NOT ALL COFFEE IS CREATED EQUAL: RESOURCE CONSTANCY AND ECOSYSTEM SERVICES IN SHADE-GROWN COFFEE PLANTATIONS

by

VALERIE PETERS

(Under the Direction of C. Ronald Carroll)

ABSTRACT

Shade-grown coffee plantations are ideal for testing ecological questions because they are more uniform than natural forest. In my dissertation I use shade-grown coffee plantations to investigate how resource constancy or the availability of resources, such as fruit and floral products influence ecosystem services. Specifically I focus on the ecosystem services of pollination and seed dispersal, and the providers of these services, bees and birds. I found that monthly fruit energy availability or FEA is strongly, positively correlated with bird species richness in shade-grown coffee plantations. I used a multi-scale occupancy model to understand the relationship of FEA to bird use of shade-grown coffee plantations. The best model included a negative effect of wind on detection and a positive effect of FEA on bird use of shade-grown coffee plantations. Conservation professionals should encourage coffee growers to plant shade trees based on their contribution to yearly or monthly FEA rather than focusing on the number of tree species per hectare only.

I experimentally planted the steady-state floral resource, *Hamelia patens*, in three of six sites. I found that bee species richness was higher in farms with the steady-state resource. Bee visitation to coffee flowers was measured during early and mass flowering periods in both farms with and without the steady state resource. While the steady state resource had a positive effect on bee conservation, the steady state resource had a negative effect on coffee production during the early flowering period. I recommend farmers to cover flowers on the steady state resource while the focal crop is flowering.

INDEX WORDS: Ecosystem services, fruit resources, frugivory, pollination, tropical ecology, FEA

NOT ALL COFFEE IS CREATED EQUAL: RESOURCE CONSTANCY AND ECOSYSTEM SERVICES IN SHADE-GROWN COFFEE PLANTATIONS

by

VALERIE PETERS

B.S. Pennsylvania State University, 1996

A Dissertation Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

DOCTOR OF PHILOSOPHY

ATHENS, GEORGIA

2009

NOT ALL COFFEE IS CREATED EQUAL: RESOURCE CONSTANCY AND ECOSYSTEM SERVICES IN SHADE-GROWN COFFEE PLANTATIONS

by

VALERIE PETERS

Major Professor:	C. Ronald Carroll
Committee:	James Affolter Robert Cooper Carl Jordan Kathy Parker

Electronic Version Approved:

Maureen Grasso
Dean of the Graduate School
The University of Georgia
December 2009

ACKNOWLEDGEMENTS

Doctoral Committee

I really want to express my gratitude towards the wonderful people who make up my committee; who have advised me for the past six years while working on my PhD. I very much appreciate all their fantastic support and advice. I especially want to thank Ron, Bob and Russ, who have been extraordinarily supportive, kind, inspiring, helpful and instructive. I feel truly honored and privileged to have had these three great men advising and supporting me throughout my PhD. It is in knowing that I must leave from their shelter that makes these final stages of my doctoral program feel bittersweet.

Family and Friends

I would like to thank my family and friends.

EarthWatch as a funding source for graduate research

From July 2006 to July 2009 I led 16 teams of EarthWatch volunteers in the field. In July 2005 I wrote a grant for equipment, travel and volunteer support to the EarthWatch Institute. Each year I received funds for equipment and travel, as well as between 4 and 10 volunteer field assistants for 15 day periods in July 2006, November 2006, February 2007, April 2007, June 2007, July 2007, November 2007, February 2008, April 2008, June 2008, November 2008, March 2009, April 2009, May 2009, July 2009 and August 2009. Working with EarthWatch volunteers has been both difficult and rewarding. Because of their backgrounds and sometimes age, EarthWatch volunteers can be limited in the type of data that they can collect. For instance some volunteers are not able to see birds clearly through binoculars because they use bifocals and have not had sufficient practice. If they cannot see the birds then they are unable to identify them, even with extensive training. The same is true for bees. Many native bee species are extremely small and are not easily identified by inexperienced volunteers. This has taught me to be inventive and station volunteers with jars so that they can catch the bee and bring it to me for identification. Volunteers have been extremely helpful in moving things between farms such as mist-nets, potted basil plants, malaise traps, and other equipment, as well as building structures, such as exclosures. There have also been some volunteers who either learn quickly or have relevant experience and so therefore have been invaluable in counting pollen grain slides, tracking radio-tagged Emerald Toucanets, catching bees for the bee reference collection, or other important data collection tasks. Although I have found their participation in my research to be highly rewarding, it is clear that in some more difficult tasks and for some participants that their data is less reliable and should not be utilized. Data collection methods have to be constantly repeated and monitored by the principal investigator in the field in order to ensure accurate data.

All in all, the most important and valuable aspect of leading an EarthWatch volunteer project is the environmental education component. I would commonly receive letters from volunteers after they returned home stating that the experience had impacted or changed their lives significantly. I hosted many teacher fellows who took careful notes during their EarthWatch volunteer experience so that they could teach their classrooms for years to come about the ecology of coffee farms. I also hosted fellows from different corporations such as British American Tobacco and Alcoa. These volunteers had to keep blogs, journals, or other detailed notes as part of their fellowship experience. They were also responsible for presenting details of their experience to other employees and leaders in the corporations who would then be challenged to incorporate conservation into the workplace or their individual lives. Some groups were even composed entirely of college students who were receiving college credit for their participation, and those students had to write papers about their experience. Many volunteers were older and they shared what they learned with family, friends, and co-workers. Spending two weeks in the field and participating in conservation research is really the best way to drive the message home for many conservation issues, and EarthWatch takes the lead in this method of conservation education. For that reason, I would highly recommend that other graduate students consider this non-traditional funding source during their graduate studies.

TABLE OF CONTENTS

Page

LIST OF TABLES

Page

LIST OF FIGURES

Page

CHAPTER1: INTRODUCTION AND LITERATURE REVIEW

Ecosystem Services

I investigated the complex interactions that birds and bees have with plants that constitute the shade-grown coffee agro-ecosystem in northwestern Costa Rica. Conceptually, I explored this system from the paradigm of ecosystem services. Ecosystem Services are generally divided, according to the Millennium Ecosystem Assessment, into the following four broad categories: provisioning, regulating, supporting, and cultural (Chan *et al.* 2006). Ecosystem services can include pest control (supporting), carbon sequestration (regulating), purification of water (regulating), pollination (supporting), timber production (provisioning), clean air (regulating), decomposition of waste (regulating), preservation of soils (supporting), biodiversity maintenance (supporting), nitrogen fixation (supporting), recreation (cultural) and seed dispersal (supporting) among others (Daily 1997). Even the regulation of diseases affecting human populations, such as Lyme disease, is an ecosystem service provided freely by intact ecosystems (Keesing and Ostfeld 2005). The Natural Capital Project, a partnership between Stanford University, The Nature Conservancy, and the World Wildlife Fund, was recently established to help integrate ecosystem services into everyday decision making around the world (Daily *et al*. 2009).

Costanza *et al*. (1997) estimated the annual global worth of natural goods and ecosystem services to be 33 trillion dollars per year, a value that exceeds the conventional market worth of the gross world product. These estimates were based on previous research from a total of 17 ecosystem services which include both non-market and market values, based on willingness-to-pay estimates. For marketed ecosystem services such as timber production, these willingness-to-pay estimates are values traced through current market prices, while the non-market ecosystem services such as recreation have been estimated through studies aimed at determining their value based on the responses from the recipients of that service in a particular region (Costanza *et al*. 1997). Assigning a concrete economic value to the services that ecosystems provide can prove to be quite difficult, however these authors proposed several clever ways to understand logically an estimated value of ecosystem services. One example was to determine what it would cost to replicate the particular service in a technologically produced, artificial biosphere, that is, the substitution value of the ecosystem service. This ground-breaking study demonstrates the enormous potential value of ecosystem services to society; however, the science of ecosystem valuation still lacks basic information regarding the affects of land-management decisions on ecosystems or multiple ecosystem services simultaneously (Daily *et al*. 2009). The rapid rate of ecosystem degradation through human activity further hinders efforts to study and assess the true value of many ecosystem services (MA 2005).

Determining the value of these services has proven to be an effective tool for engaging the public in conservation science. The Science Director for the Nature Conservancy in Frontiers of Ecology (2006), states that "Conservation will fail unless it better connects to people, and ecosystem services is the way to do that" (Gewin 2006). As conservation biology becomes more appropriately linked with human life and livelihoods, understanding ecosystem services becomes even more pressing (Kremen and Ostfeld 2005). Unfortunately, despite the fact that human life could not exist without these essential services provided freely by the environment, human domination of the landscape is quickly altering the capacity of ecosystems to provide these services (Kremen and Ostfeld 2005). For example, only recently have researchers begun to look at the role that native bees play in the pollination of crops and their habitat requirements despite the fact that more than 85% of global food production either benefits from or requires animal pollinators (Kremen *et al*. 2004, Kremen *et al*. 2007, Klein *et al*. 2008). New interests, such as that of pollination, often spring from the realization that a particular ecosystem service may be threatened or lost. For example, "colony collapse disorder", and other diseases of honeybees (refs), as well as its hybridization with the aggressive "Africanized" strains have raised awareness of the importance of pollinators. Thus, as honeybees decline and, in some places, become more dangerous to work with, the need to protect native bee species becomes more evident. However, many native bee species in the United States are considered to be in decline (Cane and Tepedino 2001) threatening the ecosystem service of pollination and food production.

Studies have shown that proximity to forest or natural areas may influence plant-animal interactions providing ecosystem services in agricultural lands, such as seed dispersal or pollination (Tewksberry 2002, Perfecto and Vandermeer 2002, Ricketts 2004). However, because it is not always feasible to have agricultural lands within close proximity (<100 meters) to natural forest, it is important for land managers and conservationists to understand the parameters required for maintaining ecosystem service providers on a year-round basis within the managed landscape itself. Conservation research on managed lands should creatively seek ways to improve the habitat quality of the entire agricultural matrix (Perfecto and Vandermeer 2002) through a better understanding of the components responsible for animal species persistence (Sekercioglu *et al*. 2007, Cruz-Angon and Greenberg 2005, Manning *et al*. 2006) especially focused on those species responsible for the provisioning of ecosystem services.

A species' functional contribution to a particular ecosystem service is another novel, intriguing field of research useful for management decisions in conservation initiatives

(Balvanera *et al*. 2005). In this concept, management practices can influence the abundance of target species. Then, if an individual species' functional contribution to an ecosystem service surpasses that of a diverse suite of organisms (Roubik 2002), then management practices for the conservation of that ecosystem service should target the increased abundance of the individual species rather than biodiversity (Balvanera *et al.* 2001).

Coffee, the crop and a model Agro-forestry system for ecological research

Coffee (*Coffea arabica* and *Coffea robusta* or *canephora*) is one of the world's most heavily traded commodities, second only to oil in terms of value of international trade for most of the post World War II period (Ponte 2002; Gordon *et al.* 2007). In 2002 coffee had a retail value of US$70 billion in the U.S., which surpasses the forecast of $56 billion for *total* US agricultural exports for 2003 (Vega *et al.* 2003). Coffee is not only valuable for its contribution to the global market, but also as one of the principal land use types in the neotropics. Coffee occupies approximately 50% of all permanent croplands within the Caribbean Islands, Columbia and Central America (http://apps.fao.org). However, the importance of coffee to the global market led many producers to increase farm size, productivity, or convert pasture to coffee in the late 1990's which led to an overproduction of coffee and subsequent price decline. In the beginning of this century, an international crisis was declared for coffee producers worldwide, causing many producers to abandon their farms or convert to other agricultural uses. An estimated 100 million people, however, are still dependent on coffee for income.

Utilizing coffee plantations to test ecological theories has recently been proposed in a Special Features section of Ecology (Klein *et al*. 2008, Cruz-Angon *et al*. 2008, Perfecto *et al*. 2008, Tscharntke *et al*. 2008, Van Bael *et al*. 2008) due to the uniformity and ease of manipulation within this human managed, poly-culture system. Within this controlled, easily-manipulated system it is perhaps best to begin the disentanglement of the complex web of life which provides humans with ecosystem services. Additionally, many ecosystem services directly relate to agricultural production, such as pollination and pest control and so therefore, coffee research offers a unique opportunity to understand how croplands can be restored or managed to take advantage of these important ecological services. Coffee plantations can therefore serve as model agro-ecosystems to study the habitat requirements of ecosystem service providers and how this influences the productivity of an agricultural crop.

Not all Coffee Farms are Created Equal

In the 1990's the Migratory Bird Center of the Smithsonian Institute was created by current directors Russ Greenberg and Robert Rice to determine the reasons for the declines of migratory bird species. Research focusing on different land use types in the neotropics determined that coffee plantations with certain levels of shade tree diversity and structure, canopy cover, and buffer windbreaks would provide sufficient habitat for migratory birds (Wunderle and Latta 2000, Greenberg *et al*. 1997, Perfecto *et al*. 2004). However, not all managed, poly-culture coffee plantations are equivalent in their ability to support a diversity of animal species (Greenberg *et al*. 1997, Carlo *et al*. 2004, Perfecto *et al*. 2003). The abundance and species of trees that have been planted within a coffee plantation vary and this variation is often used to categorize farms into management schemes from rustic (most tree species) to sun grown (least tree species) coffee (Miguel and Toledo 1999). The capacity of the farm to host a species rich assemblage of animals may depend upon the abundance and species of trees planted as shade in a coffee plantation (Johnson 2000, Carlo *et al*. 2004). Native tree species can be incorporated into coffee plantations as shade cover not only to enhance coffee quality (by reducing heat stress) and provide alternative products for farmers, but also to provide year-round resources to sustain populations of important ecosystem service providers.

Previous studies have compared forest to agro-forestry systems of varying levels of complexity, typically a monoculture versus a poly-culture, in terms of species richness, abundance, and/ or basic health of target animal species (Harvey 2007, Greenberg *et al*. 1997, Perfecto *et al*. 1997, Rey 1999). However, now that we have a better understanding that management intensification decreases diversity within many different groups of animal species, it is essential to design research that focuses on managed systems under similar levels of management intensification, in order to isolate the habitat components responsible for animal species utilization and/ or persistence (Cruz-Angon and Greenberg 2005).

Seed Dispersal

The ecosystem service of seed dispersal is responsible for maintaining genetic diversity within plant populations (Howe and Smallwood 1982). This is especially relevant to agro-ecology through the maintenance of genetically viable wild relatives of cultivated species because this genetic diversity maintains vigorous cultivars, especially within crops sensitive to rapidly evolving pests. Seed dispersal across a matrix of land uses within an agricultural landscape can affect the species richness and genetic diversity of plants comprising windbreaks, scattered trees, riparian edges and other forest remnants (Harvey 2000, Manning *et al*. 2006). In countries where deforestation rates are high, shade trees in agricultural landscapes may be the only seed bank for potential future forest restoration (Slocum 2001). The survival of the seed dispersers which move these seeds within disturbed or human dominated landscapes are critical to future forest regeneration.

Seed dispersing bird species are not only valuable for the contribution to the genetic viability of plant populations, but also they are often the most beautiful or colorful of birds in a region, and therefore may be important economically for their eco-tourism value. In countries such as Costa Rica, tourism contributes the greatest value to the Gross National Product, and the majority of tourists visiting Costa Rica seek to enjoy the country's biodiversity, forests and wildlife, especially birds. International birding is estimated to have great financial impact on developing nations such as Costa Rica, i.e. the six largest birding companies have 150 birding tours per year with approximately 12 participants per trip who pay $4,000 each (Sekercioglu 2003). Many of these tour participants come from countries, such as the U.S., where bird-watching has increased 332% since 1983 (Sekercioglu 2003).

Seed dispersing bird species have been found to consume more than 20 different plant species (Carlo *et al*. 2003) and up to 95 different species for some highly frugivorous birds, like the Emerald Toucanet (*Aulacorhynchus prasinus*) (Wheelwright 1984). Many previous studies of fruit consumption in birds have aimed to determine which fruit characteristics are responsible for avian preference, or if bird species rely on some combination of complimentary resources (Whelan 1994, Witmer 1998). It is known that some fruit consuming bird species prefer fruits that are high in lipids but low in carbohydrates (i.e. flycatchers and vireos), while others prefer fruits that are high in carbohydrates but low in lipids (i.e. thrushes). Other studies have shown that some birds select fruits based on crop size or secondary metabolite composition (Tsahar *et al*. 2002, Levey *et al*. 2006, Cipollini 2000, Whelan 1994). However when modification of the forest composition is changed due to human impact, the suitability or ability of the land to sustain bird species in healthy populations may depend on the quality of the tree species within the species particular foraging range. As biologists recommend guidelines (i.e. shade tree species diversity) to farmers for the conservation of resident seed dispersing birds in tropical America, it is essential to understand if fruit resources contribute to species persistence and how.

Pollination

The ecosystem service of pollination, alone, has an estimated value of $117 million (Costanza *et al*. 1997). Approximately two-thirds of the world's food crops require animal pollination (Ricketts *et al*. 2004). Of those remaining food crops which do not require animal pollination, it is likely that animal pollination may improve crop yield in some way (Javorek 2002, Cane 2005, Bosch 2006, Greenleaf 2006). For instance, previous studies have demonstrated that in coffee agro-ecosystems where pollinator diversity or abundance is high, the free service of pollination may result in increased pollen deposition (Ricketts 2004), seed set (Klein *et al*. 2003, Roubik 2002), or the fruit quality may improve (Roubik 2002, Philpott *et al*. 2006).

Contrasting results have been obtained; however, regarding the importance of biodiversity versus single species abundance for coffee pollination (Klein *et al*. 2008). For example, a study conducted in Panama found a 25% increase in coffee fruit mass on fruits pollinated exclusively by *Apis mellifera,* whereas when other native bees were present the percentage increase was only 7% overall (Roubik 2002). In contrast, a pollination study conducted in Indonesia concluded that a more species rich community of bees could increase seed set by 25% (Klein *et al*. 2003). One potential explanation for this difference may be the different species of coffee plants used for these two studies. *Coffea arabica* is a self-compatible species grown in Latin America, while *Coffea canephora* is a self-incompatible species grown in the lowlands of Indonesia, among other areas.

Through this research science is beginning to provide evidence of the economic importance of pollinators to the coffee yield. Unfortunately other research, however, has demonstrated that arthropod diversity, including ants and flying pollinators, generally decreases with increasing management intensification in coffee agro-ecosystems (Perfecto and Snelling 1995, Perfecto and Vandermeer 1996, Klein *et al.* 2002). Intensely managed coffee plantations with a limited species of shade trees may provide some habitat for native bees, but pollinator species richness drastically declines within the plantation when no native forest is nearby (Ricketts 2004). Small native bees seldom forage over distances greater than 100 meters (Roubik 1989), it would be essential for even small scale coffee plantations to be managed in such a way as to provide suitable habitat for these bees. Habitat variables which may be critical to sustaining native bees within coffee agro-ecosystems include canopy density, number of native tree species, floral diversity and phenology, and suitability of trees to host cavities for nesting.

In Costa Rica a recent study attempted to assign economic value to several large forest patches (> 20 hectares) bordering a large coffee plantation, based on the ecosystem service of pollination. The forest patches were estimated to provide approximately $62,000 per year in pollination service due to a 20% difference in seed set and a 27% difference in coffee quality between sites nearby vs. far from the forest patches (Ricketts *et al*. 2004). These same forest patches would only be valued at approximately $6,600 per year by the Costa Rican government under their Environmental Services Payment Program, and perhaps much less by other governments not participating in such innovative programs (Ricketts *et al*. 2004). Assigning values such as these to coffee plantations themselves with appropriate shade trees could be useful evidence to convince farmers to manage their farms with habitat elements determined to support native bees within the farm. For instance if particular plants provide floral or other important resources to bees, and planting those particular species within farms increases coffee yield and quality, then that particular plant species could hold a measurable economic value for coffee farmers.

Introduction Summary

My dissertation research focuses on how ecosystem services can be maintained in fragmented agricultural landscapes. I chose to direct my study towards the habitat requirements for the ecosystem service providers of seed dispersal and pollination in Costa Rican coffee farms. I selected study sites which were similarly managed and considered traditional poly-culture based on the classification system of Miguel and Toledo (1999). Management practices such as the number of shade tree species (Table 1.1), the number of individuals of shade trees per hectare (Table 1.2), percent canopy cover (Table 1.3), mean DBH per hectare (Table 1.4), and tree height distribution (Figure 1.1 and 1.2) were quite similar across sites. My study sites, then, were six replicates of the agro-forestry system, shade coffee, which were utilized to study the following objectives, comprising my dissertation:

- Evaluate how fruit energy availability affects bird species richness and use of traditional poly-culture coffee plantations.
- Evaluate the factors influencing the seasonal use of a 30 species resident bird community in traditional poly-culture coffee plantations.
- Evaluate the factors influencing the initial occupancy, monthly immigration, and monthly emigration of a 14 species resident bird community in traditional poly-culture coffee plantations.
- Investigate how constant resource availability affects native bee abundance and diversity, through the planting of a steady-state floral resource, *Hamelia patens*.

- Investigate how constant resource availability affects coffee flower pollination and seed set, through the planting of a native shrub with steady-state flowering, *Hamelia patens.*

Literature Cited

Balvanera, P., G. C. Daily, P. R. Ehrlich, T. H. Ricketts, S. A. Bailey, S. Kark, C. Kremen, and H. Pereira. 2001. Conserving biodiversity and ecosystem services. Science **291**:2047-2047.

Balvanera, P., C. Kremen, and M. Martinez-Ramos. 2005. Applying community structure analysis to ecosystem function: Examples from pollination and carbon storage. Ecological Applications **15**:360-375.

Bosch, J., W. P. Kemp, and G. E. Trostle. 2006. Bee population returns and cherry yields in an orchard pollinated with Osmia lignaria (Hymenoptera : Megachilidae). Journal of Economic Entomology **99**:408-413.

Cane, J. H. 2005. Pollination potential of the bee Osmia aglaia for cultivated red raspberries and blackberries (Rubus : Rosaceae). Hortscience **40**:1705-1708.

Cane, J. H. and V. J. Tepedino. 2001. Causes and extent of declines among native North American invertebrate pollinators: Detection, evidence, and consequences. Conservation Ecology **5**:art. no.-1.

Carlo, T. A., J. A. Collazo, and M. J. Groom. 2003. Avian fruit preferences across a Puerto Rican forested landscape: pattern consistency and implications for seed removal. Oecologia **134**:119-131.

Carlo, T. A., J. A. Collazo, and M. J. Groom. 2004. Influences of fruit diversity and abundance on bird use of two shaded coffee plantations. Biotropica **36**:602-614.

Chan, K. M. A., M. R. Shaw, D. R. Cameron, E. C. Underwood, and G. C. Daily. 2006.

Conservation planning for ecosystem services. Plos Biology **4**:2138-2152.

Cipollini, M. L. 2000. Secondary metabolites of vertebrate-dispersed fruits: evidence for adaptive functions. Revista Chilena De Historia Natural **73**:421-440.

Costanza, R., R. dArge, R. deGroot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R. V. Oneill, J. Paruelo, R. G. Raskin, P. Sutton, and M. vandenBelt. 1997. The value of the world's ecosystem services and natural capital. Nature **387**:253-260.

Cruz-Angon, A. and R. Greenberg. 2005. Are epiphytes important for birds in coffee plantations? An experimental assessment. Journal of Applied Ecology **42**:150-159.

Daily, G. C., S. Polasky, J. Goldstein, P. M. Kareiva, H. A. Mooney, L. Pejchar, T. H. Ricketts, J. Salzman, and R. Shallenberger. 2009. Ecosystem services in decision making: time to deliver. Frontiers in Ecology and the Environment **7**:21-28.

Daily, G.C. 1997. Nature’s Services. Island Press. Washington D.C.

Gewin, V. 2006. Billion dollar bugs. Frontiers in Ecology and the Environment **5**:228-228.

Gordon, C., R. Manson, J. Sundberg, and A. Cruz-Angon. 2007. Biodiversity, profitability, and vegetation structure in a Mexican coffee agroecosystern. Agriculture Ecosystems & Environment **118**:256-266.

Greenberg, R., P. Bichier, A. C. Angon, and R. Reitsma. 1997a. Bird populations in shade and sun coffee plantations in central Guatemala. Conservation Biology **11**:448-459.

Greenberg, R., P. Bichier, and J. Sterling. 1997b. Bird populations in rustic and planted shade coffee plantations of eastern Chiapas, Mexico. Biotropica **29**:501-514.

Greenleaf, S. S. and C. Kremen. 2006. Wild bee species increase tomato production and respond differently to surrounding land use in Northern California. Biological Conservation **133**:81-87.

Harvey, C. A. 2000. Colonization of agricultural windbreaks by forest trees: Effects of connectivity and remnant trees. Ecological Applications **10**:1762-1773.

Harvey, C. A. and J. A. G. Villalobos. 2007. Agroforestry systems conserve species-rich but modified assemblages of tropical birds and bats. Biodiversity and Conservation **16**:2257-2292.

Howe, H. F. and J. Smallwood. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics **13**:201-228.

Javorek, S. K., K. E. Mackenzie, and S. P. Vander Kloet. 2002. Comparative pollination effectiveness among bees (Hymenoptera : Apoidea) on lowbush blueberry (Ericaceae : Vaccinium angustifolium). Annals of the Entomological Society of America **95**:345-351.

Johnson, M. D. 2000. Effects of shade-tree species and crop structure on the winter arthropod and bird communities in a Jamaican shade coffee plantation. Biotropica **32**:133-145.

Keesing and Ostfield 2005. Biodiversity and disease risk: the case of Lyme disease. Conservation Biology 14: 722-728

Klein, A. M., S. A. Cunningham, M. Bos, and I. Steffan-Dewenter. 2008. Advances in pollination ecology from tropical plantation crops. Ecology **89**:935-943.

Klein, A. M., I. Steffan-Dewenter, D. Buchori, and T. Tscharntke. 2002. Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. Conservation Biology **16**:1003-1014.

Klein, A. M., I. Steffan-Dewenter, and T. Tscharntke. 2003. Fruit set of highland coffee increases with the diversity of pollinating bees. Proceedings of the Royal Society of London Series B-Biological Sciences **270**:955-961.

Kremen, C. and R. S. Ostfeld. 2005. A call to ecologists: measuring, analyzing, and managing ecosystem services. Frontiers in Ecology and the Environment **3**:540-548.

Kremen, C., N. M. Williams, M. A. Aizen, B. Gemmill-Herren, G. LeBuhn, R. Minckley, L. Packer, S. G. Potts, T. Roulston, I. Steffan-Dewenter, D. P. Vazquez, R. Winfree, L. Adams, E. E. Crone, S. S. Greenleaf, T. H. Keitt, A. M. Klein, J. Regetz, and T. H. Ricketts. 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. Ecology Letters **10**:299-314.

Kremen, C., N. M. Williams, R. L. Bugg, J. P. Fay, and R. W. Thorp. 2004. The area requirements of an ecosystem service: crop pollination by native bee communities in California. Ecology Letters **7**:1109-1119.

Levey, D. J., J. J. Tewksbury, M. L. Cipollini, and T. A. Carlo. 2006. A field test of the directed deterrence hypothesis in two species of wild chili. Oecologia **150**:61-68.

Manning, A. D., J. Fischer, and D. B. Lindenmayer. 2006. Scattered trees are keystone structures - Implications for conservation. Biological Conservation **132**:311-321.

Millenium Ecosystem Assessment

Moguel, P. and V. M. Toledo. 1999. Biodiversity conservation in traditional coffee systems of Mexico. Conservation Biology **13**:11-21.

Perfecto, I., A. Mas, T. Dietsch, and J. Vandermeer. 2003. Conservation of biodiversity in coffee agroecosystems: a tri-taxa comparison in southern Mexico. Biodiversity and Conservation **12**:1239-1252.

Perfecto, I. and R. Snelling. 1995. Biodiversity and the transformation of a tropical agroecosystem- ants in coffee plantations. Ecological Applications **5**:1084-1097.

Perfecto, I. and J. Vandermeer. 1996. Microclimatic changes and the indirect loss of ant diversity in a tropical agroecosystem. Oecologia **108**:577-582.

Perfecto, I. and J. Vandermeer. 2002. Quality of agroecological matrix in a tropical montane landscape: Ants in coffee plantations in southern Mexico. Conservation Biology **16**:174-182.

Perfecto, I. and J. Vandermeer. 2008. Spatial pattern and ecological process in the coffee agroforestry system. Ecology **89**:915-920.

Perfecto, I., J. Vandermeer, P. Hanson, and V. Cartin. 1997. Arthropod biodiversity loss and the transformation of a tropical agro-ecosystem. Biodiversity and Conservation **6**:935-945.

Perfecto, I., J. H. Vandermeer, G. L. Bautista, G. I. Nunez, R. Greenberg, P. Bichier, and S. Langridge. 2004. Greater predation in shaded coffee farms: The role of resident neotropical birds. Ecology **85**:2677-2681.

