Temporal dynamics influenced by global change: bee community phenology in urban, agricultural, and natural landscapes

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Abstract

Urbanization and agricultural intensification of landscapes are important drivers of global change, which in turn have direct impacts on local ecological communities leading to shifts in species distributions and interactions. Here, we illustrate 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 in shifts in seasonal abundance of bee pollinators. Three years of data on the spatio-temporal distributions of 91 bee species show that seasonal patterns of abundance and species richness in human-altered landscapes varied significantly less compared to natural habitats in which floral resources are relatively scarce in the dry summer months. These findings demonstrate that anthropogenic environmental changes in urban and agricultural systems, here mediated through changes in plant resources and water inputs, can alter the temporal dynamics of pollinators that depend on them. Changes in phenology of interactions can be an important, though frequently overlooked, mechanism of global change.

Keywords: agricultural, bees, ecosystem services, land-use change, phenology, pollinators, seasonality, species distributions urban ecology

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Introduction

Anthropogenic landscapes and their associated biodiversity are novel ecosystems that are expanding globally. Urbanization and agriculture, particularly, are the products of growing human populations and have accelerated rates of land conversion (Vitousek *et al.*, 1997; Barnosky *et al.*, 2012). These landscapes are typically associated with transformations in habitat structure, climate, and connectivity as well as the establishment of non-native species (Gill *et al.*, 2007; Grimm *et al.*, 2008; Ash *et al.*, 2008; Shochat *et al.*, 2010). However, even with their increasing dominance as a land use, many questions remain regarding the impact of these anthropogenic landscapes on ecological communities. Particularly, although there are differences between these ecosystems and their less human-modified equivalents, there is evidence for the potential of these anthropogenic landscapes to support biodiversity in unexpected ways that in some cases may be equivalent, or even surpass the biodiversity in surrounding natural landscapes (Mckinney, 2008; Boone *et al.*, 2012; Carper *et al.*, 2014; Leong *et al.*, 2014; Baldock *et al.*,

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2015). With the continued expansion of human-modified ecosystems coupled with the inability of reserves to support more than a fraction of the world's biodiversity (Groom *et al.*, 2006), understanding the dynamics of communities in these landscapes is necessary to evaluate their conservation potential and opportunities for restoration and management (Driscoll *et al.*, 2013).

Specifically, the temporal dynamics, or phenologies, of species have been observed to be vulnerable to disruption (Post *et al.*, 2008; Visser, 2008; Thompson, 2010; Kudo & Ida, 2013). Changes in the temporal activity of species can lead to mismatches in the presence of species and their biotic or abiotic resources, which can impact the functioning of ecosystems (Both *et al.*, 2009; Burkle *et al.*, 2013). Like global climate change which has been found to result in phenological shifts (Bartomeus *et al.*, 2011), the *urban heat island effect* is a well-documented local phenomenon experienced as significantly warmer temperatures in cities relative to the surrounding landscape due to higher energy use and impervious surface area (Hart & Sailor, 2009; Oke, 1973). As a result, plants bloom earlier and more densely (Mimet *et al.*, 2009; Roetzer *et al.*, 2000) and bird migration advances earlier in urban contexts (Tryjanowski *et al.*, 2013).

Human-altered landscapes may also shift the activity of wildlife by altering the variety and timing of resource availability. Many natural areas in temperate environments experience a large burst of diverse plant growth in the spring, and by the end of the summer, there are very few resources available (Chiariello, 1989). Urban areas, while likely having less vegetative cover than less human-modified landscapes, often support many exotic plants, which are supplemented with water and nutrient inputs, allowing for an extended vegetative and flowering season. As a result, urban areas may support more limited but constant vegetative resources throughout the year (Satterfield et al., 2015). In contrast, agricultural landscapes, due to the phenology of monoculture crops, have large patches of dense (often homogenous) vegetative resources that fluctuate greatly from early spring to the end of the summer (Riedinger et al., 2014; Rundlöf et al., 2014). Such within-year differences in vegetative availability between land-use types have been documented through the use of remote sensing and may affect the seasonal population dynamics of the animal communities that rely on floral resources (Leong & Roderick, 2015).

