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Bees in a Changing World: How Land Surface Phenology, Bee Community
Distributions, and Pollinator-Plant Interactions are Impacted by Urbanization and
Agriculture

By

Misha Tomaye Leong

A dissertation submitted in partial satisfaction of the
requirements for the degree of

Doctor of Philosophy

in

Environmental Science, Policy, and Management
Organisms & the Environment

in the

Graduate Division

of the

University of California, Berkeley

Committee in Charge:

Professor George K. Roderick, Chair
Professor Claire Kremen
Professor Steve Selvin

Fall 2014

Abstract

Bees in a Changing World: How Land Surface Phenology, Bee Community Distributions, and Pollinator-Plant Interactions are Impacted by Urbanization and Agriculture

by

Misha Tomaye Leong

Doctor of Philosophy in Environmental Science, Policy, and Management

University of California, Berkeley

Professor George K. Roderick, Chair

Background

Urbanization and agricultural intensification of landscapes are influential drivers of global change, resulting in direct impacts on ecological communities and leading to shifts in species distributions and interactions. These landscapes are novel for many reasons, but an often overlooked aspect is how the phenology of vegetation can vary between land use types. Because such differences can impact floral-dependent species, I explored how human-altered landscapes affect bees, a group of high economic and ecological importance. I measured the phenological diversity of vegetation across a human-altered landscape, compared these findings to a spatio-temporal pollinator distribution dataset, and investigated how pollinator visitation translates to seed set.

Approach

I collected and observed bees for three field seasons in a peri-urban landscape on the outskirts of the San Francisco Bay Area, California, where urban, agricultural, and natural land use types interface. To assess patterns of phenological change, I used seasonal remote sensing data from MOD13Q1 vegetation indices, which I complimented with collections of 91 bee species groups across different land use types. I examined how differences in bee populations between land use types impacted plant-pollinator interactions by making standardized observations of floral visitation and measuring seed set of yellow starthistle (*Centaurea solstitialis*), a common grassland invasive abundant in all land use types.

Results & Conclusion

I found phenological patterns in vegetation indices, total bee abundance, and species richness of human-altered landscapes to be out of sync between urban, agricultural, and natural areas. Vegetation indices were significant predictors of total bee abundance, a relationship that improved when time lags were included. Bee visitation was highest in urban and agricultural land use contexts, but seed set rates in these human-altered landscapes were lower than in natural sites. These results emphasize the importance of differences in temporal dynamics between land use types, a previously overlooked mechanism of global change.

Dedication

I dedicate my dissertation work to 21,876 individuals: all 21,874 bees who became a part of this research and 2 very important humans—my parents. Thank you Mom and Dad for all of the support, from being very enthusiastic field assistants, to letting me clutter your garage with research equipment, to always trying to give me money, and to maintaining the best field car of all time (may the '88 Acura Integra live forever). I know how lucky I am, and I love you always.

“And let me tell you this, for this is very important: although Hexapods are common and easy to find, there is not one among them all that does not have a story about his life so strange and interesting that he is worth watching just to find out what his story is. Are you pleased to know that, whether you are in the country or in the city, and whether it is summer or winter, you are living right in the midst of Hexapod Land, where you have these most wonderful fairies for next-door neighbors?”

-Edith Patch, A Little Gateway to Science, 1920.

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Chapter 1

Differences in temporal patterns of the bee community in urban, agricultural, and natural landscapes

Abstract

Urbanization and agricultural intensification of landscapes are important drivers of global change which have direct impacts on local ecological communities, leading to shifts in species distributions and interactions. Here, we explored how human-altered landscapes, with novel ornamental and crop plant communities, result not only in changes to local community diversity of floral-dependent species, but also shifts in seasonal abundance. We collected 3 years of data on the spatio-temporal distributions of 91 bee species groups through pan trapping across different land use types at multiple time points across the year. We found that human-altered landscapes experience different phenological patterns from surrounding natural areas of total bee abundance, species richness, and the abundance of certain species. Total bee abundance in natural sites peaked in the spring, and then dropped dramatically towards the summer when natural areas dry up and floral resources are scarce. In contrast, total bee abundance in urban and agricultural sites remained relatively constant across the year. These findings demonstrate that differences in vegetation between land use types can alter the temporal dynamics of pollinator-plant interactions, a previously overlooked mechanism of global change.

Introduction

Growing human populations have led to accelerating rates of natural resource use and land conversion, particularly for urbanization and agriculture [1,2]. Human-altered landscapes are often associated with declining natural habitat, non-native species, fragmentation, and transformations in habitat structure, inputs, climate, and connectivity[3,4,5,6]. These changes collectively have resulted in shifts in both spatial distributions and species interactions across many taxa including birds, mammals, reptiles, amphibians, invertebrates, and plants [7,8,9].

However, many of these studies are either static snapshots of the measured community, or lumped across time, which may miss some of the dynamics of how communities respond to anthropogenic change [10,11,12]. Urban ecosystems are temporally dynamic systems, yet historical factors associated with land use legacy and time lags as a result of development have largely been overlooked [13]. Because human-altered landscapes are relatively recent, it is particularly important to recognize that the observed biodiversity may be undergoing a process of change from the previous land use type to the new one when interpreting observations [14].

Just as urban ecosystems are dynamic across years, they are also dynamic intra-annually, with resulting phenological shifts within urban landscapes compared to surrounding natural habitat. The urban heat island effect is a well-documented phenomenon where the city environment can be significantly warmer than the surrounding landscape as a result of impervious surface area that retains heat and higher energy usage [15,16], causing changes in the timing of ecological patterns. As a result, plants bloom earlier the more densely urban the surrounding habitat is [17,18] and bird migration advances earlier in urban contexts [19].

Another potential effect of land use change in urban and agricultural landscapes beyond climatic can be the variety and timing of floral resource availability. Urban areas, while having less green space, often grow many exotic plants which are supplemented with water and nutrient inputs that allow for an extended flowering season. As a result, urban areas are characterized by relatively low (due to less available growing space), but constant, floral resources throughout the year. Agricultural landscapes have large patches of dense, often homogenous, floral resources that will fluctuate greatly from early spring to the end of the summer due to mass-flowering monoculture crops [20,21]. In contrast, many natural areas in California experience a large burst of diverse floral blooms in the spring, and by the end of the summer, there are very few floral resources available.

These differences in floral availability may affect the seasonal population dynamics of the animal communities that rely on floral resources—such as local bee populations, since bees strongly depend on flowers for both nectar and pollen. Bees provide the majority of animal-mediated pollination services on which an estimated 87.5% of flowering plants depend [22]. The value of pollination in agriculture is estimated at \$200 billion worldwide [23], largely due to many foods that are essential for food security and a healthy human diet, including numerous fruits, vegetables, and nuts that require bee pollination. In addition, there has been growing interest in urban agriculture to ensure food security and access to healthy foods for urban populations. One study estimated the economic value of urban fruit trees (many of which require animal pollination) in the one city of San Jose, California to be worth \$10 million annually [24].

Honey bee populations and many bumble bee species are declining worldwide [25,26,27], while many other bee species have not been closely documented enough to determine their status [28]. One of the reasons proposed to be negatively affecting bee populations is land use change. A review of 265 papers studying the effect of land use change on pollinator

populations found more negative than positive impacts with a wide window of variability [28]. This could partially be attributed to the wide diversity of pollinators themselves, as well as the varying definitions that people use to constitute land use change.

We propose that an additional cause of high variability can be explained by investigating how the seasonal patterns of bee communities may shift in different neighboring land use types which experience highly different availability and suites of floral resources. Although bee seasonality has been documented in urban and agricultural landscapes [29,30], no studies to our knowledge have specifically investigated the differences in seasonal patterns of population abundances of bees between human-altered landscapes and neighboring natural habitat, despite the established seasonality of bees and variability of floral resource availability. Bees are often sampled throughout the season, but all of these data are typically lumped together, potentially obscuring subtleties in change (e.g. [10]).

Here, we investigate how local bee communities shift over the course of the flowering season in urban, agricultural, and natural land use types. We make use of a “natural experimental design” in which urban, agricultural, and natural areas intersect in a peri-urban landscape on the outskirts of the San Francisco Bay Area in Contra Costa County, California. To study the impact of changing land use on local bee community population dynamics, we sampled the bee community flying through the landscape at four time points over the course of the season for three years at 24 sampling locations. Using this dataset, we tested the following questions:

1. Does land use context correlate with differences in bee community composition?
2. Do different land use types exhibit different patterns of change in bee community composition throughout the year?

Methods

Study System

Our study system was located around Brentwood, in east Contra Costa County, California, where natural, agricultural, and urban areas intersect with each other within a 20 x 20 km region (Figure 1). A county water district (Los Vaqueros Watershed), regional park district (East Bay Regional Parks: Black Diamond Mines, Round Valley, and Contra Loma), and California state park (Mount Diablo) all fall within the region, leaving large areas of land protected from development. This protected (hereafter referred to as “Natural”) land consists mainly of grasslands and oak woodlands, some portions of which are managed for grazing. East Contra Costa County has had a farming community presence since the late 19th century. The agricultural areas of Brentwood, Knightsen, and Byron mostly consist of orchards (cherries, stone fruit, grapes and walnuts), corn, alfalfa, and tomatoes [31]. A housing boom in the 1990s led to massive residential growth in the area. The city of Brentwood has grown from less than 2500 people in the 1970s to over 50,000 today (2010 U.S. Census), and nearby Antioch has over 100,000 residents (2010 U.S. Census).

Site Selection

Within this region, sites were selected to be at least 1 km away from all others, based on maximum assumed bee foraging ranges [32]. Although certain bee species have been recorded

foraging over a kilometer [33], most bees have nesting and foraging habitat within a few hundred meters of each other [32,33,34]

Using NOAA's 2006 Pacific Coast Land Cover dataset (developed using 30 meter resolution Landsat Thematic Mapper and Landsat Enhanced thematic Mapper satellite imagery), a 500 m buffer was created around each site, and the number of pixels classified as agricultural, urban, natural, water, or bare land was extracted. We grouped some categories within NOAA's classification scheme and used the following definitions for urban, agricultural, and natural: Urban- "High Intensity Developed", "Medium Intensity Developed", "Low Intensity Developed", and "Developed Open Space"; Agricultural- "Cultivated", "Pasture/Hay"; Natural- "Grassland", "Deciduous Forest", "Mixed Forest", "Scrub/Shrub". For each site, we classified the proportion of each of these different land use types within the 500 m buffer, as well as classifying each buffer categorically by the dominant land use type (>50%). In 2010, we had 18 sites, with 6 each classified as types "Urban", "Agricultural", and "Natural." In 2011 and 2012, we increased to have a total of 24 sites, with 8 of each land use classification.

Bee Sampling

At each site we laid out a standardized pan trapping transect of fifteen 12 ounce bowls spaced 5 meters apart in alternating colors of fluorescent blue, white, and fluorescent yellow [35]. Bowls were filled to the brim with soapy water (0.5 tablespoon of Blue Dawn dishwasher detergent diluted in 1 gallon of water). In 2010, transects were set up for a 4 hour period between 10:30am to 2:30pm (\pm 30 minutes), with 4 sites sampled per day, and all sites sampled on consecutive days. These 2010 transects were run twice, once in the early summer, and once in the late summer. In 2011 and 2012, sampling was conducted over a 24 hour period, so that more sites could be run simultaneously and more samples could be collected per site per year. All 24 sites were sampled within two consecutive collecting windows (e.g. if transects were set-up on a Monday, they were picked up Tuesday, and the remaining sites were sampled Wednesday and Thursday), and were run four times each year: early spring, late spring, early summer, and late summer.

Because we were interested in landscape level effects, we tried to control local variables as much as possible. All sites were selected in easily accessible, open areas that received full sun. Natural areas were in grassland habitat, so we selected agricultural sites that were either weedy field margin edges or fallow fields, and urban sites that were vacant lots or green ways. The human-altered sites were deliberately selected to not be adjacent to any mass flowering plants of agricultural crops or gardens. The goal of collection was to sample the bee community that was flying through the site searching for resources.

Bees were collected from the pan traps by using a metal strainer, rinsed with water, frozen overnight or longer, and then pinned and labeled. Specimens were sorted to the genus level, and then to the species level with the assistance of Dr. Robbin Thorp, Professor Emeritus, UC Davis. The only exception to identification at the species level were bees of the genus *Lasioglossum*, due to their overwhelming abundance, limited availability of taxonomic expertise for this group, and lack of known ecological diversity. Voucher specimens and the majority of the total collection will be deposited at the Essig Museum of Entomology at UC Berkeley.

Data Management

All analyses were done in R 2.15.1 (R Development Core Team, 2011). There were a total of 228 collecting events (6 sites of each land use types sampled twice in 2010, 8 sites of

each land use type sampled 4 times each in 2011 and 2012.) Community sampling often results in high numbers of singletons, doubletons, and other “rarely collected” species (which we defined as a maximum threshold of 9 total specimens collected across all 228 collecting events), so we calculated the estimated species pool using the R package *vegan* [36]. For each collecting event, we calculated the total bee abundance, species richness, genera richness, number of “rarely collected” species, and Shannon diversity. Shannon diversity was calculated using the R package *vegan*. The spatial autocorrelation of total abundance was assessed by Mantel tests in R package *ade4* [37] by month. Spatial autocorrelation was not detected ($p = 0.3395$).

General Community Metrics Analyses

For response variables including aggregate bee abundance, species richness, Shannon diversity, and number of rare species, we tested for the effect of land use type, seasonality, and their interaction with generalized linear mixed models using the R package *lme4*. We designated collecting method (4 hour vs. 24 hour pan traps), land use type, seasonality, and the interaction of land use type and seasonality as fixed effects, and site and year as random effects. We analyzed the effect of time both categorically by collecting period (early spring, late spring, early summer, and late summer) and continuously by day of year. Day of year was normalized on a scale of 0 to 1 from the first collecting date to the last. Natural land use was the model baseline for the categorical variables of land use. Shannon diversity was fit with a Gaussian distribution while all other variables were fit with Poisson distributions.

Species-level Analyses

We also investigated each species that was represented by 10 or more collected specimens. For each of those that were collected at least once in each land use type and in 3 or more collecting periods, we built generalized linear mixed models as described above. All response variables were plotted against collecting date and land use type, and the relationship was assessed visually for accuracy.

Results

We collected and identified 21,874 specimens to 91 bee species groups (all *Lasioglossum* spp. and *Sphcodes* spp. were counted as the same “species group” respectively for these purposes). With 228 collecting events, the rarefaction curve began to flatten and the Chao estimation of the species pool was 110.04 (se=11.54), indicating that our sampling was sufficiently thorough (Figure 2). Of the 91 species groups, 58 had less than 10 collected specimens, putting them in our “rarely collected” group.

Community Metrics

Total aggregate bee abundance was strongly impacted by land use type, seasonality, and their interaction (Tables 1 and 3, Figure 3). Species richness did not vary significantly across seasons, but agricultural sites were significantly different from natural overall and there was a significant interaction between land use type and seasonality (Tables 1 and 3, Figure 3). A similar pattern was found with Shannon diversity, with the effect of agricultural land use type, and its interaction with seasonality, being significantly different from patterns found with natural land use types (Tables 1 and 3, Figure 3). Urban sites had results that mostly fell between the

agricultural and natural extremes. Rare species were collected in all three land use types (primarily earlier in the season), but were collected less often in agricultural sites (Tables 1 and 3, Figure 3).

