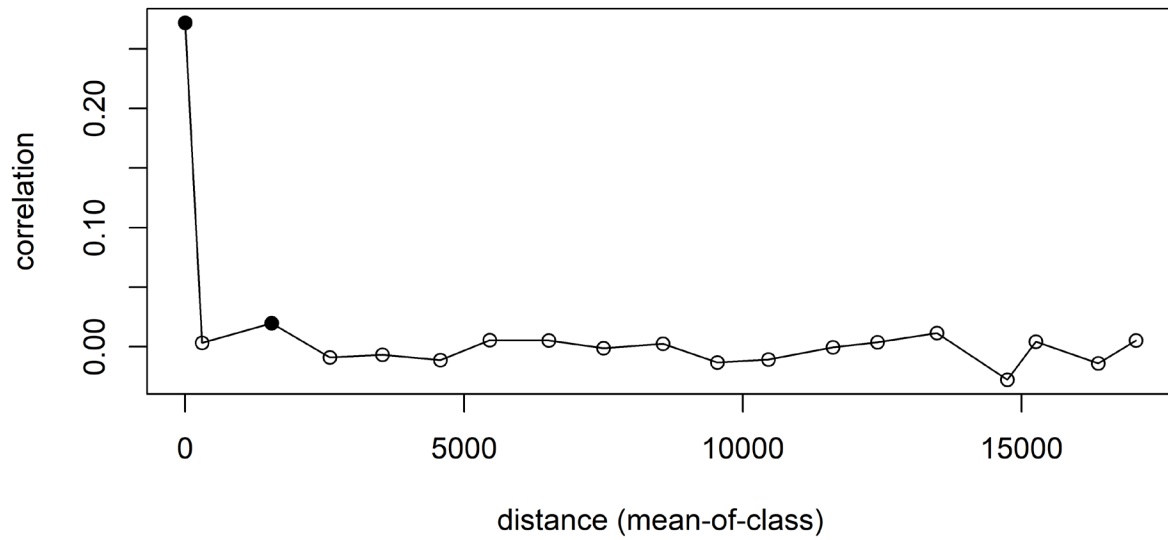


Figure D7. Correlogram of residuals from the patch size and precipitation model for the probability of fruit at 1000 m lags with 1000 permutations. The highest correlation value is 0.272 with a p-value of 0.024.

Nuisance Variable Selection

Table E1. Ranked univariate models for nuisance variable selection for the proportion of pollen tubes analysis with an 85% CI for the coefficients of models within the top 2 AIC_c. The nuisance variables included in the subsequent analysis for the proportion of pollen tubes are bolded.

	DF	AIC _c	Δ AIC _c	85% CI
Elevation	5	15.8	0.0	-0.075, -0.013
Null	4	17.5	1.7	

Table E2. Ranked univariate models for nuisance variable selection for the probability of fruit analysis with an 85% CI for the coefficients of models within the top 2 AIC_c. The nuisance variables included in the subsequent analysis for the probability of fruit are bolded.

	DF	AIC _c	Δ AIC _c	85% CI
Elevation	4	767.1	0.0	0.070, 0.401
Flower Density	4	767.5	0.5	0.059, 0.383
Flower Richness	4	767.7	0.6	0.045, 0.360
Distance to edge	4	768.9	1.8	0.011, 0.306
Null	3	769.1	2.1	
Number of bracts	4	770.4	3.3	
Distance to stream	4	770.7	3.7	
<i>H. tortuosa</i> density	4	770.7	3.7	
Height	4	771.0	4.0	

Table E3. Ranked univariate models for nuisance variable selection for the proportion of fruit analysis with an 85% CI for the coefficients of models within the top 2 AIC_c. No nuisance variables were included in the subsequent analysis for the proportion of fruit.

