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Flies to the Rescue: Improving Pollination Services through Habitat Conservation and Ecological Intensification

Author
Kearney, Emily E.

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Flies to the Rescue: Improving Pollination Services through Habitat Conservation and Ecological Intensification

by

Emily E. Kearney

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of the

University of California, Berkeley

Committee in charge:

Professor Claire Kremen, Chair
Professor Matthew D. Potts
Assistant Professor Iryna Dronova

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Abstract

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Professor Claire Kremen, Chair

The majority of crop species benefit from a plant-pollinator mutualism making animal pollination a essential part of the food system. In highly pollinator dependent crops, pollination management is important to ensure high yields. While managed pollinators can provide some of this service, in many cases, native pollinators are required to improve pollination efficiency and efficacy. Natural habitat has been shown to export native pollinators to agricultural areas as have habitat restorations. In addition, ecological intensification of management practices have been proposed as a method to increase yields through in-field interventions. I studied the effect of these three proposed solutions (habitat conservation, ecological intensification, and habitat restoration) on pollination services across two systems: cacao in Ecuador and native bee communities in California.

In my first chapter, I focused on the effect of landscape context on the pollination success of managed *Theobroma cacao* L. in Ecuador by estimating pollen limitation through hand and open pollination treatments. I found that the presence of rain forest did not alleviate pollen limitation in cacao and that other factors, such as slope or trunk circumference, were statistically more important than landscape context. In my second chapter, I studied the effect of ecological intensification on the pollination rates of *T. cacao* and incorporated data on prices and the Ecuadorean job market in order to assess the economic viability of implementing new management strategies. I found that increasing decaying plant material in fields increased pollination rates from native pollinators and that these changes in management were economically viable for farmers even when off-farm labor was readily available. In my third chapter, I switched systems to the Central Valley of California and studied the effect of restoration plantings (hedgerows) on crop-pollinating native bees. I found that hedgerows have a positive effect on the occurrence, species richness, and response diversity of crop-pollinating bees. Further, I focused in on watermelon, an economically important crop that is dependent on high efficiency pollinators, and found that hedgerows increased the abundance, occurrence, and functional redundancy of high and medium efficiency watermelon pollinators.

These findings are consistent with previous literature on pollination services that suggest that the effect of natural habitat, ecological intensification, and habitat restoration is system-

dependent. They also highlight how important the pollination syndrome of the crop, the scale of the intervention, and its feasibility are to an intervention's success. Continuing research with this data will expand upon the connections between pollinator communities and pollination services while further research should be informed by scientists, conservationists, and farmers in order to create more synergistic strategies to benefit crop pollination and native species.

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Introduction

Animal pollination is important in both natural and managed systems with 87% of flowering plants and 75% of crop species being positively affected by a plant-pollinator mutualism (Ollerton, Winfree, and Tarrant 2011; Klein et al. 2007). Higher value crops, like fruits, vegetables, and spices, are more dependent on insect pollination than staple crops (Gallai et al. 2009) and animal pollination is important in many cropping systems for larger and/or higher quality yields (Klein et al. 2007; Aizen et al. 2008). Currently, industrial agriculture meets much of its need for pollination service by relying on managed pollinators, like honey bees (*Apis mellifera*) which were a $14.4 billion dollar industry in North America in 2009 alone (Free 1993; Gallai et al. 2009). However, honey bees have experienced steep declines due to pesticide use, loss of natural habitats, simplified diets, and disease (Goulson et al. 2015) and honey bees are not always effective pollinators as they are limited by climate, crop attractiveness, the type of pollination needed, and their foraging patterns (Degrandi-Hoffman et al. 1992; Thomson and Goodell 2001; Greenleaf and Kremen 2006; Klein et al. 2007).

Wild pollinators have been shown to be integral part of a stable food system (Aizen et al. 2008; Garibaldi, Steffan-Dewenter, Winfree, et al. 2013). As honey bee stocks decline, investing in wild pollinators could ensure pollination service for farmers in changing environment conditions (Garibaldi, Steffan-Dewenter, Winfree, et al. 2013; Rodriguez 2015). Thus, the conservation of native, wild pollinator species is of global concern. In my dissertation, I focus on three types of interventions that could support native, wild pollinators and examine their effectiveness at providing valuable pollination service to farmers. These three interventions are 1) the conservation of existing natural habitat, 2) the implementation of pollinator-friendly practices on the farm (ecological intensification), and 3) the restoration of natural habitat.

Natural areas are important in the conservation of wild pollinators as they provide diverse microhabitats that can support multiple life cycle stages and/or resource needs of pollinator species (Cusser, Neff, and Jha 2016; Garibaldi, Steffan-Dewenter, Kremen, et al. 2011; Carvalheiro et al. 2010). In fact, wild pollinators, supported by and exported from natural areas, can provide complete pollination service to farms in some cases (Kremen, Williams, Bugg, et al. 2004; Greenleaf and Kremen 2006).

Increasing plant and microhabitat diversity at various levels inside the farm is another way to support local populations of pollinators (Kennedy et al. 2013). Crop rotation, polycultures, and cover-cropping increase the diversity of floral resources in fields over space and time. Practices like integrated pest management, no-till, and tolerance of or mulching non-

crop vegetation decrease disturbance and increase the availability of suitable microhabitats for beneficial insects, including pollinators (Forbes and Northfield 2017; Bommarco, Kleijn, and Potts 2013).

Many farms are in areas of intensive agriculture and are not able to benefit from natural areas in the surrounding landscape. In these cases, restorations, like planting flowering strips, installing hedgerows, and restoring riparian areas, can increase floral resources on field edges and in margins that can not be put into production. Another benefit of these restorations is that they do not require farmers to change their in-field management practices (Morandin and Kremen 2013).

Conservation, ecological intensification, and restoration can all be expensive especially if they require an investment of time or resources from farmers. While many farmers will change practices in order to conserve native, wild species without economic benefits from their actions, others will need economic incentives in order to implement new strategies. If crop pollination benefits are used to encourage farmers, it is important to fully examine these interventions for their delivery of these services.

Currently, pollination studies that quantify conservation, ecological intensification, or restoration benefits are still rare (Harrison et al. 2014, but see Kremen, Williams, and Thorp 2002; Greenleaf and Kremen 2006). In some cases, these conservation practices have been found to have no pollination benefit for farmers (Sardiñas and Kremen 2015) which show that these interventions should be evaluated on a case by case basis.

Principle Questions

In this work, I build on our understanding of the benefit of conservation, ecological intensification, or restoration to pollination service on farms. Specifically, I will ask:

1. In a non-bee pollinated crop, does landscape context affect pollen limitation?

2. Can pollen limitation be alleviated by sustainable, organic management strategies? If it can, are these interventions economically viable given farmers' constraints?

3. Does restoration benefit the pollinators of highest concern for farmers?

I approached these questions through two study systems. For the next two chapters, I focus on *Theobroma cacao* which is a high value crop limited to low-lying tropical regions with high rainfall (Purseglove 1968) and is native to the Upper Amazon Basin in northwestern South America (Columbia, Ecuador, & Peru; Richardson et al. 2015; Sereno et al. 2006). Globally, more than 2 million smallholder farmers depend on *T. cacao* as their primary source of income (ICCO 2012) but fungal diseases, low pollination rates, and insect pests limit production (Bowers et al. 2001; Toledo-Hernández, Wanger, and Tscharntke 2017). *T. cacao* is highly dependent on insect pollinators as most varieties are self-incompatible (Cope 1962; Falque et al. 1995). This dependency makes pollination management an important consideration when trying to increase yields in *T. cacao* systems (Forbes and Northfield 2017; Groeneveld et al. 2010; Tovar and Ortiz 1991; Parvais, De Reffye, and Lucas 1977).

In my third chapter, I switch systems to focus on the Central Valley of California where intensive agriculture dominates leaving few natural areas to support native, wild pollinators. In this landscape, restorations that provide abundant floral resources across the whole growing season, like hedgerows, can conserve native bee species. Hedgerows in this system have been shown to increase native bee occurrence (Morandin and Kremen 2013), promote resource specialists, increase pollinator colonization and persistence (M'Gonigle et al. 2015), and restore spatial heterogeneity of the pollinator communities to reflect what would be expected in a natural landscape (Ponisio, M'Gonigle, and Kremen 2016). I examine the native species of highest interest to farmers, bee species that pollinate crops, in order to evaluate the value of hedgerows to on-farm pollination service.

In the conclusion, I summarize my findings and draw broader conclusions from my work. I also make recommendations for future research to better understand and capitalize on native beneficial insects in agricultural areas.

Chapter 1

Natural areas do not alleviate pollen limitation in *Theobroma cacao* L.

1.1 Introduction

Globally, more than 2 million smallholder farmers depend on *Theobroma cacao*, also know as cacao, cocoa, or chocolate, as their primary source of income (ICCO 2012) but fungal diseases, insect pests, and low pollination rates limit production (Bowers et al. 2001; Toledo-Hernández, Wanger, and Tscharntke 2017). *T. cacao* is highly dependent on insect pollinators as most varieties are self-incompatible (Cope 1962; Falque et al. 1995). This dependency makes pollination management an important consideration when trying to increase yields in *T. cacao* systems (Forbes and Northfield 2017; Groeneveld et al. 2010; Tovar and Ortiz 1991; Parvais, De Reffye, and Lucas 1977).

Natural areas have been shown to have a positive effect on the pollination success of many crops by exporting pollinators into agricultural fields (Cusser, Neff, and Jha 2016; Morandin and Kremen 2013; Garibaldi, Steffan-Dewenter, Kremen, et al. 2011; Kremen, Williams, Bugg, et al. 2004; Carvalheiro et al. 2010). The documented pollinator of *T. cacao*, ceratopogonidae flies (Winder and Silva 1972; Posnette 1944; Posnette 1950; Brew and Boorman 1993), need moist decaying plant material to complete their life cycle (Borkent and Spinelli 2007). It is hypothesized that primary rain forest provides abundant habitat to host large populations of these pollinating flies. Thus, if *T. cacao* fields abutted or were embedded in primary rain forest, they might experience a benefit in pollination success from ceratopogonids being exported into the fields.

In a recent review of literature on cacao pollination and fruit production, Toledo-Hernández, Wanger, and Tscharntke (2017) emphasized that conservation of natural forest could be one way to stabilize and enhance cacao pollination. However, Frimpong et al. (2011) did not find a significant effect of distance from primary forest on pollinator abundances or pollination rates in Ghana. Still, this previous work did not focus on the immediate surrounding landscape context of the fields which could be important given that ceratopogonids can only travel a few meters per day (Kaufmann 1975). Here, I investigate the effect of natural habitat on the pollination service of *Theobroma cacao* by estimating pollen limitation on farms

across different landscape contexts in Ecuador, from farms surrounded by development to those embedded in primary rain forest.

1.2 Methods

Study Area

This study was conducted on eleven cacao farms from three villages located in the Napo Province of Ecuador: Rio Blanco (1°00'S, 77°33'W), Campo Cocha (1°05'S, 77°33'W,), and San Jose (0°55'S, 77°47'W). These villages are on the western foothills of the Andes mountains between 400m and 850m elevation. This region has a stable climate with an average monthly rainfall of 350mm and an average temperature of 21 °C. Rain forest is the primary land cover but selective logging and agriculture are important and increasingly common land uses. Cacao, coffee, and cattle are the main agricultural products. However, most farmers are small holders that grow a variety of crops, including yuca, maize, and plantains, primarily for subsistence.

Pollination System

Theobroma cacao is an understory tree native to the Upper Amazon Basin (Cope 1962; Sereno et al. 2006; Richardson et al. 2015). Cacao varieties vary in their flowering phenology which is highly dependent on climatic variables and geographic location (Lachenaud and Mossu 1985). The variety in this study (see further description in Farm Selection:Cacao Variety) flowers all year round with continuous fruit production (Kearney 2014). Flowers open around dawn and desiccate until anthers dehisce in the early afternoon. The stigma is receptive to pollen for 24 hours and ovary enlargement, or fruit set, can be observed 36-48 hours after pollination (Swanson, Carlson, and Guiltinan 2008). Flowers that do not receive compatible and/or sufficient numbers of pollen grains abscise from the trunk one day after opening, though unpollinated flowers can remain on the tree for several days if undisturbed (Swanson, Carlson, and Guiltinan 2008). Pollinated flowers mature into fruits over 6 months, and if left unharvested, mature fruits will rot on the tree (Purseglove 1968).

Flies in the family Ceratopogonidae, biting midges, are the documented pollinators of *T. cacao* (Posnette 1944; Posnette 1950; Winder and Silva 1972; Brew and Boorman 1993) and are able to access the anthers and stigma easily due to their small size (about 1mm in length). Ceratopogonids are covered in hairs that trap and carry the sticky *T. cacao* pollen. Ants, thrips, aphids and gall midges (Cecidomyiidae) are also commonly collected from *T. cacao* flowers (Frimpong et al. 2011; Winder 1978). However, these floral visitors are mostly ineffective at pollinating *T. cacao* (Winder 1978; Winder 1977).

Farm Selection

Farms were chosen based on three guiding factors: cacao variety and age, farm management, and the surrounding landscape context.

Cacao Variety

In order to be considered for this study, farms had to be growing only five self-incompatible Nacional Cacao clones distributed by a local cooperative and have trees between 5 and 7 years old.

Farm Management

Farms averaged one hectare in size (0.8 - 1.2 hectares). They consisted of polycultures with banana, plantain, and yuca as the most common inter-crops, under certified organic management. While some larger trees were left intact in all farms, shade cover, primarily provided by hardwood or fruit trees, was limited with farms experiencing 10-30% canopy cover. Management of the farms was minimal; farmers cut herbaceous vegetation about three times a year and did not apply any pesticides or fertilizers. Access to organic inputs is rare and prices are prohibitive. For this study, vegetation was cut two weeks before sampling and was cut once more halfway through the study. This improved accessibility to trees and ensured consistent vegetation management across farms.

Landscape Context

From all candidate farms, eleven were picked based on their immediate landscape surroundings (within a 100m radius). All farms were at least 500m apart. Farms were classified within four categories: (1) agricultural, (2) fragment, (3) adjacent, and (4) embedded (Table A.1). Farms classed as *agricultural* were surrounded on all sides by agriculture or other disturbed land uses (roads, houses, bare ground). Farms classed as *fragment* were next to a small fragment of primary rain forest (<1 hectare) while farms classed as *adjacent* were next to a larger tract of primary rain forest. Finally, farms classed as *embedded* were located inside large tracts of primary rain forest. There were three farms in the agricultural, adjacent, and embedded categories while there were two farms in the fragment category. Categories were not spread evenly across villages though all landscape contexts were represented in at least two villages (Table 1.1). GPS coordinates were taken at the center of each farm and 30m resolution DEMs were used to calculate the slope and aspect of each farm (Souris 2019).

Village	**Landscape Context**			
	Agricultural	Fragment	Adjacent	Embedded
Campo Cocha	2	0	2	1
Rio Blanco	0	1	1	2
San Jose	1	1	0	0

Table 1.1: Distribution of farms across villages and landscape contexts.

Sampling Design

Sampling was conducted in January and February 2016 with farms being visited at least twice and most farms being sampled three times. In each sampling round, trees were chosen every 20m along a transect bisecting the farm, resulting in at least four trees per farm, spaced about 20m apart. Trees with the most mature buds available were preferentially chosen as open flowers were necessary for the study. Trees were re-chosen in each sampling round in order to increase the probability of having usable flowers; if previously sampled trees had the most mature buds, they were sampled again. On every new tree, ten newly opened flowers on that tree were bagged and pollinated with self-pollen in order to test for self-incompatibility.

In order to account for tree and microhabitat differences, trunk circumference (at branching), canopy height, water presence, % cover (defined as the % of ground receiving filtered sunlight in a 2m radius from the trunk), and % shade (defined as the % of the study tree's canopy shaded by taller trees) was recorded for each sampled tree. For every sampling period, temperature and weather were recorded at the beginning and the end of the flower marking session.

Pollen Limitation Measurements

Pollen limitation measurements were composed of three phases: tree preparation, pollination treatments, and fruit set verification.

Tree preparation

In order to ensure only receptive flowers were used in the experiment, marked trees were prepared by clearing any open flowers the day before the application of pollination treatments; pollinated flowers (those with enlarged ovaries), cherrelles (small cacao fruits), and all other fruits were left on the tree.

Pollination treatments

Pollination treatments consisted of randomly choosing up to 16 flowers per tree and dividing these flowers between hand and open pollination. A quarter of the chosen flowers were assigned to be hand-pollinated while the rest were marked and left undisturbed for open pollination. Hand pollination was achieved by lightly rubbing the stigma of the receiving flower with two anthers, one after another, each from a different clone (Falque et al. 1995). All chosen flowers were marked with twist ties lightly twisted to the branch under the flower. In order to account for the role of resource allocation in the results, diameter of the branch and distance from the main trunk were measured and included in analyses.

Fruit Set Verification

The marked flowers were then observed after 6-10 days to record fruit set which was signalled by the enlargement of a flower's ovary. The difference in chance of fruit set between hand-

pollinated flowers and open-pollinated flowers was used to estimate pollen limitation.

Statistical Analysis

All analyses were performed in R (Team 2019). Pollen limitation was examined through binomial generalized linear mixed models (Bates et al. 2015) in a multimodel inference framework that included all possible subsets (Burnham and Anderson 2003).

Fruit set per flower, a binary variable of fruit or no fruit, was the response variable. Village, farm and tree were hierarchical random effects. As some of the variables were found to be highly colinear, these were first combined using PCA in order to avoid effect attribution issues in the multimodel inference framework. The full model included the following fixed effects: landscape context, slope, northness, and eastness at the farm level; the average weather score, and the first axis of the PCA of day of year with average temperature at the sampling event level; trunk circumference, canopy height, water presence, shade cover, and canopy cover at the tree level; and the first axis of the PCA of branch diameter with distance from trunk at the flower level. The first axis of the PCA of day of year with average temperature explained more than 85% of the variation among sampling events for these two variables, while the first axis of the PCA of diameter with distance explained around 75% of the variation among flowers for these two variables (Fig. A.2).

The full model with all possible fixed and random effects was scaled to allow for easy effect size comparisons among parameters. Model selection started with an assessment of the contribution of hierarchical random effects. Village, and then farm, were removed as their constrained parameters were on the boundary of zero which creates convergence issues (Zuur et al. 2009). Although the final model treats all trees as independent replicates, the village and farm differences were small enough to justify this choice. The full model with tree as the only random effect was then used to create all possible subsets. Since the weight of the top performing model was less than 0.9, a model averaging approach was used (Grueber et al. 2011). The top models within 2 AICc points of each other were selected, yielding a total of 12 models. The zero method, which averages parameters across all candidate models, setting the parameter estimate to zero for every model in which that parameter was not found (Burnham and Anderson 2003), was used to average these high-performing models and produce the final results presented in this paper (Table 1.2). Results from other cutoffs, including Δ5AICc, Δ10AICc, and a 95% confidence interval, were consistent with the Δ2AICc result.

1.3 Results

Over the course of the study, 1960 flowers were marked on 115 trees in 11 farms. 1442 flowers were open-pollinated, 518 were hand-pollinated, and 212 cherrelles were produced. As suspected from the low fruit-to-flower ratio, there was significant pollen limitation for all farms and trees (Figures 1.1 & 1.2). Hand pollination was 4.6 times more likely to produce fruit than flowers left open for insect pollination (Figure 1.2).