Philpott, S. M., S. Uno, and J. Maldonado. 2006. The importance of ants and high-shade management to coffee pollination and fruit weight in Chiapas, Mexico. Biodiversity and Conservation **15**:487-501.

Ponte, S. 2002. The 'latte revolution'? Regulation, markets and consumption in the global coffee chain. World Development **30**:1099-1122.

Rey, P. J. and F. Valera. 1999. Diet plasticity in blackcap (Sylvia atricapilla): The ability to overcome nutritional constraints imposed by agricultural intensification. Ecoscience **6**:429-438.

Ricketts, T. H. 2004. Tropical forest fragments enhance pollinator activity in nearby coffee crops. Conservation Biology **18**:1262-1271.

Ricketts, T. H., G. C. Daily, P. R. Ehrlich, and C. D. Michener. 2004. Economic value of tropical forest to coffee production. Proceedings of the National Academy of Sciences of the United States of America **101**:12579-12582.

Roubik, D. W. 1989. Ecology and Natural History of Tropical Bees. Cambridge University Press, N.Y., N.Y.

Roubik, D. W. 2002. Tropical agriculture - The value of bees to the coffee harvest. Nature **417**:708-708.

Sekercioglu, C.H. (2003). "Conservation through commodification" (PDF). *Birding* **35** (4): 394–402. http://www.stanford.edu/~cagan/SekerciogluBirding8-03.pdf.

Sekercioglu, C. H., S. R. Loarie, F. O. Brenes, P. R. Ehrlich, and G. C. Daily. 2007. Persistence of forest birds in the Costa Rican agricultural countryside. Conservation Biology **21**:482-494.

Slocum, M. G. 2001. How tree species differ as recruitment foci in a tropical pasture. Ecology **82**:2547-2559.

Tewksbury, J. J., D. J. Levey, N. M. Haddad, S. Sargent, J. L. Orrock, A. Weldon, B. J. Danielson, J. Brinkerhoff, E. I. Damschen, and P. Townsend. 2002. Corridors affect plants, animals, and their interactions in fragmented landscapes. Proceedings of the National Academy of Sciences of the United States of America **99**:12923-12926.

Tsahar, E., J. Friedman, and I. Izhaki. 2002. Impact on fruit removal and seed predation of a secondary metabolite, emodin, in Rhamnus alaternus fruit pulp. Oikos **99**:290-299.

Tscharntke, T., C. H. Sekercioglu, T. V. Dietsch, N. S. Sodhi, P. Hoehn, and J. M. Tylianakis. 2008. Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. Ecology **89**:944-951.

Van Bael, S. A., S. M. Philpott, R. Greenberg, P. Bichier, N. A. Barber, K. A. Mooney, and D. S. Gruner. 2008. Birds as predators in tropical agroforestry systems. Ecology **89**:928-934.

Vega, F. E., E. Rosenquist, and W. Collins. 2003. Global project needed to tackle coffee crisis. Nature **425**:343-343.

Wheelwright, N. T., W. A. Haber, K. G. Murray, and C. Guindon. 1984. Tropical fruit-eating birds and their food plants- a survey of a Costa Rican lower montane forest. Biotropica **16**:173-192.

Whelan, C. J. and M. F. Willson. 1994. Fruit choice in migrating North-American birds- Field and aviary experiments. Oikos **71**:137-151.

Witmer, M. C. 2001. Nutritional interactions and fruit removal: Cedar Waxwing consumption of Viburnum opulus fruits in spring. Ecology **82**:3120-3130.

Wunderle, J. M. and S. C. Latta. 1998. Avian resource use in Dominican shade coffee plantations. Wilson Bulletin **110**:271-281.

Wunderle, J. M. and S. C. Latta. 2000. Winter site fidelity of nearctic migrants in shade coffee plantations of different sizes in the Dominican Republic. Auk **117**:596-614

Table 1.1 List of plant species for each study site. Sites are listed by the first three letters of the farmers first name.

Plant Species	**ALV**	**GIL**	**ODI**	**OLD**	**OLI**	**RAF**
Acnistus arborensens	×	×	×	×	×	
Annona pruinosa						×
Bilia Columbiana		×	×	×		
Bursera simarouba					×	
Casimiroa edulis						×
Cecropia obtusifolia	×			×	×	×
Cestrum racemosum				×		
Citharexlym donnell-smithii				×		
Chrysophyllum brenesii		×	×	×		
Citrus spp.	×	×	×	×	×	×
Cordia eriostigma	×			×		×
Croton draco	×	×				
Croton niveus	×	×	×		×	×
Cupania glabra	×					×
Daphnopsis americana	×		×		×	
Diphysa Americana			×		×	
Diospyrus digyna			×			
Ehretia latifolia			×	×	×	×
Erybothria japoni			×			
Erythrna lancelata			×		×	×
Erytrina sp.			×			
Eugenia guatamalensis				×		
Eugenia jambos						×
Ficus costaricana	×		×			
Ficus lastericye		×		×		
Ficus pertusa		×		×		×
Guazuma ulmifolia	×					
Hamelia patens	×	×		×	×	
Inga mortoniana				×		
Inga punctata	×	×	×	×	×	×
Inga tondunzii				×		×
Lasiantha fructose	×			×	×	
Lonchocarpus olingathus	×		×			
Mangifera indica			×			
Montanoa guatamalensis	×		×		×	×
Mortoniodendron costaricense		×		×		
Musa spp.	×	×	×	×	×	×
Myrsina coriacea						×

Nectandra membranaceae				×		
Nectandra salicina		×				
Ocotea floribunda				×		
Ocotea monteverdensis		×		×		
Persea Americana		×	×	×	×	×
Psidium guayaba	×	×			×	×
Sapium glandulosum		×	×	×	×	×
Spondias sp.		×				×
Trema micrantha					×	
Trichilia martiana						
Trichilia havenensi			×			×
Xanthoxylum fagara	×	×	×			
Xanthoxylum monophyllum			×			
Total Species	**18**	**19**	**23**	**24**	**18**	**21**

Table 1.2 Number of stems per farm, listed with and without *Musa* spp., and two windbreak species, *Montanoa guatamelensis* and *Croton* sp.

Farm Name	**No. stems without windbreak sp. or Musa spp.**	**No. stems with windbreak sp. and Musa spp.**
ALVARO	57	207
GILBERT	53	646
ODILIO	44	464
OLDEMAR	71	263
OLIVIER	77	527
RAFAEL	71	473

Table 1.3 Site Percent Canopy Cover ($F_{5,95}$=1.68, p=0.15).

Farm	Percent Canopy Cover
ALVARO	62.02
GILBERT	65.97
ODILIO	64.70
OLDEMAR	62.02
OLIVIER	84.77
RAFAEL	67.39

Table 1.4 Site DBH, all trees ($F_{5,816}$=7.42, $p<0.0001$) DBH with and without two windbreak species and Musa spp. ($F_{5,379}$=4.166, $p<0.001$)

Farm Name	**Mean DBH without windbreak sp. or Musa spp.**	**Mean DBH with windbreak sp. and Musa spp.**
ALVARO	29.67	23.11
GILBERT	50.03	25.63
ODILIO	40.97	28.21
OLDEMAR	43.89	35.83
OLIVIER	30.62	29.45
RAFAEL	33.68	35.14

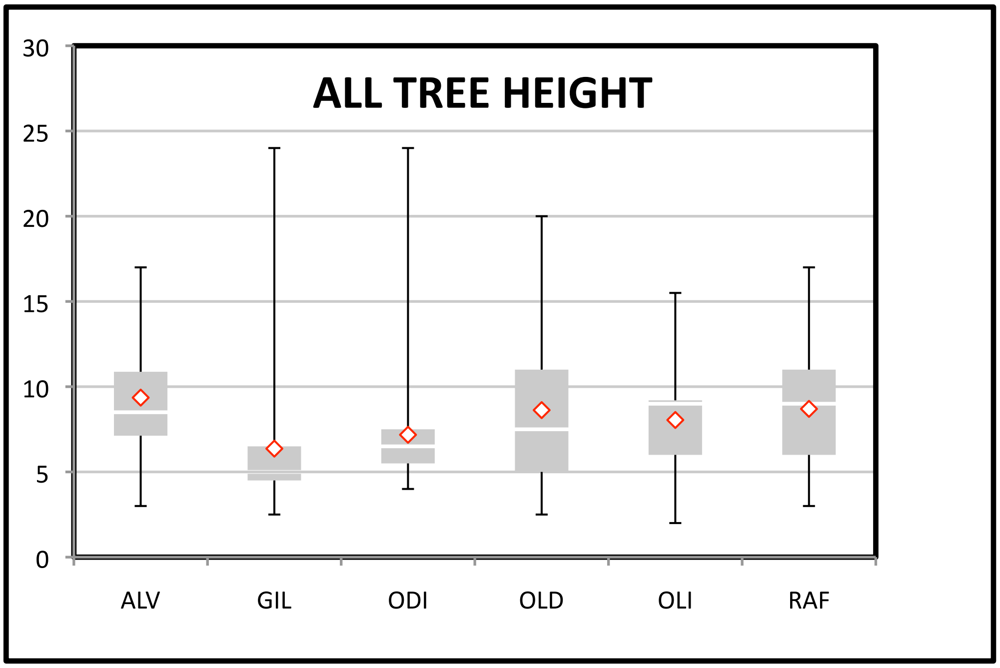


Figure 1.1 Box and whisker plot tree height. All trees, including two windbreak species and Musa spp.

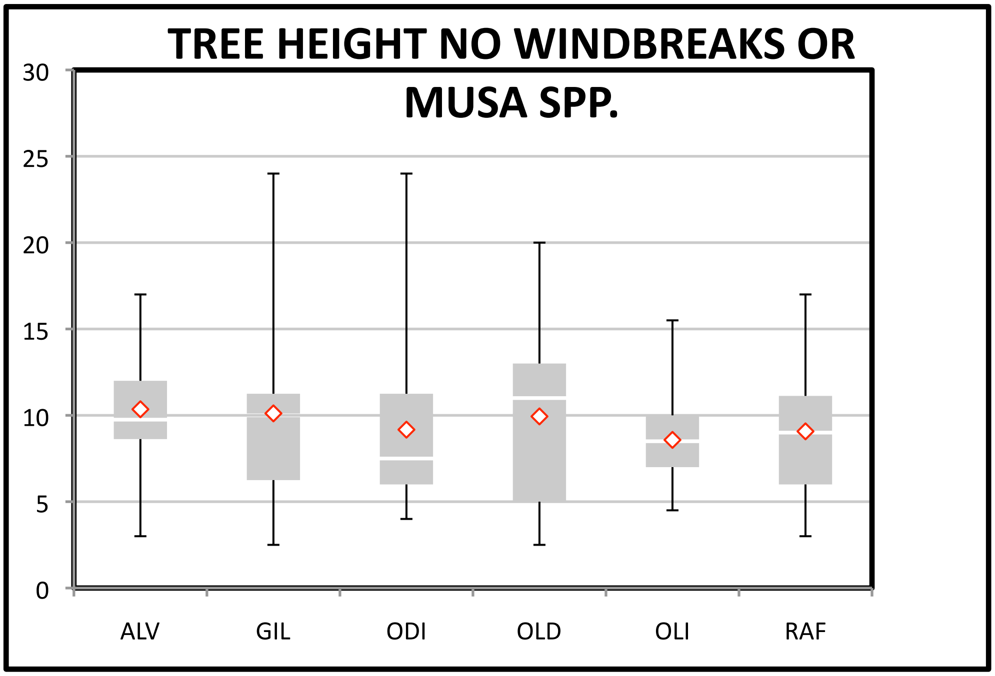


Figure 1.2 Box and whisker plot tree height, not including two windbreak species or Musa spp.

CHAPTER 2

BIRD COMMUNITY RESPONSE TO FRUIT ENERGY

Peters, V.E., C.R. Carroll, R.J. Cooper, and R. Greenberg. To be submitted to *Conservation Biology*.

ABSTRACT: Food resources have been widely studied in ecology as a limiting factor regulating animal communities; however, the heterogeneity of natural ecosystems makes it difficult to quantify this response. Additionally, the explanatory variable chosen to depict the food resource may not accurately describe the animal or community's perceived value. For example, fruit-frugivore studies utilizing the typical explanatory variable of fruit abundance have never documented a response of species richness.

Here we use Fruit Energy Availability (FEA) to demonstrate a community wide response by birds to fruit resources in replicated, one-hectare shade-grown coffee plots. The FEA of a study site mathematically combines a measure of fruit energy content with both a measure of fruit abundance and size. We found that a site's average monthly FEA was highly correlated (0.90) with a site's average bird species richness. Bird community composition turnover rates were also highly correlated with monthly changes in FEA. We used a multi-scale patch occupancy modeling approach to estimate bird detection rates at our sites. We then used these detection rates (34%) to estimate bird community occupancy (larger scale) and use (smaller scale) parameters. In our model, we estimated mean occupancy rates for the study sites at 99%, while mean bird monthly use rates were only 24%. The predictor, monthly site FEA, had a positive effect on bird community use.

These results demonstrate that fruit resources can influence the entire neo-tropical bird community, and that fluctuations of FEA can induce changes in the bird community of a particular site. This study shows that resource constancy contributes to higher levels of avian persistence, an important practical concept for management decisions. Management guidelines for agro-forestry systems could include planting fruiting species to achieve a minimum monthly FEA value which takes into account species richness as well as species persistence.

INTRODUCTION

The regulation of an animal population or community through limiting factors is a foundation of ecology (MacArthur 1958, Real and Brown 1991). Food resources have been widely studied in ecology as one primary factor constraining animal abundance or diversity (Schoener 1974, Poulin 1992, Holmes 1979, Loiselle 1991, Levey 1988, Kennedy *et al.* 2008). Depicting this relationship over a geographical scale, one ecological theory holds that the phenological gaps in fruit resource availability are responsible for the total absence of the exclusively frugivorous bird guild in the temperate zone (Stiles 1980, Stiles 1984, Kricher 2000). However, ecologists have struggled to find creative solutions to control for the experimental noise that is an implicit part of research conducted in the heterogeneous conditions of nature in order to advance a theory such as this (Wilbur 1976, Wilson and Simberloff 1969). Large-scale, replicated, manipulative experiments and mesocosm research are two examples of innovative ecological research that have successfully combated the problem of confounding factors (Morin 1981, Rowe 1995, Moegenburg and Levey 2003, Cruz-Angon 2005) though they are still limited by their abstraction from the natural world. Now, however, human agriculture has presented a new opportunity for ecologists to more rigorously test select potential factors proposed to be responsible for regulating animal populations (Perfecto 2008, Cruz-Angon 2008). Agriculture landscapes provide replicated, uniform patches where the confounding effect of natural heterogeneity can be held approximately constant while the regulating factor of interest is experimentally varied to study animal population or community response. Although many agricultural systems bear little resemblance to natural systems, shade-grown coffee, the focal system for this study, is often cited for its various similarities to a natural forest (Perfecto and Vandermeer 2008).

Human dominated landscapes comprise roughly two-thirds of all terrestrial habitats globally (Pimentel 1992), and of these, 133 million hectares is dedicated to permanent agriculture (CropLife International 2008). Under these current levels of human disturbance, on a local scale there is a potential to find the same extensive phenological gaps in fruit resource availability theorized responsible for the lack of a frugivorous bird guild in the temperate climate zone. Addressing the ecological question of how fruit resource availability or extensive time spans of fruit resource scarcity limits species richness patterns is an urgent question to ask in the face of predicted species extinctions in regions of high biodiversity (Sekercioglu 2004).

In addition to the frugivorous bird guild, habitat alteration can also be especially detrimental to omnivorous birds that use substantial amounts of fruit. Unlike insectivorous species, the nutritional intake of partial frugivores needs to be balanced between fruit and arthropod resources and among different types of fruit. Fruit resources can be low in protein, lipids and minerals (Izhaki 1993, Rode *et al*. 2006) requiring frugivores to seek these nutrients in animal matter in addition to locating fruit resources for essential fatty acids or minerals (O'Brien *et al*. 1998, Nelson *et al*. 2000). In addition, the spatial and temporal distance between fruit resources in actively managed agricultural lands can be much greater than levels that existed prior to deforestation. Therefore fruit resource or nutrient availability may be a limiting factor regulating bird populations in depauperate managed lands (Rode *et al.* 2006, Carlo and Collazo 2005).

Birds which rely on fruit to some degree may select resources, and therefore their location within the agricultural matrix, based on any or all of the following: available fruit mass or crop size (Whelan and Willson 1994, Saracco *et al*. 2005); vital nutrients or secondary metabolites (O'Brien *et al*. 1998, Tsahar *et al*. 2002, Cipollini 1997); or for their complementariness (Whelan and Willson 1994, Witmer 2001, Graham 2001). Previous research to determine the factors responsible for fruit choice by birds has focused on the selection of one of these possible explanations rather than formulating innovative ways to unite them. The gross Fruit Energy Availability (FEA) of an individual tree can combine both the available fruit mass and an indicator of nutrient value (caloric value of an individual fruit). FEA may be a better indicator of the value of a tree or location to fruit consuming birds, as well as elucidate limiting factors responsible for constraining species richness of birds within the agricultural landscape.

In Northern Latin America almost half (44%) of all permanent croplands are dedicated to the production of coffee (FAO 1991), and as such it is critical to conduct more ecological research to achieve a better understanding of the contribution towards species survival proffered by this extensive tropical agro-ecosystem. Furthermore, high-quality coffee is increasingly being grown in an agro-forestry poly-culture system where higher numbers of individual tree species can be incorporated than that typically found in other agricultural production systems, such as sugar cane or cattle pasture. These features make the coffee agro-ecosystem the most appropriate location within the agricultural matrix to test animal community response to constant versus fluctuating fruit resource availability within replicated, homogeneous plots.

Small scale agricultural lands in the tropics contribute to avian species survival because they are typically embedded within a patchwork of windbreaks, isolated trees and small forest patches or riparian zones (Luck and Daily 2003, Graham 2001, Sekercioglu *et al*. 2007, Tscharntke *et al*. 2008); however, different guilds of birds rely to differing degrees on these components of the human-dominated landscape (Sekercioglu *et al*. 2007). Understanding patterns of seasonal use by bird species of a particular component within the agricultural landscape, i.e. shade-grown coffee plots, can provide insight into answering the question *where* *within this patchwork do birds spend their time and why?* Fruit-consuming birds with higher levels of frugivory often locate more fruit resources in forest patches than in actively managed agricultural lands, and therefore may rely more heavily on these fragments (Graham 2001, Sekercioglu 2007). Generally, though ecological research within natural habitats has failed to demonstrate that the frugivore community does in fact respond to different levels of fruit resource availability (Saracco 2004, Moegenburg and Levey 2003, Haugaasen and Peres 2007). However, the heterogeneity of the natural areas where these studies have been conducted may make it difficult to detect a population or community response to changes in food resources on a local scale. Additionally, if fruit resource or gross energy availability influences bird utilization of managed coffee plantations within the agricultural matrix, then these plantations may be managed to increase their capacity to contribute to the persistence of bird populations. This study used a multi-scale patch occupancy modeling approach to answer the questions:

(1) How do bird communities respond to differences in fruit resource availability and gross Fruit Energy Availability (FEA) between similarly structured shade grown coffee plantations?

(2) Is bird community composition of coffee farms seasonal or constant and if seasonal, are seasonal changes in community composition related to monthly FEA?

METHODS

Study Site

Research was conducted at the San Luis Research Station in the San Luis valley of Northwestern Costa Rica (ca 10˚ 17’ N, 84˚ 48’ W) in the Municipality of Puntarenas. The San Luis Valley is the south-westernmost border of the Monteverde Cloud Forest Reserve, with an elevation between approximately 500 to 1200 m asl. Average monthly rainfall during dry season months (December through April) is approximately 50 mm and during wet season months (May through November) is approximately 550 mm. Due to conservation efforts in the region, the 56 hectare "environmentally-friendly" farm, Finca La Bella, was created to provide formerly landless farmers with a 1 to 2 hectare tract of land for subsistence farming. Finca la Bella (ca 900 to 1150 m asl) is a 56 hectare matrix of forest patches, windbreaks, <2 hectare pasture patches, and <2 hectare plantations of coffee. The small coffee plantations embedded within and around this matrix share similar management practices, history, and surrounding matrix quality (Perfecto 2002), and would be classified as Traditional Polyculture according to Moguel and Toledo's (1999) classification. Although plantation management practices such as high diversity of tree species and low chemical input do not differ among farms, the amount and diversity of fruit resources do differ among farms and among months thereby creating a natural experiment of variable resources in a constant structural environment.

Bird Sampling

Bird surveys were conducted during all months of 2008 except January and September, and farms were randomly visited three times per month for a total of 12 sampling surveys per month. In order to avoid observer bias, only one observer was responsible for conducting all bird surveys in 2008. This observer recorded all individual birds detected along fixed 100 meter transects, conducted by walking down slope, through the middle of each coffee plantation. Species were recorded based on sound and visual sightings. Each sampling day consisted of four rounds and each round consisted of walking slowly along the 100 meter transect for 45 minutes. Each sampling day lasted approximately four hours, between the hours of 700 and 1100AM, and only one farm was visited per day. Maximum and average wind velocity and ambient temperature were recorded, using a Weather Kestrel 2500, before the start of each transect.

Transects were initiated every hour beginning at 700AM until 1100AM. The time of day, transect number, bird species, activity and substrate were recorded for each individual observation. The bird's activity was chosen from the following categories: Perching, Vocalizing, Foraging, Moving, Nest Building, or Flew In/ Flew Out. The foraging activity category was only used when the bird was observed with a food item, and the food item was identified as Fruit; Nectar; Arthropod or Other. Substrate categories included: On ground, Coffee Plant, Croton Windbreak, Aster Windbreak, Tree or Shrub <4m, Tree >4m, Epiphyte or Vine. When possible, plant species of substrate categories were identified as well.

The top thirty most common, resident bird species were selected to evaluate a priori predictive models of seasonal occupancy based on environmental factors constraining occupancy. We also examined overall monthly bird species richness in response to available fruit resources only.

Fruit Sampling and FEA

Although tree diversity of all studied coffee plantations was approximately 20 species per hectare, there was high variation in the number of tree species which produce fleshy fruits consumed by birds (7 to 14 per farm). In addition, there was temporal variation of resource availability, and so consequently there was high variation in the mass of fruit resources available for consumption by birds, both over time and between farms. Fruit trees planted for human consumption were common on all farms with the most common species being *Psidium guayaba*, *Musa* spp., and *Citrus* spp. For the purposes of this study, *Musa* spp. was considered as a "tree" because of its large structure and the shade it provides in shade coffee farms. Although these fruit tree species are cultivated for human use, many bird species take advantage of extra fruits not harvested from these trees.

Fruit Energy Availability (FEA) indices were assigned for each coffee plantation on a monthly basis during all months of 2008 except January and September. Fruit Energy Availability was calculated by first determining the Fruit Availability Index (FAI) for each individual tree as 1= 1 to 10; 2= 11 to 25; 3= 26 to 50; 4= 51 to 100; 5= 101 to 200; 6= 201 to 500; 7= 501 to 1000; 8= 1001 to 10,000. The FAI for each individual tree or shrub was assigned by counting all fruits or, for larger trees, counting a random selection of branches and extrapolating this value to the number of branches in the entire tree. Approximately ten to thirty fruit samples were then collected from each plant species to obtain the fruit species' wet mass minus seeds and for caloric content analyses. After fruits were weighed, fruit samples were dried at 55˚C for approximately 12 h. Caloric values were determined on a per gram basis using a bomb calorimeter (Parr #1563). FEA values were then determined for each individual plant by multiplying the midpoint of the assigned individual plant FAI by the wet mass and caloric value of the fruit species so that **FEA** $= N * \hat{w} * \hat{C} \, (g^{-1})$ where N is the number of ripe fruits on an individual plant; $\hat{w}$ is the mean fruit wet mass for a plant species, and $\hat{C}$ is the mean kcal per gram of fruit for a plant species. For each month, then, the assigned FEA value for a farm represents the sum of each individual plant FEA; FEA $= \Sigma N_i w_i C_i$. We realize that bomb calorimeter derived calories may not be equivalent to the caloric value of the fruit actually assimilated. For the purposes of this analysis we assume that the calories measured in ripe fruit pulp are a reasonable approximation of the food energy gained by the birds.

Community Composition Analyses

We used the program EstimateS (Version 8.0.0 Copyright R. K. Colwell: http://viceroy.eeb.uconn.edu/estimates) which statistically estimates species richness and shared species from different samples. EstimateS computes a variety of shared species estimates and similarity indices based on either abundance or incidence-based datasets. We used summed species incidence frequencies from the entire year of the study in order to obtain an accurate estimate of shared species among farms as well as compare the similarity of the potential bird community utilizing the farms. For this analysis we used Chao Species Estimates for estimates of shared species and the Chao-Jaccard-Raw Incidence Based Similarity Index for community similarity comparisons because these calculations take into account unseen rare species and are especially useful in species rich communities, such as those of the tropics (Chao *et al*. 2005).

In order to analyze bird community monthly turnover rates for each farm, we chose the Classic Sorenson Incidence Based Similarity Index. This estimator uses summed incidence or presence/ absence data to estimate monthly community similarity or dissimilarity between two or more samples. The dissimilarity index computed for each month-to-month combination between two samples but within a site, then, is the same as the value of monthly community composition turnover rate for that site.

Occupancy Model

We used a Markov-Chain Monte-Carlo (MCMC) sampler in PyMC called MoBayes (Mordecai unpubl.) to assess model validity and examine the influence of select variables on 30 resident bird species' use (u) and occupancy (ψ) of Traditional Polyculture classified Coffee Plantations. The model MoBayes was created to address the problem of multiple scales in ecological research that seeks to understand species distributions. The model can simultaneously examine animal occupancy, (i.e. the large scale of distribution), and patterns of use, (i.e. the smaller scale). We used our biological knowledge of the study system to select a set of candidate models including the explanatory variables of Monthly FEA, Bird Substrate Use Category, Canopy Cover, Average DBH, Number of Trees >4m, and Number of Trees DBH >50cm. We compared all models using the mean Akaike's Information Criterion (AIC: Burnham and Anderson 2002). The direction and size of variable effects were determined using 95% Bayesian Credibility Intervals (2.5th to 97.5th percentile of the distribution).

A fundamental advantage for analyzing bird occupancy data with these more robust patch occupancy models is that, with repeated surveys, detection probability (p) can be estimated and then used to estimate occupancy and use parameters. In order to account for different rates of detection due to environmental factors, a Weather Kestrel 2500 was used to record temperature and maximum and average wind speeds prior to the start of each transect. For our dataset, ψ is the probability that a site, or coffee plantation, is occupied by a bird species, u is the probability that a bird species uses the site on a particular day given that the site is occupied, and p is the probability of detecting a bird species given that they are using the site on a particular day.

RESULTS

Fruit Energy Availability

Fruit caloric values were determined for 27 plant species bearing fruits consumed by birds within the six coffee plantations (Table 2.1). Ficus spp. was the most common fruit-bearing tree species, occurring in all but one coffee plantation, although the number of individuals of Ficus spp. was different among farms. Other common fruit-bearing tree species included *Inga punctata*, *Cecropia obtusifolia*, *Acnistus arborensens* and *Sapium glandulosum*. Of the 27 plant species tested for caloric values, *Ocotea monteverdenses* had the highest caloric value per gram (6.1 Kcal/ gram) and *Erybothria japonica* had the lowest caloric value per gram (3.55 Kcal/ gram).

The abundance of mature fruits varied temporally both within and among farms. Despite the fact that mid-rainy season (June- August) has typically been associated with peak fruit availability for this region, temporal variation in fruit abundance did not follow any consistent pattern among farms. Some plantations, therefore, had several monthly FEA values of 0 while the single largest monthly FEA value on any given farm was obtained during July 2008 for a farm with over 25 individuals of fruiting *Acnistus arborensens* (38,524.33 Kcal). However, for data analyses the 6 times that the monthly site FEA value exceeded 5,500 Kcal, the monthly FEA value for that particular farm was capped at 5,500 Kcal.

Birds

The total number of transects conducted on each farm from February 2008 to December 2008 was 116. Species incidence frequencies were obtained by summing all transects out of 116 for which an individual was detected. For all transects conducted (n=696), a total of 113 bird species was detected. Eighty species, or approximately 71%, were observed to consume fruit during this study (Table 2.2). For all 113 species, the total number of detections per farm was as follows: ALV= 761, GIL= 809, ODI= 684, OLD= 1401, OLI= 795, RAF= 1021 (n=116). The three letters represent the first letters in the names of the farm owners. Bird species richness varied both across months within a site and across sites, from 15 to 44 bird species when neotropical migrants were excluded, and from 18 to 55 bird species with neotropical migrants included (Fig. 2.1 and 2.2).