	DF	AIC _c	Δ AIC _c	85% CI
Null	4	2563.3	0.0	
Distance to edge	5	2563.3	0.6	-0.160, 0.014
Height	5	2564.2	0.9	-0.149, 0.023
Elevation	5	2564.4	1.1	-0.145, 0.029
Distance to stream	5	2564.6	1.4	-0.139, 0.038
<i>H. tortuosa</i> density	5	2564.7	1.4	-0.138, 0.040
Flower richness	5	2564.9	1.7	-0.057, 0.136
Number of bracts	5	2565.1	1.8	-0.119, 0.061
Flower density	5	2565.3	2.0	-0.087, 0.102

Table E4. Ranked univariate models for nuisance variable selection for the proportion of seeds analysis with an 85% CI for the coefficients of models within the top 2 AIC_c. No nuisance variables were included in the subsequent analysis for the proportion of seeds.

	DF	AIC _c	Δ AIC _c	85% CI
Null	4	-187.2	0.0	
Distance to edge	5	-186.4	0.9	-0.021, 0.003
Elevation	5	-185.5	1.8	-0.008, 0.017
Number of bracts	5	-185.5	1.8	-0.017, 0.008
Height	5	-185.3	1.9	-0.009, 0.014
<i>H. tortuosa</i> density	5	-185.3	1.9	-0.009, 0.015
Distance to stream	5	-185.3	2.0	-0.014, 0.010
Flower density	5	-185.2	2.0	-0.015, 0.011
Flower richness	5	-185.2	2.0	-0.013, 0.013

Table E5. Ranked univariate models for nuisance variable selection for the number of seeds analysis with an 85% CI for the coefficients of models within the top 2 AIC_c. The nuisance variables included in the subsequent analysis for the number of seeds are bolded.

	DF	AIC _c	Δ AIC _c	85% CI
Height	5	1664.9	0.0	0.045, 0.135
Distance to edge	5	1669.8	4.9	
Number of bracts	5	1670.0	5.1	
Elevation	5	1670.7	5.8	
Distance to stream	5	1670.8	5.9	
Null	4	1671.1	6.3	
Flower density	5	1671.9	7.0	
<i>H. tortuosa</i> density	5	1672.6	7.7	
Flower richness	5	1672.8	7.9	

Climate and Landscape Synergy Model Set

Table F1. This table represents the full model set for testing the *climate and landscape synergy hypothesis* for each response variable. All models besides the null model include nuisance variables as determined for each response variable. Random effects for year and patch were included in the listed models.

Models	Variables included
Null	N/A
Nuisance	Applicable nuisance variables
Precipitation	Precipitation
Temperature	Temperature
Forest amount	Forest amount
Patch size	Patch size and forest amount
Patch size interaction	Patch size, forest amount, and the patch size and forest amount interaction
Forest amount and precipitation	Forest amount and precipitation
Forest amount and precipitation interaction	Forest amount, precipitation, and the forest amount and precipitation interaction
Forest amount and temperature	Forest amount and temperature
Forest amount and temperature interaction	Forest amount, temperature, and the forest amount and temperature interaction
Patch size and precipitation	Patch size, forest amount and precipitation
Patch size and precipitation interaction	Patch size, forest amount, precipitation, and the patch size and precipitation interaction
Patch size and temperature	Patch size, forest amount and temperature
Patch size and temperature interaction	Patch size, forest amount, temperature, and the patch size and temperature interaction

Supplemental Models

Table G1. Patch size and precipitation interaction model for the probability of fruit.

Independent Variable	Estimate	95% CI	P-value
Forest amount	-0.271	-0.490, -0.052	0.0152*
Patch size	0.190	-0.021, 0.400	0.0770
Precipitation	-0.368	-0.539, -0.198	0.0000234*
Patch size x precipitation	0.109	-0.081, 0.300	0.2601
Distance to edge	0.080	-0.112, 0.272	0.4126
Richness	0.074	-0.187, 0.336	0.5776
Flower density	0.052	-0.224, 0.328	0.7134
Elevation	0.226	0.022, 0.431	0.0302*

Table G2. Forest amount and precipitation model for the probability of fruit.