Parameter	Relative Importance	Number of Models
Treatment	1.00	12
Eastness	1.00	12
Northness	1.00	12
PCA - Branch	1.00	12
PCA - Sampling	1.00	12
Slope	1.00	12
Trunk Circumference	1.00	12
Landscape Context	0.93	11
Treatment:Landscape Context	0.93	11
% Cover	0.40	5
% Shade	0.27	3
Weather	0.20	3
Canopy Height	0.13	2
Water	0.06	1
Start Time	0.06	1

Table 1.2: Included parameters with their relative importance and the number of models that included each parameter.

Pollen limitation & landscape effects

Fruit set success rates did not vary significantly between landscape contexts. In addition, the interaction between landscape context and pollination treatment was not significant across the four landscape contexts ($p > 0.1$, Figure 1.3). This means that pollen limitation was not alleviated in farms associated with primary forest compared to farms surrounded by agriculture or other development.

Fruit set & other parameters

Multiple factors besides the landscape context affected fruit set. Farms with steeper slopes, that were more north- and east-facing, had higher success rates ($p < 0.05$, Fig. A.1). Sampling conditions affected fruit set success with flowers marked in colder weather or later in the year being less likely to produce fruit ($p < 0.001$, Fig. A.3).

Finally, characteristics of the tree and branch on which the flower was located also had significant effects on fruit set success. Trees with thinner trunks, which often corresponds to being younger, produced more cherrelles ($p < 0.01$, Fig. A.4) while flowers on thinner branches that were farther away from the main trunk had a lower chance of fruit set success ($p < 0.05$, Fig. A.4).

1.4 Discussion

This study focused on two important questions; (1) whether *T. cacao* is pollen limited and (2) whether rain forest alleviates pollen limitation. These two points are discussed in detail in the next two sections, followed by further context on the other results from this study and discussion of the pollen limitation measurements used in this study. Finally, I give recommendations for future research directions based on the results from this and other studies that have examined the role of natural forest in pollination service in *T. cacao*.

Pollen limitation is an issue

This study shows that pollen limitation is an important issue in *T. cacao* cultivation systems even within its native range. While the success of hand pollinations was very low (10%) signaling a limited resource environment, hand pollination was still more than four times as likely to produce a cherrelle than a flower left open for insect pollination. This result was surprising not only because I had hypothesized that pollen limitation of *T. cacao* would be reduced in its native range compared to other places, but also since the farms studied are highly diverse and minimally managed. Such farms would be expected to provide large amounts of habitat for many types of pollinators, including ceratopogonids, the documented pollinators of cacao.

Primary rain forest does not alleviate pollen limitation

I found that there was no effect of the presence of primary rain forest on pollination from insects, despite recent contrary conclusions from a review on cacao pollination (Toledo-Hernández, Wanger, and Tscharntke 2017). My results are consistent with previous results that showed that distance to primary forest did not affect fruit set in cacao (Frimpong et al. 2011). While there are biological reasons to support rain forest contributing pollinators to cacao fields (e.g. abundant larval habitat; Greeney 2001) and other researchers have documented instances of natural areas exporting pollinators to agricultural fields (Cusser, Neff, and Jha 2016; Morandin and Kremen 2013; Garibaldi, Steffan-Dewenter, Kremen, et al. 2011; Kremen, Williams, Bugg, et al. 2004; Carvalheiro et al. 2010), this does not seem to be the case for *T. cacao*, even within its native range.

Many reasons could explain the lack of correlation between pollination and proximity to natural habitat. A recent study on the floral visitors of wild *T. cacao* individuals in natural areas within its native range showed that ceratopogonids were infrequent visitors to the flowers (Schawe et al. 2018). In addition, ceratopogonids are very small (<1mm) and likely face a high cost to traveling distances over a few meters (Kaufmann 1975). Further, cacao flowers rely on long-chain hydrocarbons as attraction mechanisms. Since these compounds do not volatilize easily (Young and Severson 1994), they may not be able to successfully recruit ceratopogonids from areas adjacent to the cacao farms. Finally, the difference in micro-climate between the primary forests and the cacao farms could encourage ceratopogonids to avoid the boundary, keeping them inside the primary forest.

Other factors affect fruit set

My study also showed that other factors are more important for fruit set success than the surrounding landscape context. Farm-level variables (slope, northness, and eastness), sampling conditions (the first axis of PCA of average temperature and the day of year; Fig. A.2), tree characteristics (trunk circumference) and branch position (the first axis of the PCA of branch position with diameter; Fig. A.2) were all more important than landscape context (Table 1.2).

Slope, northness, and eastness likely affect the presence of decaying, moist plant material in the farm and the presence and abundance of ceratopogonid larval habitat. Consistent with other findings, sampling conditions may also affect the likelihood of ceratopogonid flight with cloudier days later in the year being less hospitable (Winder and Silva 1972).

Finally, tree age and branch characteristics would affect the amount of resources available to a flower and would potentially affect the likelihood of fruit abortion. Smaller trunk circumferences could reflect younger trees which are known to be more productive (Purseglove 1968). Flowers located on smaller branches farther from the tree trunk were less successful at producing fruit and this is consistent with the idea that smaller branches have less access to nutrients and water (Stephenson 1981).

Considerations of pollen limitation measurements

Pollen limitation estimation is most accurate over a plant's lifespan rather than just for one season (Knight, Steets, and Ashman 2006). However, it is rarely if ever feasible to study pollination success over the lifespan of a tree crop. In addition, tree crops tend to have more complicated vascular systems that allow for resource re-allocation between branches and fruits which can lead to controlled fruit abortion based on quality of pollination (Stephenson 1981). These issues mean that most within-year estimates of pollen limitation in tree crops over-estimate pollen limitation, because some of the apparent pollen limitation observed in a one year study may actually be due to across-year resource limitation. This study could not account for these inter-year effects but the results presented here are consistent with other pollen limitation studies done on *T. cacao* which show that globally there is significant pollen limitation (Young, Erickson, et al. 1987; Groeneveld et al. 2010; Frimpong et al. 2011).

Cacao research should focus on management strategies, not natural areas

While natural areas have been shown to have a positive affect on the pollination success of other crops (Cusser, Neff, and Jha 2016; Morandin and Kremen 2013; Garibaldi, Steffan-Dewenter, Kremen, et al. 2011; Kremen, Williams, Bugg, et al. 2004; Carvalheiro et al. 2010), this does not appear to be the case in *T. cacao* cultivation systems. Given this consistent result, new research should focus on management strategies to increase pollination success. Some studies have shown success with increasing the decaying plant material in the farm through the application of discarded cacao husks (Forbes and Northfield 2017) or banana stems (Frimpong et al. 2011) which would provide more larval habitat for ceratopogonids, the documented pollinator of *T. cacao*. Both of these strategies could be easily implemented in the cultivation systems of eastern Ecuador but should be balanced against the potential

for increased disease risk and required effort or time investment from smallholder farmers. Research that focuses on interventions that are easy to communicate and implement with tools already available to farmers is most needed in these widely distributed production systems that are composed of small holder farmers who do not have the capital to invest in machinery or chemical inputs.

1.5 Figures

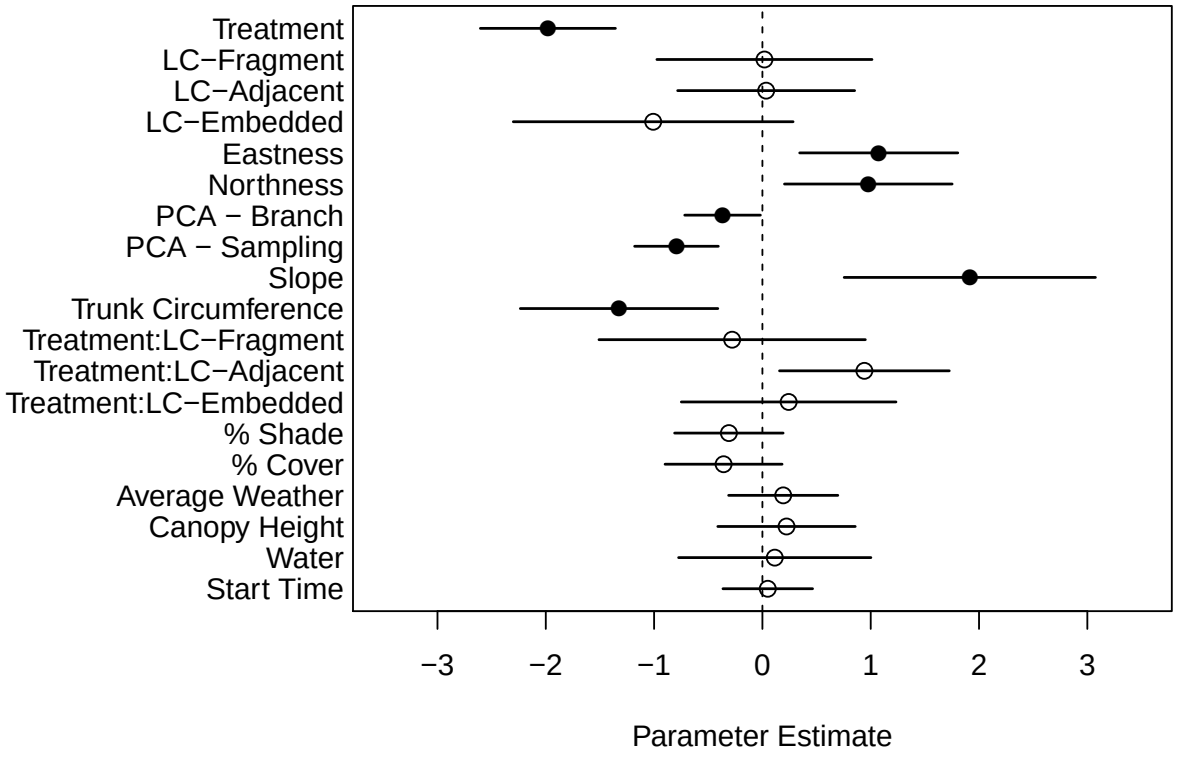

Figure 1.1: Parameter estimates with 95% confidence intervals. More positive numbers mean a better chance of successful fruit set. The intercept represents a hand-pollinated flower on a tree in a farm classed as agricultural. Estimates are scaled so that effect sizes can be directly compared. Filled circles denote parameters found to be significant. LC stands for Landscape Context.

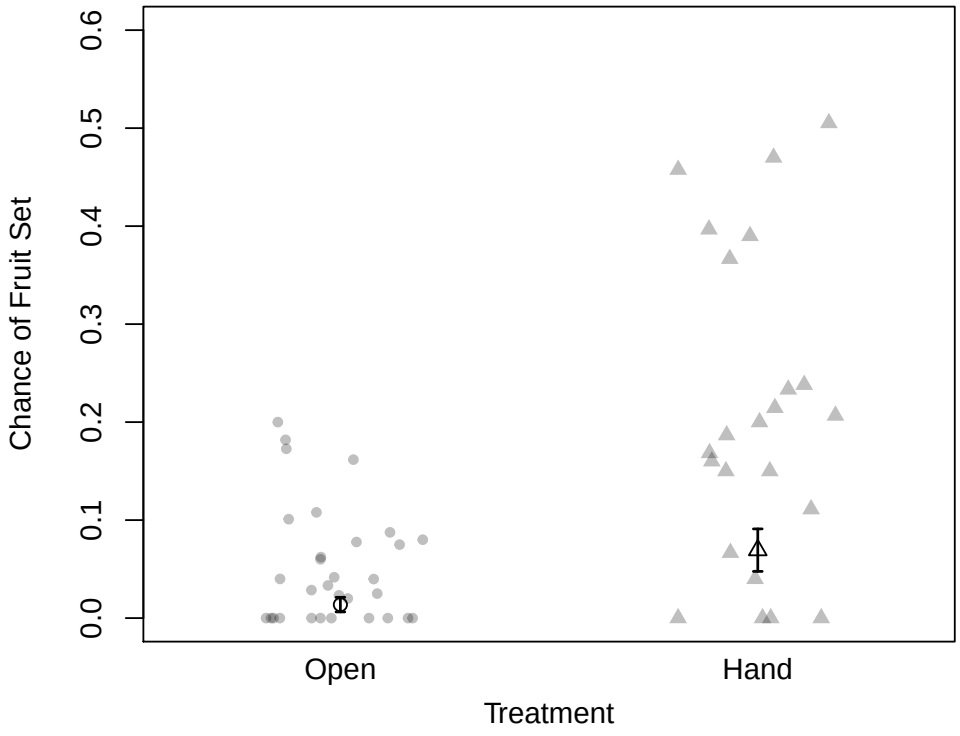

Figure 1.2: Estimated fruit set success between hand- and open-pollinated flowers regardless of landscape context. Open symbols: Back-transformed model estimates with 95% confidence intervals. Filled, transparent symbols: Fruit set success aggregated by treatment, tree, and date and then averaged by farm.

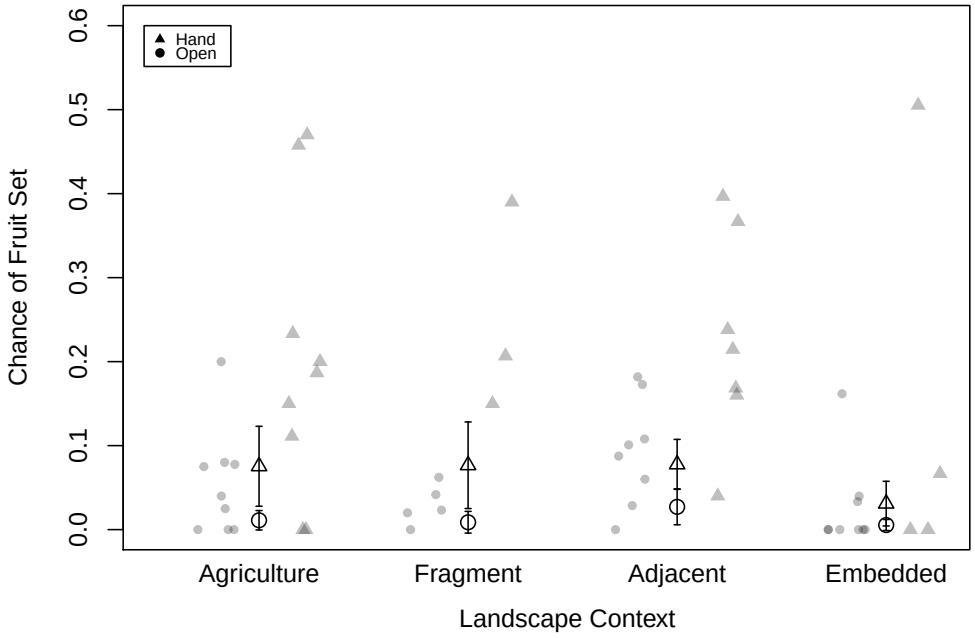

Figure 1.3: Estimated fruit set success between hand- and open-pollinated flowers among landscape contexts. Open symbols: Back-transformed model estimates with 95% confidence intervals. Filled, transparent symbols: Fruit set success aggregated by treatment, tree, and date and then averaged by farm.

Chapter 2

Ecological intensification is an economically viable way to decrease pollen limitation in *Theobroma cacao* L.

2.1 Introduction

As the global middle class expands, consumption of meat, coffee, and chocolate are expected to increase substantially (Laurance, Sayer, and Cassman 2014). In order to meet these demands, production will need to increase either through extensification or intensification. With agriculture already covering 40% of land area (Foley et al. 2005; Ramankutty et al. 2018), extensification, or the recruitment of new, previously undisturbed land into production, is not a sustainable option (Lambin and Meyfroidt 2011; Gibson et al. 2011). The extensification of crops has significant negative consequences on biodiversity. This is especially true for global commodities like coffee and cacao, that replace highly biodiverse habitat, like cloud and rain forest, respectively (Gibson et al. 2011). Instead, intensification, or increasing production on currently farmed land, along with policies that restrict forest conversion, may be needed to protect biodiversity and promote sustainability (Kremen 2015).

Conventional intensification, however, contributes substantially to negative environmental externalities contributing to marine dead zones and agricultural systems that are more vulnerable to pests and disease (Heinrichs and Mochida 1984; Mee 2006; Biello 2008; Geiger et al. 2010). Ecological intensification, in contrast, aims to increase production by harnessing biological interactions and limiting both the use of external inputs and their attendant negative consequences. Ecological intensification aims to increase yields through better ecosystem service provision (Bommarco, Kleijn, and Potts 2013). For example, increasing the abundance of wild pollinator species by restoring pollinator habitat in and around farms can increase production while preserving or even enhancing other ecosystem services (Morandin and Kremen 2013; Morandin, Long, and Kremen 2016; Ponisio, M'Gonigle, and Kremen 2016; Blaauw and Isaacs 2014).

Demand for chocolate is expected to increase as emerging markets expand but its production is severely limited by low levels of cacao (*Theobroma cacao*) pollination (Groeneveld et al. 2010; Chapter 1). Unlike other systems in which nearby natural habitats enhance pollinator abundances and services (Garibaldi, Steffan-Dewenter, Kremen, et al. 2011; Kremen, Williams, and Thorp 2002), natural areas do not enhance pollination services to cacao farms (Frimpong et al. 2011; Chapter 1). Instead, adding decaying plant material directly to cacao orchard floors has been show to increase pollination rates in Ghana (Frimpong et al. 2011; Adjaloo, Banful, and Oduro 2013) and Australia (Forbes and Northfield 2017). However, some strategies for increasing litter, like setting out rotting cacao husks, can increase fungal disease transmission, which could decrease yields even if fruit set is increased (Doungous et al. 2018). Even if litter management strategies do not increase disease risk and can be easily implemented with available tools and inputs, farmers often need incentives in order to implement recommended strategies that are labor-intensive. Small-holder farmers are particularly adverse to risk (Isakson 2015) and so practices that manage for larval habitat must present minimal financial risk through limited opportunity cost.

In this study in eastern Ecuador, I tested two management practices, leaf litter addition and banana/plantain pseudostem addition, in a full factorial experiment (Fig. 2.1). These two practices were chosen because they are unlikely to increase fungal risk (Doungous et al. 2018) and can be easily implemented by small-holder cacao farmers. I used hand and open pollination treatments to estimate pollen limitation so that I could accurately assess the effect of these management practices. In addition, I analyzed the economic viability of these practices using region-specific fruit production, wage, and price estimates. This study aims to further scientific understanding of the pollination system of *T. cacao* globally and inform management recommendations for small-holder cacao farmers in Eastern Ecuador.

2.2 Methods

Study Area

This study was conducted on six certified organic cacao farms from three different villages located in the Napo Province of Ecuador [Rio Blanco (1°00'S, 77°33'W), Campo Cocha (1°05'S, 77°33'W), and San Jose (0°55'S, 77°47'W)]. For further description of the area, please refer to Chapter 1, Section 1.2 (pg. 5).

Pollination System

For a detailed description of the pollination system, please refer to Chapter 1, Section 1.2 (pg. 5).

Farm Selection

Selected farms grew the same five self-incompatible Nacional Cacao clones distributed by a local cooperative with trees between 6 and 8 years old. For further description of farm

management, please refer to Chapter 1, Section 1.2 (pg. 5).