Seventy percent of all individual bird observations from February through August (n=4,168) were comprised of 18 bird species and the remaining approximately 90 bird species accounted for only 30% of all observations. Associations testing for preferential use of substrate categories by these two distinct groups demonstrated that the 90 bird species accounting for 30% of all observations, preferred the Tall Tree >4m category, while the 18 common birds distributed evenly across all other substrate categories: On Ground, Coffee Plant, Croton Windbreak, Aster Windbreak, and Tree or Shrub <4m (Table 2.3: χ^2=457, p<0.0000).

FEA constancy and Bird Community Stability

Estimates of bird species richness and similarity between sites using summed species incidence frequencies for the entire 10 month period indicated high similarity (0.8 to 0.94) of species composition among all sites (Fig. 2.3). Estimates of shared species between sites ranged from 55 to 90 using Chao Species Estimates (Fig. 2.4), while observed shared species ranged from 49 to 70. We expected that the bird species pool potentially occupying all sites would be highly similar, and thus allow us to examine monthly differences in utilization of a site by the bird community. Monthly Sorenson Incidence Based similarity indices between farms, utilizing monthly bird species incidence frequencies, were highly variable (0.36 to 0.75) and indicated a greater dissimilarity in bird community composition between sites when compared monthly.

We then compared monthly similarity within each site in order to determine monthly turnover rates in the bird community. For all within-site month-to-month combinations (n= 48), monthly bird community composition similarity, or the converse; turnover rates, was highly variable (0.41 to 0.85). Monthly turnover rates were correlated with monthly changes in FEA values (hereafter, ΔFEA). For almost all month-to-month combinations, a negative relationship was found between monthly within-site ΔFEA and monthly within-site species similarity, or in other words ΔFEA per month was positively correlated with bird community composition turnover rates. Strength of correlations among months differed (Fig. 2.5); however, a site's average monthly similarity index (Fig. 2.6) was negatively correlated with the site's average monthly ΔFEA (Fig. 2.7, r = -0.79).

FEA and Bird Species Richness

There was a significant difference among farms in monthly FEA (Fig. 2.8; $F_{5, 59}$= 3.47, p=0.0086), with the mean ranging from 824 Kcal to 3,743 Kcal. Additionally, monthly species richness was significantly different among sites, both for the actual number of observed bird species ($F_{5, 59}$= 11.59, p<0.0001) and for the estimated number of species ($F_{5, 59}$= 6.18, p<0.0001), (Fig. 2.9). The average monthly FEA for each site was positively strongly correlated with the average species richness per site for both observed (r=0.90) and estimated values (r=0.91), (Fig. 2.10). Monthly totals of bird species richness were graphed against monthly FEA values for each farm (Fig. 2.11a-f). Monthly totals of bird species richness were correlated with FEA for all months and all sites, (Fig. 2.12. Pearson's product-moment correlation = 0.72, CI: 0.57 to 0.82; t_{58}= 7.93, p<0.00001).

Occupancy Model

Our best model carried 100% of the weight of evidence (Table 2.4) and included the negative effect of wind on detection, no effect on occupancy, and the effects of monthly FEA, bird substrate use category and site all constraining bird community use. Model estimated occupancy rates of all sites for the 30 species bird community was very high (0.99 [BCI: 0.88 to 1.00]). Detection rates were negatively constrained by daily maximum wind speeds, with the mean model-estimated detection rate of 0.35 [BCI: 0.33 to 0.37]. We used the variable "site" to constrain the use parameter in order to obtain accurate estimates of daily use. Use of the site by the bird community was dependent upon the average monthly FEA of that site and the substrate category to which the birds belonged. The effect of monthly FEA on bird community use of a site was positive, with a BCI which did not span zero. The effect of a bird species belonging to the limited substrate category had a negative effect on use, while bird species belonging to the unlimited substrate category did not have a clear effect on use with a confidence interval that included zero.

DISCUSSION

Fruiting Phenology and Bird Response

Peak fruit abundance in the tropics typically coincides with peak rainy season, which for the region of this study occurs July through September. We found no marked periods of overall fruit abundance during July through September, or any other months, in the agro-forestry plots used in this study. However, this is not surprising, considering that a typical one-hectare patch of tropical forest harbors anywhere from 40 to over 100 tree species (Kricher 1997). In lowland forests of Costa Rica, for example, one study found 203 tree species in one hectare (Lieberman 1996). The low tree species richness of our study sites (18 to 24 tree species), when compared with tree species richness prior to human disturbance is most likely responsible for the lack of a distinct pattern in fruit seasonality. Each site had its own unique pattern of fruit resource availability, with marked variation in the availability of fruit resources both within sites and among sites. In one site, for example, 5 out of 10, or 50% of months had an FEA between 0 and only 250 Kcal, while two months had >5,000 Kcal. Due to this variation, there were extreme monthly changes in Kcal, i.e. 4,500 Kcal less in August than July. Bird species richness responded to the dramatic variation, with an average of 33 birds species present in the farm during the two months of >5,000 Kcal, and an average of only 18 during the months of <250 Kcal. Yet another farm maintained eight months of the ten with >2,000 Kcal and five months of the ten with >4,000 Kcal. Species richness at this site never fell below 26 bird species, and maintained 32 or higher bird species for seven out of ten months.

Community response

The bird community, and not just the frugivorous bird guild, responded to the temporal variation in fruit energy availability (FEA). Sites with a higher average of monthly FEA values had a higher average of monthly bird species richness, demonstrating the importance of fruit resources to a variety of bird guilds. In our model, FEA had a positive effect on bird community use in all six sites. The resident bird community used in our model included 14 frugivores, 4 flycatchers, 3 wrens, a woodpecker, 2 granivores, and 6 other bird species not classified into the frugivorous bird guild. A community wide response to fruit resources may be surprising given that no previous studies have found a response of species richness, even within the frugivorous bird guild only (Herrera 1998, Moegenberg and Levey 2003).

In our study 80 of 113 bird species were observed taking fruit, and this included bird species from virtually all bird guilds sighted during the study. The bird guild with the most species not observed to take fruit was the hummingbirds, which was comprised of 13 species. However, the two most common hummingbird species in our study sites were observed foraging on the fruits of *Cecropia obtusifolia* and *Acnistus arborensens*. The remaining 20 bird species were not observed to take fruit, however, at least ten of these species were observed less than 5 times in all sites combined. The classification of bird species into guilds is often not based on stomach content samples (Remsen *et al.* 1993), and foraging observations may be biased to more conspicuous maneuvers such as catching insects. These methods for classifying bird species may obscure the importance that fruit resources have in the diet of birds classified into the omnivorous or insectivorous guilds, such as woodpeckers or flycatchers. The results of this study underscore the lack of information available as to the degree that any bird species in any assigned guild depends upon fruit resources that would validate classification schemes such as obligate frugivore versus opportunistic frugivore (Gomes *et al*. 2008).

Some neo-tropical bird species have a greater propensity to flock when a mixed flock moves into the species home range (Pomara *et al*. 2007) possibly in an attempt to decrease predation risk. Although we observed very few mixed species flocks moving and foraging together, it is possible that bird species which were never observed to take fruit, i.e. three common wren species, were responding in a similar fashion, where the assemblage of birds gathered at the fruiting tree induced other birds, whose home range included the tree, to use that particular site within their home range more frequently. Furthermore, the relative openness of the coffee plantations has been discussed as an ecological trap for birds due to increased predation risk (Cohen and Lindell 2008), and so bird species may be more likely to use this agro-ecosystem when other bird species are present.

Bird Community Constancy

The bird community across all sites was highly similar. This high index of similarity assigned to the six sites demonstrates that the bird species pool utilizing the sites is the same. Despite this, there was a high degree of variation in community composition not only among the sites for different months, but also within the sites for different months. Monthly observed species richness ranged from 15 to 55 bird species, a difference of 40 bird species. The more dissimilar that bird community composition was at any given site was related to the amount of Kcal change, for half of all month-to-month comparisons. In some cases, however, this was difficult to assess because of the added community composition changes due to the influx or departure of migrants.

When all 8 month-to-month combinations were pooled, sites with a more constant level of FEA across the year of study had a lower average rate of change in the bird community. Stable or persistent animal populations are often supported by more consistent food resources, regardless of what level or quality of resources are available (Karr 1971, Illius and O'Conner 2000, Robb *et al*. 2008, Tremblay *et al*. 2005). This study demonstrates that resource constancy allows for higher levels of avian persistence, an important practical concept for management decisions. Management guidelines for agro-forestry systems could include a minimum monthly FEA value which takes into account species richness as well as species persistence.

Conservation Implications

Little is known about the home range size of many bird species in this region. However, of those species that have been studied to determine home ranges, several were only two to four hectares (Sekercioglu 2007). From a bird's perspective, a one-hectare coffee plantation in the middle of the two-hectare home range of a fruit-consuming bird could be especially detrimental if the necessary food resources have been removed and only non-fruit bearing tree species remain, especially during periods of low fruit abundance in surrounding forest patches. The bird species may perceive this habitat as high-quality because of the structural diversity; however, bird body condition and health could be affected through a lack of fruit resources providing essential macro or micronutrients (Rey and Valera 1999)

One third of resident avifauna in many neotropical forests are either frugivorous or granivorous and the number that occasionally consume fruits is even larger (Haugaasen and Peres 2007). Birds that consume fruit often provide the important ecosystem service of seed dispersal with approximately 70% of woody tree species dependent upon the removal of their seeds by mobile organisms (Ortiz-Pulido *et al.* 2000, Willson *et al.* 1989, Haugaasen and Peres

2007). Dispersal of seeds away from the parent plant may result in greater seedling survivability if escape from seed predators is important (Sekercioglu 2004). Seed dispersal also reduces between population heterozygosity and may affect long-term population viability by increasing the genetically effective population size (Manning *et al.* 2006). Seed dispersal across a matrix of land uses within an agricultural landscape can affect the species richness and genetic diversity of individual plants that comprise windbreaks, scattered trees, riparian edges and other forest remnants (Harvey 2000) as well as contribute to re-colonization of disturbed habitats (Sekercioglu 2004). In countries where deforestation rates are high, shade trees in agricultural landscapes become especially important pollen and seed sources for potential future reforestation (Jha and Dick 2008). The survival of the seed dispersers which move these seeds are key to future forest regeneration as well as tree species survivability. Unfortunately frugivorous birds, the major long-distance seed dispersers, are predicted to have a higher than average extinction rate over the next hundred years when compared to other bird guilds (Sekercioglu 2004).

However, this study demonstrates that bird community use of a particular component of the agricultural matrix can be increased with increasing levels of available fruit energy, as well as more constant with more constant levels of available fruit energy. Therefore, a central focus of agricultural management practices and restoration efforts tailored toward bird community conservation should include evaluating a plant species contribution to yearly fruit energy availability versus contemporary approaches tending to focus more on preferred plant species or minimum levels of plant species diversity.

Literature Cited

Anderson, D. R. and K. P. Burnham. 2002. Avoiding pitfalls when using information-theoretic methods. Journal of Wildlife Management **66**:912-918.

Carlo, T. A., J. A. Collazo, and M. J. Groom. 2004. Influences of fruit diversity and abundance on bird use of two shaded coffee plantations. Biotropica **36**:602-614.

Chao, A., R. L. Chazdon, R. K. Colwell, and T. J. Shen. 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecology Letters **8**:148-159.

Cipollini, M. L. 2000. Secondary metabolites of vertebrate-dispersed fruits: evidence for adaptive functions. Revista Chilena De Historia Natural **73**:421-440.

Cohen, E. B. and C. A. Lindell. 2004. Survival, habitat use, and movements of fledgling White-Throated Robins (Turdus assimilis) in a Costa Rican agricultural landscape. Auk **121**:404-414.

CropLife International 2008. http://www.croplife.org/PublicationDetail.aspx?Id={e8c4a241-c893-435e-afcb-f81b9842fa90}&wt.ti=Facts+and+Figures+-+the+status+of+global+agriculture+-+2008+(1.29+MB)

Cruz-Angon, A. and R. Greenberg. 2005. Are epiphytes important for birds in coffee plantations? An experimental assessment. Journal of Applied Ecology **42**:150-159.

Cruz-Angon, A., T. S. Sillett, and R. Greenberg. 2008. An experimental study of habitat selection by birds in a coffee plantation. Ecology **89**:921-927.

FAO 1991. http://www.fao.org/

Gomes, L. G. L., V. Oostra, V. Nijman, A. M. Cleef, and M. Kappelle. 2008. Tolerance of frugivorous birds to habitat disturbance in a tropical cloud forest. Biological Conservation **141**:860-871.

Graham, C. H. 2001. Factors influencing movement patterns of keel-billed toucans in a fragmented tropical landscape in southern Mexico. Conservation Biology **15**:1789-1798.

Harvey, C. A. 2000. Colonization of agricultural windbreaks by forest trees: Effects of connectivity and remnant trees. Ecological Applications **10**:1762-1773.

Haugaasen, T. and C. A. Peres. 2007. Vertebrate responses to fruit production in Amazonian flooded and unflooded forests. Biodiversity and Conservation **16**:4165-4190.

Herrera, C. M. 1998. Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: A 12-year study. Ecological Monographs **68**:511-538.

Holmes, R. T., R. E. Bonney, and S. W. Pacala. 1979. GUILD STRUCTURE OF THE HUBBARD BROOK BIRD COMMUNITY - MULTIVARIATE APPROACH. Ecology **60**:512-520.

Illius, A. W. and T. G. O'Connor. 2000. Resource heterogeneity and ungulate population dynamics. Oikos **89**:283-294.

Izhaki, I. 1993. INFLUENCE OF NONPROTEIN NITROGEN ON ESTIMATION OF PROTEIN FROM TOTAL NITROGEN IN FLESHY FRUITS. Journal of Chemical Ecology **19**:2605-2615.

Jha, S. and C. W. Dick. 2008. Shade coffee farms promote genetic diversity of native trees. Current Biology **18**:R1126-R1128.

Karr, J. R. 1971. STRUCTURE OF AVIAN COMMUNITIES IN SELECTED PANAMA AND ILLINOIS HABITATS. Ecological Monographs **41**:207-&.

Kennedy, B. P., K. H. Nislow, and C. L. Folt. 2008. Habitat-mediated foraging limitations drive survival bottlenecks for juvenile salmon. Ecology **89**:2529-2541.

Kricher 1997. A Neotropical Companion: An introduction to the animals, plants, and ecosystems of the new world tropics. Princeton University Press.

Levey, D. J. 1988. SPATIAL AND TEMPORAL VARIATION IN COSTA RICAN FRUIT

AND FRUIT-EATING BIRD ABUNDANCE. Ecological Monographs **58**:251-269.

Lieberman, D., M. Lieberman, R. Peralta, and G. S. Hartshorn. 1996. Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. Journal of Ecology **84**:137-152.

Loiselle, B. A. and J. G. Blake. 1991. TEMPORAL VARIATION IN BIRDS AND FRUITS ALONG AN ELEVATIONAL GRADIENT IN COSTA-RICA. Ecology **72**:180-193.

Luck, G. W. and G. C. Daily. 2003. Tropical countryside bird assemblages: Richness, composition, and foraging differ by landscape context. Ecological Applications **13**:235-247.

Macarthur, R. H. 1958. Population ecology of some warblers of Northeastern coniferous forests. Ecology **39**:599-619.

Manning, A. D., J. Fischer, and D. B. Lindenmayer. 2006. Scattered trees are keystone structures - Implications for conservation. Biological Conservation **132**:311-321.

Moegenburg, S. M. and D. J. Levey. 2003. Do frugivores respond to fruit harvest? An experimental study of short-term responses. Ecology **84**:2600-2612.

Moguel, P. and V. M. Toledo. 1999. Biodiversity conservation in traditional coffee systems of Mexico. Conservation Biology **13**:11-21.

Morin, P. J. 1981. PREDATORY SALAMANDERS REVERSE THE OUTCOME OF COMPETITION AMONG 3 SPECIES OF ANURAN TADPOLES. Science **212**:1284-1286.

Nelson, S. L., M. A. Miller, E. J. Heske, and G. C. Fahey. 2000. Nutritional consequences of a change in diet from native to agricultural fruits for the Samoan fruit bat. Ecography **23**:393-401.

O'Brien, T. G., M. F. Kinnaird, E. S. Dierenfeld, N. L. Conklin-Brittain, R. W. Wrangham, and S. C. Silver. 1998. What's so special about figs? Nature **392**:668-668.

Ortiz-Pulido, R., J. Laborde, and S. Guevara. 2000. Fruit-eating habits of birds in a fragmented landscape: Implications for seed dispersal. Biotropica **32**:473-488.

Perfecto, I. and J. Vandermeer. 2002. Quality of agroecological matrix in a tropical montane landscape: Ants in coffee plantations in southern Mexico. Conservation Biology **16**:174-182.

Perfecto, I. and J. Vandermeer. 2008. Spatial pattern and ecological process in the coffee agroforestry system. Ecology **89**:915-920.

Pimentel, D., U. Stachow, D. A. Takacs, H. W. Brubaker, A. R. Dumas, J. J. Meaney, J. A. S. Oneil, D. E. Onsi, and D. B. Corzilius. 1992. CONSERVING BIOLOGICAL DIVERSITY IN AGRICULTURAL FORESTRY SYSTEMS - MOST BIOLOGICAL DIVERSITY EXISTS IN HUMAN-MANAGED ECOSYSTEMS. Bioscience **42**:354-362.

Pomara, L. Y., R. J. Cooper, and L. J. Petit. 2007. Modeling the flocking propensity of passerine birds in two Neotropical habitats. Oecologia **153**:121-133.

Poulin, B., G. Lefebvre, and R. McNeil. 1992. TROPICAL AVIAN PHENOLOGY IN RELATION TO ABUNDANCE AND EXPLOITATION OF FOOD RESOURCES. Ecology **73**:2295-2309.

Real, L.A. and J.H. Brown. 1991. Foundations in Ecology. Classic papers with commentaries. University of Chicago

Remsen, J. V., M. A. Hyde, and A. Chapman. 1993. THE DIETS OF NEOTROPICAL TROGONS, MOTMOTS, BARBETS AND TOUCANS. Condor **95**:178-192.

Rey, P. J. and F. Valera. 1999. Diet plasticity in blackcap (Sylvia atricapilla): The ability to overcome nutritional constraints imposed by agricultural intensification. Ecoscience **6**:429-438.

Robb, G. N., R. A. McDonald, D. E. Chamberlain, and S. Bearhop. 2008. Food for thought: supplementary feeding as a driver of ecological change in avian populations. Frontiers in Ecology and the Environment **6**:476-484.

Rode, K. D., C. A. Chapman, L. R. McDowell, and C. Stickler. 2006. Nutritional correlates of population density across habitats and logging intensities in redtail monkeys (Cercopithecus ascanius). Biotropica **38**:625-634.

Rowe, C. L. and W. A. Dunson. 1995. Individual and interactive effects of salinity and initial fish density on a salt marsh assemblage. Marine Ecology-Progress Series **128**:271-278.

Saracco, J. F., J. A. Collazo, and M. J. Groom. 2004. How do frugivores track resources? Insights from spatial analyses of bird foraging in a tropical forest. Oecologia **139**:235-245.

Saracco, J. F., J.A. Collazo, M. J. Groom and T.A. Carlo. 2005. Crop size and fruit neighborhood effects on bird visitation to fruiting *Schefflera morototoni* trees in Puerto Rico. Biotropica **37**: 81-87

Schoener, T. W. 1974. RESOURCE PARTITIONING IN ECOLOGICAL COMMUNITIES. Science **185**:27-39.

Sekercioglu, C. H., G. C. Daily, and P. R. Ehrlich. 2004. Ecosystem consequences of bird declines. Proceedings of the National Academy of Sciences of the United States of America **101**:18042-18047.

Sekercioglu, C. H., S. R. Loarie, F. O. Brenes, P. R. Ehrlich, and G. C. Daily. 2007. Persistence of forest birds in the Costa Rican agricultural countryside. Conservation Biology **21**:482-494.

Stiles, E. W. 1980. PATTERNS OF FRUIT PRESENTATION AND SEED DISPERSAL IN BIRD-DISSEMINATED WOODY-PLANTS IN THE EASTERN DECIDUOUS FOREST. American Naturalist **116**:670-688.

Stiles, E. W. 1984. FRUIT FOR ALL SEASONS. Natural History **93**:42-&.

Tremblay, J. P., I. Thibault, C. Dussault, J. Huot, and S. D. Cote. 2005. Long-term decline in white-tailed deer browse supply: can lichens and litterfall act as alternative food sources that preclude density-dependent feedbacks. Canadian Journal of Zoology-Revue Canadienne De Zoologie **83**:1087-1096.

Tsahar, E., J. Friedman, and I. Izhaki. 2002. Impact on fruit removal and seed predation of a secondary metabolite, emodin, in Rhamnus alaternus fruit pulp. Oikos **99**:290-299.

Tscharntke, T., C. H. Sekercioglu, T. V. Dietsch, N. S. Sodhi, P. Hoehn, and J. M. Tylianakis. 2008. Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. Ecology **89**:944-951.

Whelan, C. J. and M. F. Willson. 1994. FRUIT CHOICE IN MIGRATING NORTH-AMERICAN BIRDS - FIELD AND AVIARY EXPERIMENTS. Oikos **71**:137-151.

Wilbur, H. M. 1976. DENSITY-DEPENDENT ASPECTS OF METAMORPHOSIS IN AMBYSTOMA AND RANA-SYLVATICA. Ecology **57**:1289-1296.

Willson, M. F., A. K. Irvine, and N. G. Walsh. 1989. VERTEBRATE DISPERSAL SYNDROMES IN SOME AUSTRALIAN AND NEW-ZEALAND PLANT-COMMUNITIES, WITH GEOGRAPHIC COMPARISONS. Biotropica **21**:133-147.

Wilson, E. O. and Simberlo.Ds. 1969. EXPERIMENTAL ZOOGEOGRAPHY OF ISLANDS -

DEFAUNATION AND MONITORING TECHNIQUES. Ecology **50**:267-&.

Witmer, M. C. 2001. Nutritional interactions and fruit removal: Cedar Waxwing consumption of Viburnum opulus fruits in spring. Ecology **82**:3120-3130.

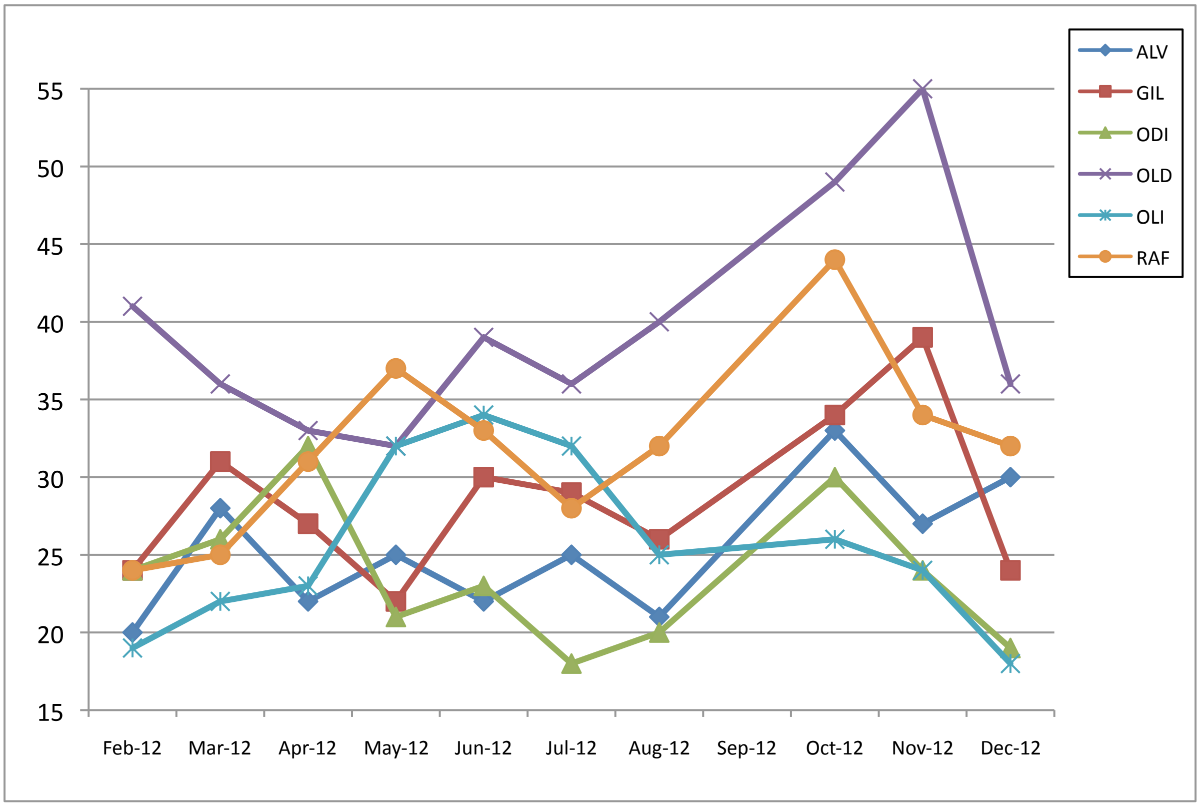


Figure 2.1. Monthly bird species richness. Includes both residents and migrants.

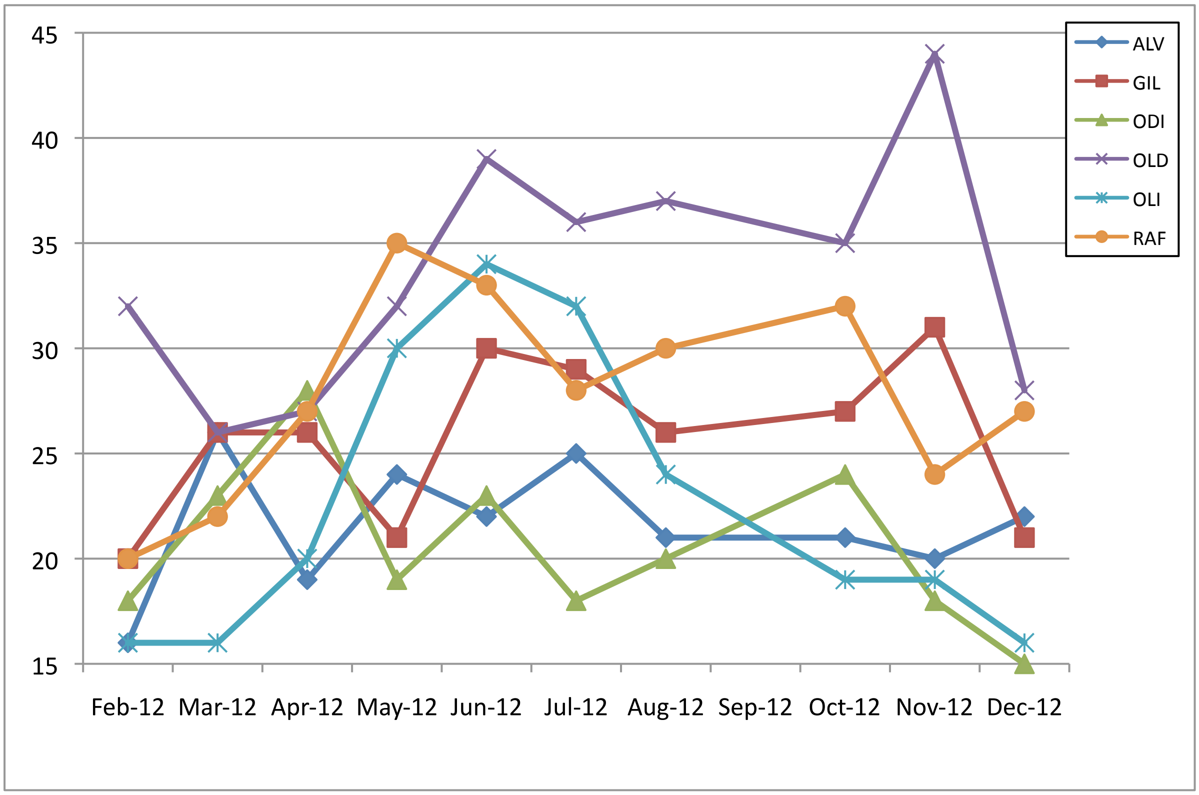


Figure 2.2. Monthly bird species richness. Includes resident species only.