Focusing on wild bees, organisms that are highly dependent on floral resources, we ask whether there are differences in the seasonal population dynamics of bee communities in urban, agricultural, and natural landscapes. Although bee seasonality and movement has been documented in urban and agricultural landscapes (Wojcik et al., 2008; Hannon & Sisk, 2009; Mandelik et al., 2012), differences in the phenological dynamics of bee communities between urban, agricultural, and natural land-use types have not been explored. Here, we evaluate the hypothesis that neighboring land-use types exhibit different patterns in bee community phenology throughout the year. We predict the temporal dynamics of bee communities in urban landscapes will be less variable than in agriculture and less human-modified areas because resources are more stable. We also predict that because the pulse of resources availability in less human-modified and agricultural area occurs at different times, the bee community phenology will shift in the different land uses to track that availability. Understanding how the novel communities in human-modified landscapes function will help to better inform restoration and conservation efforts.

Materials and methods

Study sites and collection methods

Our study landscape was located in east Contra Costa County around Brentwood, California, where natural, agricultural, and urban areas intersect with each other within a 20 × 20 km region (Fig. 1). Large areas of land remain
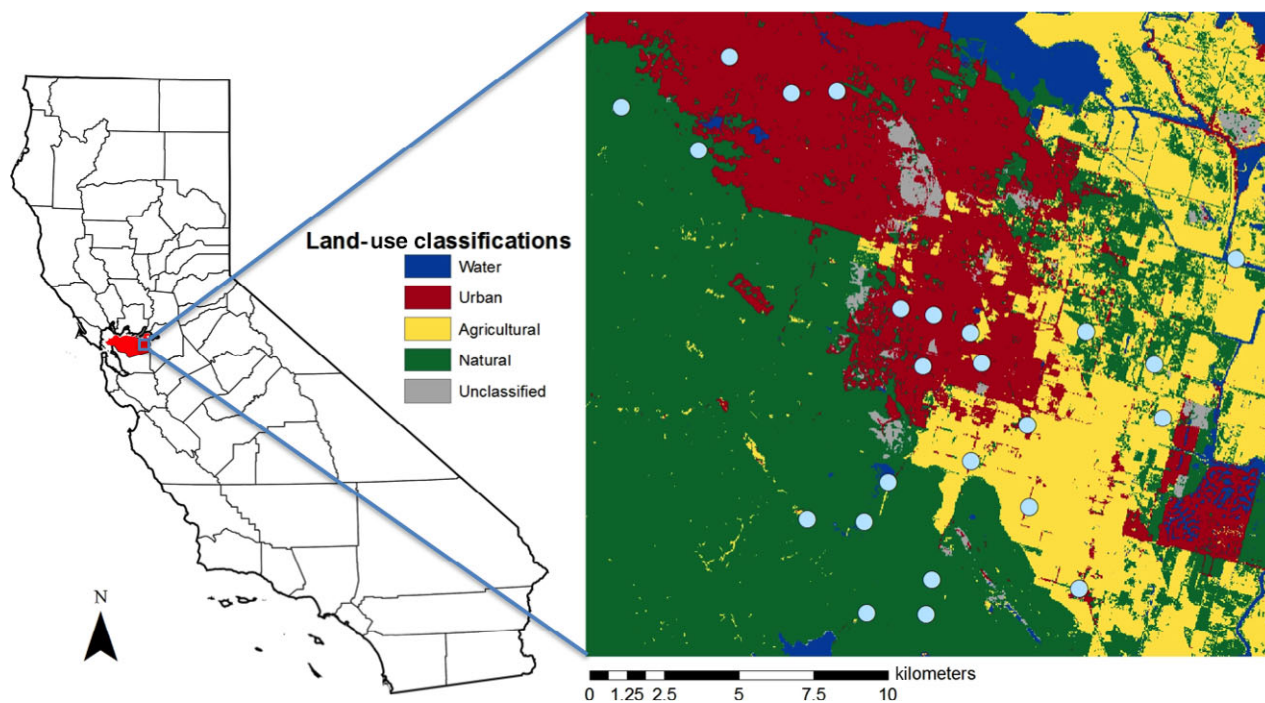
Fig. 1 Map of the study region in east Contra Costa County, CA. Based on LANDSAT classification, yellow represents agricultural land use, red represents urban land use, and green represents natural areas. Light blue dots are site locations in July 2011. Sites shifted slightly as necessary between collecting periods.

protected from development within this region by regional and state parks as well as the local water district's watershed. This undeveloped (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 (Guise, 2011). A housing boom in the 1990s led to massive residential growth in the area. The city of Brentwood has grown from <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).