Implementation of Management Practices

Two management practices were examined with a full-factorial design. The first practice manipulated the amount of leaf litter within the farm, to compare complete removal of herbaceous vegetation and cacao leaf litter with the addition of cut herbaceous vegetation to the existing leaf litter layer. Farms had herbaceous vegetation growing in most areas. In all plots, this vegetation was cut low to the ground and in half of these plots, the resulting plant material along with any fallen cacao leaves was removed from the plot. In the other half, the cut plant material was allowed to rot with the natural layer of leaf litter.

The second management practice also manipulated the amount of decaying plant material present in the farm through addition of disks of banana/plantain pseudostems (8 - 12 cm in thickness) around cacao trees in half of the plots within the farm. In plots receiving pseudostems, three disks were placed at the base of each cacao tree while in the other half, no pseudostems were placed.

Plots were 20m by 20m which encompassed about 10 cacao trees (Fig. 2.1). There were four plots per farm, one plot per practice combination (no leaves or pseudostems, leaves only, pseudostems only, leaves & pseudostems). All plots were separated by at least 10m of undisturbed buffer. Management practices were first implemented two weeks prior to the first sampling round. Pseudostem placement was repeated every week during the sampling period while vegetation cutting and removal was only repeated once more halfway through the experiment.

Sampling Design

Two trees were chosen in each treatment plot resulting in eight trees per farm. Trees were at least 5m away from the plot edge and each other. Trees were chosen at the beginning of every sampling round based on mature bud availability in order to ensure the most open flowers for use in pollination treatments. If previously sampled trees had the most mature buds, they were sampled again. In order to account for tree and micro-habitat differences, trunk circumference (5cm below branching), canopy height, water presence, % shade (defined as the percentage of the cacao tree's canopy shaded by taller trees), and % cover (defined as the percentage of the ground shaded by the cacao tree's canopy) were recorded for each sampled tree.

Sampling was conducted between September and December 2016 with farms being sampled three to four times. Temperature and weather conditions were recorded at the beginning and end of each flower marking session.

Pollen Limitation Measurements

Pollen limitation measurements were composed of three phases: tree preparation, pollination treatmetns, and fruit set verification.

Tree Preparation

In order to ensure that only freshly opened flowers were being used in the experiment, marked trees were cleared of any open flowers the day before the application of pollination treatments. Pollinated flowers and all other fruits were left on the tree.

Pollination Treatments

The following day, up to 15 flowers per tree were randomly chosen and a third of these flowers were hand-pollinated while the rest were left undisturbed for pollination by insects (the "open" treatment). All flowers were marked with twist ties lightly twisted to the branch under the flower. Flowers chosen for hand pollination were manually pollinated with anthers from two of the surrounding clones in order to ensure successful pollination as described in Falque et al. (1995). In order to account for the role of tree resource allocation in the results, diameter of the branch and distance along branch to trunk were measured.

Fruit Set Verification

The flowers were then observed after 8-13 days to record fruit set. The difference in the likelihood of fruit set between hand-pollinated flowers and those left open was the measurement of pollen limitation.

Statistical Analysis

All analyses were performed in R (Team 2019, Version 3.5.1). Pollen limitation was examined through binomial generalized linear mixed models using the lme4 package (Bates et al. 2015).

Fruit set success, a binary variable of fruit or no fruit, was the response variable. Village, farm and tree were hierarchical random effects in the starting model. The starting model was found to be singular, meaning that some of the variance-covariance Cholesky decomposition parameters were exactly zero (Barr et al. 2013). In more general but not quite equivalent terms, this means that the variances of some of the random effects were estimated to be zero. These issues signal that the starting model was over-parameterized (Bates et al. 2015; Zuur et al. 2009; Bolker 2019) and so village and then farm were removed as random effects in a sequential process following the recommendations of Barr et al. (2013). Although the final model treats all trees as independent replicates, there is evidence to show that dropping random effects whose variances are estimated to be zero does not affect the estimates or standard errors of fixed effects produced by the model (Bolker 2019; Pasch, Bolker, and Phelps 2013).

An interaction between pollination treatments (hand or open) and management strategies (no leaves or pseudostems, pseudostems only, leaves only, leaves & pseudostems) was included in order to examine the effect of management strategies on pollen limitation (defined as the difference in fruit set success between hand pollination and open pollination). The other explanatory variables included: slope, northness, and eastness at the farm level; day of year, mean temperature, mean weather, days since first management implementation, and number of pseudostem additions at the sampling level; trunk circumference, canopy height, water

presence, % shade, and % cover at the tree level; and branch diameter and distance to trunk at the flower level.

Co-linear explanatory variables were replaced with the first axis of a principal component analysis of the co-linear variables to decrease model effect attribution issues. This included seven explanatory variables resulting in three fixed effects. Day of year, days since the first management implementation, and the number of total pseudostem additions were used to create "PCA - DOY & Mgmt" which explained 87% of the total variation in these three variables. Slope and eastness were combined to create "PCA - Field" which explained 90% of the variation from these two variables. Branch diameter and distance to trunk were combined to create "PCA - Branch" which explained 82% of the variation between these two variables. All numerical variable were scaled in order to decrease convergence issues. Model results are presented in Figure 2.3.

Economic Viability

Using a Monte Carlo error propagation approach, I estimated the economic viability of the current management practice (business-as-usual) in comparison to: (1) adding leaves & pseudostems, and (2) conducting hand pollination. My Monte Carlo simulation process modeled flowering, fruit set, fruit survival to maturity, revenue (including seed weight per harvested fruit and price variability), and opportunity cost (Fig. 2.2) in order to estimate gross revenue, total costs, and net revenue of implementing each management strategy on one farm of cacao in one year. I ran the simulation for ten thousand runs to allow convergence.

Flowering

The simulation assumed 50 trees per farm and that only fruits set during a three month window would be sold to the local farmer cooperative. Many cooperatives only buy for two to three months a year in order to decrease overhead costs and have enough stock to ferment and dry the beans properly (Kearney 2014). Using flower counts from this experiment and two previous studies, I simulated the number of new flowers a tree would produce each day during this period, creating a unique distribution (Fig. 2.2:top-left). I then randomly picked from this distribution for as many tree and days as specified (4500 tree-days = 50 trees x 90 days).

Fruit Set

Once the number of flowers produced each day by each tree over the 3 month period was generated, I simulated the chance of fruit set for each group of flowers (by day and tree). The three management strategies (business-as-usual, leaves & pseudostems, and hand pollination) all had different chances of fruit set that were derived from the effect sizes and standard errors from the binomial model described above. I created a beta distribution that closely simulated the chance of fruit set given the effect size and standard error for each strategy. A beta distribution was chosen as the distribution for this step of the MC simulation because the

chance of fruit set is bounded by zero and one and the beta distribution fit the experimental model output the best.

For fruit set as well as fruit survival to maturity and job availability, a probability of a positive result (setting a fruit, fruit surviving to maturity, or securing a job) was first picked from a beta distribution and then, this picked probability was used as the probability parameter in a binomial distribution to determine the outcome for each instance (Fig. 2.2:top-right). This two step process was necessary because while experimental model outputs or expected conditions (in the case of job availability) were best represented by beta distributions, the final output of the model had to be in concrete terms such as number of fruits set/produced or days of paid work passed up. The beta distribution represents the uncertainty in the model output through producing a range of possible probabilities. In the second step, the binomial distribution step translates the picked probability into a concrete result that includes both model uncertainty and uncertainty of real-world conditions.

In the case of fruit set, each group of flowers (per tree-day) was assigned its own probability of fruit set. This probability was then used in a binomial model to determine the total number of set fruit from that group of flowers. For the business-as-usual and leaves & pseudostem strategies, I repeated this process 4500 times (for each tree-day).

To estimate the fruit set success of the hand pollination management strategy required a more complex process that accounted for the hand pollination of some flowers and the insect pollination of other flowers left undisturbed by farmers. I approached this problem using tree-days as a guide in order to simplify the simulation.

I estimated that farmers would only be willing to hand pollinate all of their trees once a week given that I estimated that it would take farmers two days to pollinate up to 20 flowers on each of their trees. Thus, farmers would hand pollinate a total of 650 tree-days (1 day/week * 13 weeks * 50 trees) and would not interfere with 3850 tree-days worth of flowers. The 3850 tree-days of undisturbed flowers were treated as tree-days in the business-as-usual strategy since hand pollination of some flowers is not expected to change the probability of fruit set for undisturbed flowers on the same tree and/or in the same farm.

For the 650 tree-days of hand pollination, my simulation treated hand-pollination as a methodical process in which farmers would pollinate as many flowers as were present on a given tree on that day (up to 20 flowers), and would not return to that tree until the next week. For hand-pollinated flowers, I modeled fruit set using a binomial distribution informed by a probability picked from the hand pollination beta distribution (Fig. 2.2:top-right). If a tree had produced more than 20 flowers on the day when it was hand-pollinated, I estimated fruit set for these undisturbed flowers using a binomial distribution informed by the beta distribution for the business-as-usual management strategy.

Fruit Survival to Maturity

After estimating fruit set, I used previously collected fruit abortion data to model the chance of a fruit aborting before maturity using another beta distribution. Fruit abortion rates were estimated by fitting a right-censored survival curve to fruit growth data collected throughout this study's duration (Fig. B.1) using the *survival* package in R (Therneau 2015). Independent of treatment plots, 227 fruits were followed from successful pollination up to sixty days

post-pollination with all instances of fruit abortion recorded. Since fruit abortion happens in the first nine weeks post-pollination (Bos, Steffan-Dewenter, and Tscharntke 2007) this survival analysis provided high-quality, local fruit abortion estimates to be used in this analysis. The average fruit survival was 49% (36.9, 65.2 - 95% CIs), consistent with other studies on cacao fruit abortion (Bos, Steffan-Dewenter, and Tscharntke 2007; Bos, Veddeler, et al. 2007).

For each group of fruits set by a tree on a particular day, a probability of survival was picked from the beta distribution created from the output of the survival analysis (Fig. 2.2:middle-left). This picked probability was used to parameterize a binomial distribution to estimate the number of mature fruits harvested from that tree from that set of flowers. My simulation did not impose a limit to the number of fruits a tree could set and did not include a mechanism where increased fruit set would result in higher fruit abortion. While these assumptions are not biologically realistic, cacao trees can produce 50 to 100 fruits per year and the average number of fruits per tree resulting from my simulations was well within this range (42.5 ± 14.8, mean $\pm$ SD).

Revenue Estimates

Once the total number of harvested fruits was determined for all trees in one farm, the weight of dried beans produced by each of these fruits was estimated by multiplying the number of fruits from a tree on a specific day by a dried weight per fruit. The weight was picked from a uniform distribution between 35g and 40g as this is the standard range of cacao fruit bean production (Fig. 2.2:middle-right; Oswald, Glasser, and Laubier 1991). For each set of fruits produced from one day of flowers on one tree, a new weight was picked from the uniform distribution in order to include uncertainty of resource investment by the tree in each fruit.

The price per kilogram of dried beans was picked from a normal distribution based on 15 years of farm-gate cacao prices for fine-flavor cacao on the craft bean-to-bar market (Fig. 2.2:bottom-left; Baranoff 2014; Baranoff 2015; Baranoff 2016; Baranoff 2017; ICCO 2019), and multiplied by the kilograms of dried beans produced to find the final total revenue.

Opportunity Costs

Since most cacao farmers and their families are the primary laborers on their farms in eastern Ecuador (Kearney 2014), the time that farmers spend on the farm implementing the leaves & pseudostems strategy or hand-pollinating flowers is time that they are not spending potentially earning other income. I modeled the opportunity cost of each of the three strategies (business-as-usual, leaves & pseudostems, and hand pollination) to determine if the increase in fruit production from the leaves & pseudostems or hand pollination strategies would offset the potential loss in income from foregoing other work opportunities.

Business-as-usual requires 2 days of labor during the flowering season which consists of farmers cutting herbaceous vegetation to maintain access to the farm and all trees. If farmers were to implement the leaves & pseudostems strategy, they would need to increase their management of the farms during the three month flowering season by 7.5 times including one day a week over the 3 months (13 weeks) cutting and distributing pseudostems and

one day a month of cutting and leaving the herbaceous vegetation after the original two days in the first month (15 additional days). Hand pollination would require farmers to cut vegetation to allow access and then to spend two days per week over 3 months to hand-pollinate up to 20 flowers on each of their trees once a week (26 additional days).

Since many farmers are unskilled laborers (Kearney 2014), they can expect to earn the minimum wage for off-farm work which is US$394 a month or around US$18 per day. This minimum is fixed by the national government and should not vary with the labor market (*Ecuador - Labor Policies & Practices* 2017). While wages do not vary, the chance of securing short-term work is variable and constantly observed by farmers using local social networks (i.e. word of mouth between family members; personal obs.).

To assess the opportunity cost of investing time in pollination management, I modeled three labor markets: low availability of off-farm work, medium availability, and high availability. I did this by creating three beta distributions with peaks at 25%, 50%, and 75% probability of securing short-term work. I decided to model single days (i.e. one day to cut and distribute pseudostems stems) or strings of days (i.e. four days at the beginning of the flowering season to clear brush and hand-pollinate trees for the first time) as separate foregone opportunities to find work. I assumed that the state of the labor market would not change drastically over the three month flowering season. In order to simulate this stability in the job market, the probability of securing a position was picked just once for each run. This probability was used to parameterize a binomial distribution. For each day or string of days, whether a job could have been secured for that time period was determined by this binomial distribution. For all the days that the farmer would have been able to secure a job, I calculated the lost income and set this as the opportunity cost of that strategy in that simulation run.

Net Revenue

The Monte Carlo simulation produced net revenue, total revenue, opportunity cost, and number of fruits produced in each instance. I used these simulation results as response variables in ANOVAs to determine whether outcomes differed significantly between management strategies, labor markets, and the interaction between the labor market and the management strategy.

2.3 Results

Over the course of this experiment, 1763 flowers were marked with 594 of those being hand-pollinated while remaining flowers were left open for insect pollination. A total of 274 fruits were produced. As expected, there was significant pollen limitation across all farms and treatments ($p<0.001$, Fig. 2.4). Hand pollinations were over seven times more likely to produce fruit than open pollinations. Single practices, like rotting leaves or just pseudostems had little effect on pollen limitation. However, the combination of rotting leaves and pseudostems tripled the fruit set of open flowers and decreased pollen limitation by 32% compared to no leaves or pseudostems plots ($p<0.05$, Fig. 2.5). There was no difference in the fruit set

rates for hand pollinated flowers across the four treatments, which indicates these practices did not affect resource availability.

Other Parameters

There were several other parameters in the model that had significant effects on fruit set (Fig. 2.3). The first axis of the PCA of branch diameter with distance to trunk ("PCA - Branch") followed previously documented patterns where flowers farther from the trunk and on thinner branches had a lower chance of fruit set ($p<0.05$, Ch. 1). Percent cover also had a significant effect on the chance of fruit set where cacao trees providing more shade to the ground underneath them had a higher chance of successful fruit set ($p<0.05$). In addition, the presence of water decreased the chance of fruit set ($p<0.05$).

Economic Viability

The ANOVAs of the MC results showed that pollination management strategy, job availability, and their interaction were all highly significant ($p < 0.001$). The strategies tested against business-as-usual in the Monte Carlo simulation (hand pollination and leaves & pseudostems) more than doubled the number of fruits produced per farm (Fig. B.2), which resulted in increased gross revenue. While the current strategy produced US$110 per farm on average, hand pollination produced US$235 and leaves & pseudostems produced US$283 (Fig. B.3). The leaves and pseudostem strategy produced the most fruits, while the hand pollination strategy was a close but significantly different second. This result suggests that a small increase in the pollination success over a continuous period is more powerful than a large increase in the pollination success once a week.

Hand-pollination was the most costly strategy while the leaves & pseudostems strategy was more costly than business-as-usual (Fig. B.4). When gross revenue and opportunity costs were combined, I found that business-as-usual provides stable returns to farmers across all labor markets. The leaves & pseudostem strategy garnered the highest net revenue of all the strategies regardless of the labor market (Fig. 2.6), while the hand pollination strategy was heavily influenced by the labor market, with medium and high availability of jobs leading to substantial net negative revenues.

2.4 Discussion

As expected, pollen limitation was significant in this system statistically, biologically, and economically (see Figs. 2.3 and 2.4). These results show that variation in pollination success on farms can translate into important yield effects (Garibaldi, Carvalheiro, et al. 2016), and more specifically, that research into ecological intensification with pollination as the leverage point is an important area of focus, especially for highly pollinator-dependent crops like cacao.

However, the management strategies tested in this experiment were not as effective as hoped. Rotting leaves or pseudostems alone were not enough to increase open pollination

rates though the combined effect of these strategies did significantly reduce pollen limitation (Fig. 2.5). Despite the lack of success with single additions, implementation of the single or dual practice over multiple years could have stronger effects. Many ecological interventions into agricultural systems require a longer continuous treatment history (> 1 year) in order to be fully effective (Pywell et al. 2015; Kremen and M'Gonigle 2015). Multi-year implementation could help to increase and stabilize habitat availability for Ceratopogonidae pollinators which would support larger populations and potentially increase pollination rates more substantially. In addition, these treatments could have a positive effect on other beneficial organisms like predators and parasitoids that reduce pest abundance and damage (Forbes and Northfield 2017; Morandin, Long, and Kremen 2014).

In my economic viability analysis, I found that a rotting leaves and pseudostem strategy would provide greater net revenue than business-as-usual even in the most competitive labor market (Fig. 2.6). I did not find hand pollination to be economically-viable as the opportunity cost of spending the required number of days in the farm outweighs the increases in yield. Thus, I would suggest that farmers implement a rotting leaves and pseudostem strategy as it requires less labor than hand-pollination while generating the greatest net revenue of any strategy. It is also more flexible to implement than hand-pollination, since herbaceous cutting and pseudostem distribution can occur at longer time intervals than hand pollination, which would be relatively continuous. One factor that I did not consider in my analysis was discounting future earnings. Instead, farmers will need to weigh the benefit of higher revenue from their fields in 6 months over wages from off-farm work in the present.

For farmers, implementation of the leaves and pseudostem practice could be limited by the availability of pseudostems from plantain plants (*Musa*). As these plants produce valuable products for farmers' subsistence livelihoods, stems that have yet to fruit are not preferred for use. Instead, stems that have already fruited should be the primary source of pseudostem disks. This means that the density of *Musa* will need to increase in most farms to provide enough material for this management practice (Kearney 2014). I recommend one *Musa* plant for every four cacao trees based on this experiment. Since *Musa* propagate vegetatively, this will require labor rather than a financial investment on the farmer's part using their existing *Musa* plants as sources of new *Musa*. While I did not estimate this cost in my economic analysis, I believe that the subsistence benefit of more plantain fruits along with the increased cacao fruit production will outweigh the opportunity cost of the labor investment.

Global demand for cacao is increasing but farmer decisions are made based on local economic forces that may not reflect the global market. Both the hand pollination and the leaves & pseudostem strategies increased fruit set substantially over business-as-usual. However, only the leaves & pseudostem strategy provides farmers with an economic incentive to change from current management. As shown by my economic analysis, farmers will substantially benefit from this strategy with its low barriers to entry, as compared to hand pollination which incurs a high opportunity cost and requires specialized tools (i.e. forceps). Implementation of the leaves & pseudostem strategy provides smallholder farmers with the opportunity to potentially double, or even triple, their cacao yield and generate higher net revenue which aligns their economic interests with rising global demand.