Independent Variable	Estimate	95% CI	P-value
Forest amount	-0.209	-0.433, 0.014	0.0665
Precipitation	-0.370	-0.541, -0.199	0.0000235*
Distance to edge	0.126	-0.065, 0.317	0.1952
Richness	0.091	-0.173, 0.354	0.4997
Flower density	0.028	-0.250, 0.306	0.8430
Elevation	0.213	-0.005, 0.431	0.0555

Table G3. Precipitation model for the probability of fruit.

Independent Variable	Estimate	95% CI	P-value
Precipitation	-0.384	-0.555, -0.213	0.0000108*
Distance to edge	0.137	-0.057, 0.330	0.167
Richness	0.075	-0.189, 0.340	0.578
Flower density	0.046	-0.233, 0.325	0.746
Elevation	0.181	-0.042, 0.404	0.113

Table G4. Forest amount and precipitation interaction model for the probability of fruit.

Independent Variable	Estimate	95% CI	P-value
Forest amount	-0.197	-0.427, 0.032	0.0916
Precipitation	-0.367	-0.539, -0.194	0.0000311*
Forest amount x precipitation	-0.042	-0.209, 0.126	0.6244
Distance to edge	0.126	-0.065, 0.317	0.1955
Richness	0.087	-0.177, 0.351	0.5187
Flower density	0.027	-0.251, 0.305	0.8479
Elevation	0.214	-0.005, 0.433	0.0556

Table G5. Patch size model for the probability of fruit.

Independent Variable	Estimate	95% CI	P-value
Forest amount	-0.261	-0.475, -0.047	0.0168*
Patch size	0.196	-0.004, 0.398	0.0552
Distance to edge	0.074	-0.115, 0.263	0.4455
Richness	0.110	-0.152, 0.372	0.4113
Flower density	0.104	-0.168, 0.377	0.4535
Elevation	0.199	-0.001, 0.398	0.0507

Table G6. Precipitation model for the number of seeds.

Independent Variable	Estimate	95% CI	P-value
Precipitation	-0.108	-0.196, -0.020	0.01644*
Height	0.093	0.032, 0.154	0.00278*

Table G7. Patch size and precipitation model for the number of seeds.

Independent Variable	Estimate	Std. Error	P-value
Forest amount	-0.042	-0.111, 0.027	0.2295
Patch size	-0.021	-0.090, 0.048	0.5465
Precipitation	-0.106	-0.194, -0.017	0.0199*
Height	0.098	0.037, 0.159	0.0016*

Table G8. Forest amount and precipitation interaction model for the number of seeds.

Independent Variable	Estimate	95% CI	P-value
Forest amount	-0.052	-0.114, 0.010	0.10077
Precipitation	-0.106	-0.195, -0.016	0.02036*
Forest amount x precipitation	-0.016	-0.079, 0.047	0.61849
Height	0.098	0.037, 0.159	0.00167*

Table G9. Models predicting the proportion of pollen tubes within the top 4 AIC_c.

Model	DF	Log Likelihood	Δ Log Likelihood	AIC _c	Δ AIC _c	Weight
Elevation	5	-2.7	1.9	15.8	0.0	0.166
Temperature	6	-1.7	2.9	16.1	0.3	0.145
Forest amount	6	-1.8	2.8	16.3	0.5	0.128
Forest amount + temperature	7	-0.9	3.7	16.8	1.0	0.101
Patch size	7	-1.2	3.4	17.3	1.5	0.079
Null	4	-4.6	0.0	17.5	1.7	0.071
Precipitation	6	-2.6	2.0	17.9	2.1	0.057
Patch size + temperature	8	-0.4	4.2	18.0	2.2	0.056
Forest amount + precipitation	7	-1.8	2.8	18.5	2.7	0.043
Forest amount x temperature	8	-0.7	3.9	18.6	2.8	0.041
Patch size x temperature	9	0.3	4.9	18.8	3.0	0.037
Patch size x forest amount	8	-1.1	3.4	19.5	3.7	0.026
Patch size + precipitation	8	-1.2	3.4	19.5	3.7	0.026

Table G10. Models predicting the proportion of fruit within the top 4 AIC_c.