Using NOAA's 2006 Pacific Coast Land Cover data set (developed using 30 meter resolution Landsat Thematic Mapper and Landsat Enhanced thematic Mapper satellite imagery, USGS Products), 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 classified each site based on the dominant land-use type within its 500 m buffer. In 2010, we had 18 sites, with six each classified as types 'urban', 'agricultural', and 'natural.' In 2011 and 2012, we increased to have a total of 24 sites, with eight of each land-use classification. Sites were selected to be at least one km away from all others, based on assumed maximum bee foraging ranges (Gathmann & Tscharntke, 2002). Although certain bee species have been recorded foraging over a kilometer (Zurbuchen *et al.*, 2010), most bees have nesting and foraging habitat within a few hundred meters of each other (Gathmann & Tscharntke, 2002; Greenleaf *et al.*, 2007; Zurbuchen *et al.*, 2010).

At each site, we designed a standardized pan-trapping transect of 15 bowls spaced five meters apart in alternating colors of fluorescent blue, white, and fluorescent yellow following a modified version of established protocols for pan-trapping bees (Lebuhn *et al.*, 2003). Bowls were filled to the brim with soapy water (0.5 tablespoon of Blue Dawn dishwasher detergent diluted in one gallon of water). In 2010, transects were set up during peak bee flying hours for the four-hour period between 10:30 and 14:30 (± 30 min), with four sites sampled per day, and all sites sampled on consecutive days. These 2010 transects were sampled at two collecting periods: once in the early summer and once in the late summer. In 2011 and 2012, transects were left out for a 24-h period (although bees fly for only a fraction of the time, i.e. generally for 6–8 h, the warmest part of the day), so that more sites could be sampled simultaneously and therefore, 24 sites could be sampled during each collecting period. All 24 sites were sampled within 4 days of each other, during four collecting periods: early spring, late spring, early summer, and late summer. There were a total of 228 collecting events (six sites of each land-use types sampled twice in 2010, eight sites of each land-use type sampled four times each in 2011 and 2012). Long-term sampling methods such as this have not been found to affect bee community structure (Gezon *et al.*, 2015).

The goal of collection was to sample the bee community that was flying through the landscape searching for resources. For this reason, the human-altered sites were deliberately selected so as not to be adjacent to any mass-flowering plants of agricultural crops or gardens to reduce potential pan-trapping biases of bees actively foraging on immediately local resources (Cane *et al.*, 2000). 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 weedy flower margins in urban and agricultural landscapes generally had equivalent flowering levels as those in the natural areas, making the adjacent floral resources similar, allowing the floral availability on a landscape scale to be the primary differentiating factor.

Bee specimens were identified to species (or morpho-species for bees in the genera *Nomada* and *Sphecodes*). The only exception was for bees of the genus *Lasioglossum*, which due to their overwhelming abundance combined with difficulty of identification, were identified to the genus level. The vast majority of *Lasioglossum* collected were primitively social generalist species of the subgenera *Dialictus* and *Evylaeus*. Voucher specimens are deposited at the Essig Museum of Entomology at the University of California, Berkeley.

Community metric analyses

To explore whether land-use types have an effect on the within-year phenology of the bee community, we asked whether aggregate bee abundance, richness (both rarified and non-rarified), and evenness (here defined as the E_{var} metric developed and described in Smith & Wilson, 1996) varied differently through time based on land-use types. To test this, we used generalized linear mixed models with the community-level metrics as response variables, and land-use type, day of the year, and their interaction as explanatory variables. We did not expect the relationship between day of the year and the community-level metrics to necessarily be linear so we also included day of the year as a quadratic term. A significant interaction between the day of the year terms and land-use type would indicate the bee community phenology differed between the different land-use types. To account for inter-annual variability and differences in collecting methods between years, we included year as a random effect. To account for sampling the same sites multiple times, we also included site as a random effect. Day of year was normalized on a scale of 0 to 1 from the first collecting date to the last across the entire dataset and then scaled. We assumed Gaussian error for the model with community evenness as a response variable, Poisson error for bee richness, and negative binomial error for aggregate abundance. All analyses were performed in R 3.1.2 (R Development Core Team, 2014). Mixed effects models were analyzed using the R package *lme4* (Bates *et al.*, 2015).