Species-level Dynamics

Of the 33 species groups (*Lasioglossum* species were lumped together in these analyses, but all other species groups are at the species level) that were represented by 10 or more collected specimens, 19 did not meet the necessary sampling criteria and were excluded from individual species analyses (11 were not represented in each of the land use types and 8 were not collected in over half of the sampling periods). Of the 11 that were not collected in each of the land use types (Appendix 1), 3 were found almost exclusively in natural sites (*Anthophorula chionura*, *Eucera lunata*, and *Ceratina sequoiae*), while 7 were almost exclusively collected in human-altered sites (*Peponapis pruinosa*, *Andrena chlorogaster*, *Megachile rotundata* [introduced species], *Andrena piperi*, *Tripeolus melanurius*, *Ashmeadiella aridula astragali*, and *Ceratina dallatorreana* [introduced species]). *Andrena cuneilabris* (considered a specialist on *Ranunculus*) was found in agricultural and natural sites, but never in urban sites. We also needed to exclude an additional 8 species for not occur in 3 or more sampling periods (Appendix 1). These included *Melissodes stearnsi* (only collected in the summer), *Tripeolus heterurus*, (only collected in late summer), *Anthophora urbana* (only collected in the late summer), *Andrena sola* (only collected in the early spring), *Andrena misella* (also only collected in the early spring), *Diadasia enavata* (only collected in the summer, and considered a specialist of *Helianthus*), *Hylaeus leptcephalus* (only collected in the summer, and an introduced species), and *Diadasia biturbiculata* (only collected in the middle of the season, considered a specialist on *Calystegia*). Despite being unable to run our statistical analyses on the above 19 species, we still could observe patterns and trends with these groups.

Of the 14 species analyzed, land use type was a significant factor determining abundances for 7 species (Table 2), seasonality was a significant factor for 11 species (Table 2), and the interaction between land use type and seasonality was significant for 9 species (Table 2 and 3). Even though the overall abundance of each of the species significantly impacted by land use type was lower in human-altered sites, of those that had an interaction with seasonality, most had a significantly more positive slope as the season continued in human altered sites.

We also discovered a few patterns graphically that were not detected in the models. In 2012, *Eucera actiosa* had collecting peaks in human-altered sites in the early spring, but didn't peak in natural sites until late spring. In contrast, *Melissodes lupina* had an earlier collecting peak in natural sites, being most abundant in natural sites in the early summer, but most abundant in human-altered sites in the late summer. *Bombus vosnesenskii* was collected in urban sites only in the spring, but was collected mostly in the summer in natural sites.

Discussion

We found that the bee communities in human-altered landscapes experienced different phenological patterns than the neighboring natural areas. Increased temperature in urbanized areas as a result of the urban heat island effect is often cited as the driving force for changed ecological dynamics. We propose another driver of local phenological shifts: the timing and quality of floral resource availability, due to irrigation that extends the flowering season through

water inputs and landscaping choices in urban residential, public, and commercial zones, as well as mass flowering crops in agricultural fields.

For example, *Eucera actiosa* (Tribe Eucerini) was collected most frequently in human-altered sites in the early spring and very little in late spring, whereas in natural sites it was collected in lower numbers in early spring and peaked in late spring. Another bee, *Melissodes lupina* (Tribe Eucerini), is a later flying bee than *E.actiosa* and experienced the opposite pattern. *Melissodes lupina* was collected most frequently in the early summer for natural areas, but was collected more often in the late summer in human-altered landscapes. Both *E.actiosa* and *M. lupina* demonstrate a pattern of relative abundance of species being shifted in different land use types. Even further, the temporal direction of relative abundance in both examples areas skew towards higher abundance during the middle of the season for natural areas and higher abundance at the more extreme ends (earlier and later) of the season in the human-altered landscapes. In other words, these are not simple patterns where species in human-altered landscapes always are collected earlier, which is generally the result of the urban heat island effect. Instead, this is likely due to irrigation effects extending flowering times in human-altered landscapes that provide bees with necessary resources for extended flight periods. This supports our theory that patterns of change in bee community distribution throughout the year are a result of the different land use types offering variable seasonal floral resources.

While ecologists have used time as an important variable in many different systems, only recently has time begun to be incorporated into urban ecology [13]. These differences in relative bee abundance throughout the year could be the result of resource tracking or a shift in emergence timing between different land use types. Shifts in plant phenology have been well documented in temperate urban landscapes [38,39,40,41]. Urban areas have been associated with earlier plant blooming closer to the city center [17,18], and the urban heat island effect also can directly affect animal populations [19,42,43]. In addition, historical temperature and museum collection records show a link between climate change and advancing bee emergences [44]. Bees could be responding to local climatic differences or floral availability respectively, with both emergence timing and length of the flight season of bee species being impacted differentially at a micro-scale between different land use types.

Pollinator responses to land use change are generally more often negative than positive, although there is high variability of outcomes due to many different experimental design types, systems, and the use of simple community metrics rather than more species specific analyses [28]. Using functional groups such as nesting type, generalized foraging, and sociality, more patterns have emerged about traits that may be most sensitive to anthropogenic disturbance, although the type of disturbance will affect bees differently [45,46,47]. For example, ground nesting species may be more successful in intensified agricultural landscapes [45], while cavity nesting species may be more common in urban landscapes because of increased nesting resources [48].

We had 7 species that were collected almost exclusively in human-altered sites (*Peponapis pruinosa*, *Andrena chlorogaster*, *Megachile rotundata*, *Andrena piperi*, *Triepeolus melanurius*, *Ashmeadiella aridula astragali*, and *Ceratina dallatorreana*). These species positively associated with anthropogenic change covered a range of functional groups for sociality, nesting type, foraging generalism, size, and distributional range. Two of these are non-native (*Megachile rotundata* and *Ceratina dallatorreana*; unlike the majority of California's estimated 1600 bee species), and as a group they have a wide diversity of life history traits. For example, *Ceratina dallatorreana*, a species of small carpenter bee originally from the

Mediterranean region first collected in California in 1949, has the unusual life history trait of female parthenogenesis in its local population here [49]. *Megachile rotundata* is another non-native bee accidentally introduced to the United States from the Mediterranean, is a solitary leaf cutter species that have become an important managed pollinator in the Western United States [50]. *Andrena chlorogaster*, is a native California bee, with a generalized life habitat and wide range [51], while the squash bee, *Peponapis pruinosa*, is a solitary specialist on cucurbits [52]. These species that favor human-altered landscapes not only fail to share many life history traits, but they are also diverse phylogenetically, comprising several different bee families.

These different patterns of bee distributions could be the result of two possibilities: either bee populations are tracking resources between the different land use types, or the bee communities in the different land use types are experiencing different emergence timing. Bee movement has been notoriously difficult to study because of the size, mobility, and life history of this group. Some species and system-specific conclusions about bee foraging distances and size-based models of foraging distances have been made [32,33,34,53]. However, these are all based on foraging movements anchored around a central nest that a female bee is provisioning, and in contrast almost nothing is known about dispersal movement—in other words, how far bees might travel from their emergence site to mate and select their own nest site. Bees are capable of passing through a variety of landscape structures [54], and bumble bees, while generally exhibiting high site fidelity, have been found to cross both natural (forest) and artificial barriers (roads and railroad tracks) with little difficulty [55,56]. Therefore, it is likely that anthropogenic land use change is not a barrier to movement.

As agricultural and urban areas continue to be the largest and fastest growing forms of land use conversion, it is critical to understand the impacts of these landscape-scale changes on species distributions in order to predict and plan for ecological impacts as global change continues. Relationships between community metrics and land use change alone do not reveal the complex interplay of land use change and seasonality. Variability in patterns due to seasonality has not been taken into account in many pollinator studies in anthropogenic landscapes, despite the known clear linkage between pollinators and floral resources.

Bringing attention to how anthropogenic landscapes experience different temporal dynamics is relevant to the numerous conservation and restoration projects being done in anthropogenic landscapes. There are many similarities between urban and agricultural landscapes, and projects being conducted within them to attract pollinators could benefit from a crossover understanding of the impacts of anthropogenic land use change. In addition to contributing to a better understanding of how change in landscape use, particularly urbanization, affects bee community population dynamics, this study illustrates the importance of observing temporal dynamics in urban ecology studies.

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Table 1. Output of GLMM models for community variables. Displayed are effect sizes, errors, and p-values for land use types (agricultural and urban) and day of the year (seasonality). The last two columns denote whether or not there was a significant interaction (and in which direction) between each land use type and day. All significant explanatory variables with p-values <0.05 are in bold.

Community Variable	AGR Effect	AGR Error	AGR p-value	URBAN Effect	URBAN Error	URBAN p-value	DAY Effect	DAY Error	DAY p-value	AGR * DAY	URB * DAY
Total Abundance	-1.4587	0.2072	>0.001	-1.1179	0.2267	>0.001	-0.8572	0.034	>0.001	+	+
Species Richness	-0.7607	0.1778	>0.001	-0.4450	0.1746	0.0189	-0.0912	0.1442	0.527	+	
Shannon Diversity	-0.4289	0.2015	0.017	-0.2536	0.2084	0.112	-0.2106	0.1647	0.101		
Rare Species	-1.5998	0.5957	0.0072	-0.9569	0.5015	0.056	-4.5264	0.7285	>0.001		

Table 2. Output of GLMM models for species groups. Displayed are effect sizes, errors, and p-values for land use types (agricultural and urban) and day of the year (seasonality). The last two columns denote whether or not there was a significant interaction (and in which direction) between each land use type and day. All significant explanatory variables with p-values <0.05 are in bold.

Community Variable	AGR Effect	AGR Error	AGR p-value	URBAN Effect	URBAN Error	URBAN p-value	DAY Effect	DAY Error	DAY p-value	AGR * DAY	URB * DAY
<i>Lasioglossum</i> spp.	-1.2779	0.23801	>0.001	-1.1202	0.2602	>0.001	-1.4735	0.0547	>0.001	+	+
<i>Halictus tripartitus</i>	-1.76662	0.293242	>0.001	-0.3507	0.3139	0.264	0.2356	0.0646	>0.001	+	
<i>Eucera actuosa</i>	-1.79304	0.562485	0.001	-2.4368	0.6170	>0.001	-1.6507	0.0893	>0.001	-	
<i>Halictus ligatus</i>	-2.80185	0.546778	>0.001	-1.3942	0.5236	0.008	-0.8849	0.1887	>0.001	+	+
<i>Osmia nemoris</i>	-2.39969	0.807668	0.003	-3.6323	0.9220	>0.001	-2.2688	0.2062	>0.001		
<i>Agapostemon texanus</i>	0.0463	0.5661	0.935	-0.0398	0.5920	0.946	2.2064	0.4046	>0.001		
<i>Melissodes lupina</i>	-4.28221	1.091057	>0.001	-4.5515	0.8378	>0.001	1.9823	0.4157	>0.001	+	+
<i>Apis mellifera</i>	0.4674	0.3919	0.233	0.3052	0.4257	0.4734	-0.7030	0.3966	0.076		-
<i>Ceratina nanula</i>	-0.8259	0.5942	0.165	-2.0313	0.6817	0.003	-1.7846	0.4399	>0.001	+	+
<i>Megachile apicalis</i>	-0.7684	1.2465	0.538	-1.3112	1.3246	0.322	1.7282	0.6964	0.013		
<i>Sphecodes</i> sp	1.7008	1.1651	0.144	0.4009	1.2618	0.751	-0.5688	1.3111	0.664		
<i>Melissodes tepida timberlakei</i>	-1.9178	2.3603	0.416	0.9687	1.3386	0.469	2.5653	1.1309	0.023		
<i>Megachile onobrychidis</i>	2.5511	2.0516	0.214	0.9459	2.5675	0.713	5.7991	1.7548	>0.001	-	
<i>Bombus vosnesenskii</i>	-1.7651	1.1990	0.141	-0.8968	0.9329	0.336	-0.8776	0.8648	0.310		

Table 3. Effect size, error, and p-values for community variables and species that were significantly impacted by interaction between land use type and seasonality ($p < 0.05$) of glmm.

Species-group	agr.day.effect	agr.day.error	agr.day.p	urb.day.effect	urb.day.error	urb.day.p
Total Abundance	1.5005	0.0521	>0.001	0.9263	0.0522	>0.001
Species Richness	0.7159	0.2206	0.0017			
<i>Lasioglossum</i> spp.	1.845432	0.073975	>0.001	1.18975	0.082005	>0.001
<i>Halictus tripartitus</i>	1.674862	0.111213	>0.001			
<i>Eucera actuosa</i>	-0.46688	0.215371	0.030			
<i>Halictus ligatus</i>	2.1115	0.439864	>0.001	0.858313	0.330315	0.009
<i>Melissodes lupina</i>	4.458791	1.199244	>0.001	5.592916	0.870275	>0.001
<i>Apis mellifera</i>				-1.62764	0.631727	0.010
<i>Ceratina nanula</i>	2.343566	0.569187	>0.001	2.582038	0.629833	>0.001
<i>Tripeolus herterurus</i>				11.90007	5.989299	0.047
<i>Megachile onobrychidis</i>	-5.58996	2.580002	0.030262			

Figure 1. Map of the study region. Based on LANDSAT classification, green represents agricultural land use, red represents urban land use, and yellow represents natural areas. Black dots are site locations in July 2011. Sites shifted slightly as necessary between collecting periods.

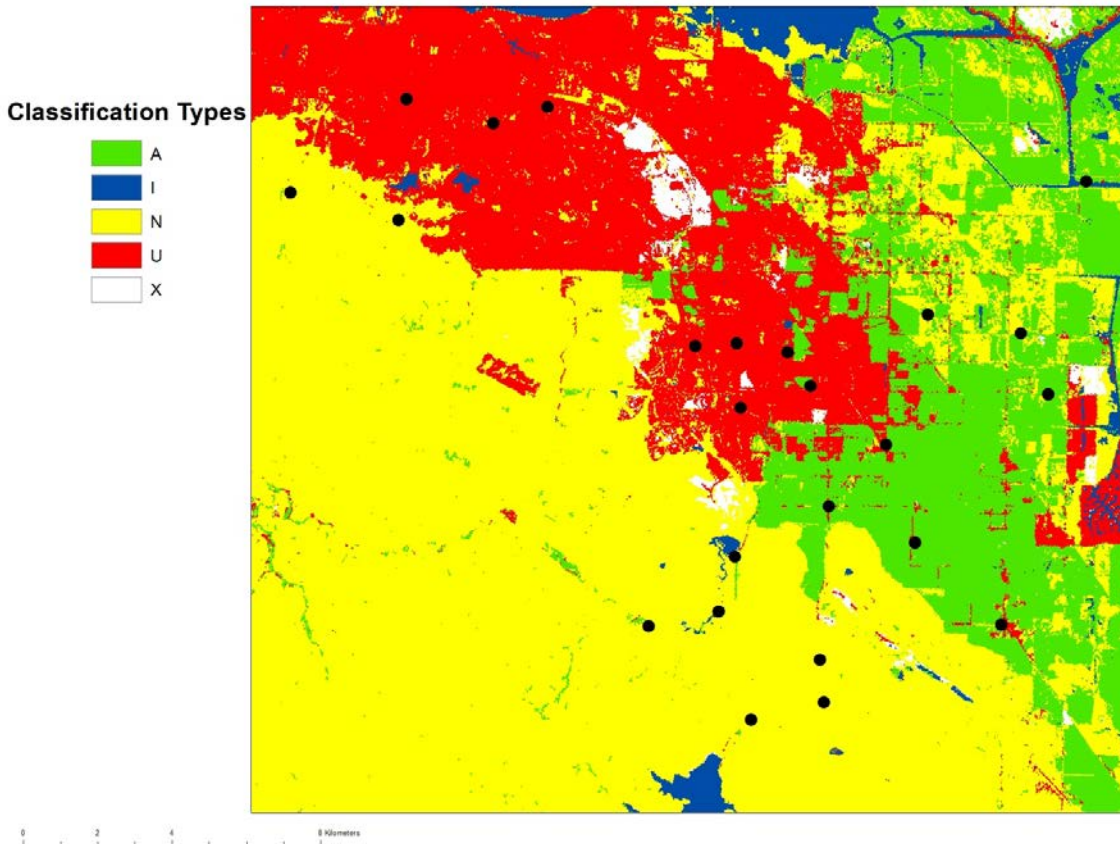


Figure 2. Rarefaction curve of combined 228 pan trapping collection events over 3 years.