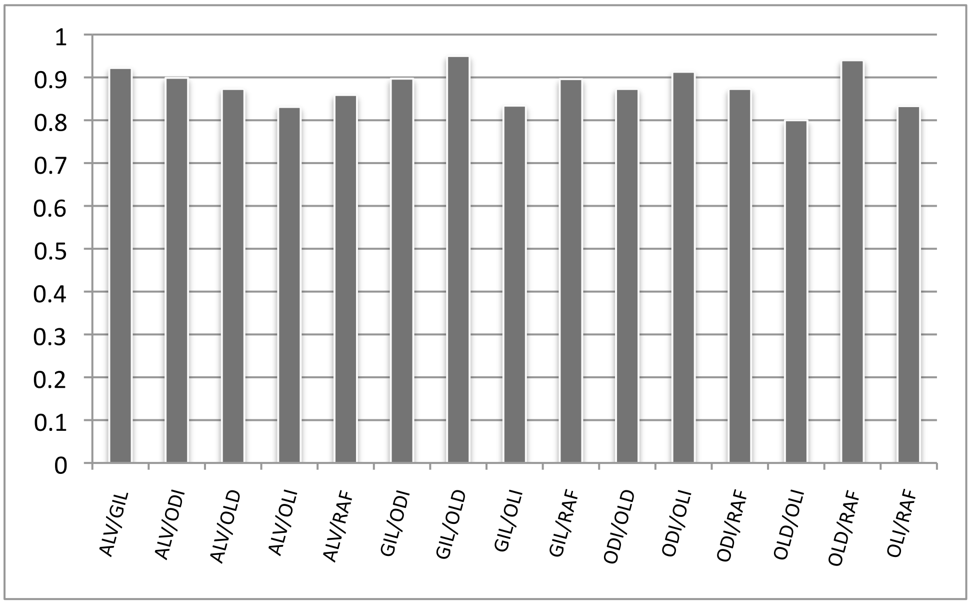


Figure 2.3. Chao-Jaccard-Raw Incidence Based Similarity Indices. The three letters represent the farmer's first name.

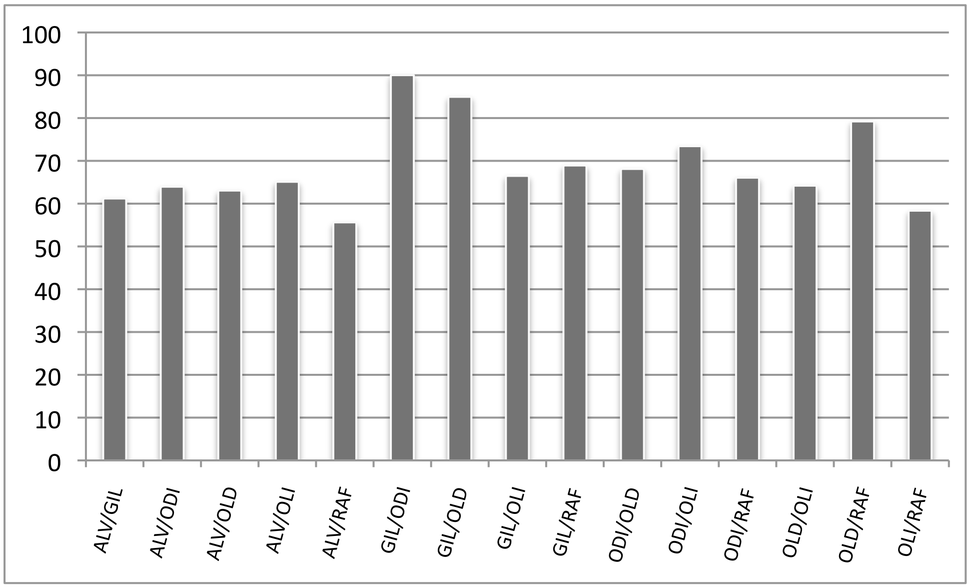


Figure 2.4. Chao Estimated Shared Species. The three letters represent the farmer's first name.

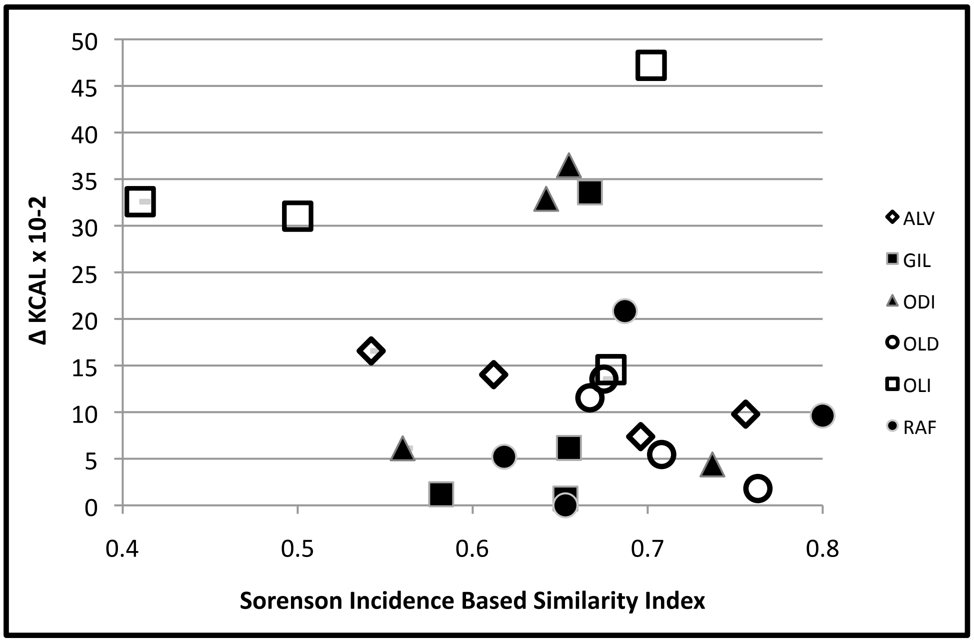


Figure 2.5. February to August bird community composition similarity within sites. Horizontal Axis: Sorenson Incidence Based Similarity Indices. Vertical axis are changes (either increase or decrease) in overall Calories per site (FEA) between the months of February and March (r = -0.77), March and April (r = -0.39), April and May (r = -0.44), and July and August (r = -0.74).

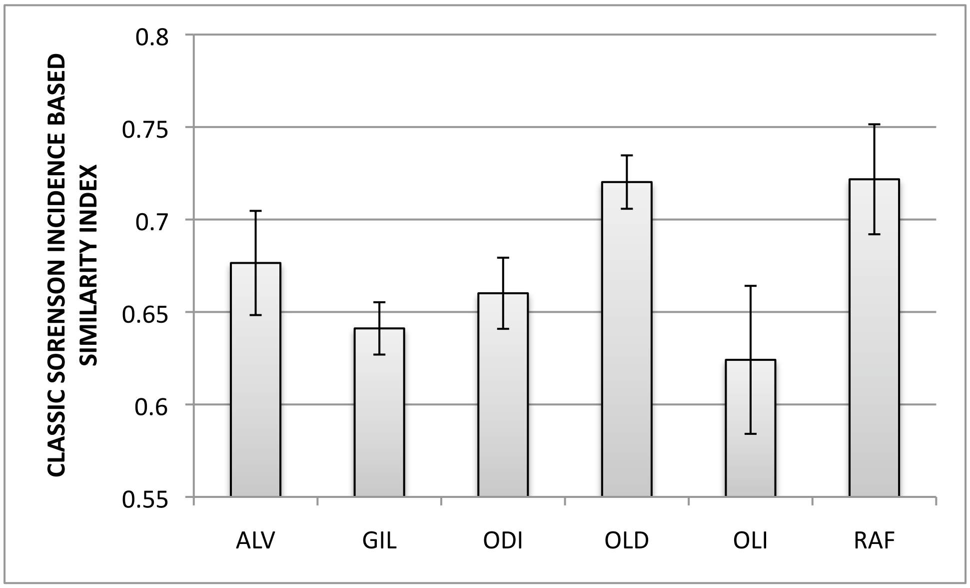


Figure 2.6. Average Monthly Turnover Rates (Classic Sorenson Similarity Indices). ($F_{5,47}$= 2.42, p=0.05)

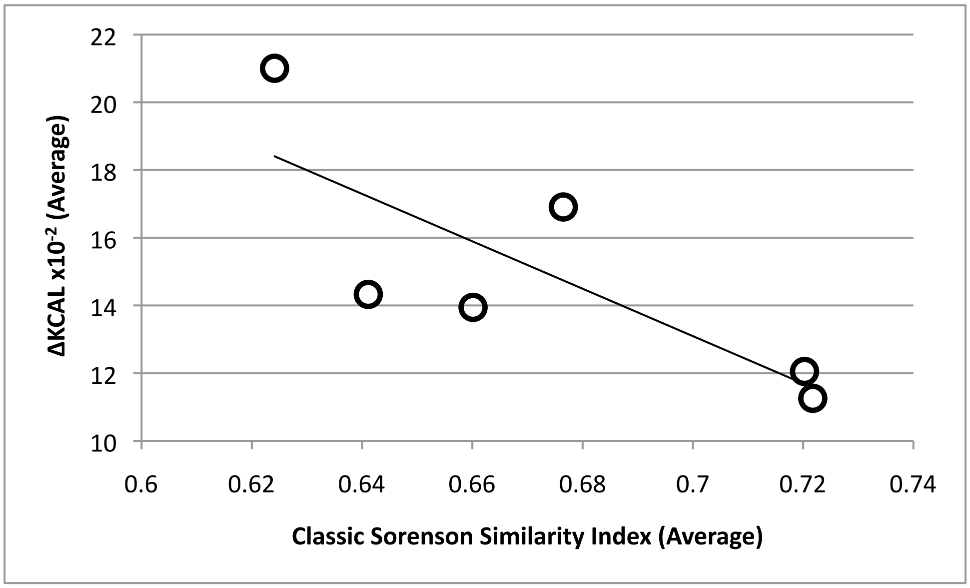


Figure 2.7. Average monthly turnover rates (Classic Sorenson Incidence- Based Similarity Indices) and Average monthly change in site Caloric Value (FEA). (r= -0.79)

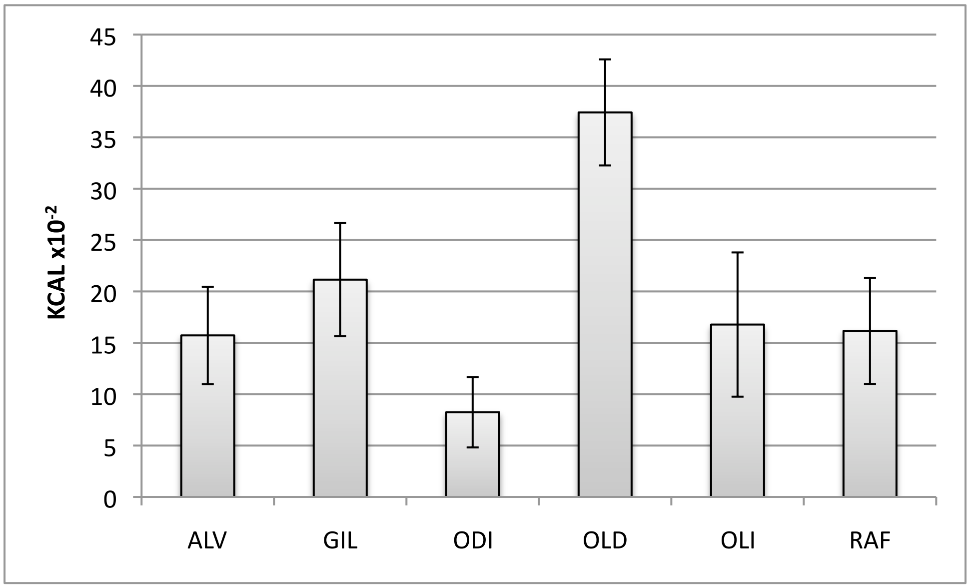


Figure 2.8. Monthly FEA per farm. **(**$F_{5,\ 59}$= 3.47, p=0.0086**)**

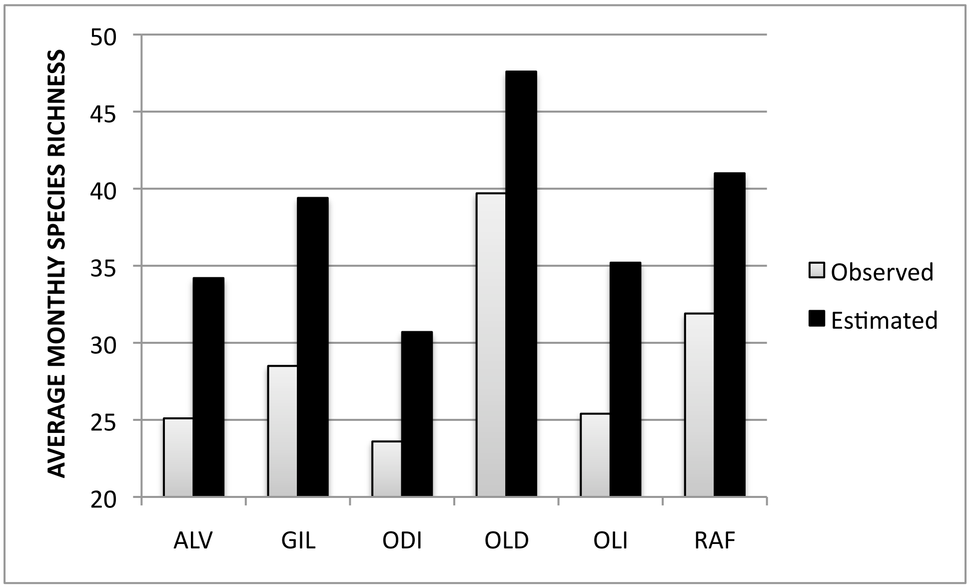


Figure 2.9. Monthly Species Richness**.** (observed species: $F_{5,\,59}$= 11.59, p<0.0001); (estimated species: $F_{5,\,59}$= 6.177, p<0.0001)

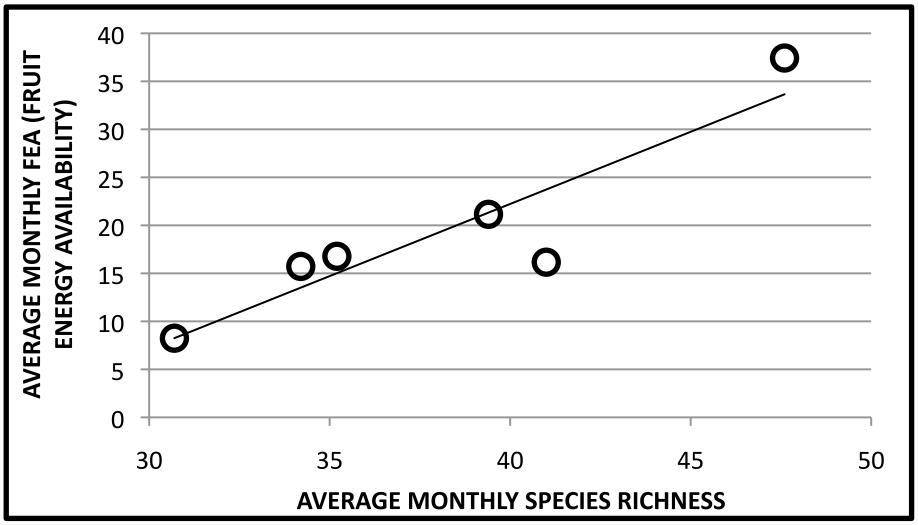


Figure 2.10. Average monthly FEA and Average monthly species richness (Estimated Species Richness; r=0.91, F=20.28, p = 0.011/ Observed Species Richness r=0.90)

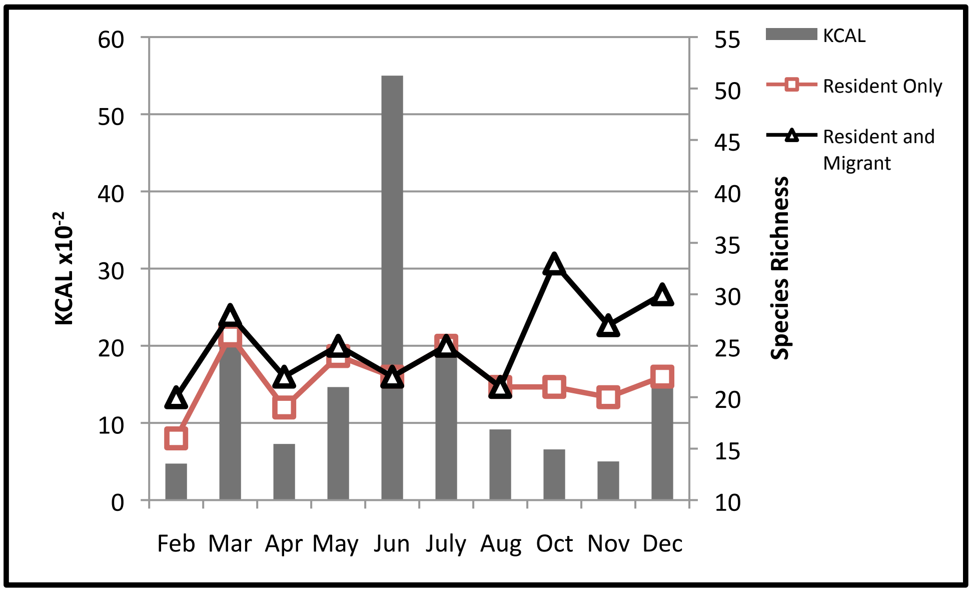


Figure 2.11a. Monthly Calories and Bird Species Richness (ALV)

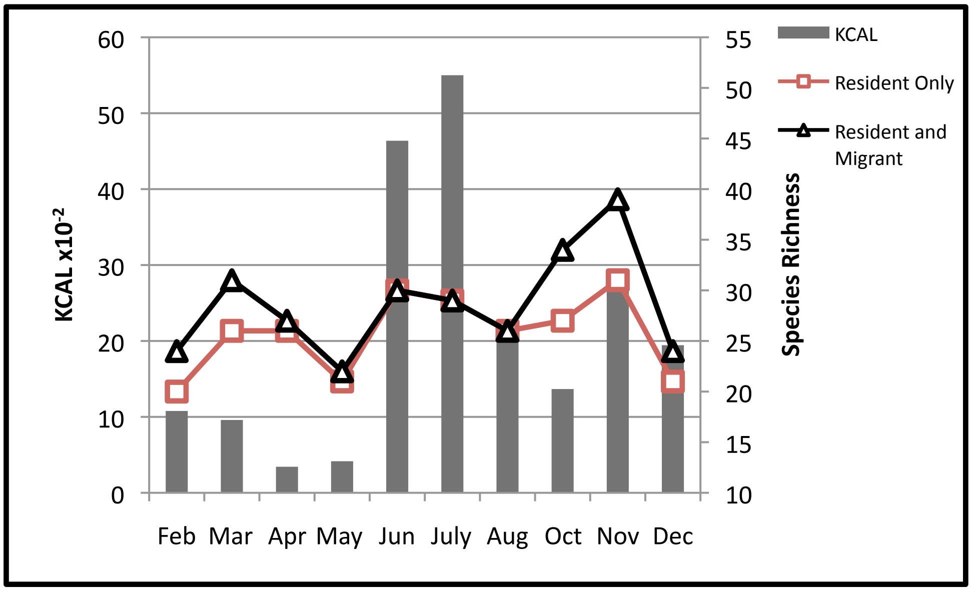


Figure 2.11b. Monthly Calories and Bird Species Richness (GIL)

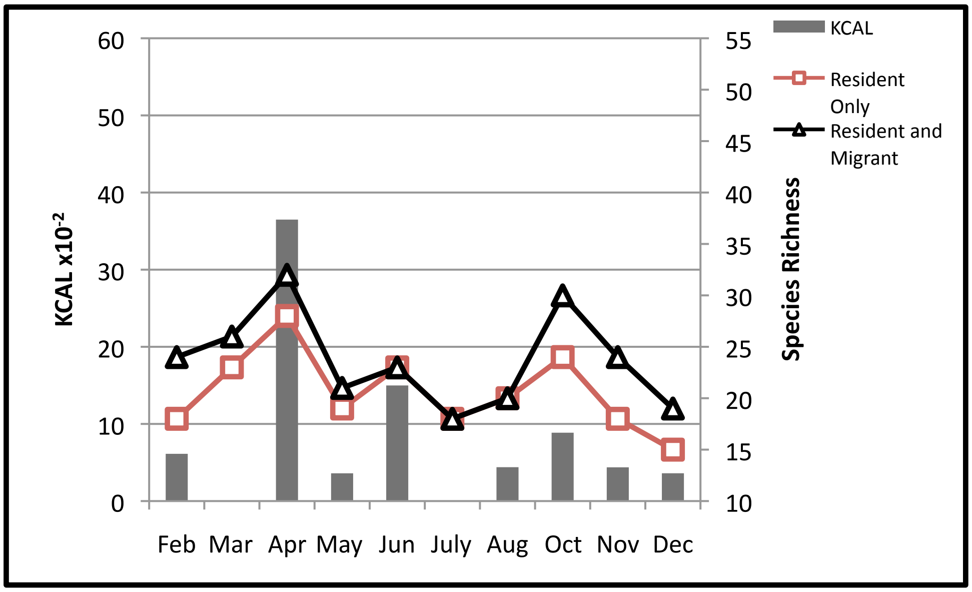


Figure 2.11c. Monthly Calories and Bird Species Richness (ODI)

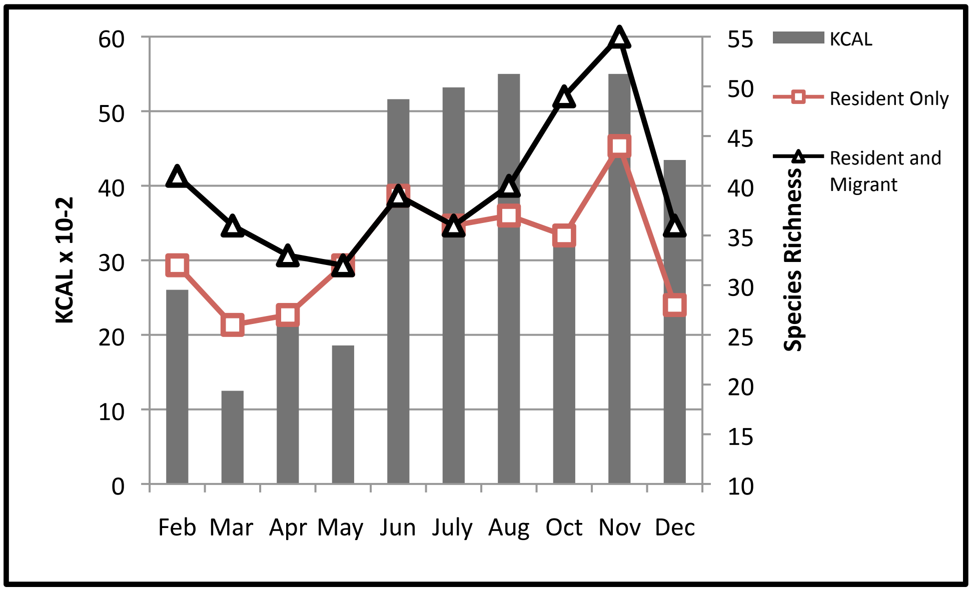


Figure 2.11d. Monthly Calories and Bird Species Richness (OLD)

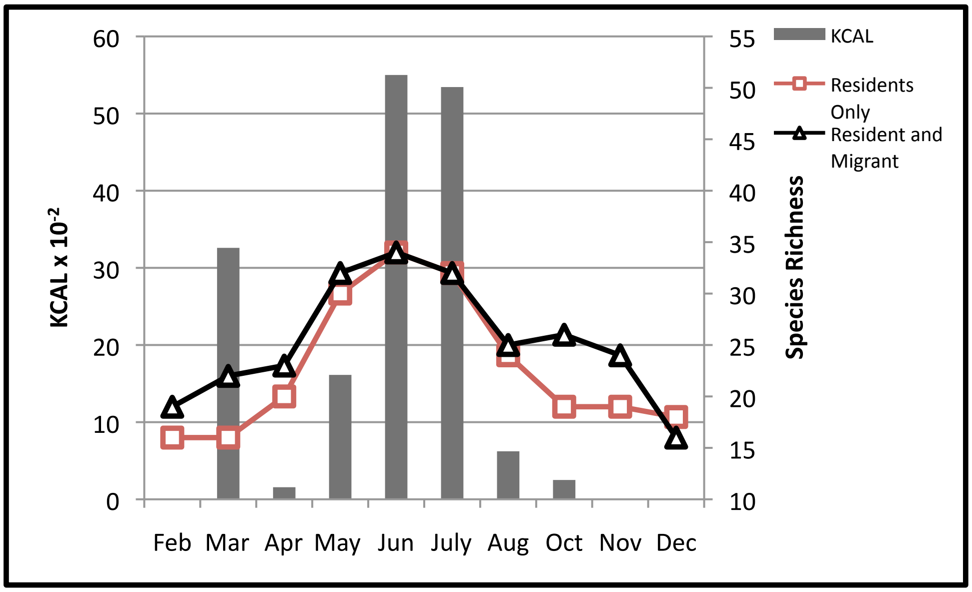


Figure 2.11e. Monthly Calories and Bird Species Richness (OLI)

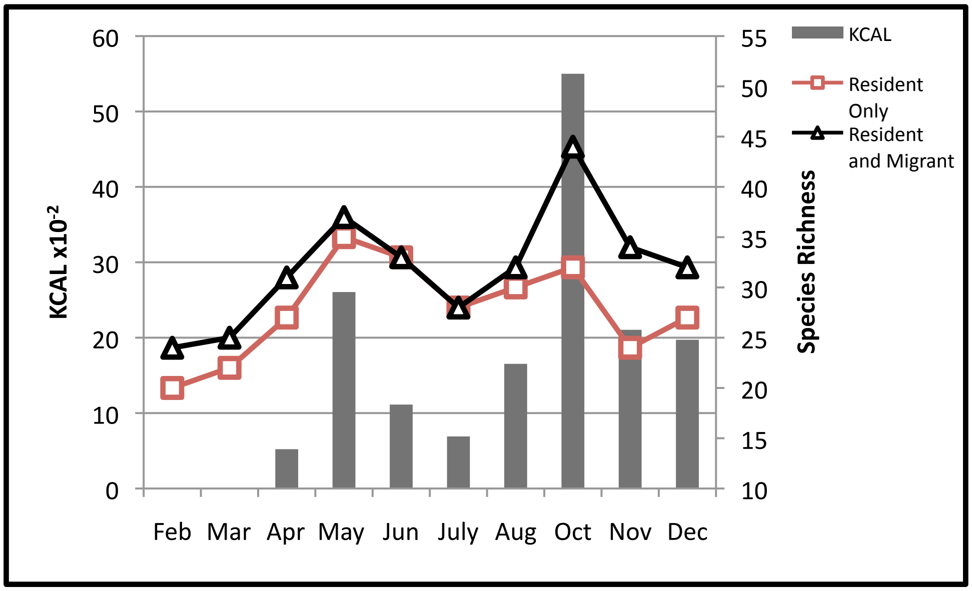


Figure 2.11f. Monthly Calories and Bird Species Richness (RAF)

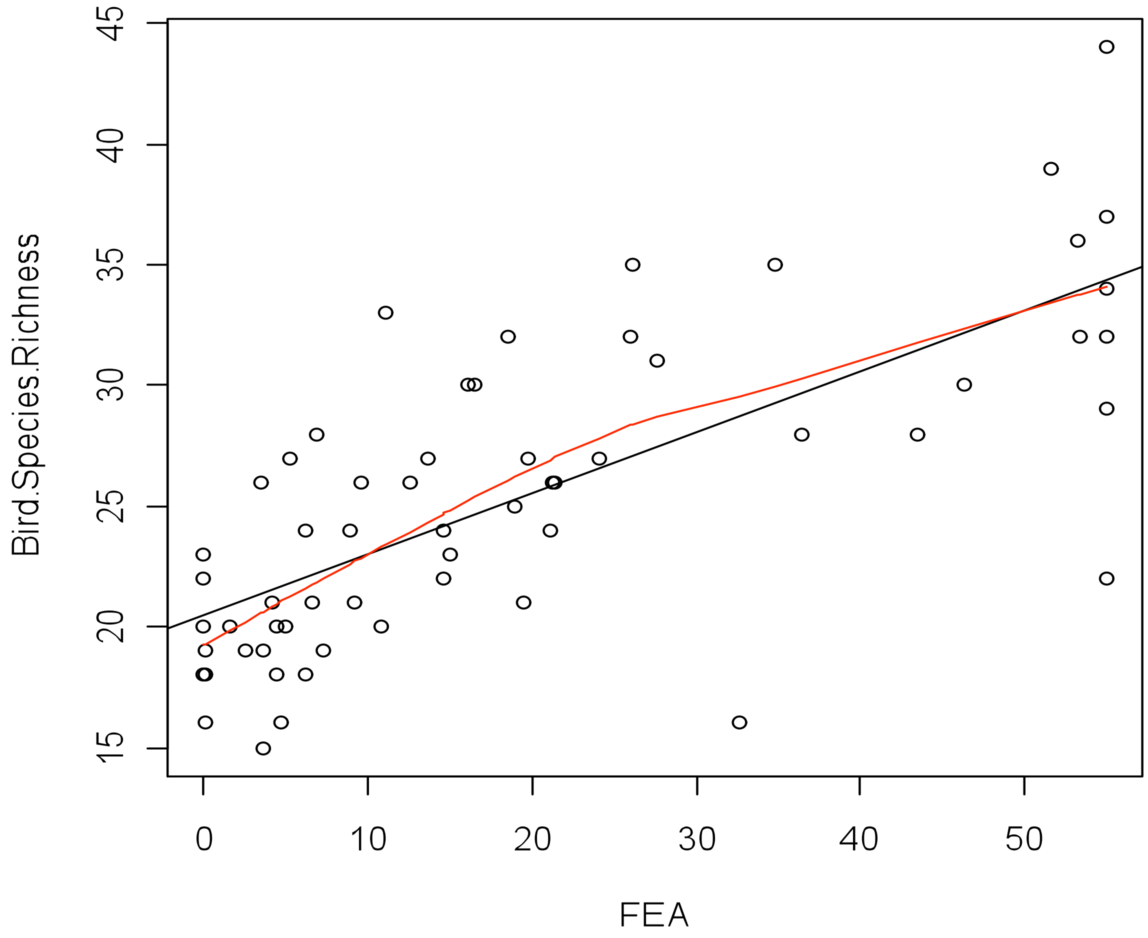


Figure 2.12. Monthly FEA and Monthly Bird Species Richness for all months from February 2008 to December 2008. Pearson's product-moment correlation = 0.72, CI: 0.57 to 0.82; (t_{58}= 7.93, $p<0.00001$)

Table 2.1. Plant Species and their Gross Energy per gram

Plant Species	**Calories per gram**	**ALV**	**GIL**	**ODI**	**OLD**	**OLI**	**RAF**
Acnistus arborensens	3,800	×	×	×	×	×	
Annona pruinosa							×
Bilia columbiana			×	×	×		
Bursera simarouba	5,200					×	
Casimiroa edulis							×
Cecropia obtusifolia	4,100	×			×	×	×
Cestrum racemosum					×		
Citharexlym donnell-smithii (Verbenaceae)					×		
Chrysophyllum brenesii	4,500		×	×	×		
Citrus spp.	3,500	×	×	×	×	×	×
Cordia eriostigma	4,200	×			×		×
Croton draco		×	×				
Croton niveus		×	×	×		×	×
Cupania glabra		×					×
Daphnopsis americana	3,700	×		×		×	
Diphysa americana				×		×	
Diospyrus digyna				×			
Ehretia latifolia				×	×	×	×
Erybothria japonica	3,550			×			
Erythrina lanceolata				×		×	×
Erythrina sp.				×			
Eugenia guatamalensis					×		
Eugenia jambos							×
Ficus costaricana	4,000	×		×			
Ficus lastericye	3,800		×		×		
Ficus pertusa	3,850		×		×		×
Guazuma ulmifolia		×					
Hamelia patens	3,900	×	×		×	×	
Inga mortoniana					×		
Inga punctata	3,700	×	×	×	×	×	×
Inga tondunzii					×		×
Lasiantha fructosa		×			×	×	
Lonchocarpus olingathus		×		×			
Mangifera indica				×			
Montanoa guatamalensis		×		×		×	×

Mortoniodendron costaricense	4,200		×		×		
Musa spp.	3,500	×	×	×	×	×	×
Myrsina coriacea	5,500						×
Nectandra membranaceae					×		
Nectandra salicina	5,700		×				
Ocotea floribunda					×		
Ocotea monteverdensis	6,100		×		×		
Persea americana			×	×	×	×	×
Psidium guayaba	3,850	×	×			×	×
Sapium glandulosum	5,100		×	×	×	×	×
Spondias sp.	3,600		×				×
Trema micrantha	4,700					×	
Trichilia martiana							
Trichilia havenensis	5,200			×			×
Xanthoxylum fagara	4,300	×	×	×			
Xanthoxylum monophyllum				×			
Total Species		**18**	**19**	**23**	**24**	**18**	**21**

Table 2.2. Bird Species. Number of Observations (n=116). An F indicates that a species was observed taking fruit.