Community composition analyses

Shifts in phenological patterns could be due to a combination of changes in the activity of individual species or to

differences in the composition of communities. To test the hypothesis that unique patterns of the bee community phenology between land-use types could be due to differences in community composition, we compared the bee communities in each land-use type during the four different collecting periods (early spring, late spring, early summer, and late summer). For each collecting period, we used PERMANOVA (Permutational Multivariate Analysis of Variance; Anderson, 2001) tests with a dissimilarity estimator that incorporates species abundances while also accounting for unobserved species (Chao *et al.*, 2005). This analysis was performed using the *adonis* function in R package *vegan* (Okansen *et al.*, 2015).

Results

We collected and identified 21 874 specimens to 91 bee species groups. 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 (Fig. S1). The community varied greatly in abundance with 13 singletons, 11 doubletons, and 33 species represented by ten or more specimens. *Lasioglossum* species made up 46.94% of all collected specimens. The other most common species, *Halictus tripartitus*, *Eucera actuosa*, *Halictus ligatus*, *Osmia nemoris*, *Agapostemon texanus*, *Melissodes lupina*, *Apis mellifera* [introduced species], *Ceratina nanula*, and *Melissodes stearnsi*, had 150 or more collected specimens.

One-third of the 33 most commonly represented species (represented by 10 or more specimens) were not collected in each of the land-use types. Three were found almost exclusively in natural sites (*Anthophorula chionura*, *Eucera lunata*, and *Ceratina sequoiae*), while seven were almost exclusively collected in human-altered sites (*Peponapis pruinosa*, *Andrena chlorogaster*, *Megachile rotundata* [introduced species], *Andrena piperi*, *Triepeolus melanurius*, *Ashmeadiella aridula astragali*, and *Ceratina dallatorreana* [introduced species]). *Andrena cuneilabris* was found in agricultural and natural sites, but never in urban sites.

Community metrics

Land-use type had strong effects on the temporal dynamics of the bee community (Fig. 2 and Fig. S2). The aggregate bee abundance had a significantly higher peak in natural areas (compare the intercepts of Eqn 1–3 in Table 1, Fig. 2a) and occurred earlier in the season (the coefficient for day of the year is negative in natural areas indicating the curve peaks before the mean day of the year), whereas the peak of urban areas was in the middle of the season and the peak of agricultural was in the latter half of the season (Eqn 1–3 in Table 1, Fig. 2a). The curvature of the relationship between abundance and day of the year was also significantly steeper in natural areas (the coefficients for the quadratic day of the year term for natural areas are

Table 1 Coefficients of GLMM models. Each equation models the curvature of the pattern with three terms: the intercept (first term in the equation), when during the season there is a slope reversal (DAY, earlier in the season has a negative coefficient, later in the season has a positive coefficient), and the steepness of the slope (DAY^2, concave curves have a negative coefficient, convex curves have a positive coefficient, values closer to zero indicate a flatter curve). If a term was not found to be significantly different from zero, it is not included in the equation. The coefficient is listed with the standard error in parentheses beside it. For urban and agricultural equations, if a term was significantly different from natural ($P < 0.05$), it is highlighted in bold. These models were built using the bee data from all 228 collecting events (six sites of each land use types sampled twice [in the early and late summer in 2010], eight sites of each land use type sampled four times each [in the early spring, late spring, early summer, and late summer] in 2011 and 2012). For species richness, because the rarified values did not cause any significant changes in the results, we decided to present the nonrarified values here for simplicity. Raw data for the figures and rarified richness data can be found in the supplementary section