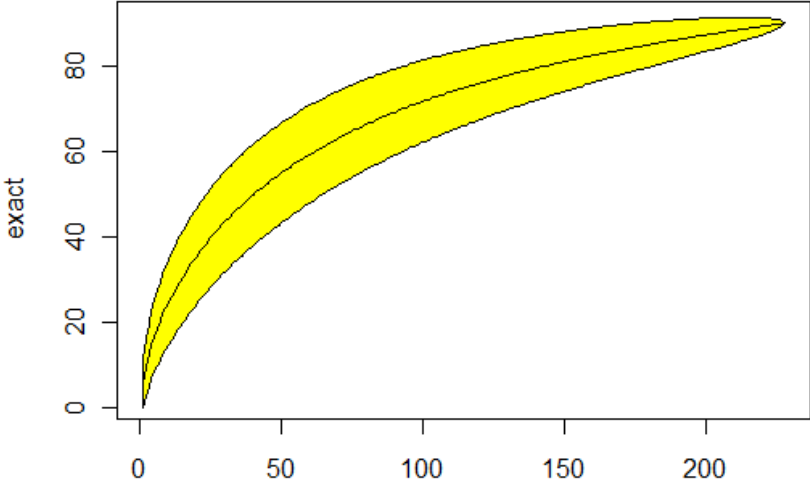
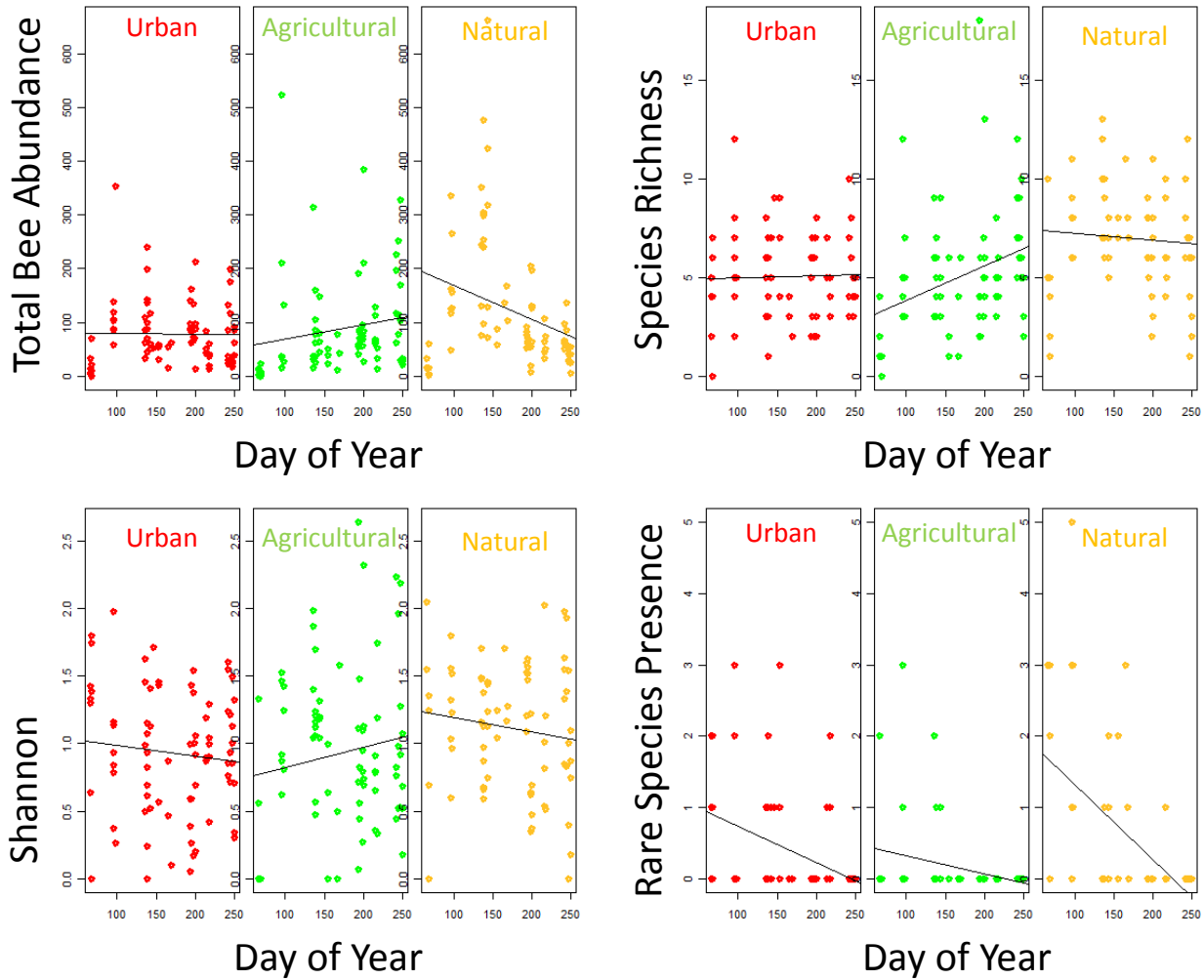


Figure 3. Scatterplots fitted with linear regression line for community metrics as a function of land use type and collecting ordinal day. In analyses, day of year is normalized on a scale from 0-1 which is reflected in start and end days of ordinal days in graph).



Chapter 2

Remote sensing and spatio-temporal pollinator distribution dataset detect vegetation phenological diversity and bee community abundance to be out of synchrony between urban, agricultural, and natural landscapes

Abstract

Global change has led to shifts in phenology, potentially disrupting species interactions such as plant-pollinator relationships. Advances in remote sensing techniques allow us to detect vegetation phenological diversity between different land use types, but it is not clear how this translates to other communities in the ecosystem. Here, we investigated the phenological diversity of the vegetation across a human-altered landscape including urban, agricultural, and natural land use types, and later compared these findings to a spatio-temporal pollinator distribution dataset. We found that the patterns of change in the vegetation indices (EVI and NDVI) of human-altered landscapes are out of synchronization with the phenology in neighboring natural California grassland habitat. In addition, EVI and NDVI were significant predictors of total bee abundance, a relationship that improved with time lags. This evidence supports the importance of differences in temporal dynamics between land use types. These findings also highlight the potential to utilize remote sensing data to make predictions for components of biodiversity that have tight vegetation associations, such as pollinators.

Introduction

Increasing temperatures as a result of global climate change have led to shifts in phenology for many species [1,2,3,4], and widespread debate over the consequences of critical interaction mismatches [5,6,7,8]. However, not all phenological change is the direct result of changing climate. Land use change, such as urbanization and agricultural expansion, includes the deliberate introduction of novel plants into communities. These plants, both exotic ornamentals and crops, are often accompanied by watering and supplemental nutrient inputs that extend survival potential in the targeted landscape, leading to different flowering seasons. Therefore, on a plant community-scale, different land use types can be expected to experience distinct patterns of phenological change.

Land surface phenology is the timing of overall surface vegetation growth [9], and differs from traditional definitions of vegetation phenology (i.e. species specific life cycle events). Major advancements in assessing phenology on a landscape scale have been made possible through the use of satellite products and improved cyber-infrastructures [9,10,11,12]. Remote sensing techniques have provided tools to detect land-surface phenology, such as data from NASA's moderate-resolution imaging spectroradiometer (MODIS), which are being used to produce 250-m spatial resolution products every 16 days (https://lpdaac.usgs.gov/data_access).

Differences in land surface phenology have been detected as a result of land use change [10,13,14,15]. In some cases, the changes in land surface phenologies between years have given insight into the history of regions that have experienced socio-economic and geopolitical transitions, such as changes in irrigation regimes in central Asia after the fall of the Soviet Union [14], or the expansion of urbanization in parts of Mexico [15]. Differences in phenology between neighboring land use types within a year also provide insights, such as vegetation phenology of urban landscapes found to be out of synchrony with patterns of phenology in the surrounding desert [13].

As a result of land use change, such phenological differences in vegetation could lead to phenological differences in other groups of organisms, especially if plants exert bottom-up control on the organisms that interact with them. Primary productivity can be linked to biodiversity [16,17,18]. Therefore, there exists great potential to use remote sensing of primary productivity data as a way to predict biodiversity [19,20]. However, early efforts to apply this technique were less powerful than expected [21]. Some evidence suggests that remote sensing data can predict biodiversity; for example, peak vegetation indices in multiple studies are correlated with higher avian diversity [22,23], although in other systems the relationship is less clear [20].

Linking remote sensing data with biodiversity has been limited despite its great potential [21]. Part of the problem may be that, in many comparisons, vegetation indices are treated statically, rather than as temporally dynamic [22]. Use of a multi-season within year vegetation index was found to be a much more accurate predictor of biodiversity [21,24]. Additionally, these indices may be more able to uncover patterns across landscape types with more dramatic differences in vegetation, such as human-altered landscapes. Also, biodiversity may be too broad, and instead, we should focus on those organisms that exhibit tight linkages with plant communities.

In this paper we focus on bees, a key pollinator group with close vegetation associations, since bees strongly depend on flowers for both nectar and pollen. Bees provide the majority of animal-mediated pollination services on which an estimated 87.5% of flowering plants depend

[25]. The value of pollination in agriculture is estimated at \$200 billion worldwide (Gallai et al. 2009), due to many foods that are essential for food security and a healthy human diet, including numerous fruits, vegetables, and nuts that require bee pollination.

Bees are closely linked to floral availability in their environment. However, the temporal dynamics of floral resources can vary between land use types. In California grasslands, there is typically a large burst of blooming in the spring, which tapers off in the summer. Urban areas often have ornamentals enhanced with external inputs that results in a steady patterns with only minor changes throughout the year, while agricultural landscapes have booms and busts of flowering that follow the pattern of local crops.

For this project, we explore how vegetation phenology varies in a human-altered California grassland landscape, and whether or not these changes in phenology correlate with those of the bee community that depends on floral resources. Specifically, we ask: 1) Do human-altered landscapes in California grasslands experience phenological diversity that is out of synchrony with surrounding natural areas?; and 2) Do these spatio-temporal patterns correlate with bee distribution data?

Methods

Study Region

Our study system was located around Brentwood, in east Contra Costa County, California, where natural, agricultural, and urban areas intersect with each other within a 50 x 50 km region (Figure 1). A county water district (Los Vaqueros Watershed), regional park district (East Bay Regional Parks: Black Diamond Mines, Round Valley, and Contra Loma), and California state park (Mount Diablo) all fall within the region, leaving large areas of land protected from development. This protected (hereafter referred to as “natural”) land consists mainly of grasslands and oak woodlands, some portions of which are managed for grazing. East Contra Costa County has had a farming community presence since the late 19th century. The agricultural areas of Brentwood, Knightsen, and Byron mostly consist of orchards (cherries, stone fruit, grapes and walnuts), corn, alfalfa, and tomatoes [26]. A housing boom in the 1990s led to massive residential growth in the area. The city of Brentwood has grown from less than 2500 people in the 1970s to over 50,000 today (2010 U.S. Census), and nearby Antioch has now over 100,000 residents (2010 U.S. Census).

Bee data collection

The bee community was sampled at multiple time points from 2010-2012. Within this region, sites were selected to be at least 1 km away from all others, based on maximum assumed bee foraging ranges [27]. Although certain bee species have been recorded foraging as far as 1400 m [28], most bees have nesting and foraging habitat within a few hundred meters of each other [27,28].

At each site we laid out a standardized pan trapping transect of fifteen 12 ounce bowls spaced 5 meters apart in alternating colors of fluorescent blue, white, and yellow [29]. Bowls were filled to the brim with soapy water (0.5 tablespoon of Blue Dawn dishwasher detergent diluted in 1 gallon of water). In 2010, transects were set up for a 4 hour period between 10:30am to 2:30pm (\pm 30 minutes), with 4 sites sampled per day, and all sites sampled on consecutive days. These 2010 transects were run twice, once in the early summer, and once in the late

summer. In 2011 and 2012, sampling was altered for transects to be set up for a 24 hour period, so that more sites could be run simultaneously and collections made more often. All 24 sites were sampled within two consecutive collecting windows of 24 hours, and were run four times each year: early spring, late spring, early summer, and late summer.

The goal of collection was to sample the bee community that was flying through the site searching for resources. Because we were interested in landscape-level effects, we tried to control local variables as much as possible. All sites were selected in easily accessible, open areas that received full sun. Natural areas were in grassland habitat, so we selected agricultural sites that were either weedy field margin edges or fallow fields, and urban sites that were vacant lots or greenways. The human-altered sites were deliberately selected to not be adjacent to any mass-flowering crops or gardens.

Bees were collected from the pan traps by using a metal strainer, rinsed with water, frozen overnight or longer, and then pinned and labeled. Specimens were sorted to the genus level, and then to the species level with the assistance of Dr. Robbin Thorp (Professor emeritus, UC Davis). The only exception to identification at the species level were bees of the genus *Lasioglossum*, due to their overwhelming abundance, limited availability of taxonomic expertise for this group, and lack of known ecological diversity. Voucher specimens and the majority of the total collection will be deposited at the Essig Museum of Entomology at UC Berkeley.

EVI and NDVI data processing

We used the MODIS land subset product MOD13Q1 for its NDVI (Normalized Difference Vegetation Index) and EVI (Enhanced Vegetation Index) data. MOD13Q1 is on a 16 day frequency and 250 meter resolution. We obtained EVI and NDVI geotif files through the Oak Ridge National Laboratory Distributed Active Archive Center [30], using a query from 2000 to 2014 in a 50km x50km zone encapsulating the study region. We calculated and plotted NDVI and EVI time series averages and standard deviations for each of the three land use types using all available data files from 2000-2014 (n=320).