Bird Species	ALV	GIL	ODI	OLD	OLI	RAF
Broad Winged Hawk	0	1	0	0	0	0
Grey Headed Chachalaca(F)	4	9	10	3	11	1
Grey Necked Wood Rail	0	2	0	1	0	0
Inca Dove(F)	0	0	1	1	0	13
White Tipped Dove(F)	17	20	37	34	30	50
Band Tailed Pigeon(F)	4	3	1	0	13	0
Red Billed Pigeon(F)	5	9	1	15	33	7
Brown Hooded Parrot(F)	0	1	0	1	0	0
Chiriqui Ground Dove(F)	0	1	0	1	0	0
Orange Chinned Parakeet(F)	1	12	5	15	2	1
Orange Fronted Parakeet(F)	0	0	0	0	3	0
Crimson Fronted Parakeet(F)	3	1	0	1	0	1
White Fronted Parrot(F)	1	1	22	5	7	5
Squirrel Cuckoo(F)	1	2	0	1	5	0
Lesser Ground Cuckoo	1	0	0	0	3	0
Groove-billed Ani	0	0	0	0	5	
Steely-vented Hummingbird(F)	40	31	12	31	4	8
Rufous-tailed Hummingbird(F)	49	55	27	102	13	33
Ruby-throated Hummingbird	1	0	1	2	1	5
Magenta-throated Woodstar	0	0	1	1	0	0
Violet Sabrewing	1	2	11	4	1	0
Fork Tailed Emerald	30	11	4	17	12	13
Green Violet-Ear	0	0	0	9	0	0
Coppery-headed Emerald	0	5	0	2	0	0
Striped-tailed Hummingbird	3	1	0	3	0	0
Plain Capped Starthroat	2	3	17	11	8	2
Blue-throated Goldentail	0	0	0	0	4	0
Green Hermit	0	0	0	2	0	1
Little Hermit	0	1	0	0	0	0
Blue-crowned Motmot(F)	27	47	23	32	36	29
Pale-Billed Woodpecker	0	1	0	0	0	0
Golden-olive Woodpecker(F)	0	4	1	1	1	6
Yellow-bellied Sapsucker(F)	0	0	0	3	0	0
Hoffmann’s Woodpecker(F)	4	12	9	22	6	13
Emerald Toucanet(F)	13	37	2	33	0	9
Keel-billed Toucan(F)	3	8	1	2	1	0

Collared Aracari(F)	0	0	0	0	1	0
Streaked-headed Woodcreeper						
Barred Antshrike	0	0	0	0	0	1
Masked Tityra(F)	2	3	1	11	4	2
Long-tailed Manakin(F)	16	24	11	11	10	4
Wood-Pewee(F)	12	2	1	11	0	3
Yellow-bellied Elaenia(F)	0	5	0	8	5	7
Yellowish Flycatcher(F)	3	0	0	0	0	0
Willow-Alder Flycatcher(F)	2	2	3	6	20	6
Boat-billed Flycatcher(F)	4	6	1	15	1	7
Ochre-bellied Flycatcher(F)	0	0	0	1	0	1
Olive-striped Flycatcher(F)	0	0	0	0	0	1
Northern Beardless Tyrannulet(F)	0	0	0	0	2	0
Social Flycatcher(F)	3	5	12	23	3	9
Dusky-capped Flycatcher(F)	34	23	19	56	45	26
Sulphur-bellied Flycatcher(F)	2	1	1	5	2	0
Great Kiskadee(F)	0	2	3	13	6	11
Common Tody-Flycatcher(F)	0	1	0	15	11	6
Tropical Kingbird(F)	0	2	2	11	2	4
Paltry Tyrannulet(F)	3	7	1	33	0	4
White-throated Magpie Jay(F)	0	0	9	1	6	1
Brown Jay(F)	40	45	42	23	48	23
Plain Wren	54	25	37	29	50	52
Rufous and White Wren	30	31	5	29	28	46
House Wren	16	4	7	40	25	54
Orange-billed Nightingale Thrush(F)	56	37	62	48	49	43
Swainson's Thrush(F)	3	1	3	7	1	6
Wood Thrush(F)	0	1	1	0	1	0
White-throated Robin(F)	6	1	0	2	0	2
Clay-colored Robin(F)	31	46	46	75	40	70
Rufous-browed Peppershrike	5	3	2	1	4	3
Lesser Greenlet	15	15	3	17	5	18
Yellow-throated Vireo(F)	4	0	5	5	4	3
Solitary Vireo(F)	0	0	0	0	0	1
Yellow-green Vireo(F)	5	10	16	12	23	24
Philadelphia Vireo(F)	9	2	1	4	0	15
Rufous-capped warbler(F)	37	28	53	29	56	45
Blackburnian Warbler(F)	5	0	2	3	3	2
Chestnut-sided Warbler(F)	2	3	0	13	0	3

Cerulean Warbler	0	0	0	1	0	2
Yellow Warbler(F)	0	4	11	12	8	2
Bay Breasted Warbler(F)	0	0	0	0	0	1
Black-throated Green Warbler	6	6	0	3	0	1
Gray-crowned Yellowthroat	0	1	0	0	0	11
Slate-throated Redstart	0	0	1	0	2	0
Waterthrush	0	0	0	0	0	1
Golden-winged Warbler	2	0	0	0	0	0
Ovenbird(F)	0	0	2	0	1	0
Tennessee Warbler(F)	12	5	12	36	5	19
Black and white Warbler	6	4	0	14	1	13
Canada Warbler	2	0	0	1	0	0
Wilson’s Warbler	30	23	13	36	15	31
Yellow-billed Cacique(F)	1	0	0	0	0	0
Melodious Blackbird(F)	11	10	15	8	19	7
Northern Oriole(F)	3	9	14	24	0	3
Eastern Meadowlark	0	0	0	0	0	1
Montezuma Oropendula(F)	0	0	2	2	3	1
Chestnut-headed Oropendula(F)	0	0	2	0	0	0
Bronzed Cowbird(F)	1	2	0	4	1	5
Golden-browed Chlorophonia(F)	0	8	0	18	0	1
Red-legged Honeycreeper(F)	0	0	0	10	0	8
Yellow-throated Euphonia(F)	24	45	15	90	8	53
Yellow-crowned Euphonia(F)	0	0	0	7	0	12
Palm Tanager(F)	0	0	0	5	0	0
Crimson-collared Tanager(F)	0	1	0	21	0	5
Summer Tanager(F)	2	1	5	33	2	4
Passerini’s Tanager(F)	0	0	0	3	0	0
Blue-gray Tanager(F)	1	11	14	77	10	35
White-eared Ground-Sparrow(F)	26	31	19	29	21	34
Prevost’s Ground-Sparrow(F)	0	0	1	0	7	0
Yellow throated Brush Finch(F)	3	4	0	3	0	0
Yellow-faced Grassquit(F)	18	14	21	25	31	44
Striped-headed Sparrow(F)	0	0	0	0	1	0
Rufous-collared Sparrow(F)	0	0	0	0	0	14
Rose-breasted Grosbeak(F)	0	1	0	4	4	2
Buff-throated Saltator(F)	4	9	2	14	1	7
Grayish Saltator(F)	0	3	0	9	0	3

Table 2.3. Contingency Table for Substrate Use (February 2008 to August 2008)

TOTAL	**Ground**	**Coffee**	**Tubu WB**	**Croton W**	**Tree <4m**	**Tree >4m**	**Total**
18 commo	515	297	359	83	616	1044	
others	49	36	96	26	165	882	
						Chisq=457	Prob=0.00

Table 2.4. Multi-scale Occupancy Model Results where p is the detection probability, ψ is the probability of occupancy and u is the probability of use.

Candidate Models	**ΔAIC**	***w*_i**
p(wind), ψ(.), u(FEA)(substrate)(site)	0	1
p(wind), ψ(.), u(FEA)(substrate)	42	0.0000
p(wind), ψ(.), u(FEA)(site)	442	0.0000
p(wind), ψ(.), u(FEA*site)	450	0.0000
p(wind), ψ(.), u(FEA)	471	0.0000
p(wind), ψ (Tree>4m), u(FEA)	472	0.0000
p(wind), ψ (Ave DBH), u(FEA)	472	0.0000
p(wind), ψ(Canopy Cover), u(FEA)	472	0.0000
p(wind), ψ (DBH>50cm), u(FEA)	472	0.0000
p(wind), ψ(Tree>4m)(Ave DBH), u(FEA)	475	0.0000
p(wind), ψ(Canopy Cover)(DBH>50cm), u(FEA)	475	0.0000
p(.),ψ, u(FEA)(site)	476	0.0000
p(wind), ψ(Canopy Cover)(Ave DBH)(Tree>4m), u(FEA)	477	0.0000
p(.),ψ(.), u(.)	518	0.0000
p(wind), ψ(.), u(.)	519	0.0000
p(wind)(wind2), ψ(.), u(.)	522	0.0000
p(wind), psi(Tree>4m), u(.)	522	0.0000
p(wind), psi(Canopy Cover)(Ave DBH), u(.)	524	0.0000
p(wind*site), ψ(.), u(.)	529	0.0000
p(wind)(site), ψ(.), u(.)	531	0.0000

CHAPTER 3

A STEADY-STATE FLORAL RESOURCE, BEE CONSERVATION, AND COFFEE PRODUCTION

Peters, V.E., C.R. Carroll, R.J. Cooper, and R. Greenberg. To be submitted to *Journal of Applied Ecology.*

ABSTRACT: The spatial and temporal distribution of pollinator resources is highly altered in human-managed landscapes, and such mobile ecosystem service providers depend upon an adequate distribution of a limited number of floral resources for survival. Bees are the primary providers of pollination, an ecosystem service of prime importance in agricultural lands because approximately 85% of crops traded on the world market either require or benefit from cross-pollination. Coffee, *Coffea arabica*, yields increase with cross-pollination by bees, however, manipulative field studies to determine best management practices for maintaining bee populations year-round within coffee farms are rare. Here we test the effects of the experimentally planted steady-state floral resource, *Hamelia patens*, on bee abundance, species richness and coffee production within six replicated coffee plantations, contrasting the small, early coffee flowering periods with the later, mass bloom coffee flowering period.

Bee species richness and abundance was higher in farms with the experimentally planted steady-state floral resource. Initial coffee fruit seed set was higher during the early coffee flowering period (74.4%) than during the mass coffee flowering period (58.9%). Native bee species were responsible for 57.1% of all bee visits to coffee flowers during the early coffee flowering period, but only 25.7% of visits during the mass coffee flowering period. The steady-state floral resource negatively affected native bee species visitation to coffee flowers during the early coffee flowering periods, however, during the mass bloom period, native bee species visitation to coffee flowers was equal among farms. In response there was a trend towards a lower initial seed set during the early coffee flowering period in farms with the steady-state floral resource. Overall, the steady-state floral resource benefits native bee conservation and persistence in coffee farms, however, this constant floral resource may strongly compete for native bee pollination during the early coffee flowering period. We propose a management

option that may balance the importance of steady state floral resources for native bee conservation with the benefits of increasing pollination by native bees during the early coffee flowering periods.

INTRODUCTION

The ecosystem service of pollination is often provided or enhanced by mobile organisms that are dependent upon an adequate quantity of floral and other resources within a limited foraging range (Kremen *et al.* 2002, Kremen *et al*. 2007, Roubik 1989). However, approximately one-third of all terrestrial ecosystems are dedicated to agricultural use (Rosen 2000) and therefore human activity has vastly altered the abundance and spatial distribution of resources. This alteration, affecting one of the principle themes of ecology, resource distribution and animal response, demonstrates how unrealistic it is to contemporarily understand terrestrial ecology without studies that examine these relationships within the globally important agricultural matrix itself (Vitousek 1997, Klein *et al.* 2008).

Generally, in agro-ecosystems, species richness and species abundance decline with intensification of management. In particular, many arthropods are affected when this intensification reduces plant diversity, resources or natural microhabitat components (Klein *et al*. 2007, Cruz-Angon and Greenberg 2005, Perfecto 1995; Perfecto *et al*. 2003; Tylianakis *et al*. 2005). For example, Root (1973) suggested that a high floral diversity is correlated with enhanced abundance and efficacy of predatory and parasitoid arthropods due to improved microhabitats or resource subsidies, and this has been supported empirically (Perfecto and Snelling 1995; Tylianakis *et al*. 2004); however, not all taxa respond equally to management practices that remove or reduce natural ecosystem components (Perfecto *et al*. 2003, Richter *et al*. 2007; Klein *et al*. 2003).

Although the interplay between ecosystem services and human benefit may be most practical and quantifiable in agricultural lands, the ecological mechanisms that maintain these relationships are often poorly understood. Only recently have ecologists begun to recognize the role that agro-ecosystems and the management practices within agro-ecosystems can play in the conservation of important ecosystem services and the organisms that provide these services (Cane and Tepedino 2001, Klein *et al.* 2002, Roubik 2002, Ricketts 2004, Klein *et al.* 2008, Van Bael *et al.* 2008, Cruz-Angon *et al*. 2008, Kremen *et al.* 2007, Sekercioglu 2006). In fact, pioneering research in the tropics with tropical plantation crops has demonstrated a positive relationship between a decrease in management intensification and an increase in ecosystem service providers (Philpott *et al*. 2006, Greenberg 2000, Perfecto and Snelling 1995, Perfecto and Vandermeer 1996; Klein *et al*. 2002), although the factors responsible for this relationship are still largely unknown (Kremen *et al*. 2007) despite the fact that this information is essential for policy makers, conservation professionals, and agricultural extensionists. Previous studies have focused on demonstrating that agro-forestry systems with diverse shade trees support higher diversities and higher abundance of bees, wasps, ants or other arthropods (Klein *et al*. 2002, Klein *et al*. 2003, De Marco and Coehlo 2004, Philpott *et al*. 2006, Veddeler *et al*. 2006), but within the “Diverse Shade” classification of plantations (Moguel and Toledo 1999) not all shade tree species provide the resources that ecosystem service providers may require. Consequently, the variation in resource quality within coffee plantations classified as “Diverse Shade” would best facilitate research to understand how agro-forestry ecosystems can be managed to benefit ecosystem service providers.

Bees are the primary providers of an ecosystem service of prime importance to agricultural lands because approximately 85% of crops traded on the world market either require cross-pollination of their flowers, or benefit from cross-pollination through enhanced seed set or seed quality (Roubik 2002, Klein *et al.* 2007, Klein *et al.* 2008). For example, the economically important cash crop coffee, *Coffea arabica*, achieves higher seed set and seed weight (= quality) with cross pollination (Roubik 2002, Klein *et al.* 2007). Coffee, however, does not require cross-pollination for seed production, and so research regarding the contribution to fruit or seed production by a diverse suite of native bees with relatively low abundance versus a single species, *Apis mellifera*, with high abundance has been inconclusive (Roubik 2002, Ricketts 2004). The flowering patterns of coffee in small farms provide a natural framework for disentangling these differences because there are both several small bloom periods which attract mainly native bees as well as a mass bloom period which draws large numbers of the non-native *Apis mellifera*.

The decreased availability of floral and/ or other resources and nesting sites have been discussed as limiting factors controlling bee populations in managed agricultural landscapes (Ricketts 2004). Foraging ranges of small, native bees are typically much smaller than those of *Apis mellifera* (Roubik 1989) and therefore native bee populations may be more sensitive to farm management practices within the agricultural matrix (Perfecto and Vandermeer 2002). Farm management practices focusing on “steady-state” floral resources (Ackerman 1983, Bawa and Beach 1983) may elucidate the relative role of floral resources to maintaining native bee populations. This study aims to investigate how floral resource availability within similarly managed coffee plantations influences bee visitation to coffee flowers during the early and mass coffee flowering periods, and furthermore how the presence of an experimentally planted “steady-state” (year-round flowering) floral resource affects bee species richness and abundance in coffee plantations. In addition, the ecosystem service of pollination in response to this management practice will be quantified using both pollen deposition rates as well as seed set.

Study Site

Research was conducted at the San Luis Research Station in the San Luis valley of Northwestern Costa Rica (ca 10˚ 17' N, 84˚ 48' W) in the Municipality of Puntarenas. The San Luis Valley is the south-westernmost border of the Monteverde Cloud Forest Reserve, with an elevation between approximately 500 to 1200 m asl. Average monthly rainfall during dry season months (December through April) is 50 mm and during wet season months (May through November) is 550 mm. Due to conservation efforts in the region, the 56 hectare "environmentally-friendly" farm, Finca La Bella, was created to provide formally landless farmers with a 1 to 2 hectare tract of land for sustenance farming. Finca la Bella (ca 900 to 1100 m asl) is a 56 hectare matrix of forest patches, windbreaks, <2 hectare pasture patches, and <2 hectare plantations of coffee. The small coffee plantations embedded within and around this matrix share similar management practices (Traditional Polyculture Classification; Moguel and Toledo 1999), history, and surrounding matrix quality. Plantation management practices similar among farms include low chemical input from fertilizers, no pesticide use, high diversity of trees and flowering ornamental species.

"Steady-state" Floral Resource Experimental planting

Hamelia patens (Rubiaceae) is a self-incompatible species occurring in secondary growth from Mexico to Bolivia (Lasso 2003), and has been introduced into gardens as an ornamental in the southern United States. It is a common species in human-altered landscapes throughout Costa Rica both because its bright orange tubular flowers have ornamental value as well as its weedy secondary growth pattern. Flowering occurs year round and individuals growing in full sun yield 20 to 60 open flowers daily during all months of the year. In contrast, shaded individuals yield approximately 20 open flowers daily from February to July and only from 2 to 10 open flowers daily from August through January. Nectar production lasts only one day beginning at dawn, with flowers detaching by late afternoon (Feinsinger 1978). The odorless, orange tubular flowers suggest hummingbird pollination; however, many insect species also can be observed foraging for pollen and nectar resources, including butterflies, bees, wasps and flies. This group includes many small solitary bees that easily fit inside the corolla, potentially of great benefit to the plant's reproductive success. Larger social bees, especially *Trigona fulviventris*, perforate the corolla in order to obtain nectar and therefore do not pollinate *H. patens*. Approximately ten *H. patens* plants were experimentally planted in July 2007 within three of six coffee plantations.

In order to quantify bee community composition and abundance differences in farms with (hereafter, H+) and without (hereafter, H-) the planted steady-state floral resource, *H. patens*, bees were observed and/ or collected at both *H. patens* flowers and three potted *Ocimum basilicum* (Basil) flowers, which attracts a generalist assemblage of many bee species. In all H+ farms, one *H. patens* plant was selected at random and observed for 15 minute periods for twelve observation periods. H- farms had by chance exactly one naturally occurring *H. patens* plant in a bordering windbreak of the plantation that was also observed for twelve observation periods. These naturally occurring *H. patens* plants were located in full shade and produced few flowers. Because the numbers of flowers of *H. patens* in H+ farms with 10 plants in full-sun were different (approximately 150 to 500 flowers) from the number of flowers of *H. patens* in H-farms with 1 plant in full shade (approximately 5 to 20 flowers), we also compared bee species richness and abundance at flowers of potted basil plants in H+ and H- farms. Three potted basil plants yielding approximately 100 basil flowers were located in each farm for a two week period, and observations of bee visitation were conducted for 15 minutes for a total of 12 observation periods at each site. Finally, one malaise trap was placed in each farm for 15 day periods during July and November 2008, as an additional method for quantifying differences in bee species richness and abundance in H+ and H- farms.

We used the software package Estimate S (Version 8.0, R. K. Colwell, http://purl.oclc.org/estimates) to find observed and predicted species richness of bees in H+ and H- farms, based on our observations at *H. patens* and basil flowers, combined. We chose to present results from both the Chao 2 Incidence Based Richness Estimator (Chao 1987) which provides a mean and 95% confidence interval of predicted richness, as well as the Classic Incidence Based Coverage Estimator (ICE).

Flowering Phenology

In the study region, *Coffea arabica* has one period of mass flowering and several smaller flowering periods during the dry season between February and early April immediately following a rain event. Each of the smaller coffee flowering periods produce approximately 20 to 30% of the total number of flowers open during the later mass bloom period. During each flowering period coffee blooms remain open for only 48 hours. For 2007, the mass bloom occurred from 19 April to 21 April, and in 2007 data were only collected during the mass bloom period. In 2008 early flowering periods were from 5 February to 7 February, 25 February to 27 February, and 17 March to 19 March, with the mass bloom occurring from 13 April to 15 April.

A site was defined as one, one hectare coffee plantation where shade tree species richness was high and approximately equal across all sites (~20 tree species per hectare). For shade tree species, time of year and duration of flowering season varied among tree species and occasionally within species among sites. An index of shade tree species flower availability was assigned to all individual trees and shrubs within each site for each month except January and September in 2008. The Flower Availability Index was assigned to all individual shrubs, trees, and ornamental plants with flowers, other than *Coffea arabica*, that are visited by bees for resources. The Flower Availability Index used was 1 = 1 to 10; 2 = 11 to 25; 3 = 26 to 50; 4 = 51 to 100; 5 = 101 to 200; 6 = 201 to 500; 7 = 501 to 1000; and 8 = 1001 to 10000. Individual plant flower availability indices were totaled monthly for each site.

Bee Visitation and Fruit Production

Much of the bee community utilizing floral resources of *H. patens* also visits the flowers of *Coffea arabica*. Bee visitation, bee species diversity, pollen deposition on coffee flower stigmas, seed set and seed weight were quantified for the coffee flowering seasons of April 2007, February, March, and April 2008 in response to the experimental plantings of *H. patens*.

Bee visitation rates were observed at coffee flowers only during the mass flowering period in 2007, but during both early flowering periods and mass flowering periods for 2008. Each observation period consisted of observing one coffee plant for fifteen minutes and recording all bee visitors. Six coffee plants with approximately 100 to 200 open flowers each were selected at random in each of the six sites and observed twice, for a total of 12 observation periods per site. To obtain seed set rates, four flower clusters per coffee plant were marked and the numbers of flowers per cluster were counted. One month later, marked flower clusters were re-visited and the numbers of swollen ovules were counted. Twenty-four coffee flower stigmas were collected at random from each site for pollen deposition rates during the mass flowering period in 2007 and 2008. Pollen grains were removed from the stigmatic surface using fushin jelly and then immediately melted over a low temperature burner onto microscope slides.

We used linear regression and AIC model selection (Anderson and Burnham 2002) in the statistical package R Version 2.8.1 to evaluate other variables potentially influencing bee visitation rates at coffee flowers. We considered the following variables: Elevation, Canopy Cover, Average Monthly Non-Coffee Flowers, Total February Flowers, Total March Flowers, Total April Flowers, and *H. patens* presence, for the four groups of bees: Native Bees Early Flowers; Native Bees Mass Flowers; Apis Early Flowers; and Apis Mass Flowers.

RESULTS

Experimental Steady-state Floral Resource

Twenty species of native social and solitary bees were collected while foraging floral resources of *H. patens* in the San Luis valley (Table 3.1). In addition, the non-native honeybee *Apis mellifera* was observed to forage occasionally at *H. patens*, but very rarely when compared to other social bees in the area. Observations of *H. patens* plants in H+ sites yielded a total of sixteen species in these farms, but only 7 species were observed visiting the single *H. patens* plants in H- farms (Fig. 3.1). In addition, each H+ farm had higher species richness for observations on individual *H. patens* plants than for individual *H. patens* plants observed in H- farms. Thirteen bee species were observed foraging on potted basil flowers in H+ farms, but only 8 bee species were observed in H- farms (Fig. 3.1). For H+ farms, the mean estimated species richness, using the Chao 2 Incidence Based Richness Estimator, was 62.3 species with a 95% confidence interval from 31.4 to 164.0, while the mean estimated species richness of H- farms was 19 species, with the 95% CI from 14.1 to 46.6 (Fig. 3.2). The Classic Incidence Based Coverage Estimator (ICE), estimated species richness in H+ farms at 39.6, and H- farms at 21.1 bee species.

Early and Mass Flowering Coffee Plants

We observed bee visitation at coffee flowers and quantified seed set for several small blooms of coffee flowers in February and March 2008, and the mass bloom of coffee flowers in both April 2007 and April 2008. Pollen deposition on the stigmatic surfaces of coffee flowers during the mass bloom periods was different among the six sites for both 2007 and 2008 (Fig. 3.3; 2008: $F_{5, 132} = 12.28$, $p<0.00001$; 2007: $F_{5, 138} = 6.21$, $p<0.0001$) although there was no significant correlation with the abundance of bee visitors or coffee seed set per farm. In addition, pollen deposition on coffee stigmas was not significantly different between H+ and H- farms for 2008 during the mass bloom period (Fig. 3.4; $t_{134} = 0.87$, $p=0.192$).

Bee community composition was different during the early and mass flowering periods, with the recruitment of *Apis mellifera* changing the overall bee visitation pattern at coffee flowers from 57.1% native bee species during the early flowering periods to 25.7% native bee species during the mass flowering period (Table 3.2). However, native bee visitation rates were not different across sites between the early and mass flowering periods. Average native bee visitation to coffee flowers during the early coffee flowering periods was 2.88 individual bees per observation period and 2.81 during the mass flowering period (log transformed data; $t_{140} = -0.60$, $p=0.55$). Average visitation rates for the non-native *Apis mellifera*, were significantly different for early versus mass coffee blooms; early coffee flowering periods averaged 2.11 individual *Apis mellifera*, and mass coffee flowering averaged 8.14 individuals (log transformed data; $t_{136} = -8.82$, $p<0.0001$).