Abundance		
Eqn 1	Natural	$5.161\ (0.257) + -0.341\ (0.088)\ \text{DAY} + -0.687\ (0.109)\ \text{DAY}^2$
Eqn 2	Urban	**4.488 (0.260)** + **−0.367 (0.088) DAY^2**
Eqn 3	Agricultural	**4.511 (0.256)** + **0.297 (0.089) DAY** + **−0.334 (0.111) DAY^2**
Richness		
Eqn 4	Natural	$2.043\ (0.097) + -0.061\ (0.049)\ \text{DAY} + -0.128\ (0.053)\ \text{DAY}^2$
Eqn 5	Urban	**1.581 (0.108)**
Eqn 6	Agricultural	**1.720 (0.099)** + **0.175 (0.056) DAY** + **−0.160 (0.062) DAY^2**
Evenness		
Eqn 7	Natural	$0.327\ (0.045) + 0.139\ (0.026)\ \text{DAY}^2$
Eqn 8	Urban	$0.392\ (0.046) + 0.097\ (0.025)\ \text{DAY}^2$
Eqn 9	Agricultural	**0.548 (0.043)** + **−0.113 (0.024) DAY**
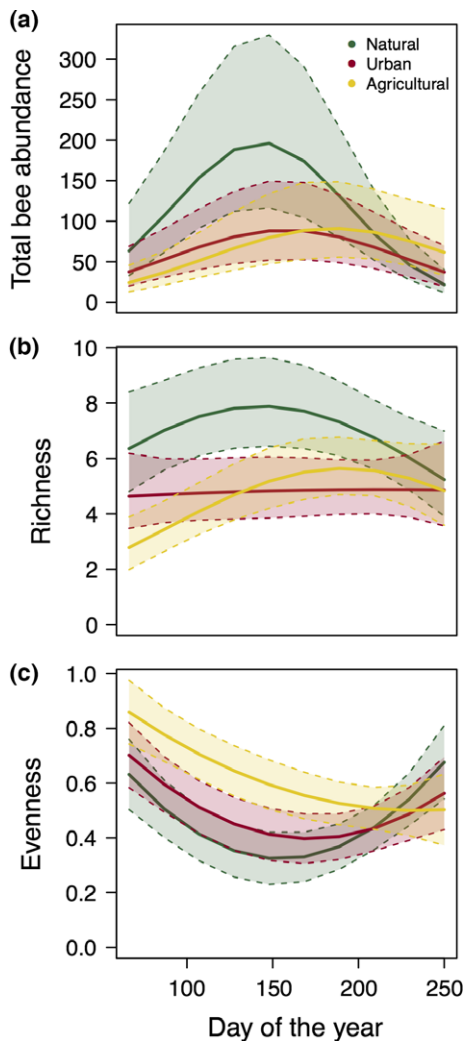
Fig. 2 Plots for community metrics as a function of land-use type and collecting ordinal day. This figure explores how land-use types vary on the within-year phenology of the bee community, based on aggregate bee abundance (a), richness (b), and evenness (c). For species richness, because the rarified values did not cause any significant changes in the results, we present only the nonrarified values here for simplicity. Evenness was calculated using E_{var}, the recommended evenness metric of Smith and Wilson (1996). Raw data of this figure and rarified richness data can be found in the supplementary section. In analyses, day of year is normalized on a scale from 0 to 1 which is reflected in start and end days of ordinal days in graph. The solid line is the mean, and the shaded area is the 95% confidence interval.

more negative than in agriculture and urban areas, Eqn 1–3 in Table 1, Fig. 2a).

Nonrarified and rarified species richness exhibited similar patterns, so for simplicity, here we use the nonrarified values when referring to species richness (rarified species richness data available in Fig. S3). Like abundance, peak richness was significantly higher in natural areas than in urban or agricultural areas and occurred earlier in the season (Eqn 4–6 in Table 1, Fig. 2b). Species richness in urban areas was constant across the season (there was no support for including a relationship with richness and day of the year, Eqn 5 in Table 1, Fig. 2b), and species richness in agricultural areas peaked in the latter half of the season (Eqn 6 in Table 1, Fig. 2b).

Bee evenness was similar for natural and urban land-use types, and slightly different for agricultural (Eqn 7–9 in Table 1, Fig. 2c). In natural and urban areas, evenness was highest at the beginning and end of the season (Eqn 7 & 8 in Table 1, Fig. 2c). In contrast, evenness was highest during the early season of agricultural areas, but steadily declined over the course of the season. (Eqn 9 in Table 1, Fig. 2c).

Community composition

The bee community was significantly different ($P < 0.001$, Fig. 3) among land-use types during all collecting periods: early spring ($F_{2,41} = 3.930$, $R^2 = 0.161$), late spring ($F_{2,45} = 16.542$, $R^2 = 0.424$), early summer ($F_{2,61} = 5.752$, $R^2 = 0.159$), and late summer ($F_{2,67} = 6.874$, $R^2 = 0.170$).