2.5 Figures

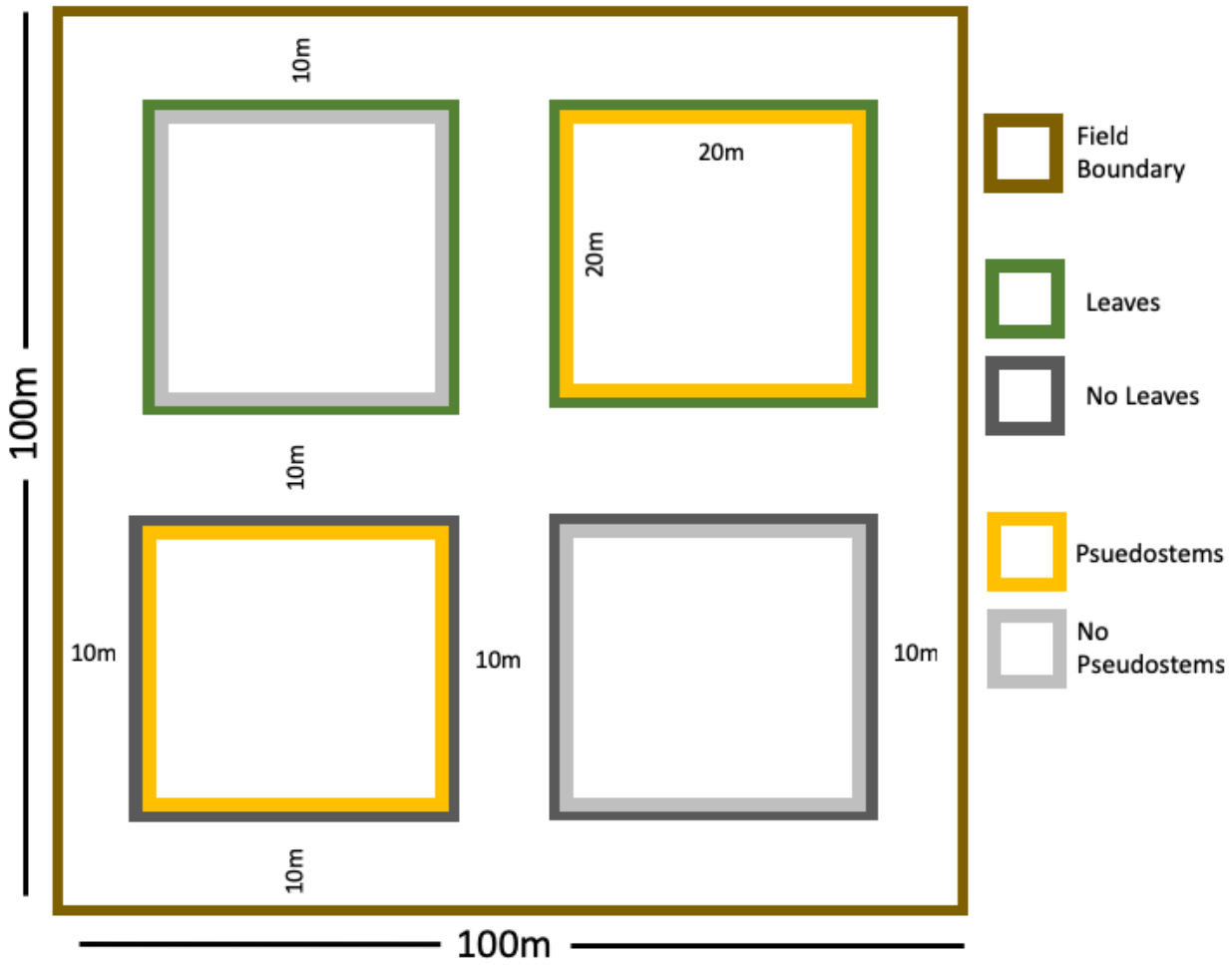

Figure 2.1: Diagram demonstrating most common formation of treatment plots within farms.

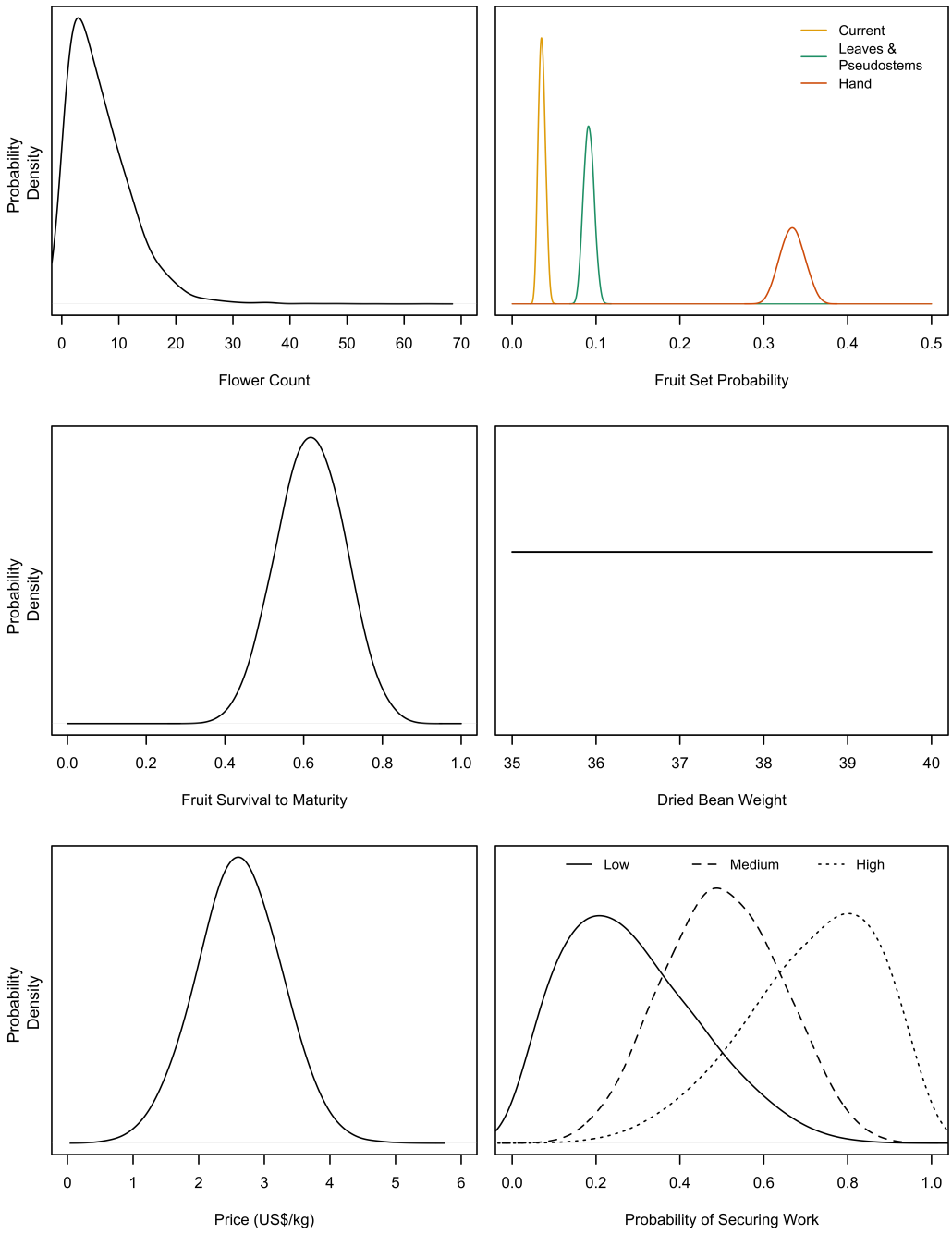

Figure 2.2: All probability distributions used in Monte Carlo simulation to examine the economic suitability of three management strategies (business as usual, leaves & pseudostems, and hand pollination) over three job market states (low, medium and high job availability).

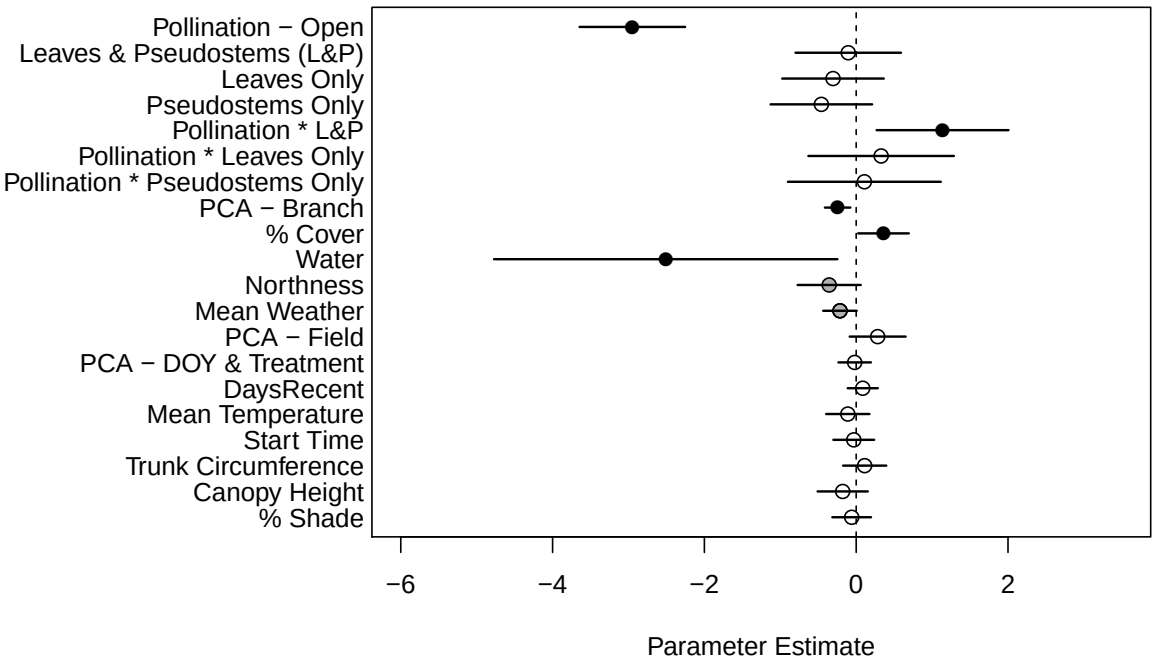

Figure 2.3: Model estimates with 95% confidence intervals. More positive numbers mean a better chance of successful fruit set, compared to the baseline of a hand-pollinated flower on a tree in a no leaves or pseudostems plot (the intercept). Estimates are scaled so that effect sizes can be directly compared. Solid-filled circles denote parameters whose p-values <0.05, grey-filled circles are parameters where $p < 0.10$, and unfilled circles are parameters where $p>0.10$.

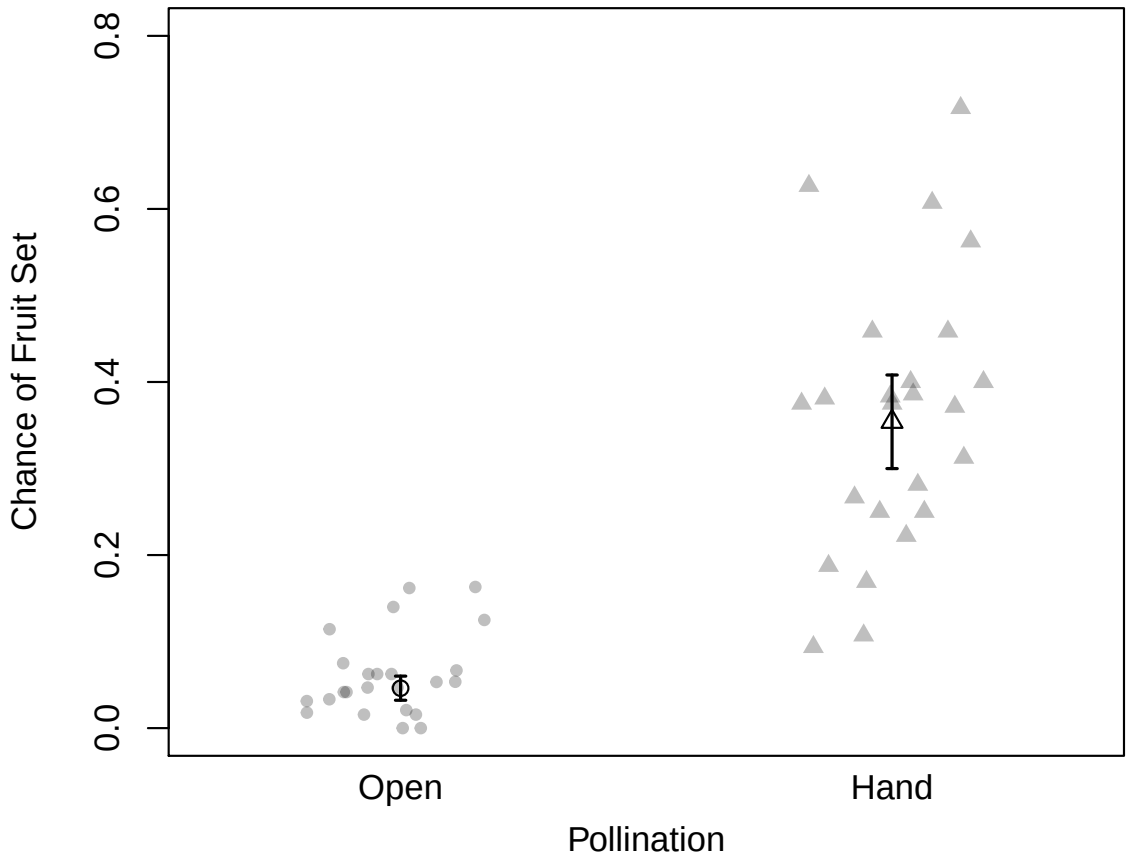

Figure 2.4: Estimated fruit set success between hand- and open-pollinated flowers regardless of management strategy. Open symbols: Back-transformed means with 95% confidence intervals. Filled, transparent symbols: The average proportion of fruits set per pollination treatment on a farm across trees on each sample date.

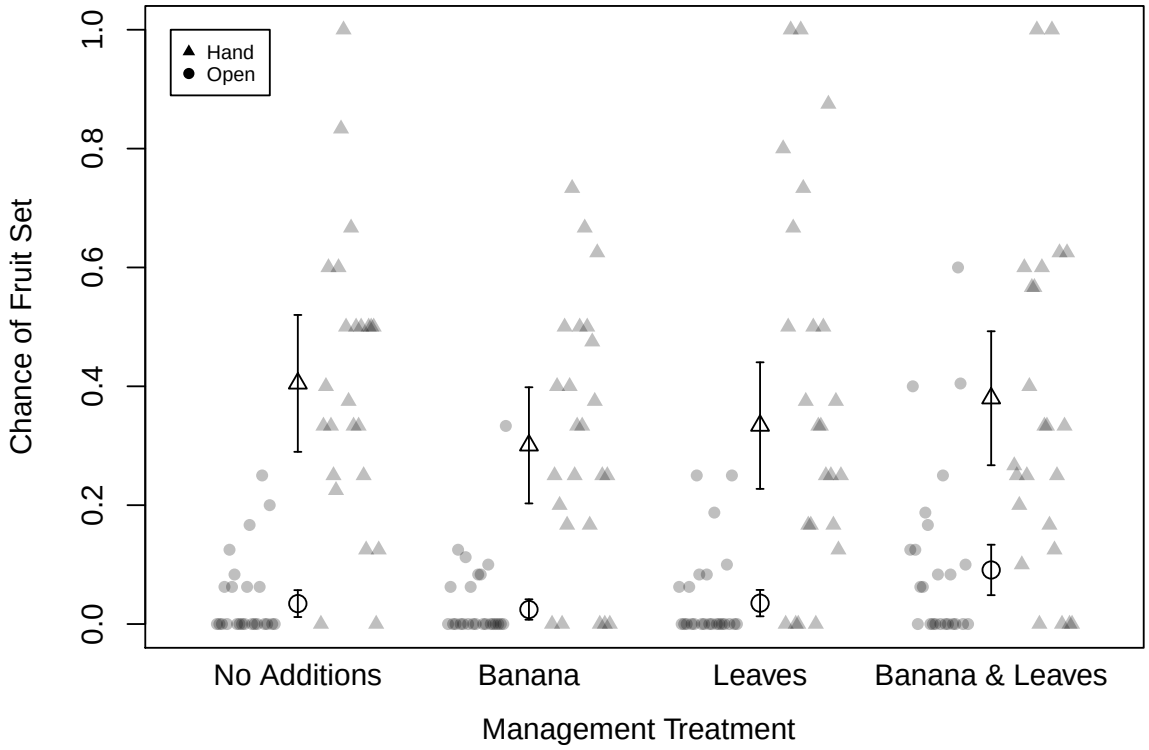

Figure 2.5: Estimated fruit set success between hand- and open-pollinated flowers across management strategies. Open symbols: Back-transformed model estimates with 95% confidence intervals. Filled, transparent symbols: The average proportion of fruits set per pollination treatment on a farm across trees on each sample date.

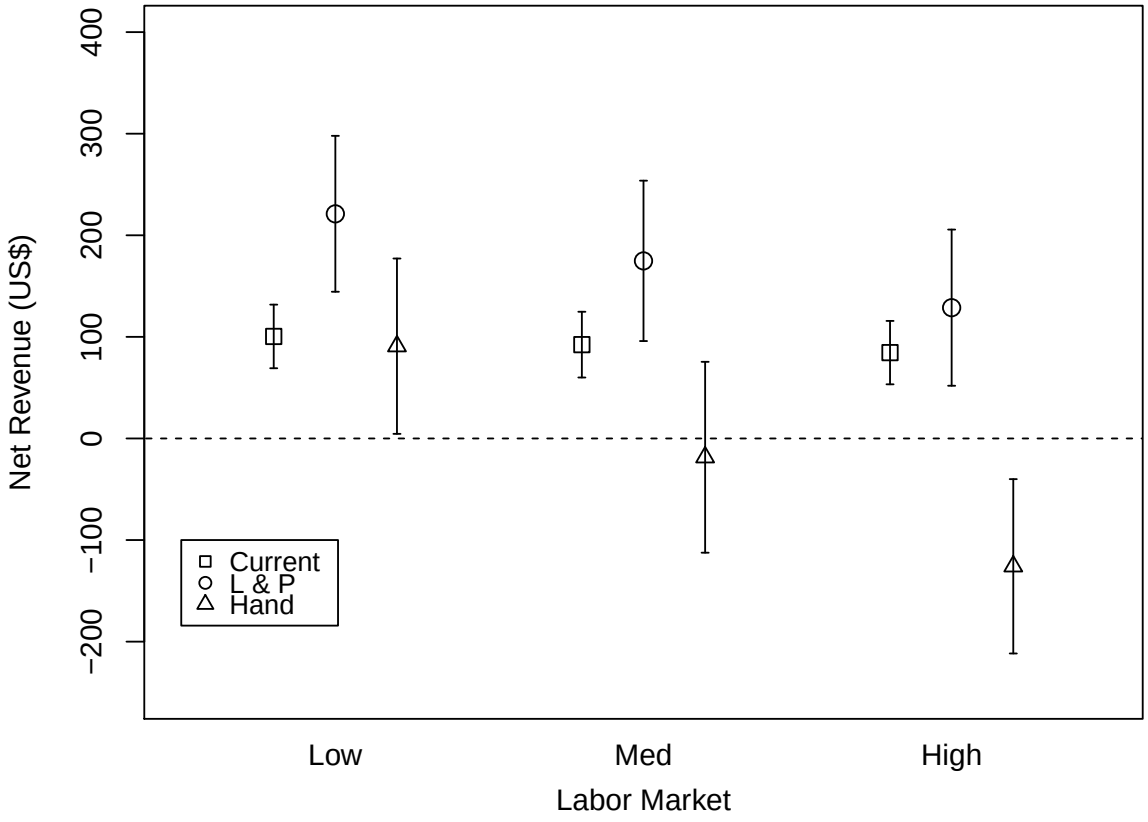

Figure 2.6: Net revenue projections in USD for a one hectare farm over one year across three different management strategies and three labor markets. Points represent the average and standard deviations from the Monte Carlo simulation that models pollination rates, fruit abortion, cacao price, and job availability.