For each bee collecting event, the closest MOD13Q1 date of collection was identified. NDVI and EVI values were extracted via bilinear interpolation at the collecting point for the closest MOD13Q1 date of collection, as well as the immediately previous three MOD13Q1 dates of collection (T-16, T-32, and T-48) to incorporate the potential effect of time lags. Some studies have demonstrated the significant impact of time lags between changes to a landscape and the subsequent ecological responses [31,32].

Analyses between EVI and NDVI variables and bee community

All analyses were done in R 2.15.1 (R Development Core Team, 2011). There were a total of 228 collecting events (2010: 6 sites of each land use type sampled twice; 2011 – 2012, 8 sites of each land use type sampled 4 times each). For each collecting event, we calculated the total bee abundance and number of species groups (species richness).

We tested for the relative significance of NDVI and EVI values on total bee abundance and species richness with generalized linear mixed models using the R package *lme4*. We used 8 possible vegetation indices represented by NDVI and EVI at the closest date of collection to bee sampling event, as well NDVI and EVI at the previous 3 dates of collection. Similar to a related study (See Chapter 1), we designated vegetation index, land use type, their interaction, and land use collecting method (4 hour vs. 24 hour pan traps) and day of year as fixed effects, and site and year as random effects. All analyses were fit with Poisson distributions.

Results

Phenological diversity of vegetation across land use types

Urban, agricultural, and natural land use types underwent different phenological patterns of vegetation “green-up”, with regards to their EVI and NDVI (Figure 1). In this region, EVI and NDVI are roughly equivalent (although EVI values are consistently slightly lower), so for the purposes of simplicity, only EVI analyses are presented. From 2000-2014 at each 16-day interval, the average EVI and NDVI for all pixels classified as each land use type underwent distinctly different, and consistent patterns (Figure 2). Natural had a large burst of high values in the early spring and then trailed off, urban was relatively constant, and agricultural had two greening peaks, the first at the same time as natural, and the second in the middle of the summer. Standard deviations (Tukey HSD, $p < 0.001$) and range (Tukey HSD, $p < 0.001$) were both larger in the human-altered landscapes than in natural (Figure 3).

Vegetation and bee community indices

For most models of total bee abundance, there was a significant impact of land use type, vegetation index value, and an interaction between the two (Figure 4, Table 1). AIC values decreased, indicating better model fit, as the time lag of vegetation data increased to 48 days prior to the collecting event. Similar patterns were not found for species richness, and there was little to no relationship between vegetation indices and species richness.

In general the relationship between higher vegetation indices and higher bee abundance was positive. However, a time lag of 16 days between the remote sensing data and the closest sampling date of bee collection exhibited differences in patterns between land use types. For natural areas, there appeared to be a positive correlation slope between EVI and higher bee abundance. The slope for bee abundance in urban sites was close to zero, and was a negative slope in agricultural sites (Figure 4c). No other scenarios of land use type, bee abundance, and vegetation index ($N=24$) was significantly negative.

Urban sites had a high amount of overlap between seasons in the correlations between vegetation indices and total abundance. Agricultural sites also had overlap between seasons, but overall variation was higher than with urban sites. Natural sites had little overlap between months and correlations were more dispersed, particularly for early and late spring (Figure 4).

Discussion

This study demonstrates the role of land use change in leading to shifts in phenology, a result often attributed to climate change [3,4,7,33]. We found major differences in land surface phenology and bee community spatio-temporal distributions between urban, agricultural, and natural land use types. The phenology of land surface vegetation human-altered landscapes are is of synchrony with surrounding California grassland natural areas. In addition to different patterns of phenological change, different land use types exhibit variability in the ranges and standard deviations of their land surface vegetation phenology. Further, these patterns correlate with spatio-temporal bee distribution data.

In California grasslands, floral availability is largely driven by temperature and rainfall, resulting in a large burst of blooms in the spring, and by the end of the summer, there are few floral resources available [34]. However, in human-altered landscapes, landscaping and water

irrigation patterns are likely even stronger influences. Vegetation in urban areas is highly diverse, and selected for aesthetic and convenience reasons. Urban areas, while having less green space, often have many exotic ornamental plants which are supplemented with water and nutrient inputs that allow for an extended flowering season. As a result, urban areas are characterized by low, but constant, floral resources throughout the year. Agricultural areas have large patches of dense, often homogenous, floral resources that will fluctuate greatly from early spring to the end of the summer. In our system, stone fruit orchards (cherries, stone fruit, grapes and walnuts) are in flower in the spring, but throughout the summer there are other crops in flower such as alfalfa, tomato, corn, and bell peppers [26].

This asynchrony in land surface phenology between neighboring land use types is similar to what Buyantuyev and Wu (2012) found in the desert landscapes of the southwestern United States. They found the timing of highest peaks of vegetation indices to be different between land use types, which they attributed to a decoupling in the urban sites from the local climatic drivers [13]. It is likely that a similar scenario occurs in California, with grasslands juxtaposed against urban and agricultural areas that have different vegetation types and additional inputs.

Beyond the different timing in vegetation indices, it is important to note the significantly different standard deviation and ranges of pixels of the same land-use type. Natural land use types were quite similar to one another given their relatively small standard deviations and ranges over time. However, in the human-altered landscapes, particularly agricultural, there was much higher variation. In other words, even though natural areas can be considered patchy, they are not nearly as patchy as urban and agricultural areas. One reason for the enhanced patchiness is that in urban and agricultural landscapes, there are many different land owners and management decisions being made on a relatively micro-scale, resulting in a wide diversity of vegetation types being selectively planted and cared for in different ways across the landscape. Instead of vegetation type shifting on the scale of a few kilometers, it might actually differ on the scale of a few meters. Such extreme patchiness of vegetation can have many implications for organisms dependent on floral resources. Additionally, varying patterns in vegetation in urban landscapes have been found to be closely tied to socio-economic factors [35], suggesting an important factor to consider when exploring biodiversity in human-altered landscapes. We were able to detect these patterns even though the resolution of the remote sensing data was limited to 250 m. As remote sensing data technology advances, we will be able to further explore these patterns.

There are clearly different patterns of bee abundance between land use types over the course of the year. We detected differences in land surface phenology between land use types through remote sensing, although the relationship between remote sensing vegetation indices and the bee community is complex due to the role of seasonality and major differences in vegetation between land use types. The strongest relationship between vegetation indices and bee abundances were in natural sites, but sites classified as natural also exhibited high colinearity between seasonality and vegetation indices, making it difficult to tease apart the differences. The overlapping points between seasons in the urban and agricultural areas (Figure 4) mean that vegetation indices are less tied to seasonality.

Despite this lack of colinearity with seasonality in human-altered landscapes, there were still significant patterns between vegetation indices and bee abundance, indicating the potential to use remote sensing to detect certain aspects of biodiversity. Further exploration into the relative contributions of different types of vegetation within each land use type and between time of year would contribute to the strength of applying these findings more broadly. In addition,

building on the idea of “scaling up from urban gardens” [36], it would be valuable to see if patterns change when the larger surrounding area of each location is investigated. No significant relationship was detected between vegetation indices and species richness as a general indicator, although focusing on certain species or functional groups may highlight which are more vulnerable to changes in phenological patterns [37].

In this study, bee collections were made approximately every two months, yet certain species peaked in abundance at different times between land use types. This lack of synchrony in peak abundance between land use types could be the result of two possibilities: either bees are moving (further than expected) between land use types in search of better resources, or localized population structuring is occurring between different land use types based on differences in timing of emergences. Perhaps on a finer temporal scale of collections, for example, on the same frequency as MODIS composite products (every 16 days), these subtleties in timing between land use types could be better captured. Additionally, the role of time lags should be further explored by investigating floral resource availability. We found better fitting models with increasing time lags, although this may still be tied to the strong effect of seasonality in natural areas. However, several other studies have shown the importance of time lags between changes and ecological responses [31,32]. In our case, this is likely the result of challenges in using vegetation indices as proxies for floral availability. Sometimes extreme floral abundance can lead to an underestimation of vegetation biomass [38]. Perhaps our time delay is the result of plants experiencing green up through leaf growth before producing floral reproductive structures. A better understanding of species associations with vegetation indices would further improve predictive power of utilizing remote sensing data to predict species distributions.

These findings have implications for how we think about human-altered landscapes and restoration. A great amount of interest and resources go into creating “green spaces” and restoring patches of land within urban and agricultural matrices [39,40,41]. However, most restoration practices are based on studies in more natural land use contexts [42,43,44]. Due to the much higher degree of patchiness in human-altered landscapes and changes in phenological patterns, restoration goals and strategies may need to be altered when working in human-altered landscape contexts. Additionally, this study highlights the importance of temporal differences in human-altered landscapes.

Understanding how human-altered landscapes impact species distributions and interactions is critical as land use change accelerates globally. In order to overcome previous limitations when using remote sensing to estimate biodiversity, it is first important to further understand the dynamics of vegetation type, phenology, and the ecology of interacting taxa. Our results clearly indicate that the phenology of vegetation in different land use types are not synchronized, and vegetation indices created through remote sensing can predict bee community abundance. Such findings suggest the potential to use remote sensing to estimate other taxa beyond bees to estimate biodiversity, as well as provide a new way of understanding the ecological challenges of urbanization and agriculture due to phenological differences.

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Table 1. Output of GLMM models for effect of EVI with varying time lags for total bee abundance. Displayed are effect sizes, errors, and p-values for land use types (agricultural and urban) and EVI value. The last two columns denote whether or not there was a significant interaction (and in which direction) between each land use type and day. All significant explanatory variables with p-values <0.05 are in bold.

Total Bee Abundance	AGR Effect	AGR Error	AGR p-value	URBAN Effect	URBAN Error	URBAN p-value	EVI Effect	EVI Error	EVI p-value	AGR * EVI	URB * EVI
Closest Collecting Period	0.03703	0.21186	0.86126	0.18141	0.24058	0.45081	0.10862	0.01371	< 0.001	-	-
Closest Collecting Period – 16 days	1.09037	0.21596	< 0.001	0.6076	0.24396	0.0128	0.40918	0.01211	< 0.001	-	-
Closest Collecting Period – 32 days	0.61977	0.20883	0.003	0.56755	0.23373	0.0152	0.44136	0.00947	< 0.001	-	-
Closest Collecting Period – 48 days	0.38849	0.20316	0.0558	0.105908	0.22515	0.6381	0.368123	0.00807	< 0.001	-	-

Table 2. Output of interaction effects between land use type and EVI value for GLMM models with varying time lags for total bee abundance. Displayed are effect sizes, errors, and p-values for land use types (agricultural and urban) and EVI value interaction effect. All significant explanatory variables with p-values <0.05 are in bold.

Total Bee Abundance	Agr.evi.effect	agr.evi.error	agr.evi.p	urb.evi.effect	urb.evi.error	urb.evi.p
Closest Collecting Period	-0.21171	0.01755	< 0.001	-0.31618	0.03469	< 0.001
Closest Collecting Period – 16 days	-0.54888	0.01782	< 0.001	-0.42078	0.03409	< 0.001
Closest Collecting Period – 32 days	-0.3695	0.01553	< 0.001	-0.34271	0.02947	< 0.001
Closest Collecting Period – 48 days	-0.275724	0.014436	< 0.001	-0.168625	0.023629	< 0.001

Figure 1. Maps illustrating the change in NDVI from March to September in East Contra Costa County, CA. Triangles represent agricultural sites, squares represent urban sites, and circles represent natural sites. As the year progresses, higher NDVI values are associated with different land use types.

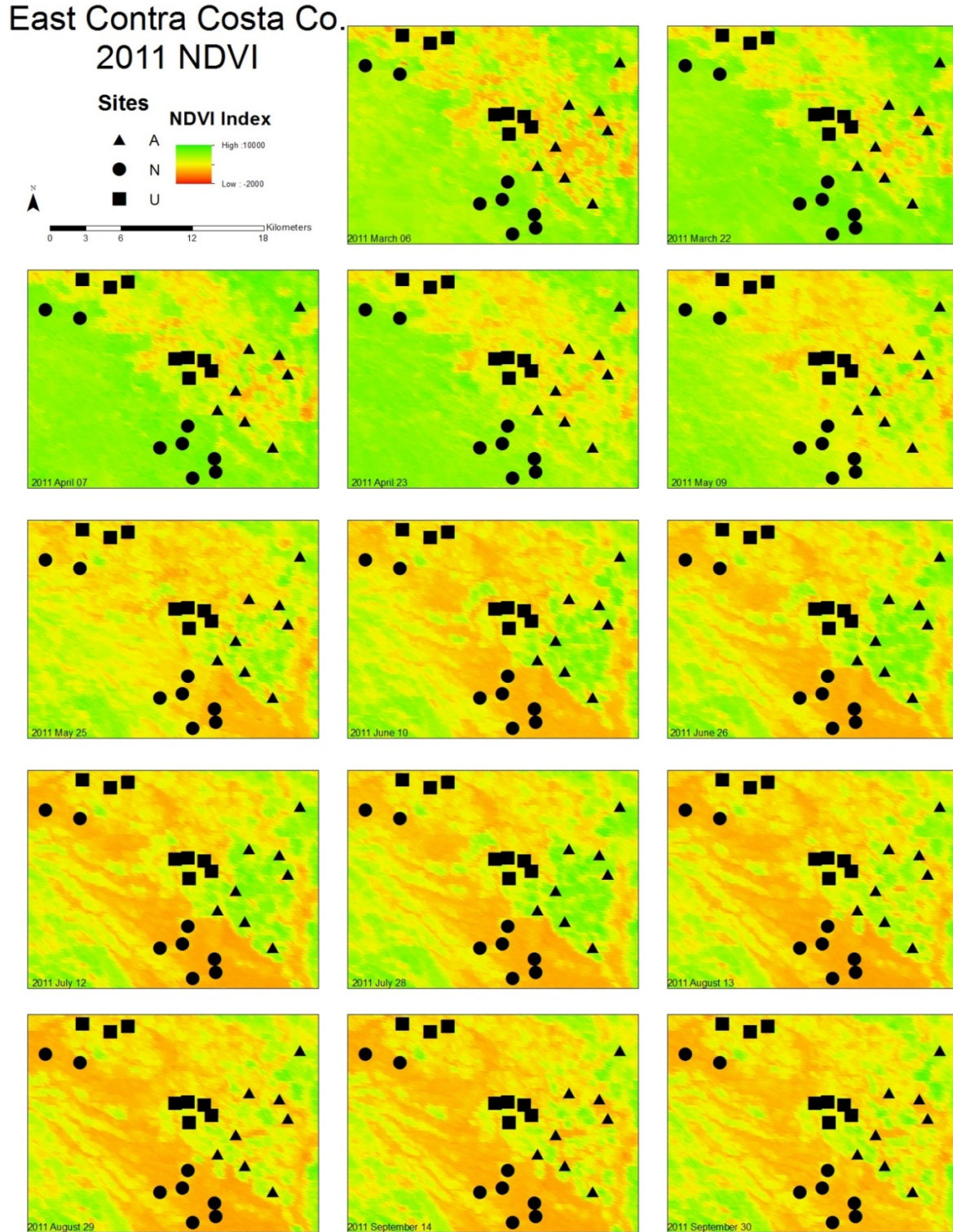


Figure 2. Different land use types exhibit different patterns of change throughout the year, from 2000-2014. Each point represents the mean EVI for all pixels of the same land use classification within the 50km x 50km region encapsulating the study site. Agricultural sites (A), have two peak EVI values, urban sites (B) remain relatively even, and natural sites (C) have one peak EVI value.