Discussion

We found that the bee communities in human-altered landscapes experienced different phenological patterns than the neighboring less modified areas. Natural areas had the largest pulse of overall abundance and species richness in the bee community in the springtime, dropping off significantly by the end of the season when bee abundance and species richness in agricultural areas were peaking. Conversely, peak bee abundance in urban areas was directly in the middle of the season and species richness of urban areas remained relatively constant throughout the year. Despite these seasonal differences of abundance and richness, the patterns of evenness of the bee communities across sites were similar between land-use types, indicating that the evenness of a community is robust to land-use change. We found bee community composition to vary between land-use types, but whether these differences drive the phenological patterns of abundance and richness, or the community composition is influenced by the phenological differences of the landscape remains unclear. While ecologists have used time as an important variable in many different systems, only recently have the effects of temporal variation been considered within urban contexts (Ramalho & Hobbs, 2012).
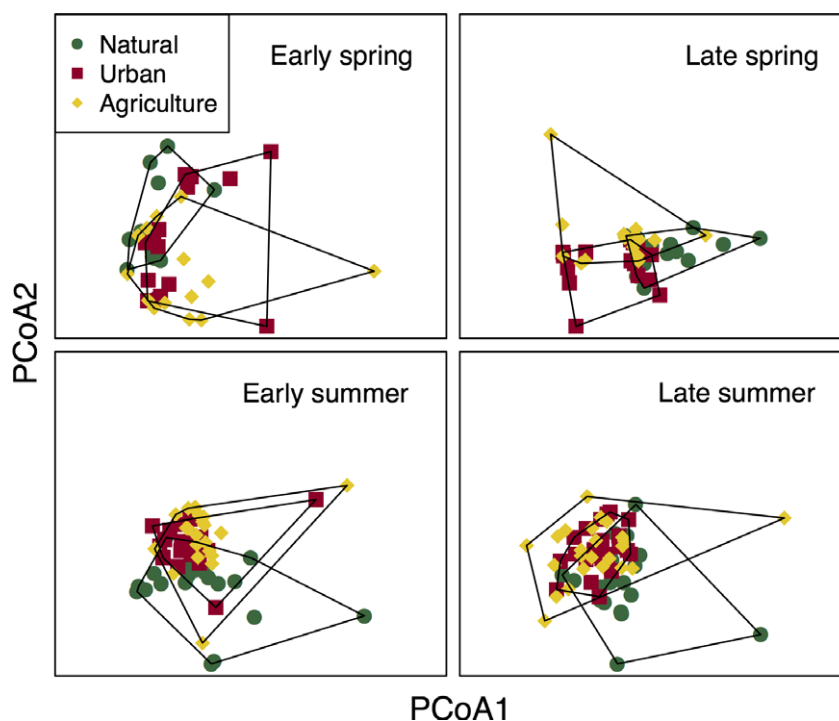
Fig. 3 The dissimilarity of communities during each collecting period in multivariate space using a principal coordinate analysis. The axes represent the first two principal coordinates. The PERMANOVA (Permutational Multivariate Analysis of Variance; Anderson, 2001) tests showed the bee community to be significantly different ($P < 0.001$, Fig. 3) during all collecting periods: early spring ($F_{2,41} = 3.930$, $R^2 = 0.161$), late spring ($F_{2,45} = 16.542$, $R^2 = 0.424$), early summer ($F_{2,61} = 5.752$, $R^2 = 0.159$), and late summer ($F_{2,67} = 6.874$, $R^2 = 0.170$).

We propose the timing of floral resource availability as a driver of local phenological shifts in different landscape types. Green vegetation in California grasslands is largely driven by temperature and rainfall, resulting in a large burst of blooms in the spring and very few floral resources at the end of the summer (Chiariello, 1989). In urban areas, the flowering season can be extended through water inputs and landscaping choices in residential, public, and commercial zones (Gill *et al.*, 2007; Satterfield *et al.*, 2015), leading to the relative stability of the bee community. In contrast, irrigation of late blooming mass-flowering crops in agricultural fields (e.g. sunflower, squash, canola) explains the shifted peak in phenology of bees in the agricultural areas. While vegetation is not a perfect surrogate for floral availability, remote sensing of the region captured similar temporal patterns of the vegetation in human-altered landscapes being out of synchronization with the phenology in the neighboring natural landscapes (Leong & Roderick, 2015). Such findings offer further supporting evidence that different land-use types offer the floral resource-dependent community unique temporal opportunities.

The extended flowering season in urban areas could explain why the species richness of the bee community remains relatively consistent from the middle to the extreme ends of the season in urban sites. Urban areas offer resources at the earliest and latest portions of the season when there is little floral availability in the other land-use types. There are several possible biological explanations of this phenomenon. Because resources are available earlier in the season, bees could be breaking diapause early to take advantage of these resources. Bees may also be able to have an additional generation due to resources available later in the season. Other consequences include the phenologies of species in these landscapes spreading out over the season, or bees flying further distances than assumed to track resources between land use types (Gathmann & Tscharntke, 2002; Greenleaf *et al.*, 2007; Zurbuchen *et al.*, 2010).