We found a significant difference in seed set rates between the early flowering and mass flowering periods. According to a previous pollination study with *C. arabica*, autonomous self-pollination led to 45% initial seed set, manual self-pollination to 60% and cross-pollination to

75% (Klein *et al.* 2003). We found a 74.4% initial seed set during the early flowering periods, and a 58.9% initial seed set during the mass flowering periods (n= 263; $t_{258} = 4.30$, $p<0.0001$). Differences between these initial seed set rates between early and mass flowering periods could be biased when comparing final production rates, through a process of competition and/ or crowding effects, whereby early flowers produced seeds which are formed one to two months prior to the mass bloom and crowd out or compete for resources with the mass flower produced seeds. We did not investigate this possibility.

Steady-State Floral Resource and Coffee Production

Fewer native bees visited coffee flowers during the early flowering periods of coffee in H+ farms than H- farms. The mean number of individual native bees visiting coffee flowers during the early flowering periods in H+ farms was 1.1, in comparison with 4.6 in H- farms (Fig. 3.5; $t_{71} =5.25$, $p<0.00001$). This difference was not observed during the mass flowering period, where the mean number of native bees visiting coffee flowers during all observation periods was 2.3 in H+ farms and 3.4 in H- farms (Fig. 3.6; $t_{69}=1.2046$, $p=0.233$). There was no difference in abundance of *Apis mellifera* between H+ and H- farms for either the early or mass coffee flowering periods.

Total pollinator species richness was different between the early flowering and mass flowering periods, and between H+ and H- farms (Fig. 3.7). In the early flowering periods, total species richness of each individual H+ farms was either 5 or 6 bee species, while the total species richness in each individual H- farms was 8 or 9 species. In the mass flowering period, total species richness increased sharply in H+ farms to 12 or 13 species, while in H- farms there was either a slight increase (2 farms increased to 10 species) or a slight decrease (one farm decreased from 8 to 7 species). In addition, we evaluated total abundance of 4 species of social Meliponini which are the most frequent visitors to *H. patens* flowers and the most common native social bees in the study region. In H+ farms total abundance during the early flowering season was only 21 individuals, while in the H- farms total abundance of the Meliponini tribe was 103 individuals. However during the mass bloom period, total abundance was more evenly distributed between H+ and H- farms with 68 individuals recorded in H+ farms and 59 individuals in H- farms (Fig. 3.8).

Coffee seed set was not significantly different between H+ farms and H- farms early and mass flowering periods are compared separately, although there was a trend for decreased seed set during the early flowering period for H+ farms. Mean percent seed set for coffee flowers in the early flowering period in H+ farms was 70% and 78% in H- farms (arcsine sqrt transformed data, t_{123}= 1.824, p=0.07). Mean percent seed set for coffee flowers from the mass flowering period was 56% for H+ farms and 62% for H- farms (t_{138}= 1.41, p=0.16).

Hamelia patens **versus Other Environmental Variables**

Out of all potential explanatory variables and bee groups, we found only two variables for two different groups to explain >20% of the variation in bee visitation rates, *H. patens* presence in Native Bees Early Flowers (R^2=0.273, p<0.0001) and Average Monthly Non-Coffee Flowers in Apis Mass Flowers (R^2=0.23). AIC model selection found the best model for each group of bees to be the following:

(1) Native Bees Early Flowers= Elevation + *H. patens* presence

(2) Native Bees Mass Flowers= Elevation + Average Monthly Non-Coffee Flowers

(3) Apis Early Flowers= Total March Flowers + *H. patens* presence

(4) Apis Mass Flowers= Elevation + Average Monthly Non-Coffee Flowers + *H. patens* presence

Finally, we wanted to evaluate whether farms with higher values of average monthly non-coffee flowers would recruit more bee pollinators during the different coffee flowering periods. We used a linear regression of mean bee visitation rates to coffee flowers against average monthly non-coffee flowers per site for all four bee groups (Fig. 3.10). The only bee group that was positively correlated to the average monthly non-coffee flowers per site was Apis Mass Flowers, (R^2=0.66, p<0.0001), which could demonstrate the higher presence of *Apis mellifera* scouts in farms with higher monthly floral abundance.

DISCUSSION

Steady-state floral resources and bee conservation

Research aimed at understanding habitat requirements for bee persistence has been primarily through mensurative field studies which focus on how varying levels of plant species richness influence the bee community (Ebeling *et al*. 2008). In this study, although all sites had similar floristic diversity, each site had a distinct flowering phenology, with different tree species producing large numbers of short-lived flowers during some months of the year while other months were absent of flowers. Despite this temporal variability in floral resources among sites, the three sites that contained the experimentally planted steady-state resource were estimated to have almost twice as many bee species than sites without. The experimental approach used in this study elucidates the importance that one plant resource, alone, can have for conservation of the bee community, when that plant species provides a constant resource.

The steady-state floral resource, *Hamelia patens*, selected for the experimental planting in this study could represent a critical resource for native bee conservation in depauparate managed landscapes. Species richness estimators predict at least twice as many bee species to be present in H+ farms. Despite the fact that *H. patens* flowers are narrow and tubular, the size (length) range of native bees utilizing the floral resources varied from tiny 4 mm solitary Halictidae to very large 24 mm Euglossinini and 16 mm Bombini. Some larger bees, such as *Ceratina* sp. #1 were long (approximately 9 mm) but narrow enough to reach floral nectar through entering the corolla, while similarly sized Euglossines had long tongues, which allowed them to reach floral nectar while hovering over the tubular flowers.

Temporal variability in pollinator populations decreases with higher plant species richness or when preferred plants are available (Ebeling *et al*. 2008). Furthermore, plant flowering strategies providing constant resources may also serve to dampen naturally-occurring fluctuations in pollinator abundances (Ackerman 1983). The only native plant species producing constant floral resources in the human-dominated landscape where this study took place was *H. patens* plants in full-sun. Despite the fact that *H. patens* is a single plant species, here we show that it has a profound influence on bee species richness. This may reveal the higher value that a constant floral resource has to the persistence of bee populations versus a variety of floral resources. In agricultural lands where space directed towards non-crop species is limited, it may be more important to understand the individual contribution of a plant species to bee species survival rather than to ascertain how plant species richness influences bee species richness levels.

Habitat edges, such as roadsides and powerline strips, have been shown to provide important resources for pollinators (Hopwood 2008; Russell *et al.* 2005). Less intensely managed agricultural lands have similar features because canopy cover is often reduced allowing retained non-crop plants such as weedy herbs and shrubs, such as *H. patens*, to invest more resources in floral production. For this reason, agricultural lands could be managed to increase their potential to act as source habitats for pollinators, through planting species similar to *H. patens*. Conservation efforts for endangered native plant species in forested lands could focus on agricultural lands adjacent to the forest as source habitats for restoring plant-pollinator relationships.

Bees are "central-place" foragers and foraging ranges are largely understood as the entire circular area surrounding the nest where the radius is the largest recorded flight distance, although this has not been fully studied (Roubik 1989). However, only a few species of tropical bees have been studied to determine maximum flight distances, but larger bees can typically fly longer distances (Roubik 1989, Marden 1987). Previous studies indicate that while large bees such as *Apis mellifera* can fly up to 13.4 km, their peak foraging range is 10 km and most worker bees work within 2 km of their nest. Smaller bee species (~6 mm to 8 mm) have been shown to have maximum flight distances of 100 meters to 1 km (Inoue *et al*. 1984). Many of the native bee species that utilized floral resources of *H. patens* in this study were small, and therefore phenological gaps in floral resource availability caused by habitat alteration could be especially detrimental to their survival.

Steady state floral resources and coffee production

In this study, bee community composition differed between the early and mass flowering periods. This result parallels other studies that have demonstrated bee community differences in coffee plantations between large blooms and single plant blooms (Stone and Willmer 1989), highlighting the different pollination service received by coffee plants with flowers open during the mass flowering period versus outside the mass flowering period (Klein *et al.* 2008). However, in our study the difference in bee community composition was due to the dramatic increase in abundance of *Apis mellifera*, while both non-native solitary and social bee abundance remained relatively constant. This shift in *Apis mellifera* abundance makes native bee species the predominant pollinators (57.1%) of coffee during floral blooms outside the mass flowering period, and *A. mellifera* the predominant pollinator (74.3%) of coffee during the mass flowering period. The change in which bee species are primarily responsible for the ecosystem service of pollination between early and mass coffee flowering periods is highlighted in our results of different initial rates of seed set between the early and mass coffee flowering periods. The higher seed set rate during the early coffee flowering period in our study may reflect the different pollination service that is provided by a diverse suite of native bees versus the single species *Apis mellifera*. This could occur because different sizes and habits of pollinators enable higher rates of cross pollination (Klein *et al.* 2007), for example through different foraging behavior patterns such as increased movement among individual coffee plants versus within an individual coffee plant. From another perspective, the increased abundance of *Apis mellifera* during the mass coffee bloom may be responsible for the lower rates of initial seed set because this species is meticulous in visiting every open flower on an individual coffee plant, thereby creating initial seed set rates similar to those of manual self-pollination by transferring pollen within individuals more often than among individual plants.

In considering the coffee harvest, farms with planted *H. patens* were negatively affected by this steady-state resource during the early coffee flowering period. Although bee species richness and abundance are higher in H+ farms, during the early coffee flowering period, both native bee species richness and abundance were lower for coffee plants in H+ farms than in H- farms. These results imply that native bees maintained in the farm by *H. patens* were not compelled to leave the steady-state floral resource to forage floral resources of coffee plants, and because of this there was a trend for lower initial seed set in H+ farms during the early flowering period. Steady-state floral resources, such as those provided by *H. patens*, can be important for the conservation and persistence of native bee species in agricultural lands, however, these floral resources may also compete with the focal crop species thereby negatively affecting production. These results suggest a management option for increasing production during the early flowering period. Steady-state resources incorporated into coffee plantations may be utilized positively to increase production if flowers are covered or removed while the focal crop species is flowering outside of the mass bloom period. This strategy is of significance to coffee producers because increased early harvests, when coffee yields are normally low, bring higher market prices.

Literature cited

Ackerman, J. D. 1983. Diversity and seasonality of male euglossine bees (Hymenoptera, Apidae) in Central Panama. Ecology **64**:274-283.

Anderson, D. R. and K. P. Burnham. 2002. Avoiding pitfalls when using information-theoretic methods. Journal of Wildlife Management **66**:912-918.

Bawa, K. S. and J. H. Beach. 1983. Self- incompatibility systems in the Rubiaceae of a tropical lowland wet forest. American Journal of Botany **70**:1281-1288.

Cane, J. H. and V. J. Tepedino. 2001. Causes and extent of declines among native North American invertebrate pollinators: Detection, evidence, and consequences. Conservation Ecology **5**:art. no.-1.

Chao, A. 1987. Estimating the population size for capture-recapture data with unequal catchability. *Biometrics* **43**, 783-791. *Download pdf.*

Cruz-Angon, A. and R. Greenberg. 2005. Are epiphytes important for birds in coffee plantations? An experimental assessment. Journal of Applied Ecology **42**:150-159.

Cruz-Angon, A., T. S. Sillett, and R. Greenberg. 2008. An experimental study of habitat selection by birds in a coffee plantation. Ecology **89**:921-927.

De Marco, P. and F. M. Coelho. 2004. Services performed by the ecosystem: forest remnants influence agricultural cultures' pollination and production. Biodiversity and Conservation **13**:1245-1255.

Ebeling, A., A. M. Klein, J. Schumacher, W. W. Weisser, and T. Tscharntke. 2008. How does plant richness affect pollinator richness and temporal stability of flower visits? Oikos **117**:1808-1815.

Feinsinger, P. 1978. Ecological Interactions between plants and hummingbirds in a successional tropical community. Ecological Monographs **48**:269-287.

Greenberg, R., P. Bichier, A. C. Angon, C. MacVean, R. Perez, and E. Cano. 2000. The impact of avian insectivory on arthropods and leaf damage in some Guatemalan coffee plantations. Ecology **81**:1750-1755.

Hopwood, J. L. 2008. The contribution of roadside grassland restorations to native bee conservation. Biological Conservation **141**:2632-2640.

Inoue, T., S. Salmah, I. Abbas, and E. Yusuf. 1985. Foraging behavior of individual workers and foraging dynamics of colonies of 3 Sumatran stingless bees. Researches on Population Ecology **27**:373-392.

Klein, A. M., S. A. Cunningham, M. Bos, and I. Steffan-Dewenter. 2008. Advances in pollination ecology from tropical plantation crops. Ecology **89**:935-943.

Klein, A. M., I. Steffan-Dewenter, D. Buchori, and T. Tscharntke. 2002. Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. Conservation Biology **16**:1003-1014.

Klein, A. M., I. Steffan-Dewenter, and T. Tscharntke. 2003a. Fruit set of highland coffee increases with the diversity of pollinating bees. Proceedings of the Royal Society of London Series B-Biological Sciences **270**:955-961.

Klein, A. M., I. Steffan-Dewenter, and T. Tscharntke. 2003b. Pollination of Coffea canephora in relation to local and regional agroforestry management. Journal of Applied Ecology **40**:837-845.

Klein, A. M., B. E. Vaissiere, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Tscharntke. 2007. Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society B-Biological Sciences **274**:303-313.

Kremen, C., N. M. Williams, M. A. Aizen, B. Gemmill-Herren, G. LeBuhn, R. Minckley, L. Packer, S. G. Potts, T. Roulston, I. Steffan-Dewenter, D. P. Vazquez, R. Winfree, L. Adams, E. E. Crone, S. S. Greenleaf, T. H. Keitt, A. M. Klein, J. Regetz, and T. H. Ricketts. 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. Ecology Letters **10**:299-314.

Kremen, C., N. M. Williams, and R. W. Thorp. 2002. Crop pollination from native bees at risk from agricultural intensification. Proceedings of the National Academy of Sciences of the United States of America **99**:16812-16816.

Lasso, E. and M. E. Naranjo. 2003. Effect of pollinators and nectar robbers on nectar production and pollen deposition in Hamelia patens (Rubiaceae). Biotropica **35**:57-66.

Marden, J. H. 1987. Maximum lift production during takeoff in flying animals. Journal of Experimental Biology **130**:235-258.

Moguel, P. and V. M. Toledo. 1999. Biodiversity conservation in traditional coffee systems of Mexico. Conservation Biology **13**:11-21.

Perfecto, I., A. Mas, T. Dietsch, and J. Vandermeer. 2003. Conservation of biodiversity in coffee agroecosystems: a tri-taxa comparison in southern Mexico. Biodiversity and Conservation **12**:1239-1252.

Perfecto, I. and R. Snelling. 1995. Biodiversity and the transformation of a tropical agroecosystem- ants in coffee plantations. Ecological Applications **5**:1084-1097.

Perfecto, I. and J. Vandermeer. 1996. Microclimatic changes and the indirect loss of ant diversity in a tropical agroecosystem. Oecologia **108**:577-582.

Perfecto, I. and J. Vandermeer. 2002. Quality of agroecological matrix in a tropical montane landscape: Ants in coffee plantations in southern Mexico. Conservation Biology **16**:174-182.

Philpott, S. M., I. Perfecto, and J. Vandermeer. 2006. Effects of management intensity and season on arboreal ant diversity and abundance in coffee agroecosystems. Biodiversity and Conservation **15**:139-155.

Richter, A., A. M. Klein, T. Tscharntke, and J. M. Tylianakis. 2007. Abandonement of coffee agroforests increases insect abundance and diversity. Agroforestry Systems **69**:175-182.

Ricketts, T. H. 2004. Tropical forest fragments enhance pollinator activity in nearby coffee crops. Conservation Biology **18**:1262-1271.

Root, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats-fauna of collards (Brassica- Oleracea). Ecological Monographs **43**:95-120.

Rosen, C. (Ed.), 2000. People and Ecosystems: the Fraying Web of Life. Elsevier Science, Oxford Press.

Roubik, D 1989 Foraging and Pollination in *Ecology and Natural History of Tropical Bees*

Roubik, D. W. 2002. Tropical agriculture - The value of bees to the coffee harvest. Nature **417**:708-708.

Russell, K. N., H. Ikerd, and S. Droege. 2005. The potential conservation value of unmowed powerline strips for native bees. Biological Conservation **124**:133-148.

Sekercioglu, C. H., G. C. Daily, and P. R. Ehrlich. 2006. Ecological implications of bird extinctions. Journal of Ornithology **147**:250-250.

Stone, G. N. and P. G. Willmer. 1989. Warm-up rates and body temperatures in bees- the importance of body size, thermal regime and phylogeny. Journal of Experimental Biology **147**:303-328.

Tylianakis, J. M., R. K. Didham, and S. D. Wratten. 2004. Improved fitness of aphid parasitoids receiving resource subsidies. Ecology **85**:658-666.

Tylianakis, J. M., A. M. Klein, and T. Tscharntke. 2005. Spatiotemporal variation in the diversity of hymenoptera across a tropical habitat gradient. Ecology **86**:3296-3302.

Van Bael, S. A., S. M. Philpott, R. Greenberg, P. Bichier, N. A. Barber, K. A. Mooney, and D. S. Gruner. 2008. Birds as predators in tropical agroforestry systems. Ecology **89**:928-934.

Veddeler, D., A. M. Klein, and T. Tscharntke. 2006. Contrasting responses of bee communities to coffee flowering at different spatial scales. Oikos **112**:594-601.

Vitousek, P. M. 1997. Human domination of Earth's ecosystems (vol 277, pg 494, 1997). Science **278**:21-21.

Table 3.1. Identified bee species collected from flowers of *Hamelia patens*. Bees were found either collecting nectar or pollen from outside the flower or from inside the flower.

Native Bee Species	H. patens +	H. patens -	Coffee flowers
Apis mellifera (11 mm)	×		×
Trigona fulviventris (7mm)	×	×	×
Trigona corvina (7mm)	×		×
Partamona orizabaensis (7mm)	×		×
Tetragonisca angustula (4.5mm)	×		
Bombus pullatus (14mm)	×		×
Exaerete frontalis (24mm)	×		
Euglossa sp. (bright green with yellow ab)	×		
Euglossa viridissima	×	×	×
Ceratina sp. 1 (9mm) black w/ bronze ab.		×	
Ceratina sp. 3 (8.5mm) all turquoise		×	
Ceratina sp. 5 (9mm) green w/ bronze ab.	×	×	
Halictidae/ Augochlorini sp. 1 (8mm) metallic green w/ gold ab.	×		×
Halictidae/ Augochlorini sp. 3 (6.5mm) green/ gold/ red	×		×
Halictidae/ Halictini sp. 1 (7mm) ♀Matte turquoise w/ glossy ab	×	×	
Halictidae/ Halictini sp. 1 (7mm) ♂metallic green/red	×		×
Halictidae/ Halictini sp. 2 (10mm) ♂ metallic green/ turquoise	×		×
Halictidae/ Halictini sp. 3 (5mm) ♀ black w/ bronze wings	×		
Halictidae/ Halictini sp. 4 (5mm)	×	×	×
Green metallic halictid sp. with bronze legs	×		×
Smaller yellow melipona	×		

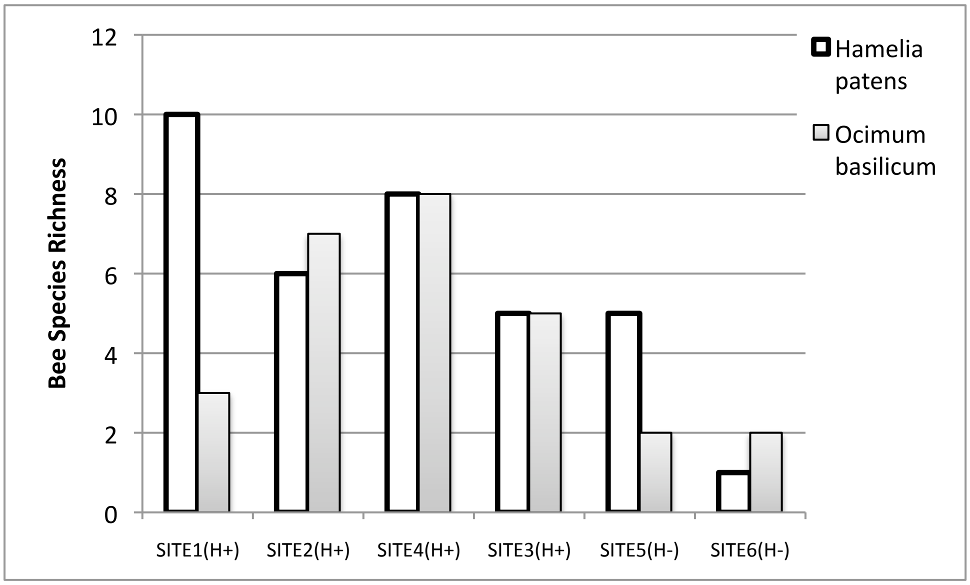


Figure 3.1. Bee Species Richness at *Hamelia patens* and *Ocimum basilicum*. No. bee species observed during all 15 minute observation periods (n=12).

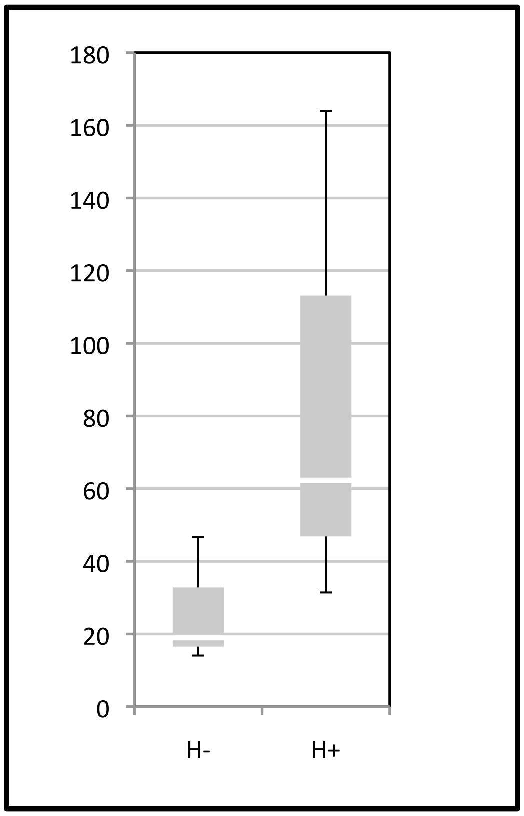


Figure 3.2. Chao 2 Species Richness Estimates using 50 Randomizations in EstimateS, Version 8.0; Mean Species Richness is white line with 95% Confidence Intervals.

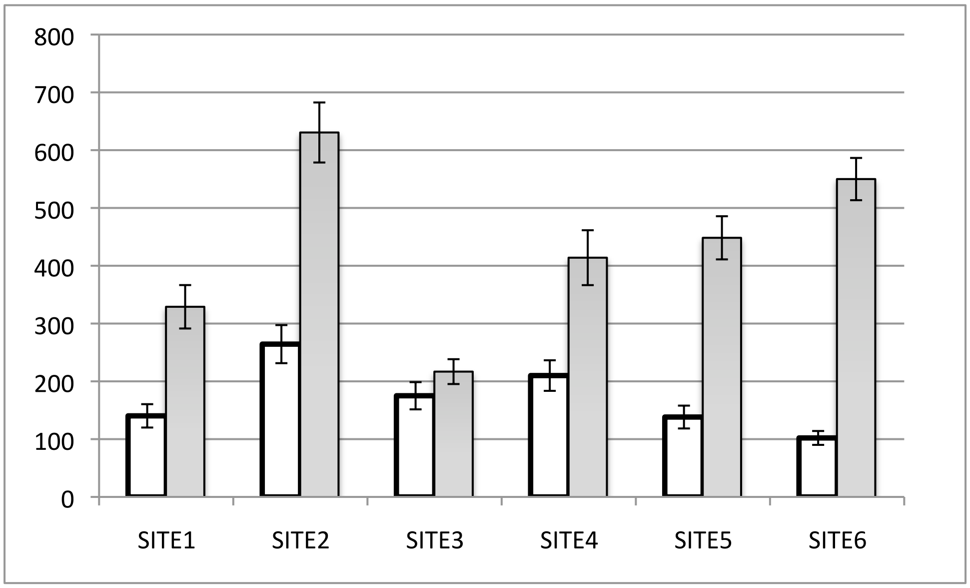


Figure 3.3. Number of Pollen Grains deposited on the stigmatic surface of coffee flowers during mass bloom periods, 2007 (n= 144) and 2008 (n= 138).