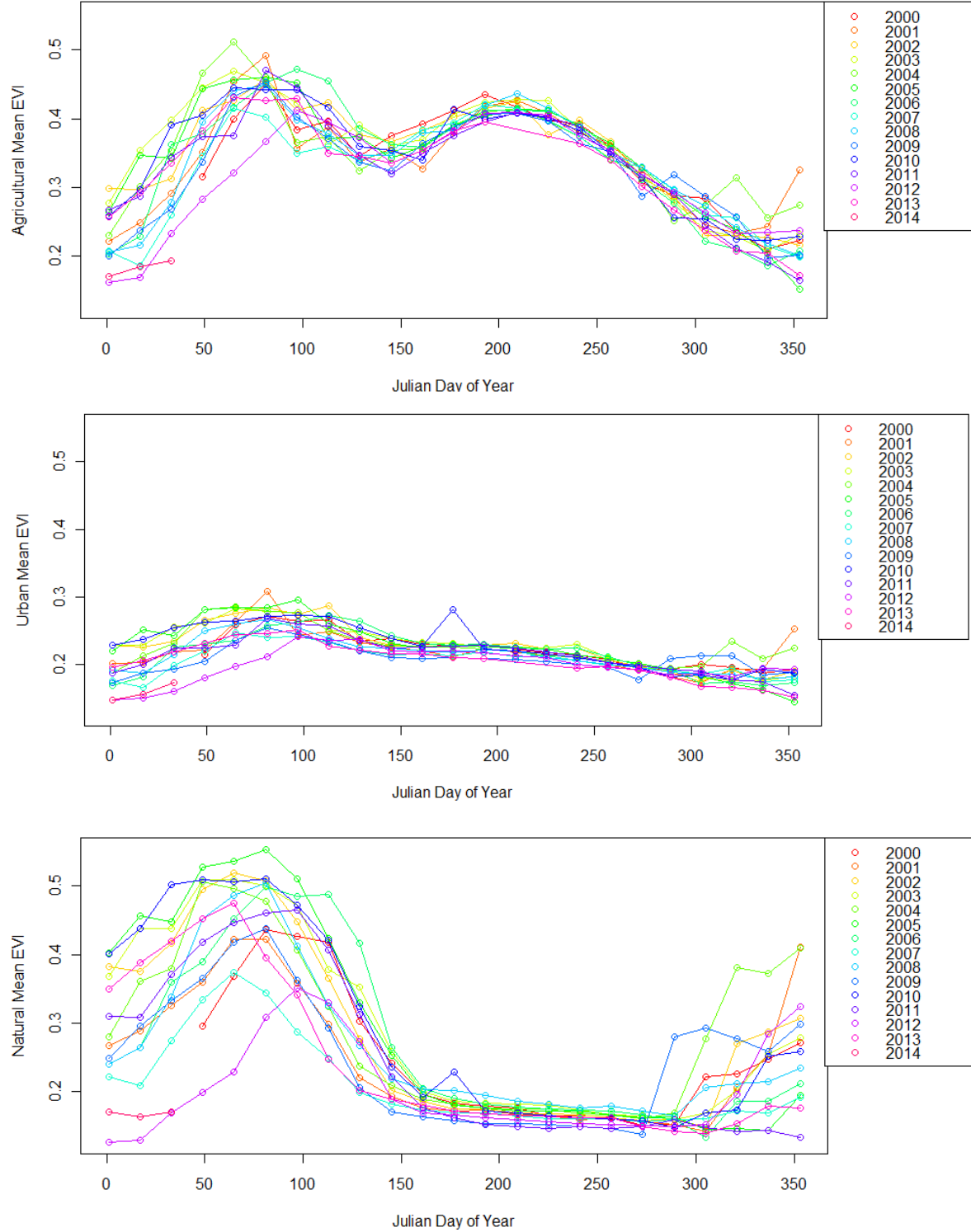


Figure 3. Standard deviation (A) and range (B) of different land use types are quite different. Agricultural sites (green) consistently have the highest standard deviations and ranges, natural (yellow) have the lowest, and urban is in between (red).

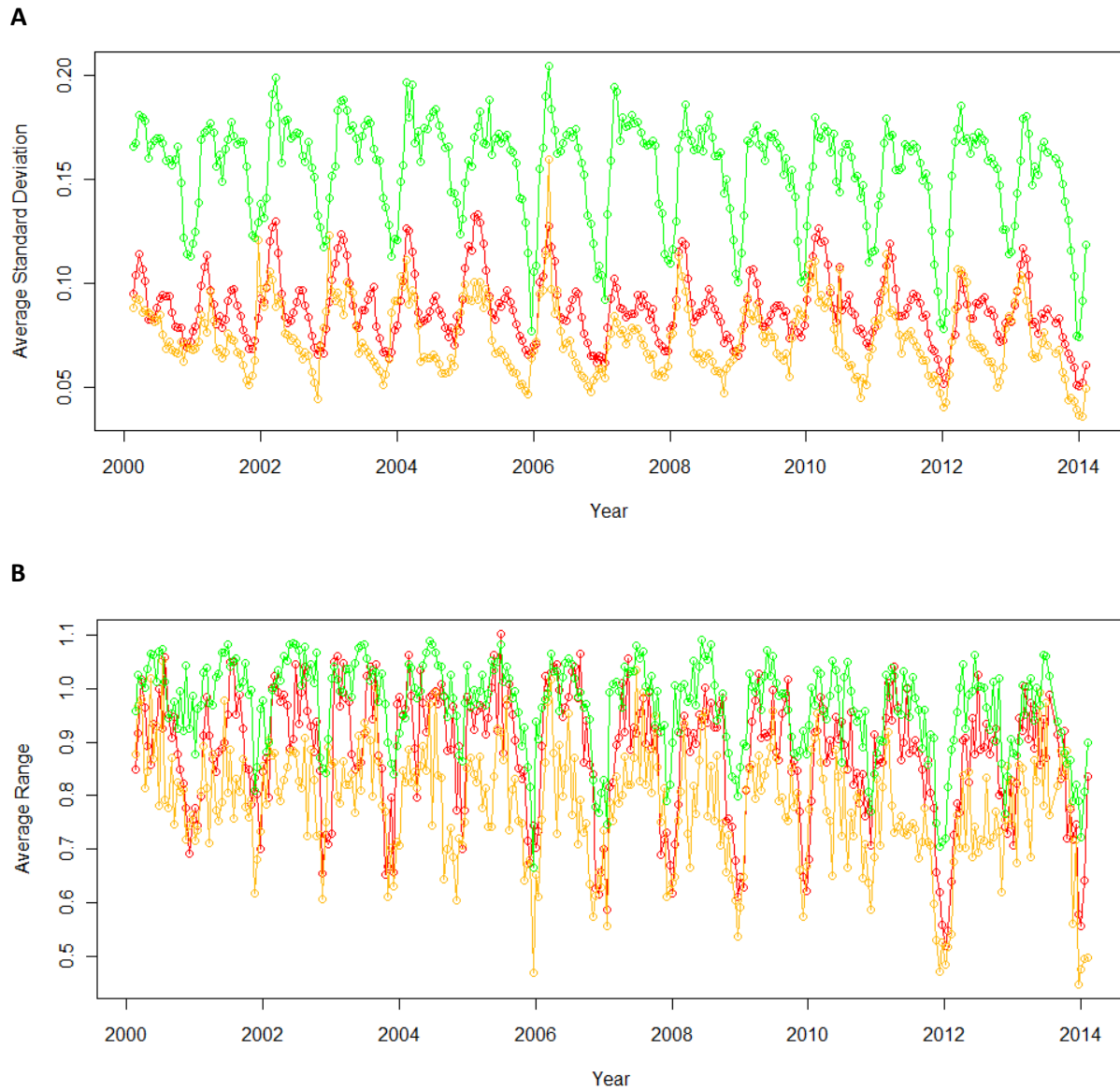
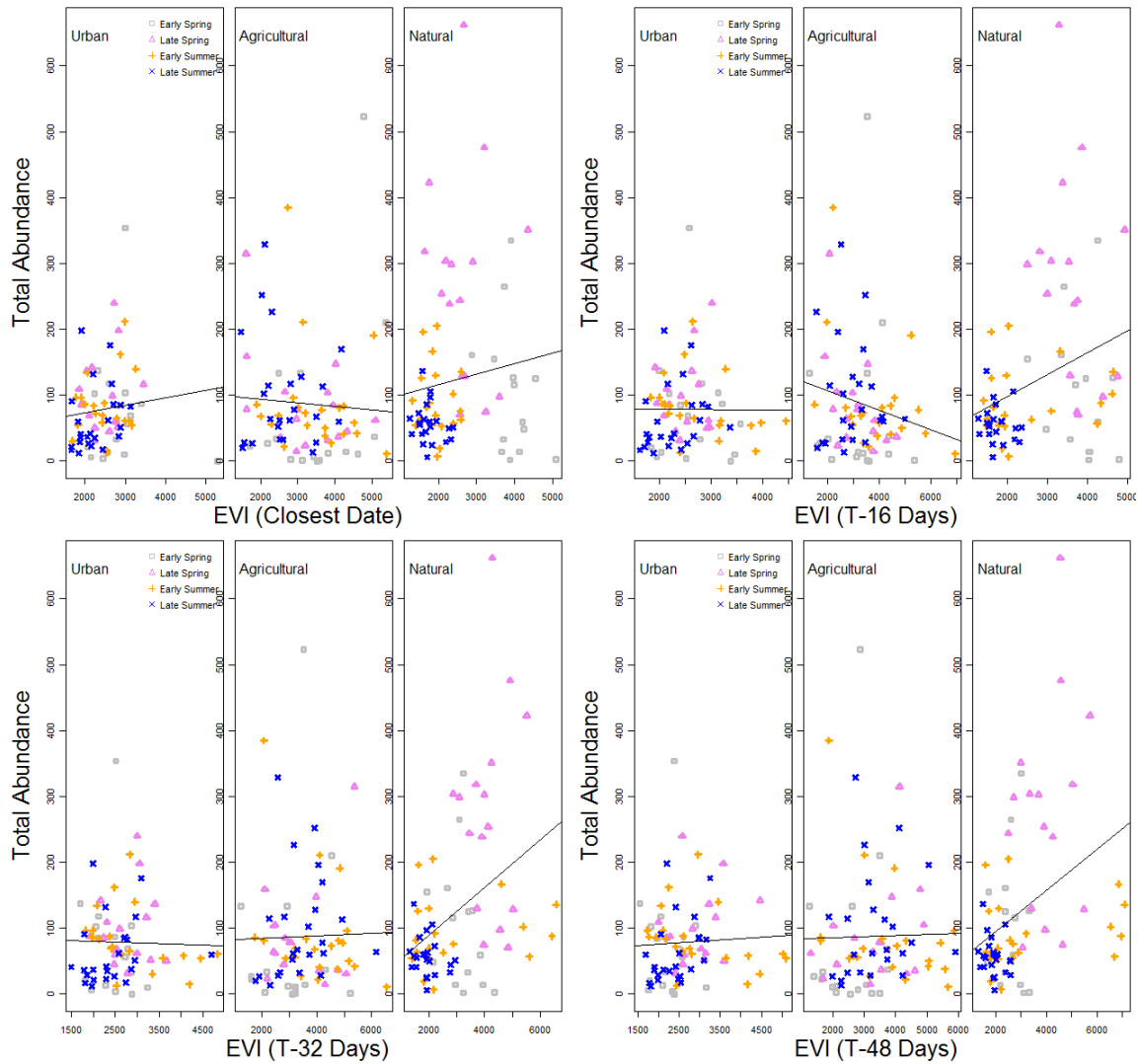


Figure 4. Plotting total abundance against EVI values by land use type illustrates different patterns based on season and time lag. The first plot are the EVI values closest to the date of collection, and each subsequent plot represents a 16-day time lag between remote sensing data and bee collection.



Chapter 3

Pollinator Interactions with Yellow Starthistle (*Centaurea solstitialis*) across Urban, Agricultural, and Natural Landscapes

Abstract

Pollinator-plant relationships are found to be particularly vulnerable to land use change. Yet despite extensive research in agricultural and natural systems, less attention has focused on these interactions in neighboring urban areas and its impact on pollination services. We investigated pollinator-plant interactions in a peri-urban landscape on the outskirts of the San Francisco Bay Area, California, where urban, agricultural, and natural land use types interface. We made standardized observations of floral visitation and measured seed set of yellow starthistle (*Centaurea solstitialis*), a common grassland invasive, to test the hypotheses that increasing urbanization decreases 1) rates of bee visitation, 2) viable seed set, and 3) the efficiency of pollination (relationship between bee visitation and seed set). We unexpectedly found that bee visitation was highest in urban and agricultural land use contexts, but in contrast, seed set rates in these human-altered landscapes were lower than in natural sites. An explanation for the discrepancy between floral visitation and seed set is that higher plant diversity in urban and agricultural areas, as a result of more introduced species, decreases pollinator efficiency. If these patterns are consistent across other plant species, the novel plant communities created in these managed landscapes and the generalist bee species that are favored by human-altered environments will reduce pollination services.

Introduction

Human-altered landscapes are expanding globally and are often associated with declining natural habitat, non-native species, fragmentation, and transformations in structure, inputs, climate, and connectivity [1,2,3,4]. These changes collectively have resulted in shifts in both spatial distributions and species diversity across many taxa including birds, mammals, reptiles, amphibians, invertebrates, and plants [5,6]. One common driver of global change is urbanization, which in the extreme is associated with a reduction in biodiversity compared to habitats in their more natural state [7]. However, in moderately urbanized areas, the effects of urban impacts on species distribution and diversity can vary greatly and depends on region, type of change, and taxonomic group, among other factors [8,9].

Documenting the effects of urbanization compared to natural communities has proven problematic, making predictions of community change associated with urbanization difficult. Human-altered landscapes are often associated with many non-native species which add to species diversity [6,10,11] but also can obscure changes in community dynamics. Thus, to assess accurately the complex impacts of land use change on ecological communities, one must look beyond species richness to investigate ecological processes themselves. Ecological processes are the links between organisms in a functioning ecosystem, and are critical in understanding how altered biodiversity can lead to changes in ecosystem functioning [12].

Global environmental change has been found to have a wide variety of impacts on ecological processes in different systems [13]. Pollinator-plant relationships in particular are found to be particularly vulnerable to land use change, resulting in decreases in interaction strength and frequency [14]. Pollination services are crucial ecosystem processes in natural systems, but also in agricultural and urban areas [15]. Bees provide the majority of animal-mediated pollination services on which it is estimated 87.5% of flowering plants depend [16]. The value of pollination in agriculture is estimated at \$200 billion worldwide [17], largely due to many foods that are essential for food security and a healthy human diet, including numerous fruits, vegetables, and nuts that require bee pollination. As urban areas expand, there has been increasing interest in urban agriculture to ensure food security and access to healthy foods for growing populations, and these systems also depend on pollination. For example, Kollin [18] estimated that the economic value of urban fruit trees (many of which require pollination) to be worth \$10 million annually in San Jose, California.