Chapter 3

Hedgerows support resilient and diverse communities of crop-pollinating bees

Authors: E. Kearney, L. Ponisio, A. Lu, L. M'Gonigle, and C. Kremen

3.1 Introduction

Natural areas have been shown to support and export enough wild pollinators to provide complete pollination service to farms (Kremen, Williams, Bugg, et al. 2004; Greenleaf and Kremen 2006). However, many farms are in intensified areas, like those in the Central Valley of California, and are unable to benefit from wild pollinators because of the surrounding landscape. In these cases, increasing plant diversity at various scales on and around the farm is another way to support local populations of wild bees in order to capitalize on their pollination service (Kennedy et al. 2013). Crop rotation, polycultures, and cover-cropping increase the diversity of floral resources in fields (Kuussaari, Hyvönen, and Härmä 2011; Isbell et al. 2017) while flowering strips, hedgerows and riparian area restoration can increase floral resources on field edges and other areas that can not be put into production (Morandin and Kremen 2013; Kremen, Iles, and Bacon 2012).

Hedgerows, or strips of flowering shrubs and trees planted on field edges and margins, are one restoration technique that is gaining popularity in the Central Valley. In this region, hedgerows have been shown to increase pollinator abundance (Morandin and Kremen 2013) and occurrence (Kremen and M'Gonigle 2015), promote resource specialists, increase pollinator colonization, persistence and species richness (M'Gonigle et al. 2015), and restore spatial heterogeneity of the pollinator communities to reflect what would be expected in a natural landscape (Ponisio, M'Gonigle, and Kremen 2016). Hedgerows export crop pollinators to fields (Morandin and Kremen 2013) and improve fruits set in some crops (Morandin, Long, and Kremen 2016) but have no effect on other crops (Sardiñas and Kremen 2015). Given varied responses of adjacent crops to the well-documented enhancement of native bee communities, it is of interest to focus on the effect of hedgerows on the subset of the native

bee community that visits crops and provides pollination services. Do hedgerows support resilient communities of native crop-pollinating bees? And do these species provide a diversity of pollination services to farmers?

For farmers interested in native bees as crop pollinators, four aspects of the potential service provision are important: the amount of service provision, the stability of service, the diversity of services provided and service provision resilience.

Service provision amount is how much pollination an intervention would provide to a farmer (i.e. how many additional flowers are being sufficiently pollinated). Visitation, abundance, and/or occurrence of a bee species are commonly used proxies for the amount of service a farm is experiencing (Kremen, Williams, Bugg, et al. 2004).

Service provision stability is how even service provision will be over time. Using the abundance as a proxy for service provision, we can define the stability of service provision as the stability of abundance over time or the coefficient of variation in abundance.

Service provision diversity can be defined in many different ways but for this study, we define it as the diversity of crops likely to be pollinated by an intervention. Every bee species has a slightly different service profile because every species visits different crops and has different pollination efficiencies for each crop. Thus, species richness can be used as a simple measure of service provision diversity.

Service provision resilience is the likelihood that a service will be provided even if there is an environmental change or disturbance. Service provision resilience could be indicated simply by the number of species present at a site that provide the same service (the functional redundancy). This simple measure of resilience assumes that a larger number of species providing the service will allow greater stability for the service, due to random or directed changes in populations of different species. Random effects include portfolio effects (Thibaut and Connolly 2013), while directed effects could include density compensation or response diversity (Winfree and Kremen 2008).

A more targeted assessment of resilience could be obtained by assessing response diversity directly. This approach requires focusing on traits that are likely to mediate a species' response to environmental change (response traits: body size, specialization, etc.; Ponisio, M'Gonigle, and Kremen 2016): the more dispersion in response traits between individuals in the same community (Schleuter et al. 2010) the more response diversity and the more likely it is that some species survive to provide service even after a disturbance (Mori, Furukawa, and Sasaki 2013; Cariveau et al. 2013; Rogers, Tarpy, and Burrack 2014).

In this study, we compared crop pollinating bees at hedgerows and unrestored control sites to determine how hedgerows affect these four aspects of service provision in the Central Valley of California. Across all crop pollinating bees, we asked the following questions:

1. **Amount** Do hedgerows increase *abundance* and/or *occurrence* of species?

2. **Stability** Do hedgerows decrease the *the variation in abundance* of species?

3. **Diversity** Do hedgerows increase *species richness*?

4. **Resilience** Do hedgerows increase the *response diversity* of all crop-pollinating bee species? Do hedgerows increase the *functional redundancy* and/or the *response diversity* of groups of interest?

3.2 Materials & Methods

Study System

We surveyed pollinators from 23 restored sites and 28 unrestored control sites (Table C.1), located in the Central Valley of California (Yolo, Colusa, and Solano Counties) from 2006 to 2015 as published in Ponisio, M'Gonigle, and Kremen (2016). The Central Valley is intensively managed for agriculture and is dominated by conventional row crops, vineyards, and orchards. Restoration was accomplished through establishing hedgerows on farms. Hedgerows are plantings of native, perennial shrubs and trees where the plant species were chosen to ensure continuous bloom from early spring to late fall to provide both nectar and pollen resources to floral visitors. Hedgerows are ca. 3-6m wide, approx. 350m long and border large crop fields (ca. 30 hectares) and differ in age from maturing ($2-5$ years post-planting) to mature (>6 years post-planting). Our unrestored control sites consisted of unmanaged strips that represent a variety of field edges found in the region (bare, or with volunteer grasses, forbs, shrubs and trees, mostly non-native). We sampled pollinator communities between April and August each year, simultaneously at restored and unrestored sites. Each year, sites were sampled between two and six times depending on funding availability.

Identifying Crop Pollinators

To determine the service provision potential of over 180 native bee species collected at our sites in the Central Valley of California, we collected data on known crop visitors for four different crops commonly grown in the Central valley (Table C.2). From our literature search, we identified 82 native bee species that also visited at least one of our crops (almond, watermelon, sunflower, and tomato; Kremen, Bugg, et al. 2002; Kremen, Williams, Bugg, et al. 2004; Sardiñas and Kremen 2015; Greenleaf and Kremen 2006). This list is not exhaustive as we only included species that pollinate four crops while there are hundreds grown in this region but it is the best information available for this taxa for the region to date. In our surveys of hedgerows and control sites in the Central Valley, we found 43 species of the 82 in our master list. These 43 species were used in as the basis for all of the following analyses.

Watermelon Pollination: A Case Study

In order to gain greater understanding of the effects of hedgerows on pollination services, we investigated a subset of our 43 crop-pollinating bee species by looking only at those species that pollinate watermelon. By focusing in on only one crop, we could include more information about the service provision role of each bee species in our analyses. Our measure of service provision was pollination efficiency defined as the median number of pollen grains

left on a flower after one visit from one individual of that species (Kremen, Bugg, et al. 2002; Kremen, Williams, Bugg, et al. 2004). 24 of our 43 crop-pollinating bees species pollinate watermelon but we only have pollination efficiency data for 19 of these species. Watermelon needs 800-1000 grains of pollen per flower to be sufficiently pollinated and so pollinators that leave more pollen in each visit will sufficiently pollinate the crop with fewere visits (Kremen, Bugg, et al. 2002). For the 19 species with pollination efficiency data, we separated them into three groups - low (leaving less than 45 grains of pollen per visit), medium (45 - 90 grains per visit), and high efficiency pollinators (more than 90 grains per visit). We used these groups to examine the effect of hedgerows on species with differing service provision profiles.

Statistical Analyses

All statistical analyses were performed in R (Team 2019; Version 3.5.1). Models for analyses of the whole crop-pollinating community and just for watermelon pollinators was very similar and are described together below. Any differences in model formulas between the two groups are noted. For the rest of the chapter, these two groups will be described as the whole community (all crop-pollinators, 43 species) and the watermelon case study (just watermelon pollinators, 19 species). Models were tested for goodness of fit using expert review of q-q plots for linear mixed models and bootstrapped residual plots from the DHARMa package for generalized linear mixed models (Hartig 2019). Interactions between fixed effects were tested for inclusion in models through AICc comparisons where the model with the lowest AICc score (within 2 points) and secondarily, the simplest set of fixed effects was chosen as the final model.

Amount of Service

In order to investigate effect of restoration on the service provision amount, species abundance was used as the response variable in generalized linear mixed model (GLMM) with a Poisson error distribution with site status (unrestored control, maturing hedgerow, or mature hedgerow), day of year, and day of year squared as fixed effects along with random effects of year, site and species (Bates et al. 2015). For the watermelon case study, the best model based on AICc scores was one that included an interaction between site status and pollination efficiency (PE) group which was chosen as the final model presented in this chapter. This final model also included day of year and day of year squared as fixed effects and site, year, and species as random effects.

We also used occurrence as a proxy for service provision amount. In both cases, species occurrence was modeled with a GLMM with the same fixed and random effects as its abundacne counterpart but with a binomial error distribution.

Stability of Services

We used the coefficient of variation (CV) of abundance for each species across sampling events at each site in each year as our proxy for service provision stability. The CV of

abundance is dependent on how many sampling events were used to calculate it and in our data set, the number of sampling events for one site in one year varied from two to six. To create a data set of comparable sampling events across sites and years, we limited our data to site-year combinations with at least three sampling events. If there were more than three sampling events in a year at a site, three events were picked to most closely resemble the date distribution of sites with only three sampling events. For the first two sampling events, we took the earliest and the latest sampling events between 110 and 230 days into the year. The third sampling date was the one closest to the mean of the days of year of all sampling events for that site in that year. If two events were equidistant from the mean, then one was randomly picked to be the third sampling event. This representative set of sampling events and sites was also used as the basis for the service provision resilience analyses (Section 3.2).

For the whole community, the effect of hedgerows on the stability of services was modelled using a linear mixed model (LMM) with site status as a fixed effect and site, year and species as random effects. For watermelon pollinators, it was also modeled as a linear mixed model (LMM) with site status, PE group, and an interaction between the two as fixed effects and site, year and species as random effects. This model was compared to one without the interaction and one without PE groups. The one that only contained site status as a fixed effect (but retained the original random effects) has the lowest AICc and so is the model presented here.

Diversity of Services

For the whole community, we used species richness as a proxy for service provision diversity as each species has a slightly different service provision profile. Species richness was modeled in a GLMM with a Poisson error distribution, site status, day of year, and day of year squared as fixed effects, and site and year as random effects.

Resilience of Service

We calculated two measures of resilience for our analyses. For the whole community, we calculated response diversity while for watermelon pollinators, we calculated both response diversity and functional redundancy.

To determine how bee species would be influenced by their environment, we selected resource capture and use traits including resource specialization (d), body size (intertegular span, mm), sociality (eusocial, solitary, cleptoparasitic), nest location (above ground, below ground or mix), and nest construction (excavate or rent; as in Ponisio, M'Gonigle, and Kremen 2016). We also included two phenological estimates which approximated the width and the peak of species detectability in the environment based on an occupancy model (M'Gonigle et al. 2015). For some species, there were very few collection records to inform the occupancy model. In these cases, the peak centralizes towards the average peak of all species and the width measure widens in order to signal that there is the lack of information for that species. These traits were then used to calculate response diversity for the whole community and just watermelon pollinators. We used unweighted trait dispersion, or the average distance of individual species from the center of the whole group in principal compo-

nent analysis space, as our responde diversity metric (Anderson 2006; Schleuter et al. 2010). It is not influenced by species abundance or richness and so measures a different aspect of the community than abundance or species richness.

We calculated response trait dispersion (our metric of response diversity) for each site by year (Schleuter et al. 2010; Laliberté and Legendre 2010; Laliberté, Legendre, and Shipley 2014). Response trait dispersion was calculated at the year level because it was highly unlikely that enough species were collected at just one sampling event to result in a meaningful community for which dispersion could be calculated (i.e. there would be too many zeros). To control for different sampling efforts in different years, we used the same set of sampling events as used to analyze service stability (see Section 3.2). In both models (for the whole community and just watermelon pollinators), we used a log transformation on the raw response trait dispersion numbers to increase the fit of the residuals to a normal error distribution. For all crop pollinators, we modeled the effect of restoration on response diversity with a LMM with site status as a fixed effect, and site and year as random effects. For watermelon pollinators, response trait dispersion was calculated at the PE group level and the final model included site status, PE group, and their interaction as fixed effects and site and year as random effects.

Functional redundancy was only modeled for watermelon pollinators. We defined functional redundancy as a binomial variable where a site in a given year for a given PE group received a one if two or more species from that group had been collected or a zero if less than two species had been collected at that site in that year. It was modeled using a GLMM with a binomial error distribution with site status, PE group, and an interaction between the two as fixed effects and site and year as random effects. This full model was compared to more parsimonious models and the model without an interaction between site status and PE group is the model presented in this chapter.

3.3 Results

We collected 43 species of crop pollinating bees in our 23 hedgerows and 28 unrestored sites over 10 years. Over eleven thousand individual specimens were collected and identified from 456 sampling events in unrestored control sites, 84 events in maturing hedgerows, and 275 events in mature hedgerows (Table C.1).

Service Provision

Amount

For the whole community, abundance was not significantly different across site types though abundance in mature hedgerows was slightly elevated ($p < 0.1$, Fig. 3.1:top-left & Table 3.1). Species occurrence was significantly higher in both maturing and mature hedgerows ($p < 0.001$, Fig. 3.1:top-right & Table 3.2). Collecting a crop-pollinating species was 85% and 125% more likely to occur in a mature or maturing hedgerow, respectively, than at an unrestored control.

Two native bee species, *Lassioglossum (Dialictus) incompletum* and *Halictus tripartitus* are both generalist crop-pollinators and have high abundances across all site types which could be affecting the power of the abundance GLMM to identify differences in abundance of other species across site statuses. When these two species were removed from the analysis, the results of the abundance analysis more closely resembles the occurrence results with maturing hedgerows having significantly higher abundances ($p < 0.01$) and mature hedgerows having marginally significantly higher than unrestored controls ($p < 0.1$, results not shown).

For watermelon pollinators, there was a significant interaction effect between site status and pollination efficiency groups on species abundance as well as a significant difference between the low and high PE groups (Tab. 3.1). For the low efficiency pollinators, there was no significant difference between the three site types. However, for the medium and high efficiency pollinators, both maturing and mature hedgerows had significantly higher abundances compared to control sites (Fig. 3.2:top-left). The abundance of medium efficiency pollinators was 3.7 times greater at mature hedgerows compared to controls and the abundance of high efficiency pollinators was 2.8 times greater at mature hedgerows.

Species occurrence for watermelon pollinators followed a similar pattern (Table 3.2). In this case, low efficiency pollinators had significantly higher occurrence at maturing hedgerow sites while both medium and high efficiency pollinators had higher occurrences in both maturing and mature hedgerows compared to controls (Fig. 3.2:top-right). We were 3 times more likely to find a medium efficiency pollinator in a mature hedgerow compared to a control and 3.7 times more likely to find a high efficiency pollinator there.

Stability

For the whole community, there was no effect of hedgerows on stability of abundance (Tab. 3.3 & Fig. 3.1:middle-left). For watermelon pollinators, the final model did not contain PE groups as a fixed effect and so CV of abundance was only compared across site status. There was no significant difference between any of the site types though there was a negative trend in CV with hedgerow maturation (or a non-significant increase in stability as hedgerows matured; Tab. 3.3 & Fig. 3.2:bottom-left).

Diversity

For all crop pollinating bees, there were significant differences between unrestored and hedgerows sites in species richness. Species richness in maturing and mature hedgerows increased by 50% and 40%, respectively, compared to unrestored sites ($p < 0.01$, Fig. 3.1:middle-right & Table 3.4). There was no measure for service diversity for watermelon case study.

Resilience

There was a significant difference between hedgerow and control sites for response diversity of the whole crop-pollinating community (Fig. 3.1:bottom-left & Table 3.5). Both maturing and maturing hedgerows were about 35% more diverse in the response traits of their bee communities than unrestored sites.

For watermelon pollinators, our model showed that functional redundancy was significantly affected by site status and PE groups (Table 3.6). Maturing and mature hedgerows were around 10% more likely to be redundant than their unrestored counterparts (Fig. 3.2:bottom-right). For response diversity, we found that mature and maturing hedgerows had higher response diversity across all PE groups (Tab. 3.5). This effect was most pronounced for low efficiency pollinators with maturing and mature hedgerows being 11 and 4 times, respectively, more diverse in response traits than their unrestored counterparts (Fig. 3.2).

3.4 Discussion

Restoration in intensified landscapes, like the Central Valley of California, is important for native species conservation (M'Gonigle et al. 2015; Ponisio, M'Gonigle, and Kremen 2016; Kremen and M'Gonigle 2015). Restorations that are designed for insect conservation, like hedgerows, have also been praised for their benefit to farmers through ecosystem service provision like pest control and pollination. This chapter quantified the effect of hedgerows on the community of native bees that would provide pollination services to farmers. From these results, it is clear that hedgerows have an overall positive effect on crop-pollinating bees.

Amount

Abundance, our first proxy for service provision amount, was not affected by restoration status across all crop-pollinating bees. However, occurrence was significantly increased in both maturing and mature hedgerows compared to unrestored sites. This suggests that hedgerows are attracting rare species more often and that unrestored sites are frequented by highly abundant species in similar amounts to hedgerows. Thus, the benefit of hedgerows is highly context dependent. If a farmer's crop is well pollinated by *L. incompletum* and *H. tripartitus*, then hedgerows may not provide significant benefit. However, many crops benefit from rarer but more efficient pollinators that visit less frequently but have a larger impact when they do (Larsen, Williams, and Kremen 2005). In these cases, hedgerows could provide significant pollination benefit.

In our watermelon case study, this is exactly what we see. Hedgerows significantly increase the abundance of medium and high efficiency pollinators while not affecting the abundance of low efficiency pollinators like *H. tripartitus*. Hedgerows do significantly increase the occurrence of species in all three efficiency groups which is also beneficial for watermelon pollination since no single pollinator can sufficiently pollinate a watermelon flower from just one visit (Kremen, Bugg, et al. 2002; Kremen, Williams, Bugg, et al. 2004).