Model	DF	Log Likelihood	Δ Log Likelihood	AIC _c	Δ AIC _c	Weight
Temperature	5	-1276.4	1.2	2563.0	0.0	0.257
Null	4	-1277.6	0.0	2563.3	0.3	0.223
Forest amount + temperature	6	-1276.3	1.3	2564.8	1.8	0.103
Forest amount	5	-1277.5	0.1	2565.1	2.1	0.090
Precipitation	5	-1277.5	0.1	2565.1	2.1	0.088
Forest amount * temperature	7	-1276.0	1.6	2566.1	3.2	0.053
Patch size + temperature	7	-1276.3	1.3	2566.8	3.8	0.038
Forest amount + precipitation	6	-1277.4	0.2	2567.0	4.0	0.035

Table G11. Models predicting the proportion of seeds within the top 4 AIC_c.

Model	DF	Log Likelihood	Δ Log Likelihood	AIC _c	Δ AIC _c	Weight
Temperature	5	99.0	1.4	-188.0	0.0	0.163
Forest amount + temperature	6	99.7	2.1	-187.3	0.7	0.115
Null	4	97.6	0.0	-187.2	0.8	0.112
Precipitation	5	98.7	1.0	-187.2	0.8	0.111
Forest amount x temperature	7	100.6	2.9	-187.0	1.0	0.100
Forest amount + precipitation	6	99.4	1.8	-186.8	1.2	0.089
Forest amount	5	98.3	0.7	-186.5	1.4	0.079
Patch size + temperature	7	100.0	2.4	-185.9	2.1	0.058
Patch size + precipitation	7	99.7	2.1	-185.2	2.8	0.041
Patch size + forest amount	6	98.6	1.0	-185.1	2.9	0.038
Forest amount x precipitation	7	99.5	1.8	-184.8	3.2	0.033
Patch size x temperature	8	100.1	2.5	-184.0	3.9	0.023
Patch size x precipitation	8	100.1	2.4	-183.9	4.0	0.022

Table G12. Temperature model for the proportion of seeds.

Independent Variable	Estimate	95% CI	P-value
Temperature	0.017803	-0.001, 0.037	0.0661

Table G13. Elevation model for the proportion of pollen tubes.

Independent Variable	Estimate	95% CI	P-value
Elevation	-0.044	-0.086, -0.002	0.0402*

Table G14. Elevation and temperature interaction for the proportion of pollen tubes.

Independent Variable	Estimate	95% CI	P-value
Elevation	-0.041	-0.084, -0.001	0.0557
Temperature	0.038	-0.016, 0.093	0.1652
Elevation \times temperature	-0.02	-0.063, 0.021	0.3214

Table G15. Elevation and precipitation interaction for the proportion of pollen tubes.

Independent Variable	Estimate	95% CI	P-value
Elevation	-0.044	-0.086, -0.001	0.0448*
Precipitation	0.007	-0.056, 0.071	0.8167
Elevation \times precipitation	0.011	-0.032, 0.054	0.6220

Table G16. Elevation and temperature interaction for the probability of fruit.

Independent Variable	Estimate	95% CI	P-value
Elevation	0.032	0.001, 0.063	0.0433*
Temperature	0.017	-0.035, 0.069	0.5174
Elevation \times temperature	0.012	-0.013, 0.037	0.3459

Table G17. Elevation and precipitation interaction for the probability of fruit.

Independent Variable	Estimate	95% CI	P-value
Elevation	0.033	0.002, 0.063	0.0355*
Precipitation	-0.062	-0.088, -0.036	0.00000249*
Elevation \times precipitation	0.009	-0.035, 0.018	0.5231