Despite the important role of pollinators and concerns about bee declines [19,20], there remain many uncertainties regarding the impact of land use change on pollinators [21]. Urbanization has resulted in more interfaces with both natural and agricultural landscapes, creating new transitional zones of peri-urbanization [22]. While there has been extensive pollinator research in agricultural and natural systems [23,24,25,26,27], less attention has focused on pollination in neighboring urban areas and how the changing landscape has impacted pollination [9,28]. In addition, very few studies of urban areas have looked beyond changes in bee diversity to understand explicitly the effect of urbanization on pollinator-plant interactions [10,29,30].

Here, we investigate the effect of land use change on pollinator-plant ecosystem processes. We make use of a “natural experimental design” in which urban, agricultural, and natural areas intersect. Bees visit flowers for both pollen and nectar resources, and floral visitation is a commonly used as an index of pollination services. However, depending on the flower, certain bee groups are much more effective pollinators than others [9,21,31]. Thus,

while visitation is important, it alone does not definitively indicate whether pollination services were received by the plant [32]. When pollen is limited by other factors, consequences for plant fitness can include failure to set seed, production of smaller fruits, and even complete lack of reproduction [33,34]. By looking at rates of bee visitation and comparing this with other measures of plant fitness, such as seed set, we can develop a more complete understanding of how shifts in bee distributions between areas that differ in land use are impacting pollination services.

To study the impact of changing land use on pollinator-plant interactions, we focus on bee pollination of a widespread plant, yellow starthistle (*Centaurea solstitialis*), a common weed found in natural, agricultural, and urban habitats. Using standardized observations of floral visitation and seed set measurements of yellow starthistle, we test the hypotheses that increasing urbanization decreases 1) rates of bee visitation, 2) viable seed set, and 3) the efficiency of pollination (relationship between bee visitation and seed set). In addition to contributing to a better understanding of how change in landscape use, particularly urbanization, affects pollination-plant interactions, the study illustrates the importance of use of neighboring lands for pollination services.

Methods

Ethics Statement

No protected species were sampled in this field study. Permits and approval were obtained for field observations on public land from the East Bay Regional Park District, Contra Costa County Flood Control and Water Conservation District, and the Los Vaqueros Reservoir.

Study System

Our study system was located around Brentwood, in east Contra Costa County, California, where natural, agricultural, and urban areas intersect with each other within a 20 x 20 km region (Figure 1). A county water district (Los Vaqueros Watershed), regional park district (East Bay Regional Parks: Black Diamond Mines, Round Valley, and Contra Loma), and California state park (Mount Diablo) all fall within the region, leaving large areas of land protected from development. This protected (hereafter referred to as “natural”) land consists mainly of grasslands and oak woodlands, some portions of which are managed for grazing. East Contra Costa County has had a farming community presence since the late 19th century. The agricultural areas of Brentwood, Knightsen, and Byron mostly consist of orchards (cherries, stone fruit, grapes and walnuts), corn, alfalfa, and tomatoes [35]. A housing boom in the 1990s led to massive residential growth in the area. The city of Brentwood has grown from less than 2500 people in the 1970s to over 50,000 today (2010 U.S. Census), and nearby Antioch has now over 100,000 residents (2010 U.S. Census).

We selected 12 sites dominated by yellow star thistle in a stratified design to span the different land use types (Figure 1). Yellow starthistle (*Centaurea solstitialis*) is a common weedy plant that forms homogenous flowering patches in grassy areas throughout this region. Many different bee taxa in a range of functional groups and size classes have been observed to visit yellow starthistle [36], in part because it flowers late in the season relative to other floral resources [37]. Despite being considered a serious introduced weed, yellow starthistle is unusual as an invasive species in that it depends on animal pollinator visits in order to set seed [38].

Within each site we selected a 50 m x 50 m plot such that each plot was at least 2 km away from all others, a distance larger than the maximum assumed typical bee foraging ranges [39]. Although certain bee species have been recorded foraging as far as 1400 m [40], most bees in this type of habitat have nesting and foraging habitat within a few hundred meters of each other [39,40,41]. Within each plot we estimated number of flowering yellow starthistle blooms by randomly placing 10, 1 m x 1 m quadrats and counting the number of flowering blooms in each. We also measured the spatial area of yellow starthistle patches within each 50 m x 50 m plot to obtain an estimate of total flowering blooms within each plot. We categorized total blooms/plot on a log scale: $<10^3$ (Category 1), 10^3 - 10^4 (Category 2), and $>10^4$ (Category 3).

Using NOAA's 2006 Pacific Coast Land Cover dataset (developed using 30 meter resolution Landsat Thematic Mapper and Landsat Enhanced thematic Mapper satellite imagery, USGS Products), a 500 m buffer (representing estimated bee foraging ranges [39,40,41]) was created around each plot, and the number of pixels classified as agricultural, urban, natural, water, or bare land was extracted. These categories were obtained by lumping finer categories in NOAA's classification scheme using the following definitions: Urban—"High Intensity Developed", "Medium Intensity Developed", "Low Intensity Developed", and "Developed Open Space"; Agricultural—"Cultivated", "Pasture/Hay"; Natural—"Grassland", "Deciduous Forest", "Mixed Forest", "Scrub/Shrub". Each plot was classified as a proportion of each of the 3 different land use categories, as well as for the category that was dominant. By this latter measure, of our 12 sites, 4 of each were classified as "urban", "agricultural", and "natural".

Bee Visitation

We observed visits by all bee species to yellow starthistle at all sites 3 times (AM, mid-day, and PM) for a 30 min period for a total of 90 min of total observation time per site within the same 2 wk period in August 2011. AM was defined as being between the hours of 9:30-11:30, Mid-Day as between 11:30-13:30, and PM as between 13:30-15:30. All observations were conducted by the same individual (ML) to avoid sampling biases. Also recorded at each observation period were approximate number of blooms, and wind and temperature simultaneously (using a Kestrel 3000 Pocket Weather Meter). Bees were not netted for later identification as we did not want to interfere with visitation to starthistle during this study. Instead, we used a modified protocol of citizen scientist observation surveys [42] with 15 expected bee morphotypes (Table 1) that correspond to 30 possible genera known to occur in the region (Leong, unpublished data). The observer slowly walked through the yellow starthistle patch, and upon reaching patch edge, returned on a path at least 3 m away from the previous, and recorded the morphotype classification of all bee visitors within 1.5 m on either side of the transect.

Seed Set

Yellow starthistle (Asteraceae) has composite flowers, which are aggregations of anywhere from 20-80 florets [43]. At each site, 12 yellow star thistle buds were randomly selected from different plants and covered with a mesh bag. Yellow starthistle blooming cycles have been described in detail in other publications [43]. We selected buds at stage BU-4 [43], when buds had no yellow petals exposed, but had well-developed straw-colored spines. When in full flowering, 10 bags were opened for a 4 hour period from 10am to 2pm, while 2 were kept closed as controls to verify that self-pollination was not occurring. At the opening and re-closing of the bags, the number of florets that had their stigmas extended (and thus, available for

pollination) were counted. Later, when flowers were fully mature (dry and straw-colored), seed heads were collected, and later dissected in the lab. Viable and non-viable seeds in yellow starthistle seed heads are easily distinguishable based on color and shape [38]. Because yellow starthistle requires pollination to produce viable seeds (also confirmed by our controls), non-viable seeds represent pollen limitation occurring during the 4-hour period that the flowers were exposed to pollinators. All seeds were counted to compare ratios of viable to non-viable seeds. Any seed predation was noted, and when possible, the seed predator was identified.

Analyses

All analyses were done in R 2.15.1 (R Development Core Team, 2011). Because each site had an AM, Mid-Day, and PM observation event, there were a total of 36 observation events, each with unique wind and temperature recordings, and visit observations of the 15 bee morphotypes. From these, we calculated the total number of bee visitors, total number of bee morphotypes, Shannon diversity of morphotypes, and morphotype evenness. Shannon diversity and evenness were calculated using the R package *vegan* [44]. The spatial autocorrelation of all bee visitor response variables (each morphotype abundance, total abundance, morphotype richness, diversity, and evenness) was assessed by Mantel tests in R package *ade4* [45], using the average values for each time of day at each site. Spatial autocorrelation was not detected ($p \geq 0.14$).

To test for the effect of land use type on each of the response variables we used a generalized linear mixed model using the R package *lme4* [46]. We designated land use type, bloom category of flowering patch, observation time period, wind, and temperature as fixed effects and site as a random effect. Natural land use and AM observation time period were the model baselines for the categorical variables of land use type and observation time. Shannon diversity and evenness were fit with Gaussian distributions while all other variables were fit with Poisson distributions.

In comparing the ratios of viable seeds to total seeds vs. the ratio of viable seeds to counted stigmas, we found that there was a strong correlation between these metrics. To look at the effect of land use type on seed-set, we therefore decided to utilize the ratio of viable seeds to total seeds in each seed head that did not experience seed predation, because of error in counting the number of stigmas (in some cases, we had slightly more viable seeds than counted number of stigmas, suggesting errors in this measurement). We then used a generalized linear mixed model fit with a Binomial distribution, with land use type as a fixed effect and site as a random effect.

Finally, we tested for an effect of floral visitor observations on yellow starthistle seed set at each site. We averaged the number of visits from each morphotype across temporal observation events at the same site. Morphotypes that averaged at least one visit per 30 minute observation window were included as fixed effects in a linear mixed model fit with a binomial distribution, with site as a random effect and the ratio of viable to total seeds as the response variable. We also modeled the effects of total bee visitation, morphotype richness, and morphotype diversity on seed set ratios.

Data on bee visitation rates for all observation events and seed set ratios for each plant are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.b5np1> [47].

Results

Bee visitation and land use

A total of 2816 total bee visits were recorded, representing 15 bee morphotypes. Total bee visitation was significantly higher in urban and agricultural areas with respective effect sizes (\pm standard errors) of 0.885 ± 0.26 ($p=0.0007$) and 0.813 ± 0.22 ($p=0.0002$) (Figure 2, Tables 2 & 3). The effect of land use type on visitation rates when analyzed separately for each bee morphotype, was a significant variable for 6 of 15 morphotypes. Bloom category, time of observation, wind, and temperature were only occasionally significant in some of the models.

Agricultural sites (Table 2) had the highest total bee visitation; 62% of total bee observations were honey bees (*Apis mellifera*), which were observed significantly more often in agricultural, than managed or urban sites (effect size \pm SE = 1.26 ± 0.33 , $p=0.0002$). Agricultural sites also had significantly higher visitation rates from shield-tipped small dark bees (effect size \pm SE = 1.83 ± 0.78 , $p=0.02$) and medium striped hairy belly bees (effect size \pm SE = 1.53 ± 0.62 , $p=0.01$). However, agricultural sites, compared to natural and urban sites, had significantly lower morphotype Shannon diversity (effect size \pm SE = -0.488 ± 0.193 , $p=0.009$) and morphotype evenness (effect size \pm SE = -0.264 ± 0.086 , $p=0.002$).

Visitation by native bees (here measured as visitation by non-honey bees, although there are a few other non-native species that may be included within the other morphotypes) was highest in urban sites (Table 3) compared to those in the other land use types (effect size \pm SE = 1.389 ± 0.273 , $p<0.0001$). Medium and small striped sweat bees were the most abundant groups after honey bees, which made up 12% and 7% of total bee observations respectively. When analyzed by morphotype, urban sites had the highest visitation levels from medium striped sweat bees (effect size \pm SE = 3.213 ± 0.268 , $p<0.0001$), small striped sweat bees (effect size \pm SE = 1.74 ± 0.53 , $p=0.001$), and small striped hairy belly bees (effect size \pm SE = 1.055 ± 0.536 , $p=0.04$). Urban areas had higher morphotype richness (effect size \pm SE = 0.369 ± 0.199 , $p=0.06$), but this effect was not significant. None of the morphotypes were observed significantly most often in natural sites, although 2 of 3 sites where bumblebees were observed were natural sites.

To examine in more detail the effect of land use on bee visitation, we created a continuous variable for land use with an index ranging from agriculture to urban use based on proportional area of each type within a 500 m radius. We then used this measure of land use to assess the response of total bee visitation, native bee visitation, morphotype richness, evenness, and Shannon diversity using previously described mixed model techniques. We found that while there was no significant effect of land use on total bee visitation, native bee visitation observations increased with more surrounding urban area (effect size \pm SE = 0.963 ± 0.22 , $p<0.001$). We also saw the same effect of increasing surrounding urban area on morphotype richness (effect size \pm SE = 0.27 ± 0.12 , $p=0.02$), Shannon diversity (effect size \pm SE = 0.55 ± 0.144 , $p<0.01$) and evenness (effect size \pm SE = 0.237 ± 0.069 , $p<0.01$) (Figure 3, Table 4).

Seed Set

Natural sites had the highest average rates of seed set, and urban areas had the lowest (effect size \pm SE = -0.756 ± 0.371 , $p=0.042$, Figure 4), in direct contrast to the pattern found with floral visitation where urban sites had the highest rates of native bee visitation and natural sites had the lowest. In total 140 yellow starthistle seed heads were collected and dissected; 4 lost mesh bags in the field and were eliminated from the study. Of these, 43% of the collected seed heads experienced some type of seed damage, largely due to biological control efforts in the area

involving tephritid flies and weevils. Seed predation decreased with amount of surrounding agricultural area (simple linear regression, $p < 0.01$). Of the 79 seed heads that were intact, 73 had received the 4-hour treatment of being exposed to pollination. Only 6 flowers in the control group which were never exposed to pollinators experienced no predation. Of those, 3 had no viable seeds, and 3 had 4.7%, 8.3%, and 20% viable seeds respectively.

Bee visitation and seed set

Of the 8 morphotypes that averaged at least one visit per 30 minute observation period, 3 exhibited significant relationships between visitation abundance at a site and seed set, although there was no significant relationship between site seed set and total bee visitation, morphotype richness, or morphotype diversity. Increased seed set ratios correlated with sites that had more visitation from medium hairy leg bees (effect size \pm SE = 0.284 ± 0.069 , $p < 0.001$) and to a smaller extent, round-tipped small dark bees (effect size \pm SE = 0.127 ± 0.074 , $p = 0.04$), despite there not being significant relationships between land use type and either of these bee groups. However, visitation by shield-tipped small dark bees (effect size \pm SE = -0.155 ± 0.051 , $p = 0.002$) had a significant negative effect on proportion of viable seeds (Figure 5).

Discussion

Our results show that rates of bee visitation and seed set vary among urban, agricultural, and natural landscapes, demonstrating the importance of land use in the dynamics of plant-pollinator interactions. We suggest that these effects are at least in part explained by floral availability, a vital bee resource, which can be highly variable among different land use types. For example, in August there are few plants in flower besides yellow starthistle in the natural areas of Contra Costa County, California, whereas in urban and agricultural areas there are many exotic plants and supplementary inputs available (personal observation). From pan-trapping of bee specimens in the region (Leong, unpublished data), we know that total bee abundance is highest in the spring in natural areas. However, towards the end of the summer when yellow starthistle is in flower, there is little difference in collected bee abundance between human-altered landscapes and natural areas, and human-altered areas may even exhibit overall higher bee abundance.