Stability

Hedgerows did not increase the stability of species abundance for the whole community or watermelon pollinators. However, this is not unexpected given the following two explana-

tions. First, we had to drop all species-site-year combinations that had zero abundance across all sampling events. This meant that our data set was much smaller for the CV of abundance analyses than our other measures which greatly decreases our ability to discern the significance of any effect. Second, our measure of stability, the coefficient of variation in abundance, was calculated across dates in the same year which could be an in effective scale at which to test this question. We could have also calculated it across years at a site for a species and this scale could be better matched to the biological cycles experienced by the community in question.

Diversity

Hedgerows increase species richness in comparison to unrestored sites which means that they are also increasing the diversity of services provided. While we did not break out specific services to examine, each bee species provides a slightly different complement of services and has slightly different response profile to environmental conditions. Thus, the more species a farmer can attract to their farm, the more likely the crop in question will benefit from native, wild pollinators.

Resilience

Finally, we were interested in if hedgerows could increase the resilience of the crop-pollinating community and stabilize the provision of crop pollination by attracting either more species (redundancy) or more diverse species (response diversity). For both groups and measures, hedgerows had a positive effect. While neither of these resilience measures can fully represent how species will respond to environmental change, hedgerows increasing both measures for each group suggests that communities supported by hedgerows are more likely to continue to provide service even after environmental change compared to unrestored sites.

Thus for the vast majority of our metrics, hedgerows did provide statistically and biologically significant benefits to farmers. It is important to recognize that these benefits will be crop dependent in their effect but for crops that are dependent on a diverse set of pollinators for sufficient pollination, like watermelon, hedgerows could provide important benefits. While the direct effect of hedgerows on watermelon pollination has not been tested, our results combined with previous research on the effect of natural areas on watermelon pollination (Kremen, Bugg, et al. 2002; Kremen, Williams, Bugg, et al. 2004; Larsen, Williams, and Kremen 2005) suggest that hedgerows would likely increase yield in watermelon farms if there was insufficient pollination from managed honey bees.

As a counter example, hedgerows have been shown not to increase yield in some systems, like sunflower (Sardiñas and Kremen 2015). Sunflower specialists primarily visit male flowers within this hybrid seed production system to collect pollen, and thus visit and pollinate the female, seed-producing flowers rarely; their main contribution to pollination is via interactions with managed honey bees that increase their movement and efficacy as pollinators (Greenleaf and Kremen 2006; Sardiñas and Kremen 2015). Thus, benefits from hedgerows in increased occurrence or abundance for sunflower pollinators is unlikely to result in yield increases for farmers.

In future work, we would like to examine the effect of hedgerows on tomato pollinators as tomato flowers need to be buzz pollinated (the flower requires vibration at a certain frequency to release pollen; McGregor 1976; Buchmann 1983) which honey bees can not effectively accomplish (Banda and Paxton 1991; Sabara and Winston 2003; Higo et al. 2004). Several native, wild bee species, especially *Bombus* spp., are capable of buzz pollination and increases in their abundance from hedgerows could have significant positive impact on yields. Scientists should continue to explore a wide range of interventions and focus in on the direct benefit of intervention to agriculture if they want to develop recommendations that demonstrate clear synergies. This study shows that interventions planned for conservation can provide significant benefits to communities of crop-pollinating bees and secondarily, farms. Thus, we encourage scientists, conservationists, and farmers to use hedgerows as an example to follow while they continue to work together to design interventions that balance the need for biological conservation with agricultural benefit.

3.5 Tables

Table 3.1: Model output from species abundance GLMMs for all crop-pollinating bees and watermelon pollinators.

	All Crop Pollinators				
Effects	Estimate	Std. Error	z.value	p.value	
Intercept (Unrestored)	-4.145	0.358	-11.578	<0.001	***
Status-Maturing	0.234	0.164	1.421	0.155	
Status-Mature	0.276	0.160	1.728	0.084	.
(Day of Year)^2	-2.999	0.117	-25.741	<0.001	***
Day of Year	3.523	0.123	28.745	<0.001	***
Status-Maturing:(Day of Year)^2	-0.147	0.035	-4.208	<0.001	***
Status-Mature:(Day of Year)^2	-0.002	0.024	-0.098	0.922	

	Watermelon Pollinators				
Effects	Estimate	Std. Error	z value	p value	
Intercept (Unrestored)	-2.540	0.746	-3.404	<0.001	***
Status-Maturing	0.059	0.207	0.285	0.775	
Status-Mature	-0.227	0.213	-1.064	0.287	
PEGrp-Medium	-1.471	1.028	-1.431	0.152	
PEGrp-High	-4.312	1.027	-4.198	<0.001	***
Day of Year	3.731	0.163	22.916	<0.001	***
(Day of Year)^2	-3.152	0.155	-20.379	<0.001	***
Status-Maturing:PEGrp-Medium	1.250	0.098	12.698	<0.001	***
Status-Mature:PEGrp-Medium	2.002	0.118	17.019	<0.001	***
Status-Maturing:PEGrp-High	0.986	0.239	4.131	<0.001	***
Status-Mature:PEGrp-High	2.192	0.253	8.678	<0.001	***

Table 3.2: Model output from the species occurrence GLMMs for all crop-pollinating bee species and watermelon pollinators.

	All Crop Pollinators				
Effects	Estimate	Std. Error	Z value	p value	
Intercept (Unrestored)	-4.746	0.350	-13.568	<0.001	***
Status-Maturing	0.816	0.211	3.870	<0.001	***
Status-Mature	0.624	0.182	3.429	<0.001	***
Day of Year	-2.109	0.316	-6.680	<0.001	***
(Day of Year)^2	2.568	0.322	7.972	<0.001	***

	Watermelon Pollinators				
Effects	Estimate	Std. Error	z value	p value	
Intercept (Unrestored)	-2.908	0.683	-4.261	<0.001	***
Status-Maturing	0.386	0.245	1.575	0.115	
Status-Mature	0.602	0.298	2.023	0.043	*
PEGrp-Medium	-1.581	0.931	-1.698	0.09	.
PEGrp-High	-4.051	0.952	-4.255	<0.001	***
Day of Year	3.121	0.451	6.919	<0.001	***
(Day of Year)^2	-2.543	0.440	-5.775	<0.001	***
Status-Maturing:PEGrp-Medium	0.777	0.195	3.991	<0.001	***
Status-Mature:PEGrp-Medium	0.853	0.284	3.006	0.003	**
Status-Maturing:PEGrp-High	0.937	0.351	2.668	0.008	**
Status-Mature:PEGrp-High	1.257	0.451	2.788	0.005	**

Table 3.3: Model output from the CV of abundance LMMs for all crop-pollinating bee species and watermelon pollinators.

	All Crop Pollinators					
Effects	Estimate	Std. Error	df	t.value	p value	
Intercept (Unrestored)	1.633	0.043	70.001	38.075	0.000	
Status-Maturing	-0.046	0.048	91.106	<0.001	0.338	***
Status-Mature	-0.064	0.037	53.805	<0.001	0.088	***

	Watermelon Pollinators					
Effects	Estimate	Std. Error	df	t.value	p value	
Intercept (Unrestored)	1.620	0.061	35.313	26.406	<0.001	***
Status-Maturing	-0.080	0.053	55.198	-1.509	0.137	
Status-Mature	-0.027	0.067	89.619	-0.398	0.692	

Table 3.4: Model output from species richness GLMM for all crop-pollinating bees.

Effects	Estimate	Std. Error	Z value	p value	
Intercept (Unrestored)	0.754	0.087	8.681	<0.001	***
Status-Maturing	0.399	0.122	3.278	0.001	**
Status-Mature	0.330	0.098	3.358	<0.001	***
Day of Year	-1.200	0.237	-5.069	<0.001	***
$(\text{Day of Year})^2$	1.455	0.242	6.007	<0.001	***

Table 3.5: Model output from the response diversity linear mixed model for all crop-pollinating bees and watermelon pollinators.

	All Crop Pollinators					
Effects	Estimate	Std. Error	df	t value	p value	
Intercept (Unrestored)	0.149	0.013	21.013	11.379	<0.001	***
Status-Maturing	0.053	0.023	85.869	2.314	0.023	*
Status-Mature	0.051	0.017	54.894	2.951	0.005	**

	Watermelon Pollinators					
Effects	Estimate	Std. Error	df	t value	p value	
Intercept (Unrestored)	-5.329	0.404	43.037	-13.199	<0.001	***
Status-Maturing	2.418	0.781	294.577	3.097	0.002	**
Status-Mature	1.371	0.570	166.689	2.407	0.017	*
PEGrp-Medium	-5.403	0.387	559.523	-13.968	<0.001	***
PEGrp-High	-6.117	0.387	559.523	-15.816	<0.001	***
Status-Maturing:PEGrp-Medium	-0.224	0.952	558.957	-0.235	0.814	
Status-Mature:PEGrp-Medium	0.798	0.654	558.985	1.222	0.222	
Status-Maturing:PEGrp-High	-2.018	0.952	558.957	-2.121	0.034	*
Status-Mature:PEGrp-High	-1.002	0.654	558.985	-1.533	0.126	

Table 3.6: Model output from the functional redundancy GLMM for watermelon pollinators.

	Watermelon Pollinators				
Effects	Estimate	Std. Error	df	t value	p value
Intercept (Unrestored)	0.743	0.416	1.785	0.074	.
Status-Maturing	1.938	0.673	2.879	0.004	**
Status-Mature	1.567	0.527	2.974	0.003	**
PEGrp-Medium	-3.547	0.372	-9.543	<0.001	***
PEGrp-High	-7.637	1.103	-6.925	<0.001	***

3.6 Figures

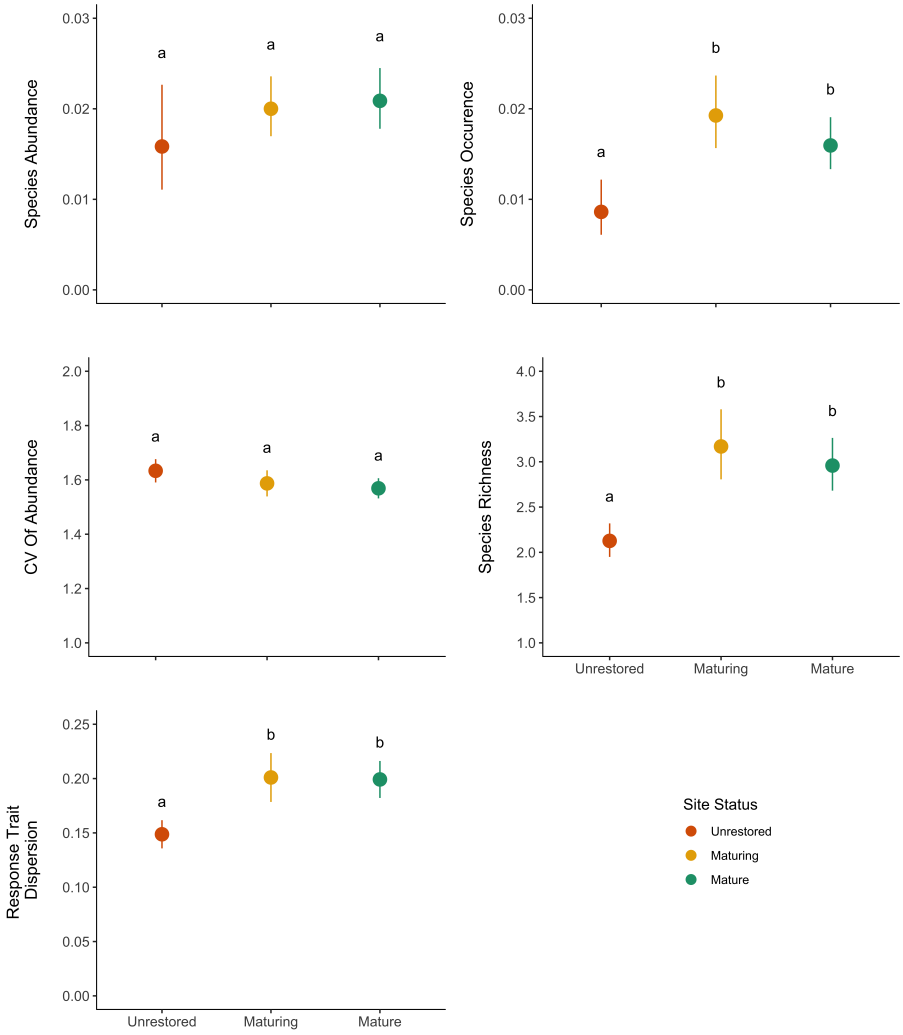

Figure 3.1: Left to right, top to bottom: Means of model estimates and standard errors of abundance, occurrence, CV of abundance, species richness, and response diversity across unrestored controls, maturing hedgerows, and mature hedgerows.

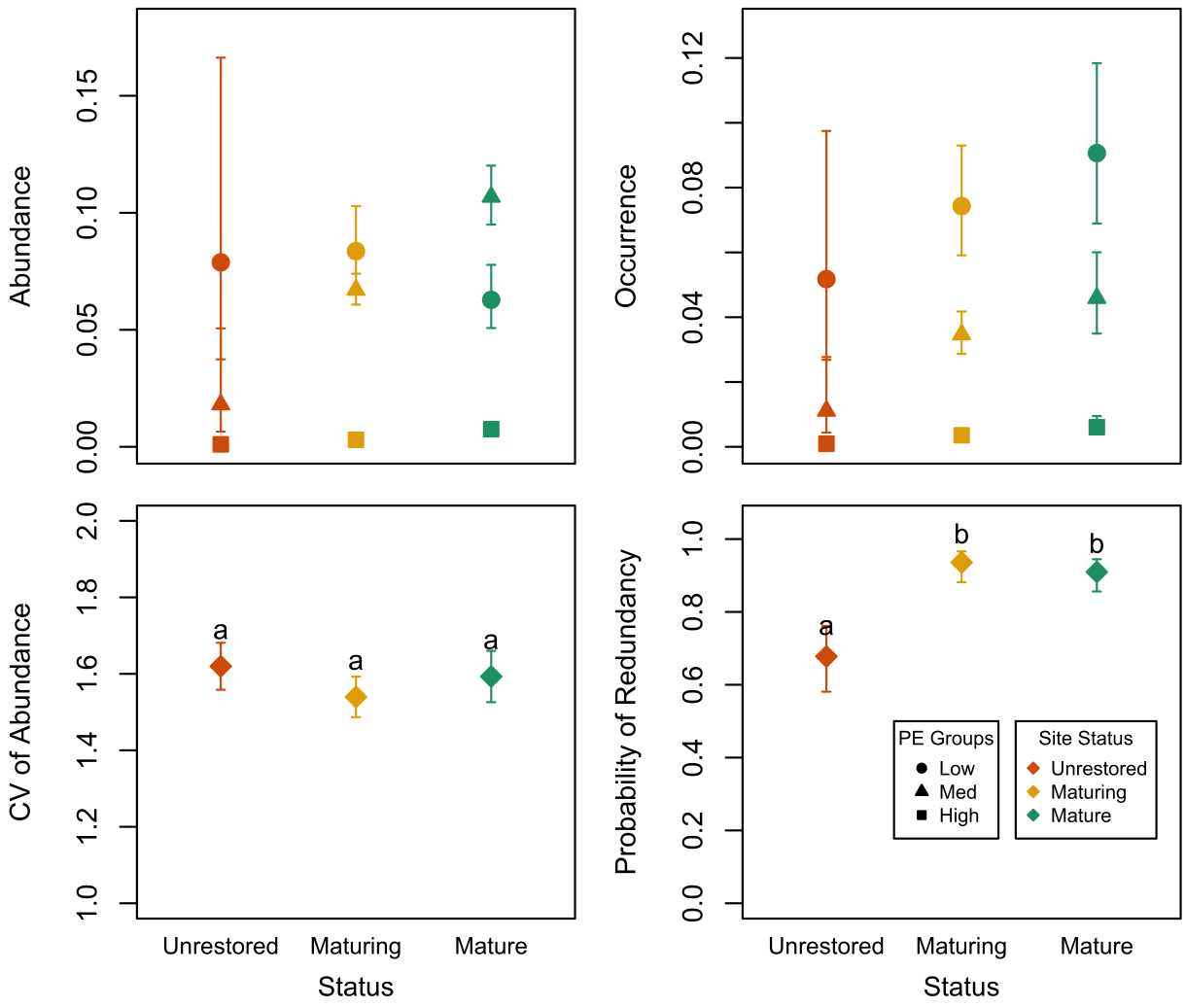

Figure 3.2: Left to right, top to bottom: Means of model estimates and standard errors of abundance, occurrence, CV of abundance, and functional redundancy at unrestored, maturing, and mature sites and across pollination efficiency groups (low, medium, high). The interaction between site status and PE group was significant for both abundande and occurrence($p < 0.01$).

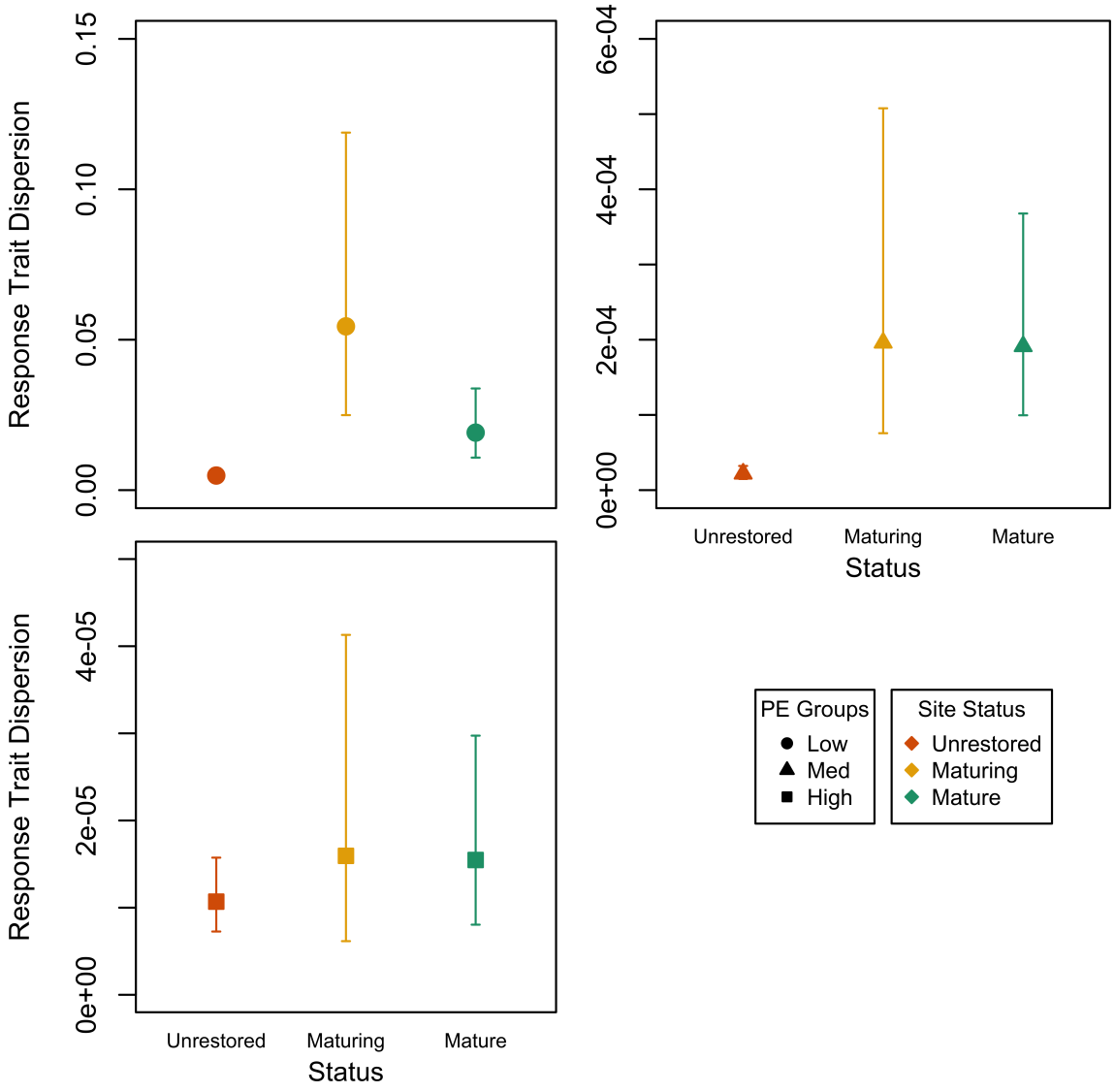

Figure 3.3: Means of model estimates and standard errors of response diversity at unrestored, maturing, and mature sites and across pollination efficiency groups (low, medium, high). Pollination efficiency groups are plotted on different plots in order to demonstrate the similar pattern across groups even though the scale of response diversity is very different across PE groups.