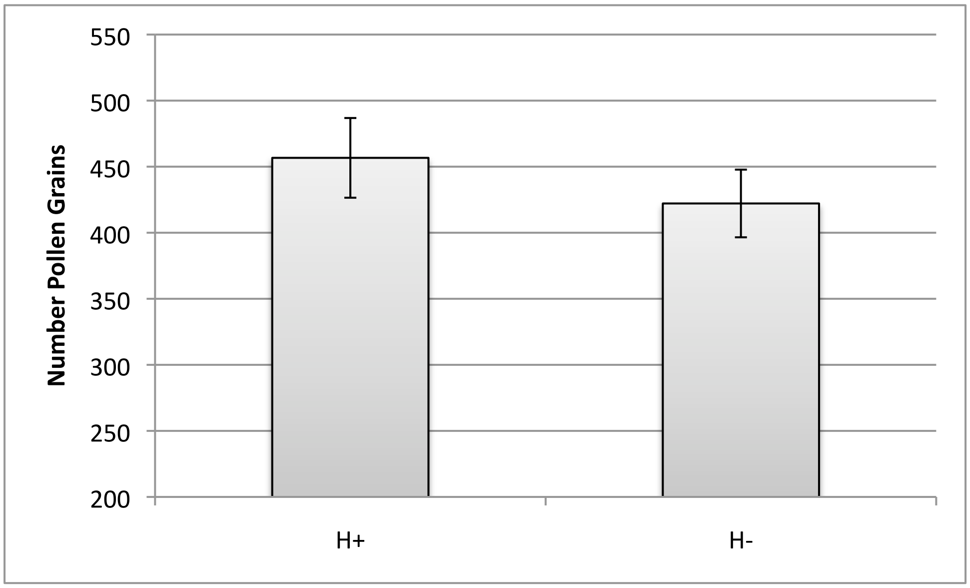


Figure 3.4. Number of Pollen Grains deposited on the stigmatic surface of coffee flowers during mass bloom period, April 2008 (n= 138), in response to experimental planting of *H. patens*

Table 3.2. No. Bee Species and Abundance for coffee plantations comparing *Apis mellifera*, other Non-apis social bees and Solitary bees for Early-bloom and Mass-bloom periods. ($X^2 = 105$, $p=0.000$)

	No. Species	**No. Individuals**
Early-bloom Coffee Plants		
Apis mellifera	1	151
Non-Apis Social bees	6	189
Solitary bees	2	12
Mass-bloom Coffee Plants		
Apis mellifera	1	565
Non-Apis Social bees	6	177
Solitary bees	5	18

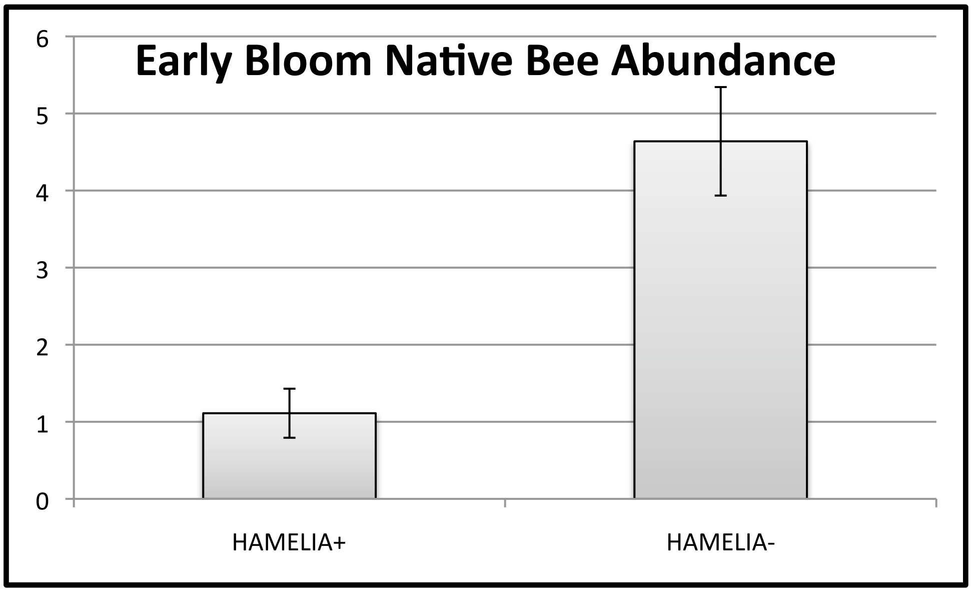


Figure 3.5. Native bee visitation rates to coffee flowers during Early Bloom in farms with planted *Hamelia patens* (HAMELIA+) and without (HAMELIA-); No. native bee visits to coffee flowers during 15 minute observation periods. (t_{71} =5.25, $p<0.00001$)

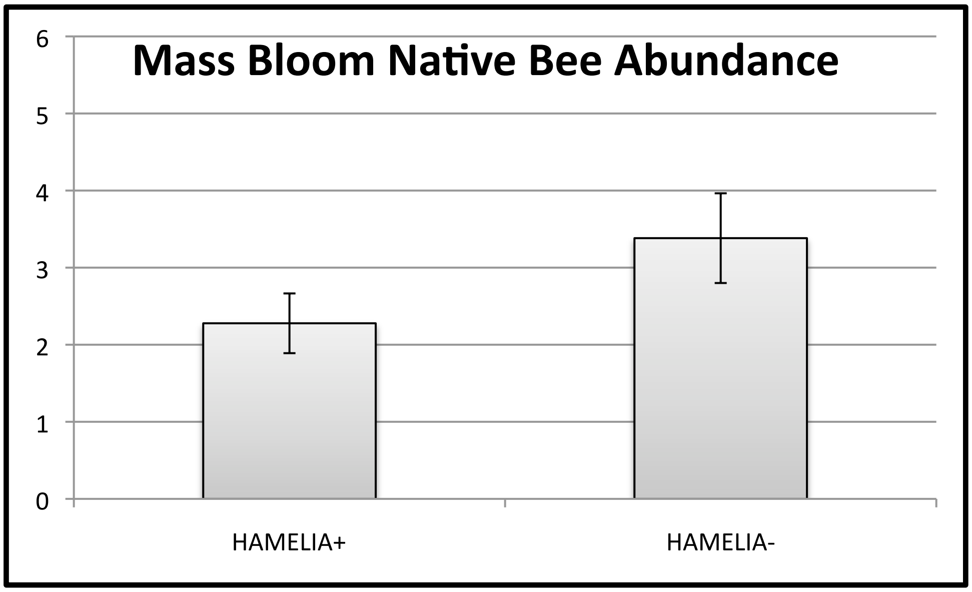


Figure 3.6. Native bee visitation rates to coffee flowers during Mass Bloom in farms with planted *Hamelia patens* (HAMELIA+) and without (HAMELIA-); No. native bee visits to coffee flowers during 15 minute observation periods. (t_{69}=1.20, p=0.233)

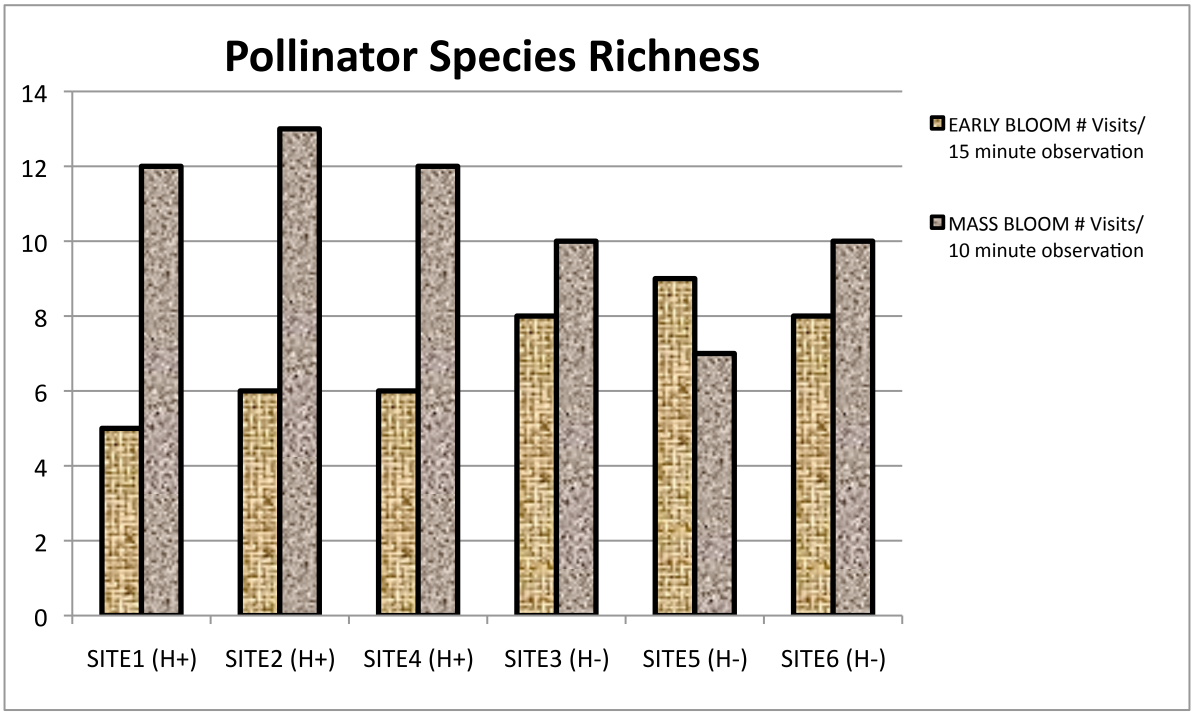


Figure 3.7. Total Pollinator Species Richness for all sites. (H+) denotes sites with steady-state floral resource *Hamelia patens* and (H-) without.

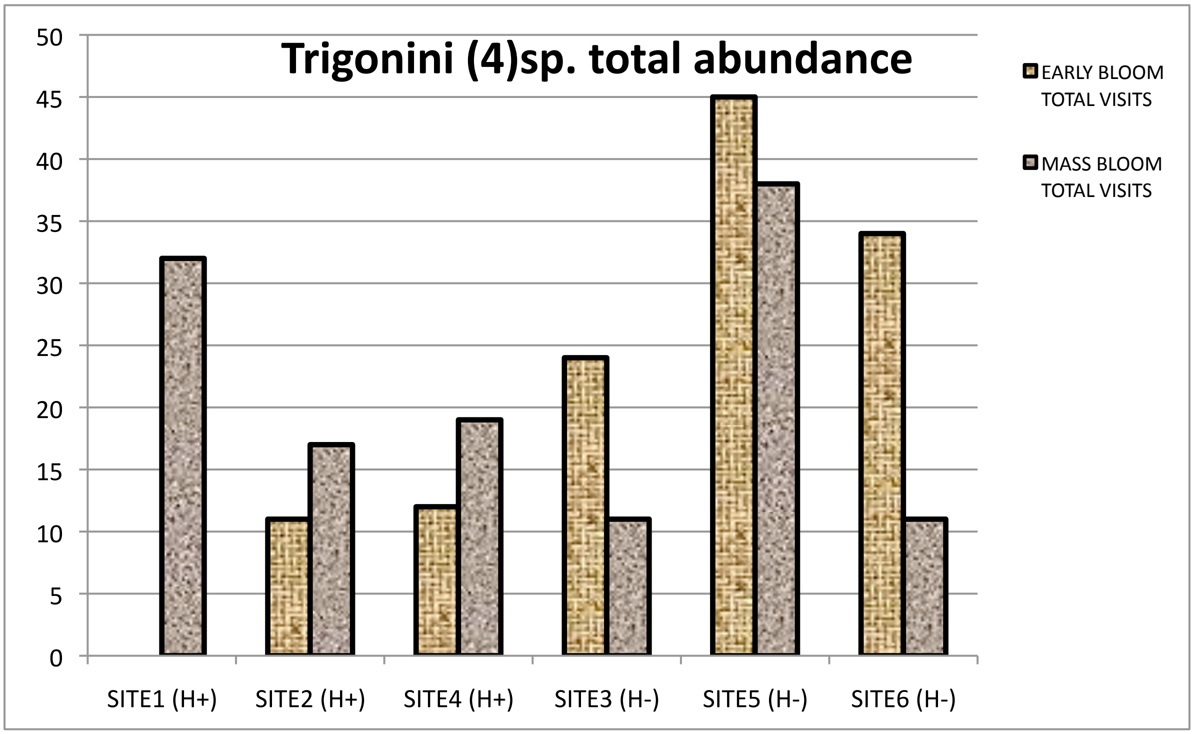


Figure 3.8. Total abundance of 4 species in the Trigonini group in H+ and H- farms, for the early bloom and mass bloom coffee flowering periods.

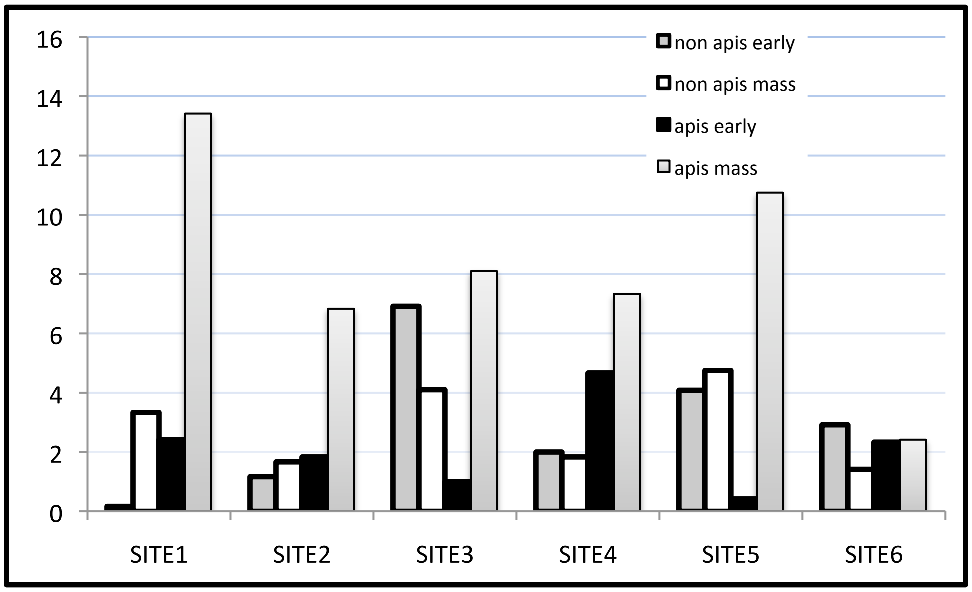


Figure 3.9. Average Number of Bee Visits per site in each group of 4 groups; Native Bees Early Flowering, Native Bees Mass Flowering, Apis Early Flowering and Apis Mass Flowering.

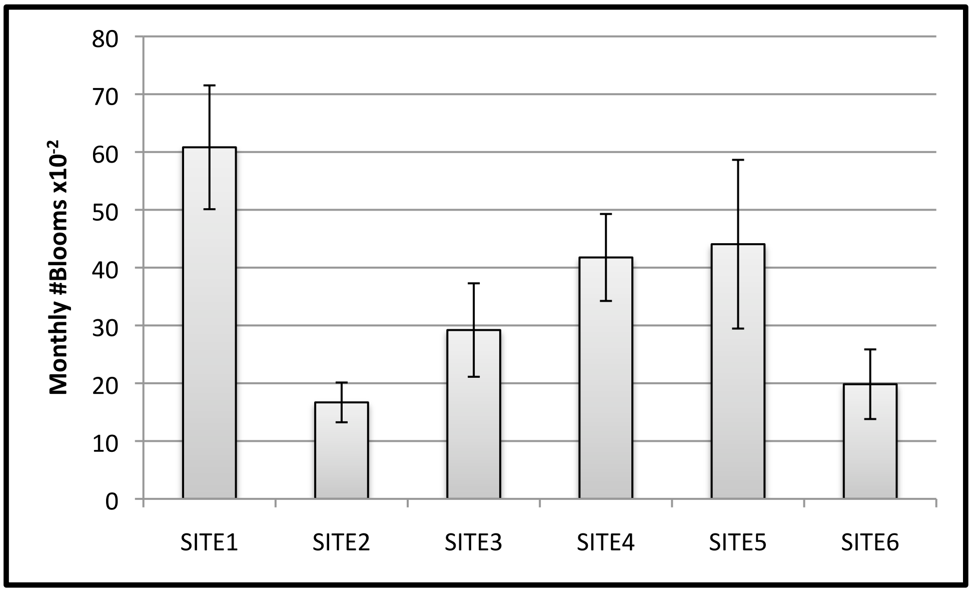


Figure 3.10. No. Monthly Blooms per site from February 2008 to December 2008. Number of blooms is shown as actual value x10^{-2}.

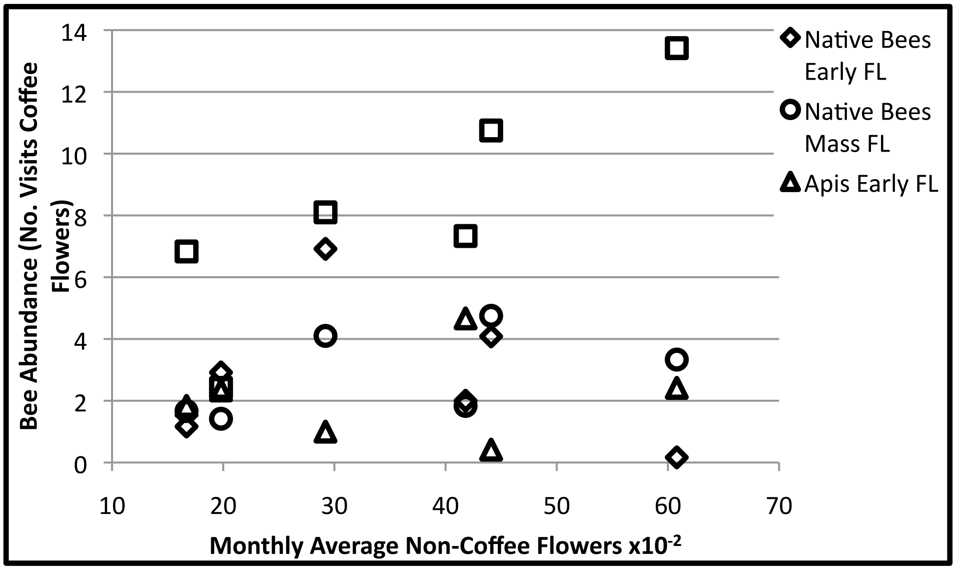


Figure 3.11. Average Monthly Number of Non-Coffee Flowers per site and Four Bee groups. Only *Apis mellifera* bee abundance during the Mass Bloom period displays a correlation with monthly average flowers (*Apis mellifera* Mass, F=10.56, p=0.03, R^2=0.66); (Native bees Mass, F=1.35, p=0.31, R^2=0.07); (*Apis mellifera* Early, F=0.087, p=0.78, R^2= -0.22); (Native bees Early, F=0.36, p=0.58, R^2= -0.15)

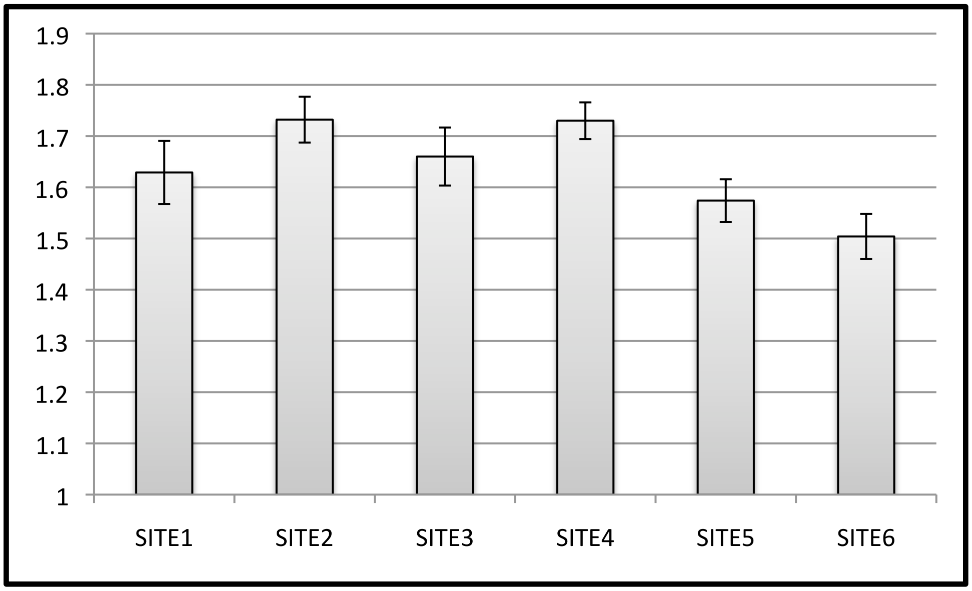


Figure 3.12. Coffee Fruit Weight per site. (F_{287}= 3.72, p=0.0028)

CHAPTER 4: CONCLUSIONS, RECOMMENDATIONS AND FUTURE RESEARCH PLANS

In the broadest sense my dissertation research provides some best practices for the conservation or restoration of ecosystem services in managed landscapes. More specifically, I selected shade-grown coffee plantations as case study sites for two reasons, because they were proposed in a working session of the 2003 ESA conference as a model agro-ecosystem for ecological research and because they are a managed system where the findings of my research could be applied. I selected coffee plantations which would be classified as traditional poly-culture, according to Moguel and Toledo (1999), because these farms had sufficient shade tree species diversity to allow an investigation into how the shade grown coffee agro-ecosystem influences the biodiversity of birds and bees. It was my goal to use structurally similar coffee plantations as replicates so that the variation in anything other than seasonal resource availability was reduced. In minimizing structural variation and variation in diversity of shade tree species, I was also able to create more rigorous experiments where I manipulated some aspect of the environment (i.e., the planting of a steady-state floral resource).

The scope of research related to the conservation or restoration of ecosystem services in managed lands is extensive, and for that reason often includes modeling the response of multiple ecosystem services to various, large-scale land management scenarios (Nelson *et al*. 2009). My dissertation research, however, was focused on one, small-scale aspect of ecosystem service research: determining habitat requirements for the animal species provisioning ecosystem services and how local ecological variables contributed to the provisioning of ecosystem services. This type of research is essential because without this knowledge models would incorrectly predict how different land-use scenarios affect ecosystem services. However, even on the small scale level, my research has only scratched the surface of the myriad research topics possible relating to the conservation and provisioning of ecosystem services in managed lands (Swinton *et al*. 2006). Although the ecosystem services I chose for my dissertation research were all animal mediated, how different agricultural management practices contribute to the provisioning of other non-animal mediated ecosystem services, such as climate regulation, water purification, nutrient renewal and carbon sequestration, is equally poorly understood.

Basic Research Conclusions

I selected six coffee plantations that were all approximately one hectare and that were all embedded within a similar quality of surrounding habitat which included cattle pasture, forest patches and single and/ or multiple species tree windbreaks. Additionally, tree species richness and canopy cover within each coffee plantation was similar. Despite the high degree of similarity in tree species richness as well as farm structural characteristics such as canopy cover and tree DBH, I found significant differences among the farms for almost all variables sampled or tested: monthly bird diversity, bee diversity, bee species abundance, monthly fruit energy availability, monthly floral availability, coffee plant seed set, and pollen deposition on coffee flower stigmas. Many previous studies have compared one specific dependent variable, such as bird abundance or ant species diversity, across a gradient of management intensification, (i.e., forest, shade-grown coffee, sun-grown coffee). My research is significant because it demonstrates that even within the classification of shade-grown coffee plantations having similar shade tree species diversity there is variation in the availability of food resources for both birds and bees. Understanding that there is a difference and that this difference can affect the community of organisms that can be supported by the coffee plantation is important knowledge for conservation managers and farmers who want to manage their coffee plantations for biodiversity. Prior to this research a conservation professional may have directed landowners to plant shade-grown coffee with diverse shade tree species only; however, it is my hope that with this research the conservation professional may encourage landowners to more carefully select shade tree species based on the type of resources provided by the plant species, and how those resources contribute throughout the year to providing a constant resource base for animals, such as birds and bees.

Bird Response to Fruit Energy Availability

All sites were sampled for birds in July 2006, November 2006, February 2007, April 2007, June 2007, July 2007 and November 2007 as a preliminary investigation in order to determine which bird species would be target species for the full year of study in 2008. Contrary to what I had originally expected, in 2008, I decided to include all bird species and use species richness as the response variable rather than the abundances of focal "frugivorous" bird species. Furthermore, I selected 14 bird species from many different guilds for the analysis in a multi-season occupancy model. My results clearly indicate that a community-wide response by birds to fruit energy availability was observed in the coffee plantations. Monthly bird species richness was strongly correlated with monthly fruit energy availability. Additionally, in the multi-season occupancy model, both emigration and immigration of birds into a coffee plantation were dependent on fruit energy availability. The probability of emigration exceeded the probability of immigration into a coffee farm when the monthly fruit energy availability value was below 500 calories; however, above 12,000 calories the probability of immigration was almost 100% and the probability of emigration 0% for the bird community used in the model. The Smithsonian Migratory Bird Center Bird-Friendly Certification requires only 10 different tree species per hectare while the farms where I conducted my research had between 18 and 23 different tree species per hectare. Despite this tree diversity, only four farms each had only one month when fruit energy availability exceeded 12,000 calories and several farms had many months where fruit energy availability was less than 500 calories. Only one farm did not have any months with fruit energy availability values less than 500 calories.

The home range or foraging range of many neotropical birds is still unknown, and so it is unclear how different bird species depend upon the availability of resources within a one hectare tract of land; for example, the Orange-billed Nightingale-Thrush is estimated to have a home range of approximately one hectare (Sekercioglu *et al*. 2008) while the Keel-billed Toucan has been estimated to have a home range between 18 and 111 hectares (Graham 2001). The fourteen bird species used in the multi-season occupancy model most likely vary between these two very different home range sizes. Even so, the bird species in this community were all found to be more likely to use and to remain within a hectare of land (coffee plantation) as the number of calories increased.

One goal of my dissertation research was to contribute to the guidelines available for coffee farmers who are interested in managing their farms for the conservation of bird species, mainly through the certification criteria for the Smithsonian's Bird-Friendly Coffee program. My research has demonstrated the importance of fruit resources to the bird community in shade-grown coffee plantations, and that the monthly availability of fruit resources is due to which tree species are selected as shade trees and not the diversity of shade tree species planted. I would therefore recommend that Bird-Friendly guidelines focus on the types of tree species selected as shade trees, based on their contribution to monthly fruit energy availability, and not focus as much on a specific number of tree species diversity per hectare, e.g., ten tree species per hectare.

For example, an individual *Ficus pertusa* tree contributes approximately 7,000 or 8,000 calories each year to the farm's yearly fruit energy value, and therefore contributes much more than most other tree species to bird use of the coffee farm.

Previous research has shown that the abundances of some bird species do respond to fluctuations in fruit availability (Moegenberg and Levey 2003), but my study is unique because it is the first to demonstrate a community wide response to fruit availability. There are several likely explanations why other studies have not detected a community response. One explanation is that previous studies have taken place in natural areas or extensive forest where this type of response either doesn't occur because fruit resources are too widespread and therefore not limiting, or the response cannot be detected because there is too much extraneous variability in natural forest, as opposed to the more uniform, managed coffee plantation. Another possible explanation is that the explanatory variable used in other studies to represent the fruit resource did not accurately reflect the value perceived by the study organism. In my study, I used the explanatory variable of fruit energy availability, which mathematically combines the fruit size, the fruit calories per gram, and the number of ripe fruits on an individual tree. Most previous studies relating frugivore abundance to fruit resources have used only the number of ripe fruits as the explanatory variable.

Bee Conservation and Coffee Production

In three out of six coffee plantations I planted, for experimental purposes, the native shrub *Hamelia patens*, Family Rubiaceae, because it produces fruits and flowers during all months of the year and its red tubular flowers are visited by both hummingbirds and bees. The experimentally planted steady-state resource, *H. patens*, used in this study had both a positive effect on native bee conservation and a negative effect on coffee production, but only during some flowering periods. We found 21 bee species foraging floral resources of *H. patens*, both in farms with the enhanced resource (H+) and without (H-). Based on bee observations on *H. patens* plants, species richness estimators predicted twice as many native bee species in H+ farms over H- farms. The native bee species found utilizing floral resources of *H. patens* included both social, stingless bees as well as a diversity of rare solitary bees from the Family Halictidae and from the Family Apidae: Tribe Ceratinini. Due to time constraints I was not able to investigate the difference in bee species abundances between farms with and without planted *H. patens*; however, based on personal observations over the past several years, as well as some preliminary data from Malaise traps placed in these two types of farms, it seems likely that farms with *H. patens* (H+) support higher abundances of these bees as well. It is my plan to investigate this further in upcoming years (see Future Research Plans below).

I also investigated the influence of the experimentally planted steady-state resource, *H. patens*, on the production of coffee. I selected three response variables: bee visitation during ten minute periods, seed set, and the number of pollen grains deposited on the stigmatic surface of coffee flowers. I also divided the flowering periods into early flowering blooms and the mass bloom. Early flowering blooms occurred during February or March, and only about 20 to 30% of plants produced flowers. The mass bloom occurred during April and all plants in the coffee plantation were in full bloom. This mass bloom coincided with the first week of heavy rains marking the beginning of the rainy season and can typically occur in late April or early May. I found that the number of native bee visits to coffee flowers did not change significantly between early and mass flowering periods; however, the non-native European honeybee, *Apis mellifera*, did respond to the mass bloom. There was a significantly higher visitation rate of *Apis mellifera* to coffee flowers during the mass bloom period over the early bloom periods. This difference changed who was mainly responsible for providing the ecosystem service of pollination to coffee plants during the mass bloom and the early bloom periods. Native bees provided 57% of the service during the early blooms, but only 25.7% during the mass bloom. I also found a significant difference in seed set values between the early bloom and the mass bloom, 74% and 59%, respectively. These numbers correspond to differences in pollination of coffee found from previous research where 75% seed set was obtained through cross-pollination and 60% seed set from manual self-pollination. Our difference in seed set values may indicate that native bees offer the ecosystem service of cross pollination more often and that *Apis mellifera* bees pollinate coffee plants in a fashion more comparable to manual self-pollination. This matches with observed behaviors between these two groups, as *Apis mellifera* were often observed to visit all flowers on a particular coffee plant, while native bees were observed to only visit a few flowers before moving on to another plant.

I further divided and compared my data for bee visitation rates to coffee flowers during the mass bloom and early bloom periods between farms with (H+) and without (H-) *H. patens*. I found no difference in *Apis mellifera* visitation rates to coffee flowers between H+ and H- farms for either the early or the mass bloom periods. I did find a significant difference, however, between native bee visitation rates to coffee flowers in H+ and H- farms, during the early bloom periods only. This is likely due to that the smaller bloom of coffee flowers did not represent a sizeable enough resource to compete with the steady-state flowers of *H. patens*. This result shows that the steady-state resource can actually compete with coffee flowers for pollinators during the early bloom, and that perhaps a management practice in coffee plantations could involve covering or cutting flowers from a steady-state floral resource when coffee is flowering.

In the San Luis Valley there are other planted steady-state floral resources within the managed landscape; however, many of these plant species are non-native ornamentals and vary greatly between households. *H. patens* is a native plant found throughout the valley in almost every household as well as growing naturally in forest patches, windbreaks and roadsides. It is the only native steady-state resource found in the managed landscape and it has been shown to be valuable for native bee conservation. In addition, many species of hummingbirds, wasps, and butterflies are often seen foraging resources from *H. patens*. Although I found that it can have negative consequences to the coffee harvest, I would not recommend that the farmers remove the plants from their coffee farms but instead that they manage their *H. patens* plants during early bloom periods if they find that they have a noticeably reduced coffee harvest. It is likely that there is a similar species of Rubiaceae in other coffee growing regions throughout Latin America and that the practice of planting a steady-state floral resource in coffee plantations throughout the neotropics could be extremely beneficial for the conservation of native bee species.

Future Research: Pest control service providers and resource constancy

Pest control is yet another ecosystem service which can be assigned value directly through a demonstrated increase in production, and different agricultural management practices may affect the provisioning of this agriculturally important ecosystem service. In coffee farms of the Dominican Republic, seventeen bird species, primarily Nearctic migrants, were responsible for the reduction of coffee bean borer infestation on coffee plants by up to 14% (Kellermann *et al*. 2008). Furthermore, the abundance and diversity of these bird species were found to increase with increasing shade-tree cover (Kellermann *et al.* 2008). Several other recent studies have examined pest control by native and migratory birds in coffee farms. One study found that migratory birds decrease herbivory and arthropod abundances on shade trees within shade grown coffee plantations, but not necessarily on the coffee plants themselves (Van Bael *et al.* 2008). Another study found that only migratory birds, not resident birds, were responsible for this effect of arthropod reduction (Van Bael *et al.* 2008). However these studies were restricted to one location, and therefore much more research would be necessary to determine if these effects are true for all regions, even where resident bird diversity is higher or in coffee plantations capable of sustaining greater abundances of those resident birds responsible for removing arthropods from coffee.