Our results of bee visitation to yellow starthistle support this pattern. Agricultural areas have large populations of managed honey bee colonies, so one would predict visitation to yellow starthistle by honey bees to be positively associated with surrounding agricultural land use. By contrast for native bees (total bee visitation excluding honey bees), the highest rates of visitation to yellow starthistle were in sites with more surrounding urban land use. Urban gardens have many exotic plants, often selected for aesthetic purposes, many of which are in flower later in the season than most California native plants. In addition, many of the plants in urban areas both directly and indirectly receive supplementary resources, particularly water, that further extend their flowering time. Even though agricultural areas also have supplementary resources, the main crop in flower in East Contra Costa County later in the season is maize, which is wind-pollinated. There may be multiple impacts of exotic plants in urban areas. By filling the phenological flowering gap [48] noted above, they may help attract even larger populations of bees into the urban landscape. In addition, bees in urban sites may be behaviorally more likely to visit non-native plants due to the increased encounters they have with novel plants [49].

In agricultural and natural landscapes, a positive correlation between pollinator visitation and seed set is typical [50]. Surprisingly in our system, in human-altered landscapes, higher total observed bee visitation did not result in higher proportions of seed set, as would be expected. In fact, urban areas, despite receiving the highest rates of native bee visitation, exhibited the lowest rates of seed set. Conversely, natural areas, which received the lowest amount of total bee visitation, had the highest rates of seed set.

We suggest 2 possible explanations for this discrepancy between pollinator visitation and rates of seed set: 1) pollinator efficiency; and/or 2) the composition of the local flowering community. Depending on the plant, certain pollinator species are much more effective than others [51]. For example, *Osmia*, *Habropoda*, and *Apis*, have been found to produce varying amounts of seed set as a result of a single visit to blueberry, but these results vary slightly depending on the blueberry variety [52]. In the case of yellow starthistle, it is likely that the most frequent visitors are perhaps not the most efficient. When we directly compared average seed set at each site against visitation rates, we found a significant positive association with the medium hairy leg bees. The medium hairy leg bee morphotype includes those species which fall in both the Tribes Emphorini and Eucerini. Emphorini are known to largely be oligolectic (Michener 1999), meaning they specialize on certain plant groups, which theory suggests would make them more efficient pollinators than generalists [51].

The medium hairy leg bee morphotype was not significantly associated with any of the land use types. It was also the only group that was observed most frequently during morning (AM) sampling, perhaps reflecting a difference in when yellow starthistle is most receptive to pollination. Despite the overwhelming abundance of honey bees in agriculture areas, we did not observe higher seed set in those regions, consistent with the observation that honey bees can be poorer pollinators than other species [53,54].

It is also important to note that this study used a morphotype classification, and there may be multiple species that fit within the same morphotype that provide varying degrees of pollination services [55]. It is possible there are rare, but highly efficient, pollinators that were rarely observed during the sampling period, or were lumped together with a more frequently observed morphotype.

An alternative explanation for the lack of an association between floral visitation and seed set is that higher plant diversity in urban and agricultural areas may decrease pollinator efficiency. Previous research has shown that invasive alien plants can have a negative effect on native plant communities by acting as attractors for pollinators, or decreasing pollinator efficiency by providing a wider range of resources for pollinators to visit, with the consequence that visitors transfer pollen from non con-specifics, potentially clogging stigmas and reducing pollination success [56,57,58]. In this case, our target plant, yellow starthistle is indeed considered an invasive alien plant, but the hypothesis of it being in a novel diverse community could lead to a similar effect on the frequency and quality of pollination services that it receives. In sites where there are many other potential plants to visit and accompanying decreased floral fidelity leading to diverse pollen loads, one predicts decreased pollinator efficiency. Abundant sources of exotic plant pollen could occur in areas where there is a greater diversity of nearby plants for pollinators to visit. This explanation might account for the observation that shield-tipped small dark bees were negatively correlated with seed set.

We selected yellow starthistle as the target plant for this study because of its ubiquitous distribution, reliance on pollination, and its attraction for a wide set of visitors; it is also a highly invasive and undesirable plant [59]. Previous research on yellow starthistle has found that its

invasion can be facilitated other non-native pollinator species such as the honey bee, *Apis mellifera*, and the starthistle bee, *Megachile apicalis* [36,38], which is included in the medium striped hairy belly bee morphotype. However, the abundance of bees in both of these 2 morphotypes were most closely associated with agricultural areas, which did not have the highest rates of seed set as would be predicted by visitation alone.

Our results indicate clearly that bee visitation in human-altered landscapes can be higher than that in comparable natural areas, especially towards the end of the flowering season when there are few resources available in natural landscapes. Because the response of bee visitors to land use change depends on species-specific requirements and these pollinators also have variable effects on plants, understanding the effect of land use change on pollination services requires knowledge not only of which pollinator groups shift to the human-altered landscapes, but also the rate of pollination that those groups have on the plant species in those landscapes. Future research will benefit from looking at a wider range of plants with a different range of target pollinators and that flower earlier in the year to better tease out these hypotheses. If the patterns of bee visitation and seed set that we observed are indeed consistent across other plant species, the novel plant communities created in these human-altered landscapes and the generalist bee species that are favored in such landscapes will lead to a reduction in overall pollination services.

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Table 1. The 15 bee morphotypes observed and their associated genera and species in East Contra Costa County, California.

Morphotype	Possible Species
Honey bee	<i>Apis mellifera</i>
Bumblebee	<i>Bombus spp.</i>
Carpenter bee	<i>Xylocopa spp.</i>
Hairy leg bee, medium	<i>Melissodes spp., Anthophora spp., Eucera spp., Peponapis spp., Exomalopsis spp., Diadasia spp.</i>
Hairy leg bee, large	<i>Svastra spp.</i>
Green sweat bee	<i>Agapostemon texanus</i>
Striped sweat bee, medium	<i>Halictus ligatus, Halictus spp., >0.5 cm</i>
Striped sweat bee, small	<i>Halictus tripartitus, Halictus spp., < 0.5 cm</i>
Small dark bee, rounded tip	<i>Lasioglossum spp.</i>
Small dark bee, shield tip	<i>Ceratina spp.</i>
Striped hairy belly bee, small	<i>Ashmeadiella spp., Megachile spp., <0.5 cm</i>
Striped hairy belly bee, medium	<i>Megachile, >0.5 cm, <1.5 cm</i>
Striped hairy belly bee, large	<i>Megachile, >1.5 cm)</i>
Wasp-like hairy belly bee	<i>Dianthidium app., Anthidium spp.</i>
Cuckoo bee	<i>Sphecodes spp., Nomada spp., Nomia spp., Calliopsis spp.</i>

Table 2. Statistical output table for response variables having significant relationships with the agricultural land use type. Bee morphotype visitation data and calculated community metrics were collected in East Contra Costa County, California. Significant relationships with the agricultural land use type were calculated based on generalized linear mixed models with land use type, bloom category of flowering patch, observation time period, wind, and temperature as fixed effects and site as a random effect. The natural land use type and morning (AM) observation time period were the model baselines for the categorical variables of land use type and observation time. Shannon diversity and evenness were fit with Gaussian distributions while all other variables were fit with Poisson distributions.

Response Variable	Effect size	Standard error	p- value
Total bee visitation	0.813	0.22	0.0002
Honey bees	1.26	0.33	0.0002
Shield-tipped small dark bees	1.83	0.78	0.02
Medium striped hairy belly bees	1.53	0.62	0.01
Morphotype Shannon diversity	-0.488	0.193	0.009
Morphotype evenness	-0.264	0.086	0.002

Table 3. Statistical output table for response variables having significant relationships with the urban land use type. Bee morphotype visitation data and calculated community metrics were collected in East Contra Costa County, California. Significant relationships with the urban land use type were calculated based on generalized linear mixed models fit with Poisson distributions with land use type, bloom category of flowering patch, observation time period, wind, and temperature as fixed effects and site as a random effect. The natural land use type and morning (AM) observation time period were the model baselines for the categorical variables of land use type and observation time.

Response Variable	Effect size	Standard error	p- value
Total bee visitation	0.885	0.26	0.0007
Native bee visitation	1.389	0.273	<0.0001
Medium striped sweat bees	3.213	0.268	<0.0001
Small striped sweat bees	1.74	0.53	0.001
Small striped hairy belly bees	1.055	0.536	0.04
Morphotype richness	0.369	0.100	0.06

Table 4. Statistical output for response variables having significant relationships with the gradient of agricultural to urban land use. To examine in more detail the effect of anthropogenic land use on bee visitation, we created a continuous variable for land use with an index ranging from agriculture to urban land use based on proportional area of each type within a 500 m radius. Generalized linear mixed models were created with this calculated anthropogenic land use metric, bloom category of flowering patch, observation time period, wind, and temperature as fixed effects and site as a random effect. The morning (AM) observation time period was the model baseline for the categorical variable of observation time. Shannon diversity and evenness were fit with Gaussian distributions while all other variables were fit with Poisson distributions.

Response Variable	Effect size	Standard error	p- value
Native bee visitation	0.963	0.22	<0.01
Morphotype richness	0.27	0.12	0.02
Morphotype Shannon diversity	0.55	0.144	<0.01
Morphotype evenness	0.237	0.069	<0.01

Figure 1. Map of study area and locations of plots in East Contra Costa County, California. Light blue dots represent a 500 m radius around the center point of each of the 12 sites. The sites were chosen to be located in agricultural (green), urban (red), and natural (yellow) land use types.

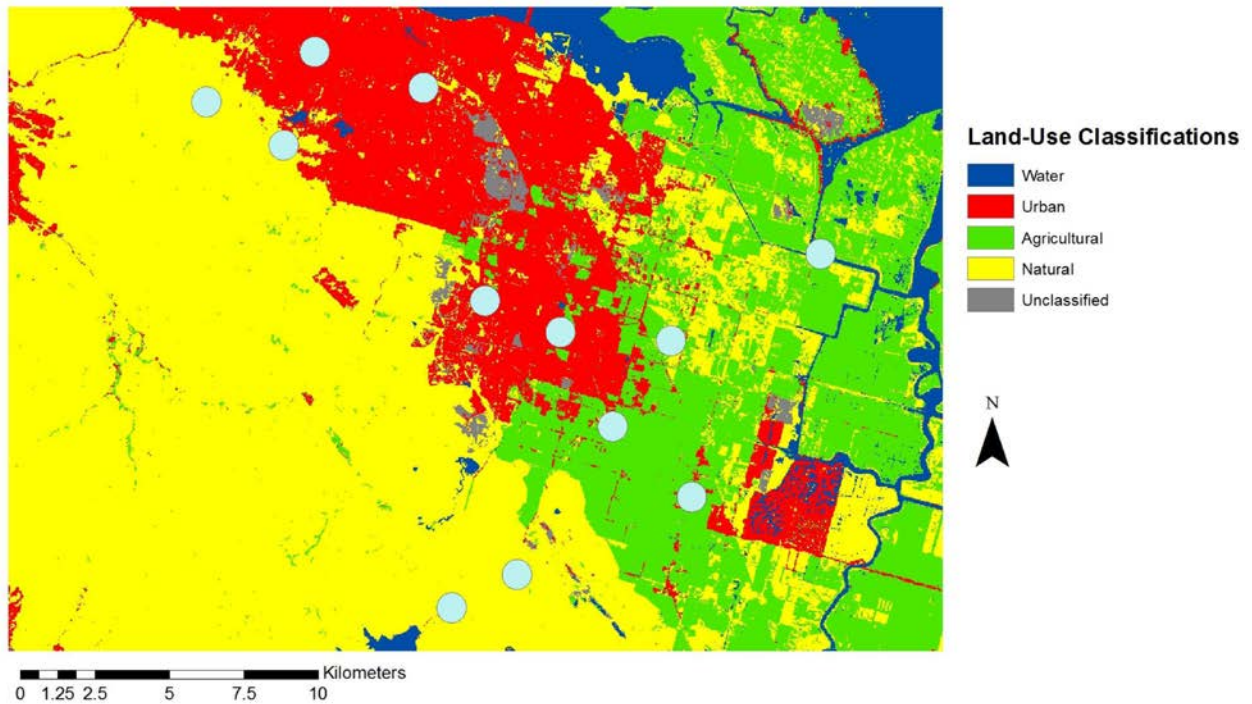


Figure 2. Box plots of bee visitation response variables in natural, agricultural, and urban sites. Bee morphotype visitation data and calculated community metrics were collected in East Contra Costa County, California.

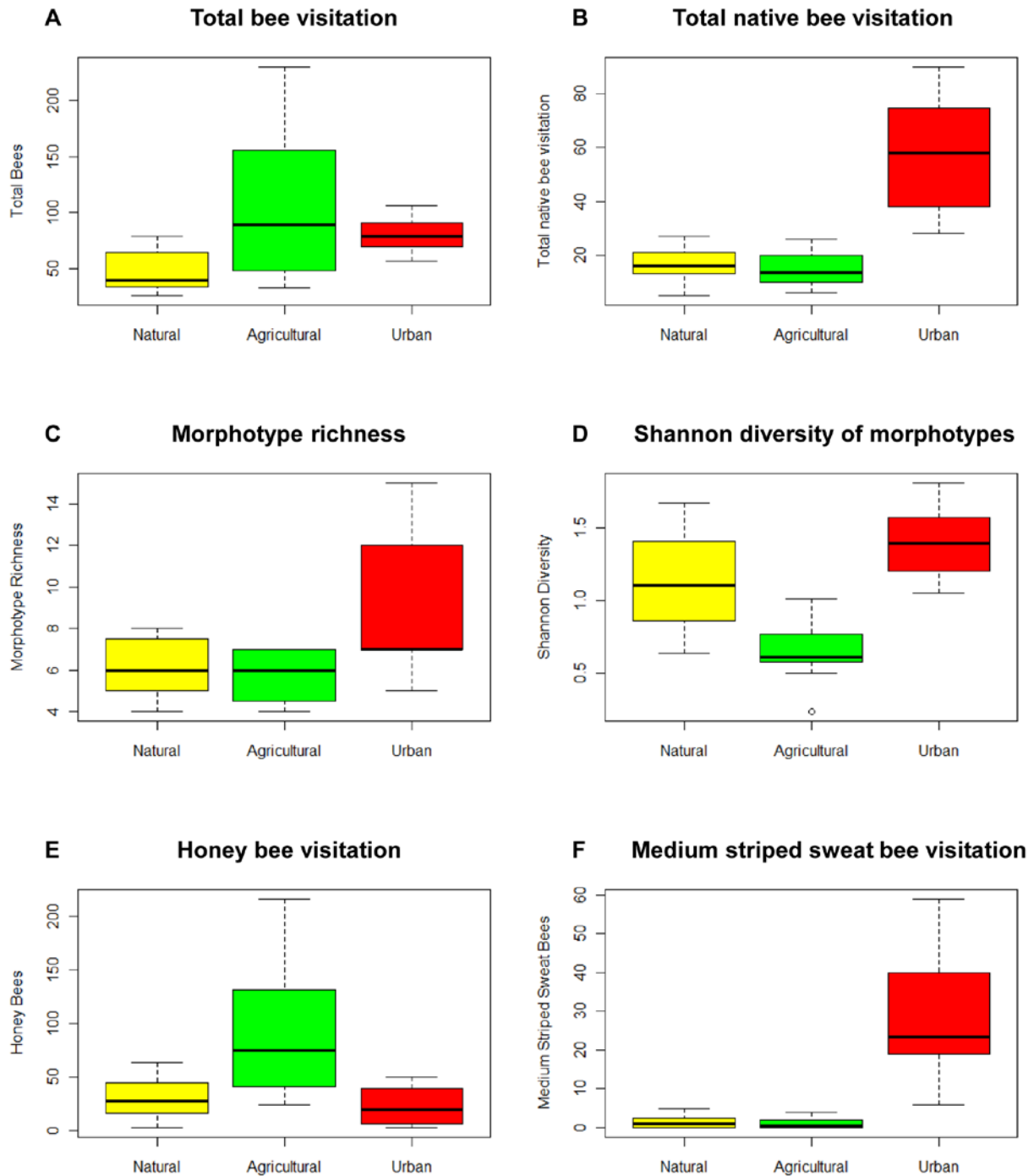


Figure 3. Bee visitation response variables as a function of surrounding anthropogenic land use. Bee morphotype visitation data and calculated community metrics were collected in East Contra Costa County, California. To examine in more detail the effect of anthropogenic land use on bee visitation, we created a continuous variable for land use with an index ranging from agricultural to urban land use based on proportional area of each type within a 500 m radius. As the x-axis moves from left to right, sites go from being more agricultural to more urban.