Conclusion

This body of work shows that conservation, ecological intensification, and restoration can support crop-pollinating insects in ways that are important to farmers. However, these results vary greatly by context and system. This means a deep understanding of the crop and the system in which it is grown is needed in order to design a conservation or ecological intensification strategy that will effectively improve crop pollination and support pollinator communities. From this work, I believe there are three major areas on which researchers, conservationists, and farmers should focus when designing and testing a new intervention: the crop's pollination syndrome, the scale of the intervention, and the feasibility of any proposed actions.

Pollination Syndrome

While it seems obvious, knowing by whom and for what a crop is pollinated is of the utmost importance in designing an effective intervention. There are many ways that crops are easy or difficult to pollinate and understanding these factors for the specific crop(s) will help to smooth the rest of the design process. Some crops, like tomato and cranberry, are buzz-pollinated where the pollinator must vibrate the flower at the correct resonance frequency in order to release pollen from the anthers for collection and pollination (McGregor 1976; Buchmann 1985). Others, like almond and cacao, are self-incompatible and need pollen from individuals that are genetically different in order to set fruit (Fenster et al. 2004; Cope 1962). Still others, like vanilla, have evolved to be completely dependent on just a few pollinators and these pollinators have not been introduced into the non-native range of vanilla (Lecomte 1902; Ridley 1912; Purseglove et al. 1981; Soto Arenas 1999).

For example, from my work, *T. cacao* pollination is performed by tiny biting midges (Ceratopogonidae) that need moist, decaying leaf-litter as larval habitat. These pollinators do not visit flowers other than *T. cacao* flowers and so would not benefit from many of the common pollinator-supporting interventions (e.g. flowering strips). Instead, interventions need to focus on increasing larval habitat through increasing rotting plant material on or near the farm. In my third chapter, I highlighted another example of this principle with the difference in benefits of hedgerows for watermelon pollinators versus sunflower pollinators. While both groups may experience a benefit from the floral resources provides by hedgerows, watermelon has a much higher chance of being positively affected by the increased abundances and occurrences of species on the hedgerows since is it very dependent on a diversity of pollinators for sufficient pollination (Kremen, Williams, Bugg, et al. 2004). Since sun-

flower bees tend to nest in sunflower fields and visit just male flowers, hedgerows do not have an effect of sunflower yields (Sardiñas and Kremen 2015).

Scale of Intervention

The scale of the intervention is also very important. In *T. cacao*, I found that conservation of natural habitat outside of the farm was not effective at providing pollination services. This is most likely because *T. cacao* pollinators can only fly a few meters (Kaufmann 1975) and experience a large microhabitat change at the field boundary that prevents them from crossing from natural rainforest into *T. cacao* fields. Thus, effective interventions in this system are at the farm scale, like the leaves and pseudostem strategy described in Chapter 2.

On the other hand, crop-pollinating bees can fly up to several hundred meters in search of floral resources (Greenleaf, Williams, et al. 2007)and so while I examined a local, on-farm intervention in this work, landscape scale interventions could be beneficial in supporting increases abundances and species richness for all farms in the area. Networks of local interventions could also provide a landscape scale benefit from farmers supporting hedgerows or flowering strips on their farms and exporting native, wild pollinators to other farms (Ponisio, Valpine, et al. 2019). The scale of impact can determine at what level incentives should be used to encourage implementation of interventions. While in *T. cacao* it will be the farmer deciding to adopt a practice or not, for hedgerows and crops in the Central Valley, these decisions might be best made at a county or grower cooperative level in order to create landscape-level interventions that result in the desired effect on pollination services.

Feasibility

While I only examined feasibility explicitly in my second chapter and only focused on economic viability, it is just as important as the pollination syndrome and the scale of the intervention in determining the best intervention (Long, Garbach, and Morandin 2017; Sellers et al. 2018). For on-farm practices that require investment or change on the part of farmers, suggested practices must be acceptable in terms of disease and pest interactions, skill and equipment limitations, and economic concerns.

Future Work

I will continue to explore the effect of rain forest and on-farm management practices in *T. cacao* by linking floral visitors to changes in pollination success rates and microhabitat qualities. I am also working on developing effective tools with which I will disseminate my results and supporting information so that it will be available to the farmers that it would affect most. Finally, I will continue to quantify the value of hedgerows for different crops in the intensified system of the Central Valley, starting with tomato.

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Appendix A

Supplemental Materials - Chapter 1

A.1 Tables

Farm	Week of Sampling						Landscape Context	Land Use			
	1	2	3	4	5	6		Side A	B	C	D
CC1	1	1	-	-	-	1	Agricultural	Cacao	Banana	Cacao	Cacao
CC2	1	1	-	-	-	1	Agricultural	Cacao	Fish Pond	Houses	Road
CC3	1	1	-	-	1	-	Adjacent	PRF	Cacao	River	Cacao
CC4	1	1	-	-	1	-	Adjacent	PRF	Cacao	River	PRF
CC5	1	-	-	-	2	-	Embedded	PRF	PRF	PRF	PRF
RB1	-	-	2	-	-	-	Fragment	PRF fragment	Cacao	Yuca	Houses
RB2	-	-	2	-	-	-	Embedded	PRF	PRF	Yuca	PRF
RB3	-	-	2	-	-	-	Adjacent	PRF	Cacao	Road	Cacao
RB4	-	-	2	-	-	-	Embedded	PRF	PRF	Cacao	PRF
SJ1	-	2	-	-	-	1	Agricultural	Cacao	Houses	Cacao	Cacao
SJ2	-	1	-	-	-	2	Fragment	PRF fragment	Cacao	Cacao	Cacao

Table A.1: Farm Information: Distribution of sampling across weeks, landscape context classification, and land use surroundings. PRF stands for primary rain forest. CC is Campo Cocha, RB is Rio Blanco, and SJ is San Jose.

A.2 Figures

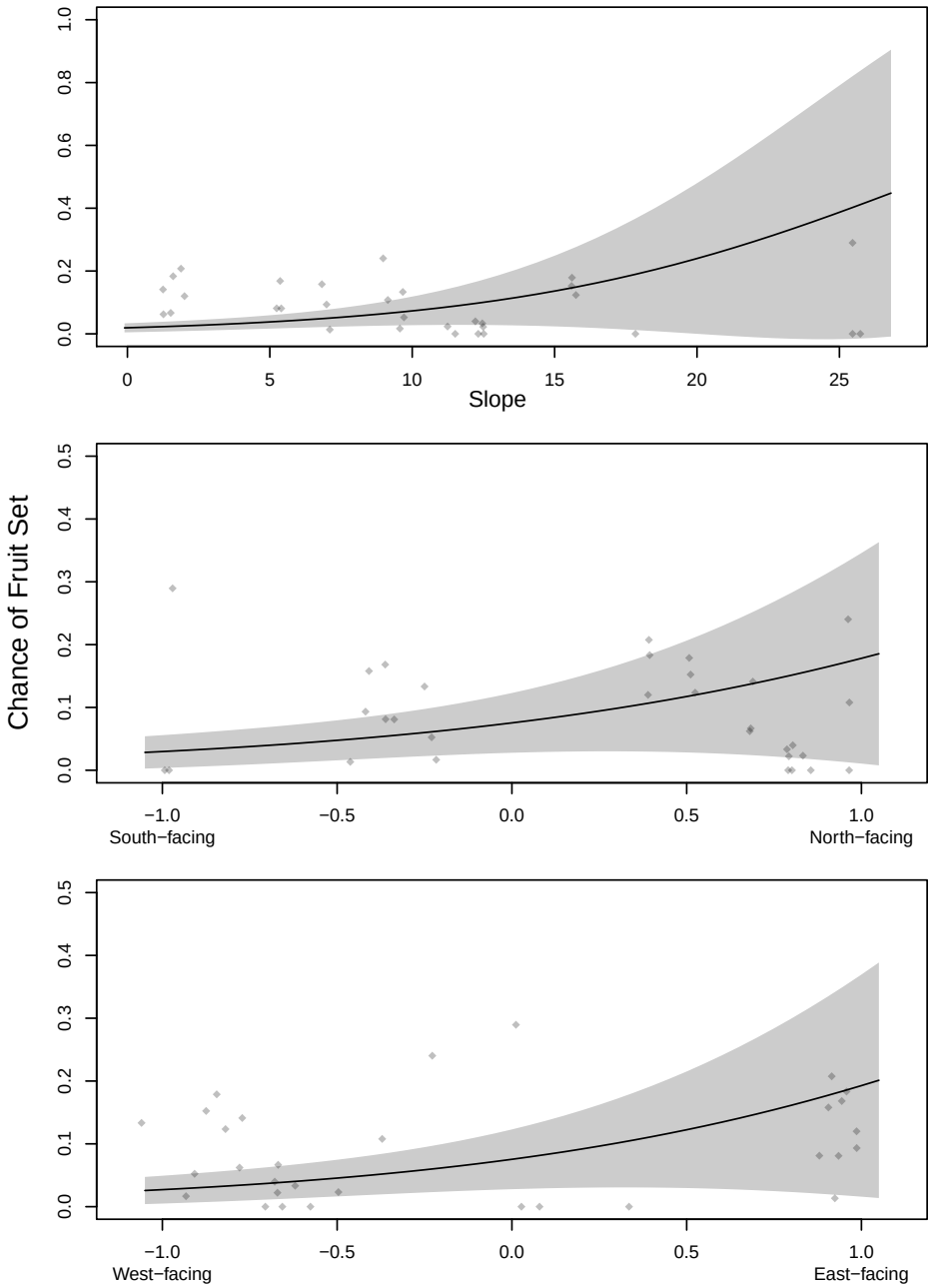

Figure A.1: Line and shaded area: Back-transformed model estimate and 95% confidence interval. Filled, transparent symbols: Fruit set success aggregated by tree and date and then averaged by farm.

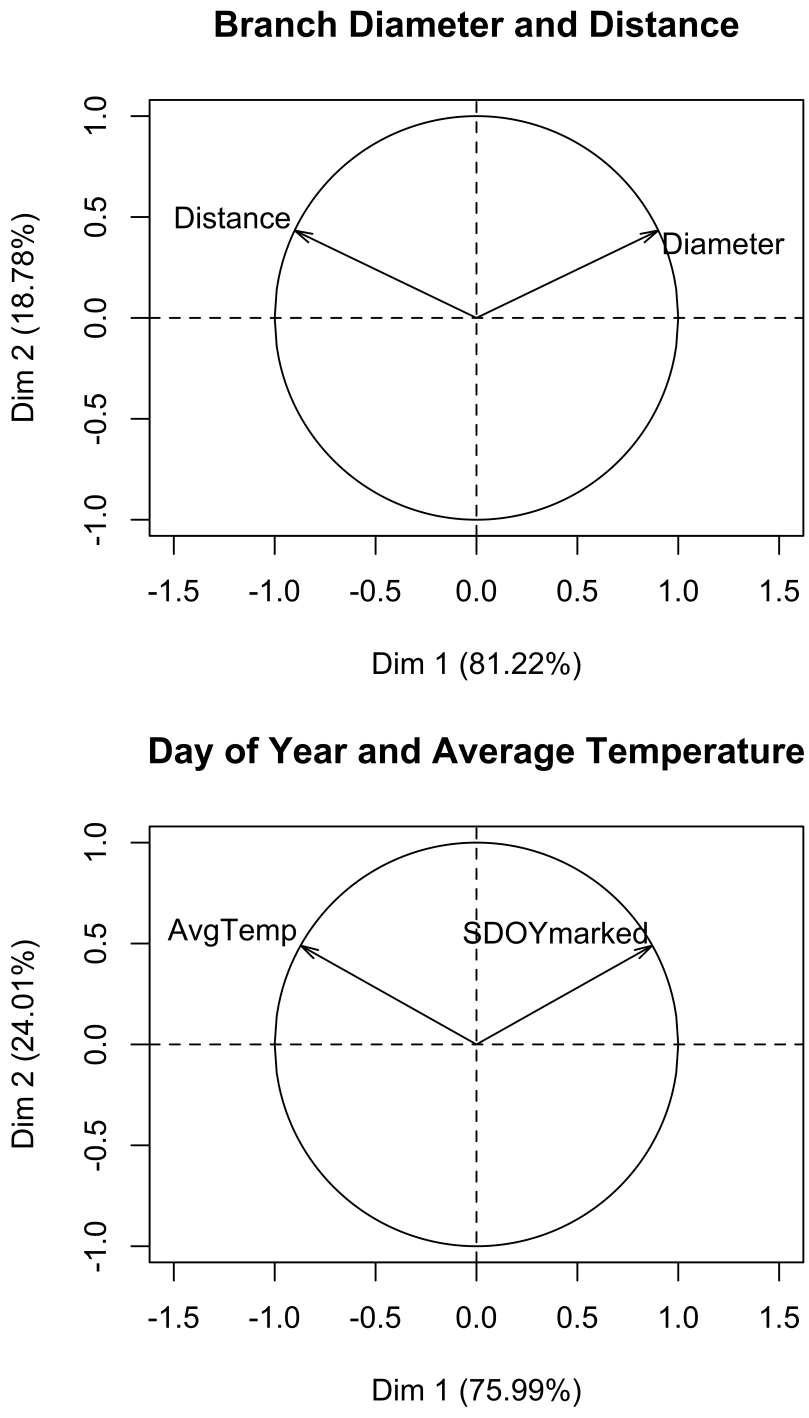

Figure A.2: Graphs of the first two axes of the PCAs for a) branch diameter and distance and b) day of year and mean temperature.

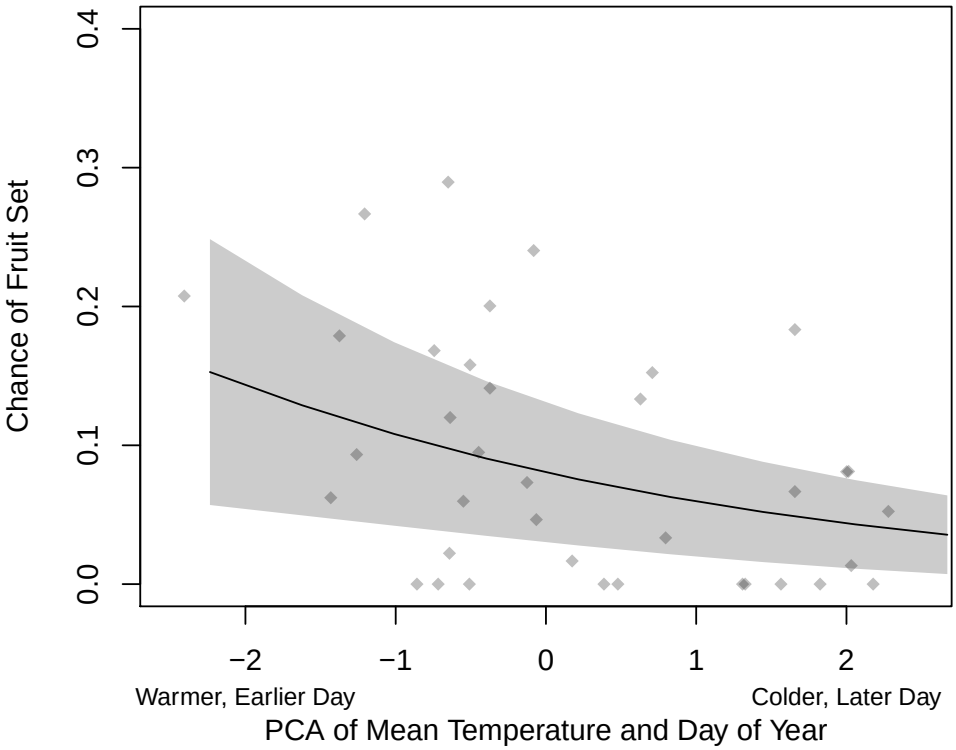

Figure A.3: Line and shaded area: Back-transformed model estimate and 95% confidence interval. Filled, transparent symbols: Fruit set success aggregated by tree and date and then averaged by farm. X-axis is the first axis of the PCA of mean temperature and the day of year.