Research addressing predation by birds in coffee plantations thus far has not addressed how fruit resource availability influences different bird species abundances within the farm throughout the year, and in turn how this affects the ecosystem service of pest control. In my study area, it is common to observe several resident bird species gleaning insects from coffee plants. Some of these resident birds additionally consume fruit resources when they are available within the plantation, but their abundance or presence in the farm may depend upon the availability of these other resources. For example, Rufous-capped Warblers (*Basileuterus rufifrons*) were observed gleaning insects from coffee plants on approximately 50% of all observations during all transects conducted for my dissertation research in 2008, and this same species was observed to consume *Musa* spp. fruit whenever available in the farm. Additionally, Rufous-capped Warblers were detected about twice as often on some coffee farms over other farms. Two other resident bird species that were commonly observed gleaning insects from coffee plants were the Blue-crowned Motmot (*Momotus momota*) and the Dusky-capped Flycatcher (*Myiarchus tuberculifer*), both also abundant consumers of fruits such as *Ficus sp.*, *Acnistus arborensens*, *Hamelia patens*, *Trema micrantha*, and *Cecropia obtusifolia* (personal observation). Finally three species of resident wrens were observed commonly feeding on insects on coffee plants: the Rufous-and-white Wren (*Thryophilus rufalbus*), the Plain Wren (*Thryothorus modestus*), and the House Wren (*Troglodytes aedon*). At least five additional migratory bird species also participate in gleaning insects from coffee plants: Wilson's Warblers (*Wilsonia pusilla*), Tennessee Warblers (*Vermivora peregrine*), Chestnut-sided Warblers (*Dendroica pensylvanica*), Yellow Warblers (*Dendroica petechia*), and Alder Flycatchers (*Empidonax alnorum*). Several of these migratory bird species were more abundant or more commonly utilized a particular coffee plantation when a fruiting resource was also available. Thus, my future research on ecosystem services in coffee plantations will focus on the question: Does the presence of fruit eating birds at fruit resources increase the level of active insectivory on coffee plants?

Future Research: Native bee population monitoring and climate change

The San Luis Valley is an optimal location for long-term research relating to tropical native bees and climate change for two reasons. The first reason is that the San Luis Valley is comprised of steep elevation gradients and native bee species have been observed to display elevation restrictedness. In my dissertation research I discovered that at least 5 to 10 bee species found within the elevation range of 900 to 950 msl were no longer present at 1000 msl. Furthermore, climate change is predicted to more rapidly affect elevation restricted species, with range shifts averaging 6.1 meters per decade upward (Parmesan and Yohe 2003). Long-term monitoring stations can therefore be set up at 50 meter intervals throughout the San Luis Valley from 850 msl to 1100 msl, as well as within different micro-habitats such as shade-grown coffee farms, forest patches, and cattle pastures.

Future Research: Insect diversity and a steady-state floral resource

Another of my current research projects focuses on the differences in overall insect diversity between farms with and without the planted steady-state floral resource, *Hamelia patens*, which was planted in July 2007 as part of my dissertation research focusing on bee conservation and coffee production. In a collaborative effort with the Costa Rican National Institute of Biodiversity, in July 2008, I placed one Malaise trap per farm for 15 days in each of six coffee farms. The main intention of placing Malaise traps was to determine differences in bee species abundance or diversity within the coffee farms, both those with and without *Hamelia patens*. Preliminary results, however, indicated that overall species richness and abundance of insects may differ among farms with and without *Hamelia patens* (Table 4.1 and 4.2). In order to evaluate differences in overall insect diversity and abundance between H+ and H- farms, I will conduct several more insect collections in the two types of coffee farms, utilizing Malaise traps, between November 2008 and November 2009.

Table 4.1. Diptera diversity, number of species per family collected in Malaise traps for farms with (H+) and without (H-) planted *Hamelia patens* (Rubiaceae).

DIPTERA/ FAMILY	ALV (H+)	GIL (H+)	OLD (H+)	ODIL (H-)	OLIV (H-)	RAFA (H-)
MUSCIDEAE	5	17	7	15	8	5
SARCOPHAGIDEAE	3	10	4	3	4	3
TACHINIDEA	11	37	17	10	13	8
TABANIDEAE	3	3	3	1	1	0
CALLIPHORIDEAE	0	4	1	1	0	0
SYRPHIDEAE	0	6	2	0	2	0
ASILIDEAE	0	1	1	0	0	0
STRATIOMYIDEAE	0	1	3	0	0	0

Table 4.2. Dry mass in grams of various insect orders from Malaise traps placed in farms with (H+) and without (H-) planted *Hamelia patens* (Rubiaceae).

INSECT ORDER	ALV (H+)	GIL (H+)	OLD (H+)	ODIL (H-)	OLIV (H-)	RAFA (H-)
DRY MASS DIPTERA	1	6.2	2.5	1.2	1.6	0.9
DRY MASS SPIDERS	0.2	0.1	0.3	0.2	0.5	0.2
DRY MASS ORTHOPTERA	0.7	0.8	1.1	0.8	3.6	1.9
DRY MASS LEPIDOPTERA	0.8	4.2	2.5	0.7	1.4	1.2
DRY MASS COCKROACHES	0.3	0.7	0.7	0	0.3	0
DRY MASS SYMPHYTAS	0.3	0.3	0.1	0	0.2	0.1
DRY MASS WORMS	0.8	0	0.1	0	0.1	0

Table 4.3. Bee species diversity and abundance from Malaise traps placed in farms with (H+) and without (H-) planted *Hamelia patens* (Rubiaceae)

Bee Species	**ALV (H+)**	**GIL (H+)**	**OLD (H+)**	**ODIL (H-)**	**OLIV (H-)**	**RAFA (H-)**
Trigona fulviventris	0	9	5	0	3	0
Trigona corvina	0	0	0	0	1	0
Scaptotrigona lateipennis	0	3	0	0	1	0
Partamona orizabaensis	0	4	1	0	0	0
Apis mellifera	0	0	1	0	0	1
Halictid: Augochlorini sp.1	0	4	1	0	1	0
Halictid: Halictini sp. 1	0	6	1	0	0	0
Halictid all green metallic	0	0	0	1	0	0
Megachilidae: Coelioxys sp.	0	0	0	0	0	1
Small black halictid	1	0	1	0	1	0
Colletidae: Hylaeinae sp.	0	0	0	0	0	1
Colletidae: Ptiloglossa costaricana	0	1	0	0	0	0
small black ceratini (7mm)	0	1	0	0	0	0
Halictid small metallic green (6 mm)	0	1	0	0	0	0
Halictid matte green metallic (9mm)	0	1	0	0	0	0
Examolopsis sp.	0	1	1	0	0	0

Melipona costaricensis	0	1	0	0	0	0
metallic green cuckoo bee or wasp	0	0	3	0	0	1
Halictidae: Halictini sp. 2	0	0	0	0	0	1

Future Research: Restoration ecology and natural capital

It is estimated that in the decade following the World Summit on Sustainable Development in 1992, six global biomes have suffered a mean rate of land conversion of approximately -11.4% (Balmford *et al*. 2002), and in 1995 it was estimated that approximately 43% of the world's vegetated terrestrial surface was so degraded that it had diminished capacity to supply benefits to humanity (Daily 1995). As the negative impacts of land degradation continue to accumulate, the restoration of lands to re-establish our lost natural capital is of utmost importance (SER 2004). Restoration projects, however, are typically carried out with limited funds and so it is increasingly necessary to assess the return-on-investment on different types of restoration projects in order to meet targeted outcomes (Goldstein *et al*. 2008), especially in highly degraded lands that are more costly to restore. A key measure of return-on-investment for restoration projects would be the restored land's capacity to provision ecosystem services, such as pollination, carbon sequestration or timber production (Daily *et al*. 2009).

One potential way to reduce funds spent in restoration activities is to reduce the number of tree species planted in reforestation activities. Forest regeneration and recruitment occurs differently under different focal tree species (Janzen 1988, Chapman and Chapman 1999, Slocum 2001), however many restoration projects haphazardly select tree species for use in reforestation. Furthermore, many times individual trees are lost due to competitive interactions with non-native grasses, seedling predation, or poor abiotic conditions (Chapman and Chapman 1999, Aerts *et al*. 2007), causing great monetary loss for the restoration project. An improved method for diminishing costs associated with planting trees for reforestation would be to select tree species based on their effectiveness and/ or rapidity in re-establishing target ecosystem services. As the different plant communities regenerate under planted tree species, these various species compositions and abundances provide different levels of fuel wood, forage for range animals, habitat for pollinators, carbon and water storage, functional biodiversity or biodiversity for eco-tourism (Milton *et al*. 2003, Aerts *et al*. 2007).

Beginning August 2009, I will begin an Andrew W. Mellon Postdoctoral Teaching and Research Fellowship in Environmental Restoration at Rollins College in Central Florida. Rollins College owns two different restoration sites in Central Florida, both in differing degrees of restoration, and nearby is the 19,000 acre Lake Apopka Restoration Area owned by the St. John's Water Management District. All three of these are potential sites for my future post-doctoral research, relating to restoration ecology and natural capital. The ideal site would be 10 to 30 years post reforestation, where several different tree species were utilized and the regenerating community surrounding these focal trees can be studied for provisioning of selected ecosystem services which may represent targeted outcomes or original goals of the restoration project.

Literature Cited

Aerts, R., A. Negussie, W. Maes, E. November, M. Hermy, and B. Muys. 2007. Restoration of dry afromontane forest using pioneer shrubs as nurse-plants for Olea europaea ssp cuspidata. Restoration Ecology **15**:129-138.

Balmford, A., A. Bruner, P. Cooper, R. Costanza, S. Farber, R. E. Green, M. Jenkins, P. Jefferiss, V. Jessamy, J. Madden, K. Munro, N. Myers, S. Naeem, J. Paavola, M. Rayment, S. Rosendo, J. Roughgarden, K. Trumper, and R. K. Turner. 2002. Ecology -

Economic reasons for conserving wild nature. Science **297**:950-953.

Chapman, C. A. and L. J. Chapman. 1999. Forest restoration in abandoned agricultural land: a case study from East Africa. Conservation Biology **13**:1301-1311.

Daily, G. C. 1995. Restoring Value To The Worlds Degraded Lands. Science **269**:350-354.

Daily, G. C., S. Polasky, J. Goldstein, P. M. Kareiva, H. A. Mooney, L. Pejchar, T. H. Ricketts, J. Salzman, and R. Shallenberger. 2009. Ecosystem services in decision making: time to deliver. Frontiers in Ecology and the Environment **7**:21-28.

Greenberg, R., P. Bichier, A. C. Angon, C. MacVean, R. Perez, and E. Cano. 2000. The impact of avian insectivory on arthropods and leaf damage in some Guatemalan coffee plantations. Ecology **81**:1750-1755.

Janzen, D. H. 1988. Tropical Ecological And Biocultural Restoration. Science **239**:243-244.

Kellermann, J. L., M. D. Johnson, A. M. Stercho, and S. C. Hackett. 2008. Ecological and Economic Services Provided by Birds on Jamaican Blue Mountain Coffee Farms. Conservation Biology **22**:1177-1185.

Milton, S. J., W. R. J. Dean, and D. M. Richardson. 2003. Economic incentives for restoring natural capital in southern African rangelands. Frontiers in Ecology and the Environment **1**:247-254.

Moguel, P. and V. M. Toledo. 1999. Biodiversity conservation in traditional coffee systems of Mexico. Conservation Biology **13**:11-21.

Nelson, E., G. Mendoza, J. Regetz, S. Polasky, H. Tallis, D. R. Cameron, K. M. A. Chan, G. C. Daily, J. Goldstein, P. M. Kareiva, E. Lonsdorf, R. Naidoo, T. H. Ricketts, and M. R. Shaw. 2009. Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. Frontiers in Ecology and the

Environment **7**:4-11.

Parmesan, C. and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature **421**:37-42.

Slocum, M. G. 2001. How tree species differ as recruitment foci in a tropical pasture. Ecology **82**:2547-2559.

Swinton, S. M., F. Lupi, G. P. Robertson, and D. A. Landis. 2006. Ecosystem Services from Agriculture: Looking Beyond the Usual Suspects. American Journal of Agricultural Economics **88**:1160-1166.

Van Bael, S. A., S. M. Philpott, R. Greenberg, P. Bichier, N. A. Barber, K. A. Mooney, and D. S. Gruner. 2008. Birds as predators in tropical agroforestry systems. Ecology **89**:928-934.

APPENDIX 1: BEE SPECIES

Family: Apidae Subfamily/ Tribe: Apinae/ Meliponini

Tetratrigona angustula (3.5 mm)
Olivier/ Odilio; Coffee flowers

Plebia sp. (3.5 mm)
Olivier/ Odilio; Coffee flowers

Trigona corvina (6 mm)

Partamona orizabaensis (6 mm)

Scaptotrigona lateipennis (6 mm)

Trigona fulviventris (6.5 mm)

Trigonisca buyssoni (2.5 mm)
Odilio; coffee flowers

Melipona costaricensis (11 mm)
coffee flowers

Apis mellifera (11 mm)

Family: Apidae Subfamily/ Tribe: Apinae/ Euglossini

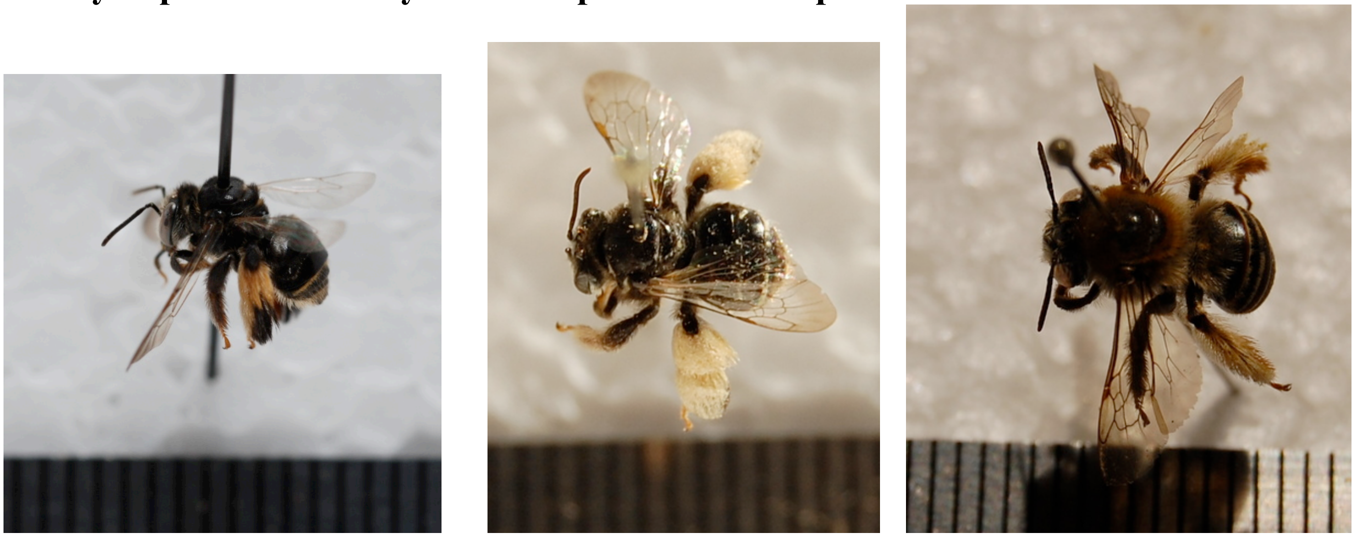

Exaerrette frontalis (24 mm)


Euglossa sapphirrina (11 mm)
Odilio; Ocimum basilicum


Euglossa sp. (11.5 mm)
Oldemar; Coffee flowers

(same euglossine as green above but with diff. lighting)

Family: Apidae Subfamily/ Tribe: Apinae/Exomalopsini



Exomalopsis sp. (7 mm) Odilio; Ocimum basilicum and coffee

Family: Apidae Subfamily/ Tribe: Apinae/ Centridini

Centris (Melacentris) sp. (21 mm) Oldemar;
Ocimum basilicum

Epicharis angulosa (16 mm)
Oldemar; purple flower verbena

Family: Apidae Subfamily/ Tribe: Bombinae

Bombus pullatus (14 mm)

Family: Apidae Subfamily/Tribe: Xylocopinae/ Xylocopini

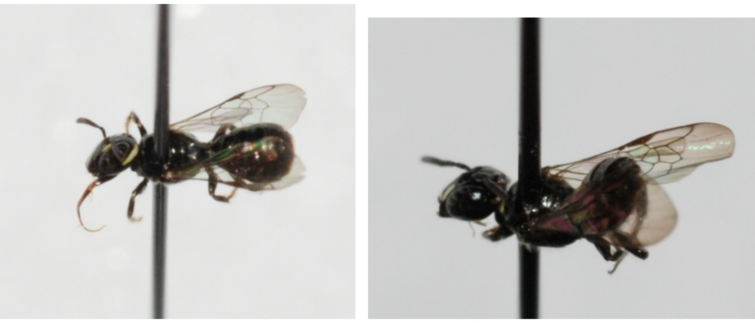
Xylocopa (Neoxylocopa) sp. (30 mm)
Oldemar; coffee flowers

Xylocopa (Schonnherria) sp. 1(16 mm)
Oldemar; coffee flowers

Xylocopa (Schonnherria) sp. 2 (20 mm)
Oldemar; Purple flower verbena

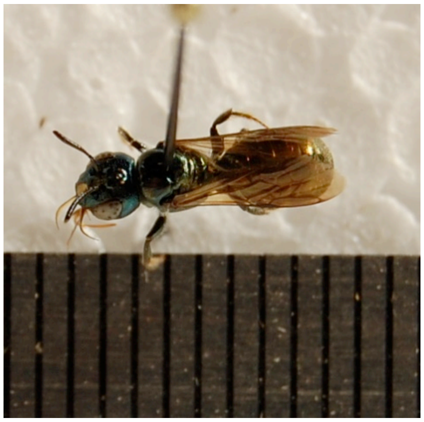
Family: Apidae Subfamily/Tribe: Xylocopinae/ Ceratinini

Ceratina sp. 1 (9 mm; black w/ bronze ab.)
Olivier; Hamelia patens



Ceratina sp. 2 (5mm; all black ♂&♀ w/ diff. yellow on face)
Gilbert; Ocimum basilicum

Ceratina sp. 3 (8.5 mm)
Olivier; Hamelia patens



Ceratina sp. 4 (8.5 mm)
Odilio; Ocimum basilicum

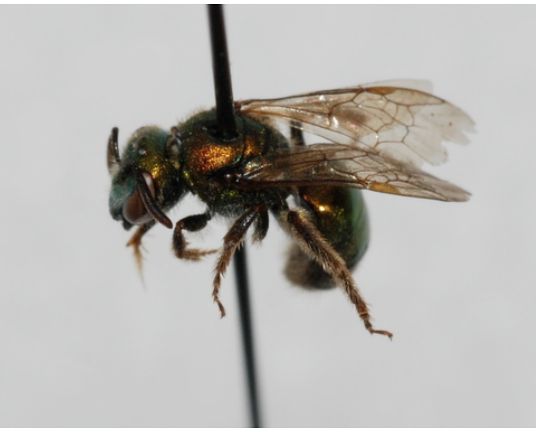
Ceratina sp. 5 (9mm)
Olivier; Hamelia patens

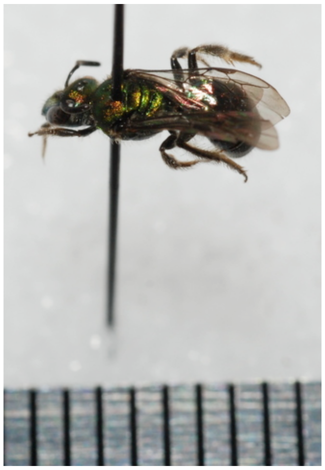
Ceratina sp. 6 (4.5mm; all black with one yellow spot on clypeus)
Olivier; Ocimum basilicum

Ceratina sp. 7 (5mm)
Olivier; Ocimum basilicum

Family: Halictidae Subfamily/ Tribe: Halictinae/ Augochlorini


Species 1 (8 mm)
Gilbert; Ocimum basilicum


Species 2 (6 mm)
Rafael; Ocimum basilicum


Species 3 (6.5 mm)
Hamelia patens

Family: Halictidae Subfamily/ Tribe: Halictinae/ Halictini


Species 1 ♂ (7 mm)
Hamelia patens


Species 1 ♀ (7 mm)
Odilio/ Alvaro; Hamelia patens


Species 2 ♂ (7 mm)
Alvaro; Hamelia patens

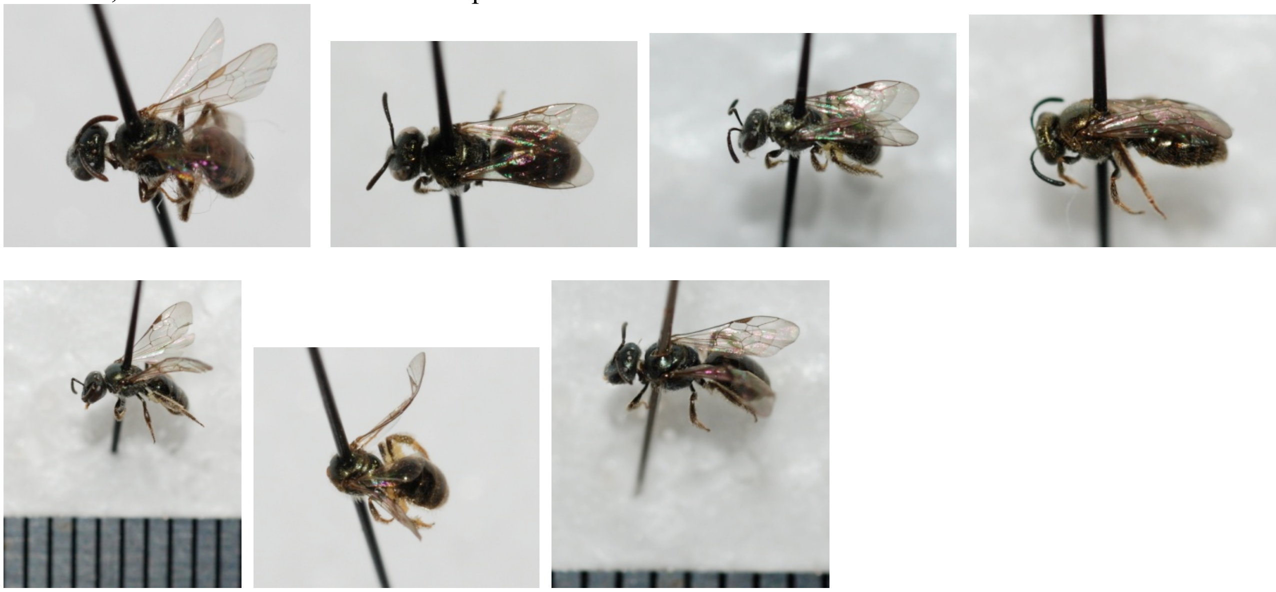

Species 2 ♀ (9 mm)
Ecolodge


Species 3 ♂ (10 mm)
Oldemar; Ocimum basilicum


Species 3 ♀ (5 mm) (goldish small black)
Oldemar; Hamelia patens/ Coffee flower

Family: Halictidae Subfamily/ Tribe: Halictinae/ Halictini

Species 4 (5 mm)- all photos
All farms; Ocimum basilicum/ Hamelia patens/ Coffee flowers

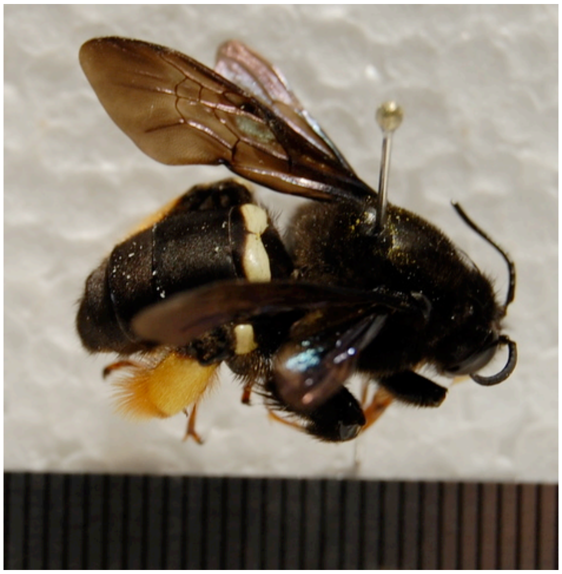


Halictidae: Auglochlorini sp.4
Odilio; coffee flowers

Family: Megachilidae Subfamily/ Tribe: Megachilinae/ Megachilini

Coelioxys sp. (11 mm)
Oldemar; Ocimum basilicum

Bees still to identify:



(21 mm)
Oldemar; coffee flowers

Xylocopa sp. (31 mm)
Oldemar; coffee flowers

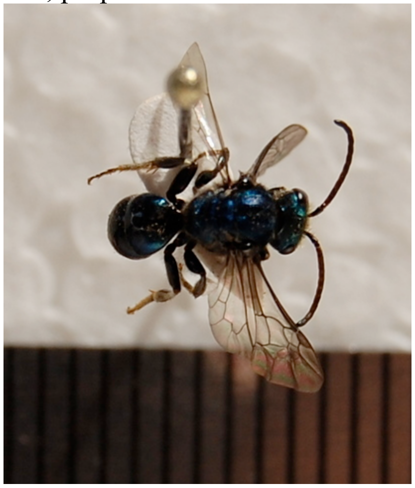
Apidae: Centridini (17 mm)
All farms; coffee flowers

Face shot; bee on left

Apidae: Centridini (13 mm)
Oldemar; purple verbena

Halictidae: (7.5 mm)
Gilbert; coffee flowers
Gilbert; malaise trap November

Halictidae: (9 mm)
Oldemar; coffee flowers

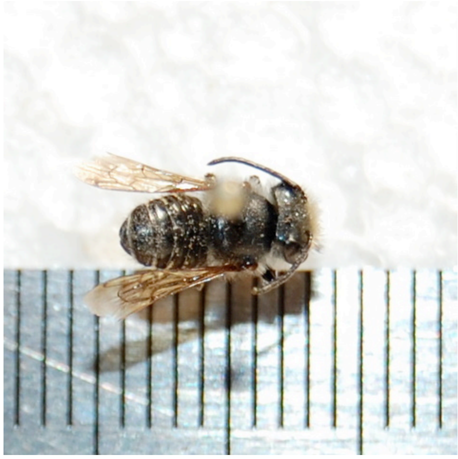


Halictidae: (7 mm)
Rafa; coffee flowers

Halictidae: (2.5 mm)
Rafa; coffee flowers

Apidae: Exomalopsis sp. (5 mm)
Rafa; coffee flowers

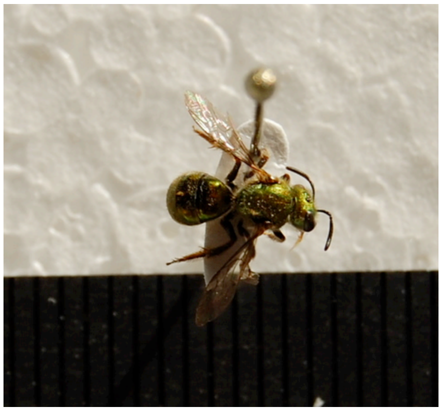
Apidae: Exomalopsis (7.5 mm)
Oldemar; coffee flowers



Megachilidae:?? (7 mm)
Gilbert; coffee flowers

Megachilidae: ?? (10 mm)
Oldemar; Ocimum basilicum

Apidae: Centridini (22.5 mm)
Olivier; coffee flowers

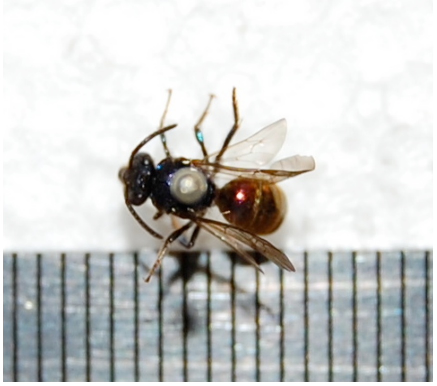


Halictidae: (6 mm)
Gilbert; coffee flowers

Halictidae: (6 mm)
Coffee flowers

Halictidae: (6.5 mm)
Rafa; coffee flowers

Halictidae: (9 mm)
Gilbert; coffee flowers



Apidae: Ceratinini? (7.5 mm)
Odilio; malaise trap May

Halictidae: (8.5 mm)
Odilio; malaise trap May

Halictidae: (10 mm)
Olivier; malaise trap November

Apidae: Bombinae (19 mm)
Gilbert; malaise trap November

?? (15 mm)
Odilio; malaise trap November