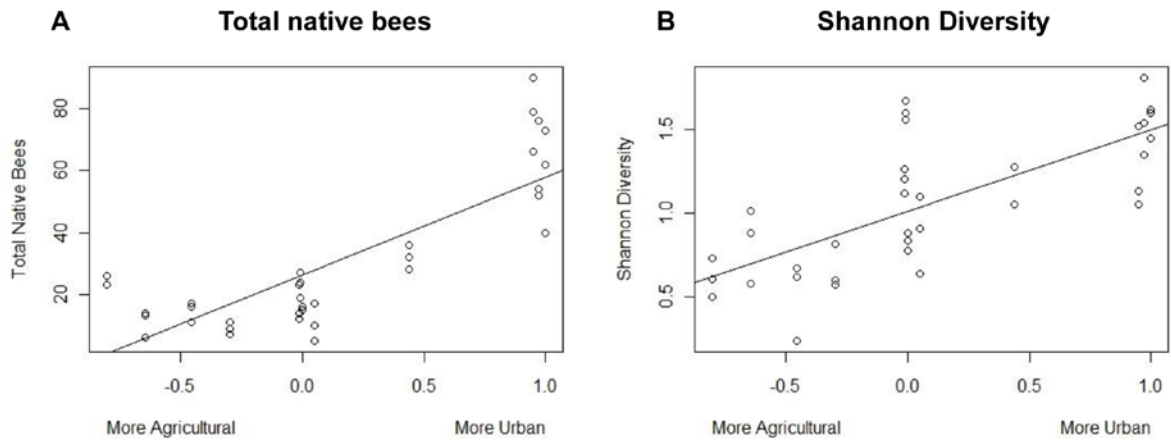


Figure 4. Box plot demonstrating the effect of land use type on percentage of viable seeds. Yellow starthistle seed heads were collected in East Contra Costa County, California and dissected in the lab after maturity. We calculated significance using a generalized linear mixed model fit with a binomial distribution, with land use type as a fixed effect and site as a random effect. With natural sites as the baseline, urban areas had significantly lower rates of seed set (effect size \pm SE = -0.756 ± 0.371 , $p=0.042$).

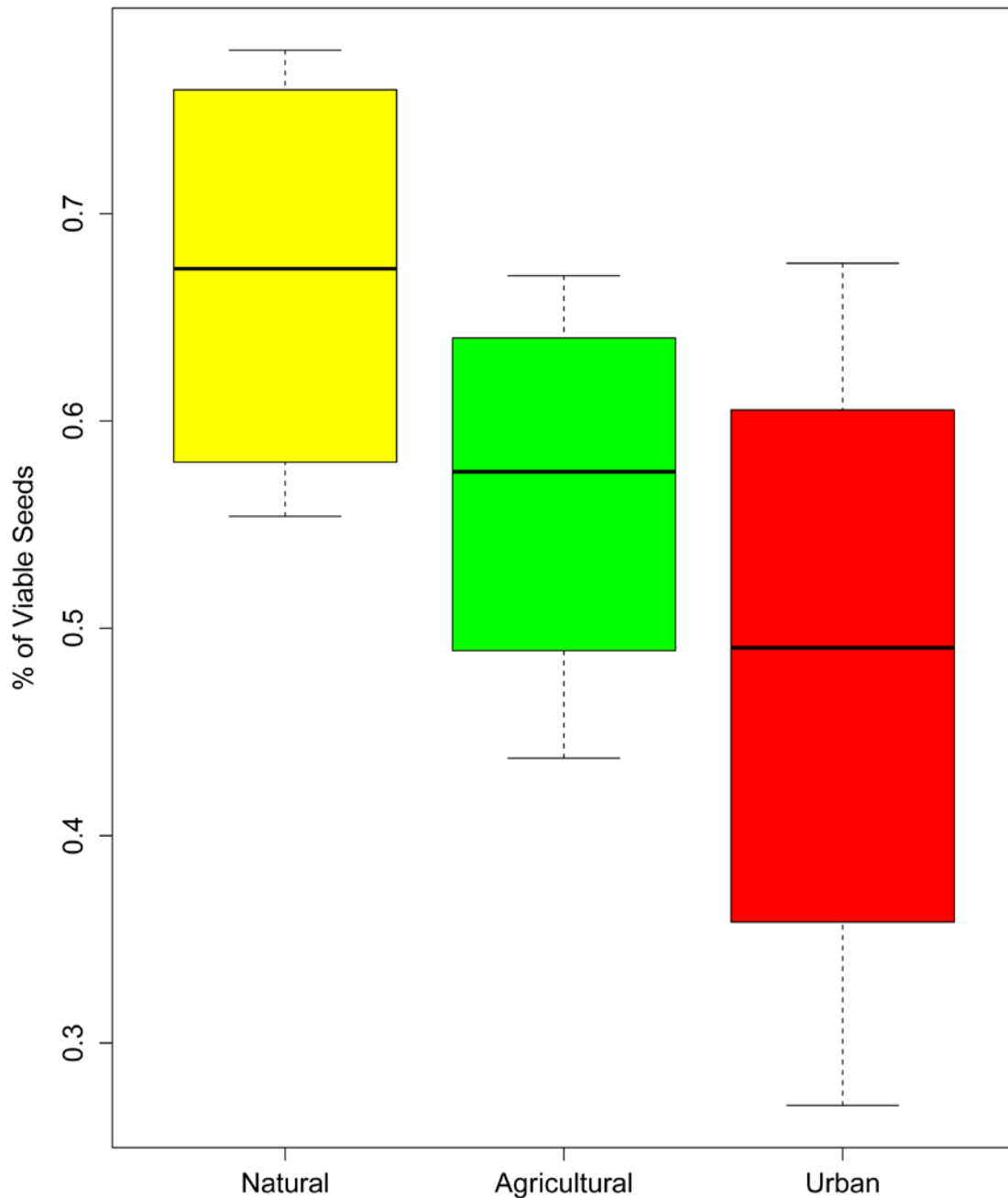
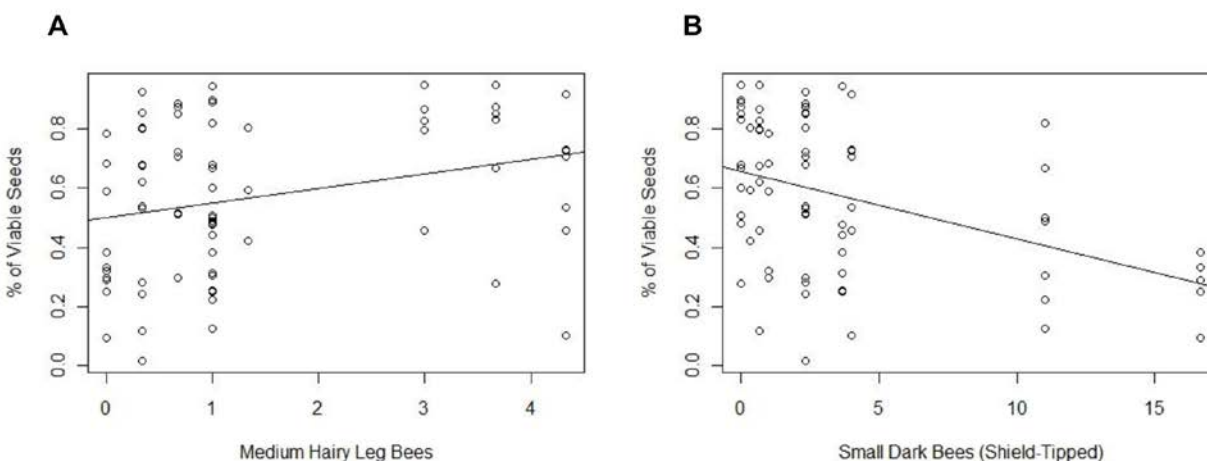


Figure 5. Correlation between the percentage of viable seeds in each yellow starthistle seed head and the average number of site visits by morphotype. Bee morphotype visitation data, calculated community metrics, and yellow starthistle seed heads were collected in East Contra Costa County, California. Bee morphotypes that averaged at least one visit per 30 minute observation window were included as fixed effects in a linear mixed model fit with a binomial distribution, with site as a random effect and the ratio of viable to total seeds as the response variable. Medium hairy leg bees (effect size \pm SE = 0.284 ± 0.069 , $p < 0.001$) and shield-tipped small dark bees (effect size \pm SE = -0.155 ± 0.051 , $p = 0.002$) had significant effect sizes in the model. Regression lines were added to illustrate relationships.



Appendix

List of bee species collected in east Contra Costa County, CA (2010-2012)

List of bee species collected in east Contra Costa County, CA (2010-2012)

Determined by Robbin W. Thorp, UC Davis

Referenced with:

Ascher, J. S. and J. Pickering. 2014. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila).
http://www.discoverlife.org/mp/20q?guide=Apoidea_species

ANDRENIDAE

Andrena angustitarsata Viereck, 1904
Andrena caerulea Smith, 1879
Andrena cerasifolii Cockerell, 1896
Andrena chlorogaster Viereck, 1904
Andrena chlorosoma Linsley & MacSwain, 1961
Andrena cuneilabris Viereck, 1926
Andrena fuscicaudata (Viereck, 1904)
Andrena misella Timberlake, 1951
Andrena nigrocaerulea Cockerell, 1897
Andrena orthocarpus Cockerell, 1936
Andrena perimelas Cockerell, 1905
Andrena piperi Viereck, 1904
Andrena semipunctata Cockerell, 1902
Andrena sola Viereck, 1917
Andrena suavis Timberlake, 1938
Andrena submoesta Viereck, 1917
Calliopsis scitula Cresson, 1878
Panurginus melanocephalus (Cockerell, 1926)
Panurginus niger Nylander, 1948
Perdita californica (Cresson, 1878)

APIDAE

Anthophora curta Provancher, 1895
Anthophora edwardsii Cresson, 1878
Anthophora urbana Cresson, 1878
Anthophorula chionura (Cockerell, 1925)
Apis mellifera Linnaeus, 1758
Bombus californicus Smith, 1854
Bombus melanopygus Nylander, 1848
Bombus vandykei (Frison, 1927)
Bombus vosnesenskii Radoszkowski, 1862
Ceratina acantha Provancher, 1895
Ceratina arizonensis Cockerell, 1898
Ceratina dallatorreana Friese, 1896
Ceratina nanula Cockerell, 1897

Ceratina punctagena Cockerell, 1916
Ceratina sequoiae Michener, 1936
Diadasia bituberculata (Cresson, 1878)
Diadasia consociata Timberlake, 1939
Diadasia enavata (Cresson, 1872)
Diadasia rinconis Cockerell, 1897
Eucera actiosa (Cresson, 1878)
Eucera frater albopilosa (Fowler, 1899)
Eucera lunata (Timberlake, 1969)
Melecta separata callura (Cockerell, 1926)
Melissodes agilis Cresson, 1878
Melissodes lupina Cresson, 1878
Melissodes microsticta Cockerell, 1905
Melissodes stearnsi Cockerell, 1905
Melissodes tepida timberlakei Cockerell, 1926
Nomada sp.
Peponapis pruinosa (Say, 1837)
Svastra obliqua expurgata (Cockerell, 1925)
Triepeolus melanarius Rightmyer, 2008
Triepeolus utahensis (Cockerell, 1921)
Xylocopa varipuncta Patton, 1879

COLLETIDAE

Hylaeus episcopalis (Cockerell, 1896)
Hylaeus leptcephalus (Morawitz, 1871)

HALICTIDAE

Agapostemon texanus Cresson, 1872
Halictus farinosus Smith, 1853
Halictus ligatus Say, 1837
Halictus rubicundus (Christ, 1791)
Halictus tripartitus Cockerell, 1895
Lasioglossum incompletum (Crawford, 1907)
Lasioglossum kincaidii (Cockerell, 1898)
Lasioglossum mellipes (Crawford, 1907)
Lasioglossum olympiae (Cockerell, 1898)
Lasioglossum sisymbrii (Cockerell, 1895)
Lasioglossum tegulariforme (Crawford, 1907)
Lasioglossum titusi (Crawford, 1902)
Lasioglossum (Dialictus) sp. B
Lasioglossum (Dialictus) sp.
Nomia melanderi Cockerell, 1906
Spechodes sp.

MEGACHILDAE

Anthidium edwardsii Cresson, 1878

Anthidium utahense Swenk, 1914
Ashmeadiella aridula astragali Michener, 1939
Dianthidium parvum schwarzi Timberlake, 1943
Hoplitis producta gracilis (Michener, 1935)
Megachile apicalis Spinola, 1808
Megachile brevis Say, 1837
Megachile concinna Smith, 1879
Megachile fidelis Cresson, 1878
Megachile gentilis Cresson, 1872
Megachile lippiae Cockerell, 1900
Megachile montivaga Cresson, 1878
Megachile onobrychidis Cockerell, 1908
Megachile perihirta Cockerell, 1898
Megachile rotundata (Fabricius, 1787)
Osmia aglaia Sandhouse, 1939
Osmia atrocyanea Cockerell, 1897
Osmia californica Cresson, 1864
Osmia clarescens Cockerell, 1911
Osmia gaudiosa Cockerell, 1907
Osmia glauca (Fowler, 1899)
Osmia granulosa Cockerell, 1911
Osmia laeta Sandhouse, 1924
Osmia lignaria propinqua Cresson, 1864
Osmia montana Cresson, 1864
Osmia nemoris Sandhouse, 1924
Protosmia rubifloris (Cockerell, 1898)

MELITTIDAE

Hesperapis regularis (Cresson, 1878)