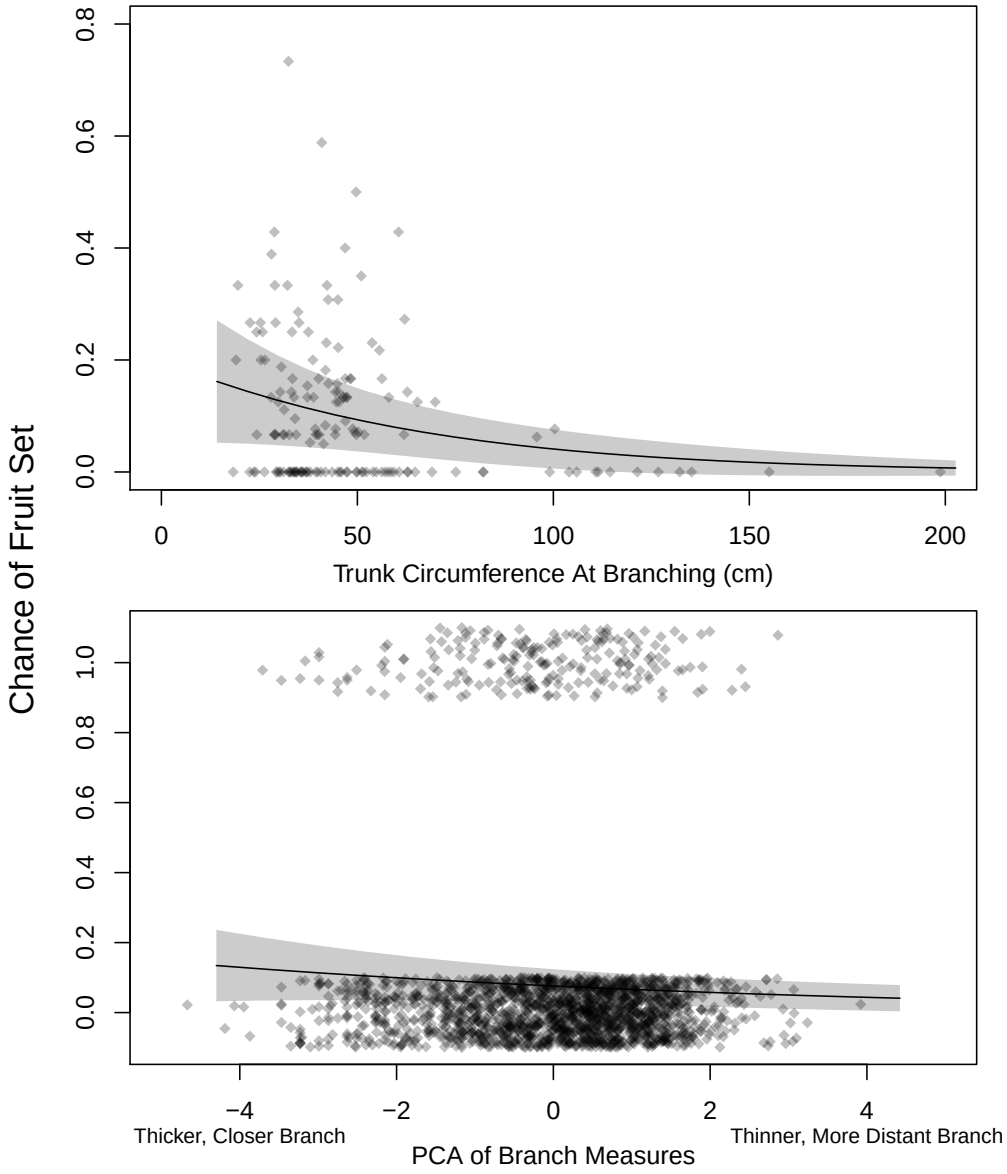

Figure A.4: Line and shaded area: Back-transformed model estimate of fruit set success and adjusted 95% confidence interval. Top: Filled, transparent symbols represent fruit set success aggregated by tree and date. Bottom: Filled, transparent symbols represent fruit set success of individual flowers. X-axis is the first axis of the PCA of branch diameter with distance from the trunk.

Appendix B

Supplemental Materials - Chapter 2

B.1 Tables

Farm	Week of Sampling						
	1	2	3	4	5	6	7
CC1	1	0	1	1	1	0	0
CC2	1	0	1	1	1	0	0
RB1	0	0	1	1	0	1	1
RB2	0	0	0	1	1	1	1
SJ1	1	0	1	0	1	1	0
SJ2	1	0	1	0	1	1	0

Table B.1: Distribution of sampling across weeks and farms. CC is Campo Cocha, RB is Rio Blanco, and SJ is San Jose.

B.2 Figures

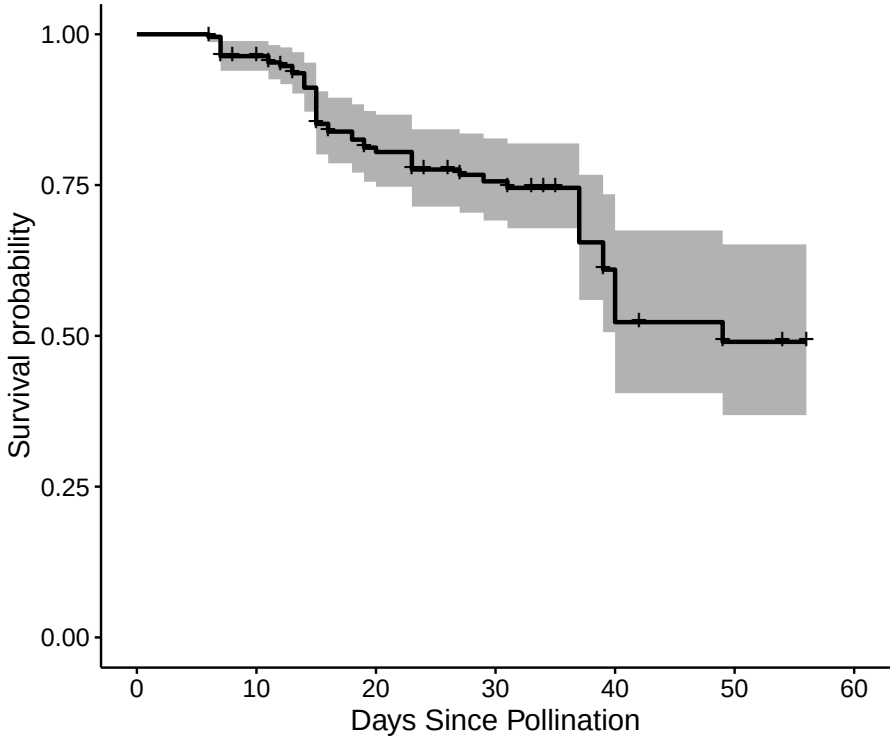

Figure B.1: Survival curve of young cacao fruits. Shaded area represents 95% confidence intervals.

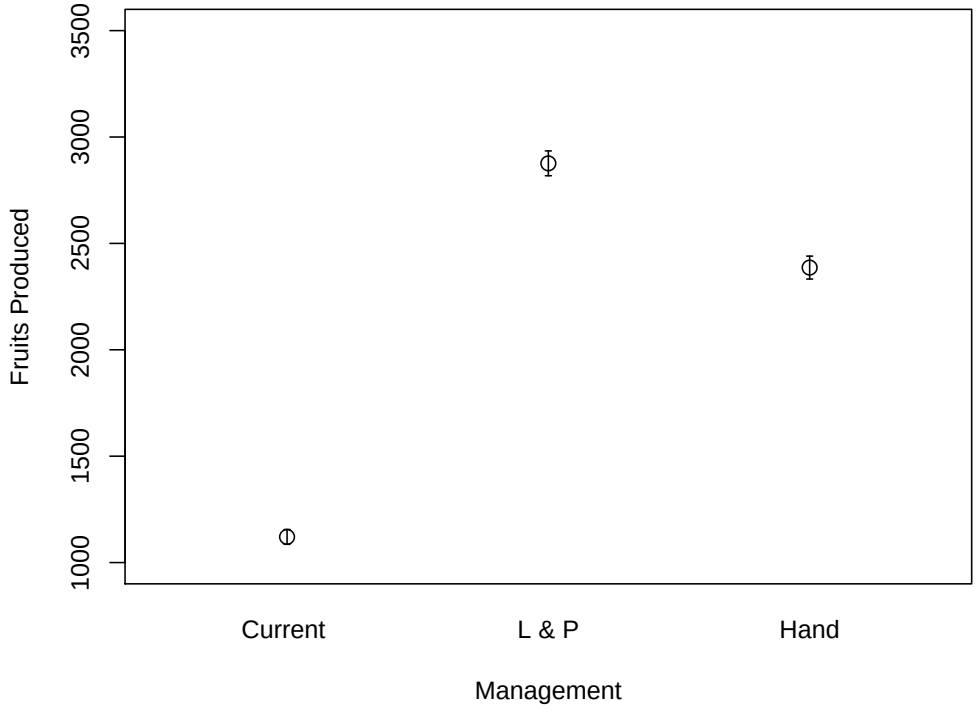

Figure B.2: Fruit production projections for a one hectare farm over one year across three different management strategies. Points and error bars represent the average and standard deviations from the Monte Carlo simulation that models pollination rates, fruit abortion, cacao price, and job availability.

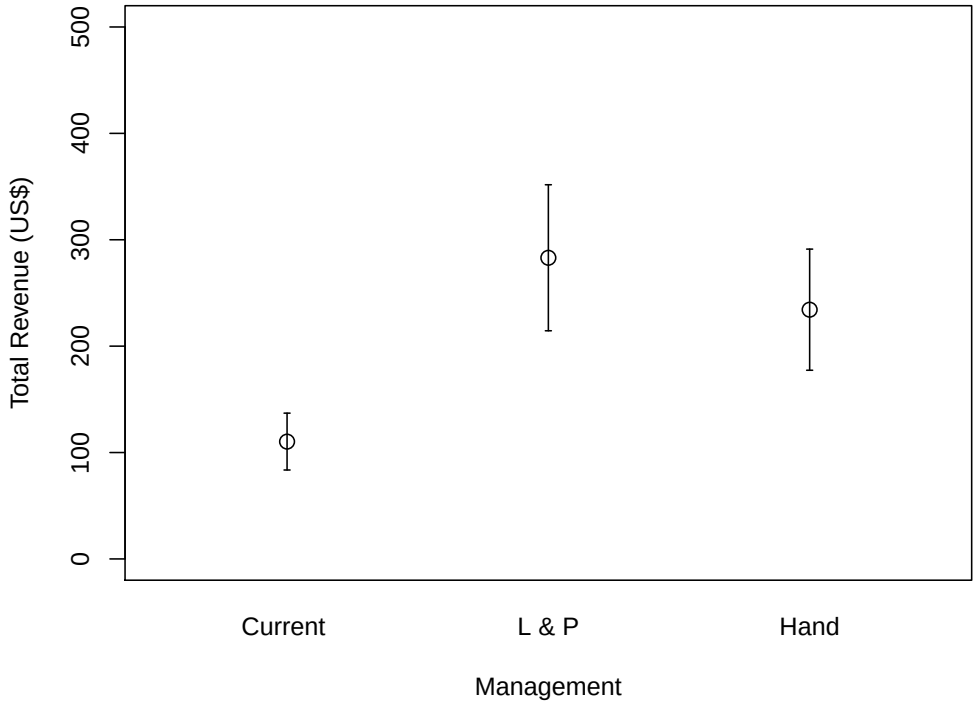

Figure B.3: Total revenue projections in USD for a one hectare farm over one year across three different management strategies. Points and error bars represent the average and standard deviations from the Monte Carlo simulation.

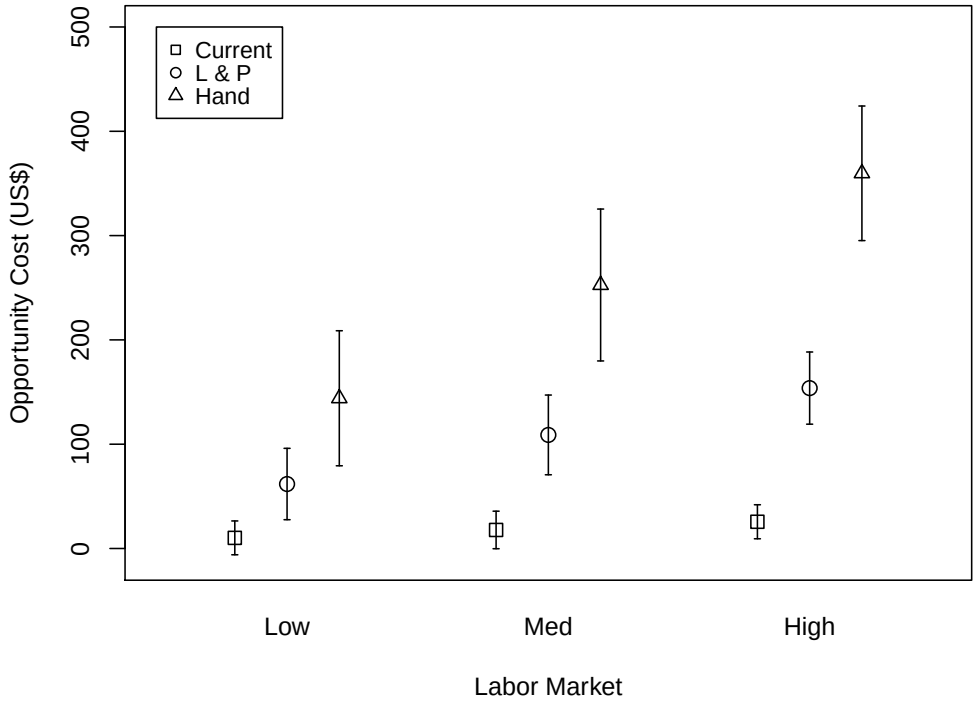

Figure B.4: Opportunity cost projections in USD for a one hectare farm over one year across three different management strategies. Points and error bars represent the average and standard deviations from the Monte Carlo simulation.

Appendix C

Supplemental Materials - Chapter 3

C.1 Tables

Table C.1: Table of sampling events for all sites and all site statuses across years from 2006 to 2015. For service provision stability, functional redundancy, and response diversity (both for all crop-pollinators and just watermelon pollinators), site and year combinations with three or more sampling events were pulled from this complete data set in order to form a representative data set where all site-year combinations had three sampling events.

Status	SiteID	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
Unrestored	B1	0	0	0	4	4	0	4	5	3	0
Unrestored	B2	4	3	3	0	0	0	0	0	0	0
Unrestored	B3	0	3	3	3	0	3	4	5	3	0
Unrestored	B4	0	0	0	0	0	0	4	5	3	0
Unrestored	C5	0	3	3	3	0	3	4	5	3	4
Unrestored	C6	0	0	0	4	0	0	4	6	3	0
Unrestored	C7	0	0	0	0	0	0	3	5	3	0
Unrestored	D8	4	3	3	3	0	3	4	5	3	4
Unrestored	G9	4	0	0	0	0	0	0	0	0	0
Unrestored	G10	4	0	0	0	0	0	0	0	0	0
Unrestored	G11	0	3	3	3	0	3	4	5	3	4
Unrestored	H12	4	3	3	3	0	3	4	5	3	4
Unrestored	H13	0	0	0	4	0	0	4	5	3	0
Unrestored	H14	0	0	0	0	0	0	4	1	0	0
Unrestored	H15	0	3	3	3	0	3	0	0	0	0
Unrestored	J16	0	0	0	4	4	0	4	5	3	0
Unrestored	J17	0	0	0	0	4	0	0	0	0	0
Unrestored	L18	0	0	0	0	0	0	0	5	3	0
Unrestored	M19	0	0	0	0	0	0	0	5	3	0

Status	SiteID	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
Unrestored	M20	0	0	0	0	0	0	4	0	0	0
Unrestored	M21	0	3	3	3	0	3	4	5	2	4
Unrestored	R22	4	0	0	0	0	0	0	0	0	0
Unrestored	R23	0	0	0	0	0	0	4	5	3	0
Unrestored	S24	0	3	3	3	0	3	4	5	3	0
Unrestored	T25	4	3	3	3	0	3	4	5	3	4
Unrestored	U26	4	3	3	3	0	3	4	5	3	0
Unrestored	Y27	0	0	0	0	0	0	4	5	3	0
Unrestored	Z28	0	0	0	0	4	0	6	5	3	0
Maturing	B29	0	0	0	3	0	3	4	0	0	0
Maturing	B30	0	0	3	3	0	3	0	0	0	0
Maturing	G31	0	0	0	0	0	0	4	5	3	4
Maturing	H32	0	0	0	3	0	3	4	0	0	0
Maturing	J33	0	0	0	0	0	0	0	5	3	0
Maturing	M34	0	0	3	3	0	3	0	0	0	0
Maturing	R35	0	0	0	0	0	0	4	5	3	0
Maturing	S36	0	0	0	3	0	3	4	0	0	0
Mature	A37	0	0	0	0	4	0	0	0	0	0
Mature	B29	0	0	0	0	0	0	0	5	3	4
Mature	B38	0	0	0	0	0	0	4	5	3	4
Mature	B30	0	0	0	0	0	0	4	5	3	4
Mature	C39	4	0	1	0	0	0	0	0	0	0
Mature	C40	0	0	0	0	0	0	3	5	3	0
Mature	C41	0	0	0	0	0	0	4	5	3	0
Mature	F42	0	0	1	4	4	2	4	5	3	0
Mature	F43	0	0	0	0	0	0	4	5	3	0
Mature	H44	0	0	0	4	0	2	4	5	3	0
Mature	H32	0	0	0	0	0	0	0	5	3	4
Mature	M45	0	0	0	0	0	0	4	5	3	0
Mature	M34	0	0	0	0	0	0	4	5	4	4
Mature	M46	0	0	0	0	4	2	6	5	3	0
Mature	O47	0	0	0	0	0	0	4	5	0	0
Mature	P48	0	0	0	0	0	0	4	5	3	4
Mature	R49	0	0	0	4	4	2	4	5	3	4
Mature	S36	0	0	0	0	0	0	0	5	3	4
Mature	T50	0	0	0	4	0	2	4	5	3	0
Mature	V51	0	0	0	0	0	0	4	0	0	0

Table C.2: Crop-pollinating native bees with corresponding crop pollination traits. For *Lassioglossum* spp., (D) stands for Dialictus and (E) stands for Evylaeus. Alm = Almond, Water = Watermelon, Sun = Sunflower, and Tom = Tomato.

Species	Pollination Traits				
	Binary				Efficiency
	Alm	Water	Sun	Tom	Water
Agapostemon texanus	0	1	1	0	40.29
Andrena cerasifolii	1	0	0	0	
Andrena chlorogaster	1	0	0	0	
Andrena w-scripta	1	0	0	0	
Anthophora urbana	0	1	1	1	22.50
Bombus californicus	1	1	1	1	76.69
Bombus crotchii	0	0	1	0	
Bombus melanopygus	1	0	1	0	
Bombus vandykei	0	0	1	0	
Bombus vosnesenskii	1	1	1	1	55.88
Ceratina dallatorreana	0	0	1	0	
Ceratina nanula	0	1	0	0	
Diadasia enavata	0	1	1	0	
Eucera actuosa	1	0	0	0	
Eucera frater albopilosa	1	0	0	0	
Halictus farinosus	1	1	1	0	181.85
Halictus ligatus	0	1	1	0	18.01
Halictus tripartitus	1	1	1	1	14.30
Hylaeus conspicuus	0	1	0	0	21.00
Hylaeus rudbeckiae	0	1	0	0	21.00
Lasioglossum mellipes	0	1	0	0	91.00
Lasioglossum titusi	0	1	0	0	91.00
Lasioglossum (D) incompletum	1	0	1	0	
Lasioglossum (D) megastictum	0	1	0	0	4.27
Lasioglossum (E) diatretum	1	1	0	0	101.00
Lasioglossum (E) granosum	1	1	0	0	101.00
Lasioglossum (E) sp. B	1	1	0	0	101.00
Megachile apicalis	0	0	1	0	
Megachile fidelis	0	0	1	0	
Megachile gentilis	0	1	0	0	
Megachile parallela	0	0	1	0	
Melissodes agilis	0	0	1	0	
Melissodes lupina	0	1	1	0	46.74
Melissodes robustior	0	1	1	0	46.74

Species	Pollination Traits				
	Binary				Efficiency
	Alm	Water	Sun	Tom	Water
Melissodes stearnsi	0	1	1	0	46.74
Melissodes tepida timberlakei	0	1	0	1	46.74
Osmia atrocyanea	0	0	1	0	
Osmia lignaria propinqua	1	0	0	0	
Osmia regulina	0	1	0	0	
Osmia texana	0	0	1	0	
Peponapis pruinosa	0	1	1	0	51.76
Xylocopa varipuncta	0	0	1	0	
Xylocopa tabaniformis	0	0	1	0	