The phenologies of two frequently collected species further support the important role of changing floral resources, by peaking in abundance in urban landscapes at the extreme ends of the season: *Eucera actuosa*, a ubiquitous spring bee, was collected most frequently in urban sites in the early spring, whereas in natural sites, its abundance peaked in late spring. Conversely, *Melissodes lupina*, a summer bee, was collected most frequently in the early summer for natural areas, but was collected more often in the late summer in urban landscapes. Urban areas adjacent to natural areas therefore may actually help support bees to experience longer

flight seasons when resources are most limited. In our study, collecting periods occurred every two months – it is likely that finer-scale temporal collecting would have captured this pattern for more species.

Understanding how the dynamics of bee populations are altered by land-use change is critical because bees provide essential pollination services to managed and wild plant populations (Ollerton et al., 2011). The value of pollination in agriculture is estimated at $200 billion worldwide (Gallai et al., 2009), 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 (Eilers et al., 2011). In urban areas specifically, there has been growing interest in urban agriculture to ensure food security and access to healthy food. For example, the estimated economic value of urban fruit trees (many of which require animal pollination) in the one city of San Jose, California, is worth $10 million annually (Kollin, 1991). However, honey bee populations and many bumble bee species are declining worldwide (Allen-Wardell et al., 1998; Williams & Osborne, 2009; Vanbergen, 2013), while many other bee species have not been closely documented sufficiently to determine their status (Winfree et al., 2011; Irwin et al., 2013; Carper et al., 2014).

Resource availability is different in urban and agricultural areas than in less modified areas, and these human-dominated landscapes are supporting bee communities with novel patterns of activity. Although not explored here, resource quality will also strongly vary due to differences in plant species composition between land-use types. Management of pollinator communities requires an understanding of the dynamics of these systems and how to best target restoration and conservation work to meet the unique needs of each landscape (Menz et al., 2011). For example, knowing that the peaks in bee community activity occur during different times of the year in different land-use types can help prioritize efforts. It is important to recognize that restoration goals may have different desired outcomes, for example, to support the largest pollinator community, or, alternately, to replicate the dynamics of the natural environment within the human-altered landscapes. Knowledge of when resources are most limiting is necessary in planning for either outcome. In agricultural areas, restoration techniques such as enhancing floral resources may benefit from a focus on providing flowers that bloom early in the season. In contrast, the floral and subsequently the bee community in urban areas are relatively stable through time, so efforts can focus on enhancing bloom availability year round. Supporting other animal populations in the different land-use types will likely involve similar considerations if the temporal dynamics of these populations are also shifted.

As shifts of land use to agricultural and urban purposes continue to be the largest and fastest growing forms of land-use conversion (Barnosky et al., 2012), it is critical to understand the impacts of these landscape-scale changes on species' temporal and spatial distributions in order to predict and plan for ecological impacts. While the implications of the shifts in the phenology of bee communities in human modified areas on the resilience and productivity of these populations need further exploration, the temporal dynamics of communities in anthropogenic landscapes must be considered.

References

Allen-Wardell G, Bernhardt P, Bitner R et al. (1998) The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. Conservation Biology, 12, 8–17.

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecology, 26, 32–46.

Ash C, Jasny BR, Roberts L, Stone R, Sugden AM (2008) Reimagining cities. Science, 319, 739.

Baldock KCR, Goddard MA, Hicks DM et al. (2015) Where is the UK's pollinator biodiversity? The importance of urban areas for flower-visiting insects. Proceedings of the Royal Society B-Biological Sciences, 282, 20142849.

Barnosky AD, Hadly EA, Bascompte J et al. (2012) Approaching a state shift in Earth's biosphere. Nature, 486, 52–58.

Bartomeus I, Ascher JS, Wagner D, Danforth BN, Colla S, Kornbluth S, Winfree R (2011) Climate-associated phenological advances in bee pollinators and bee-pollinated plants. Proceedings of the National Academy of Sciences, 108, 20645–20649.

Bates D, Maechler M, Bolker B, Walker S (2015) LME4: Linear Mixed-Effects Models Using Eigen and S4. R package version 1.1-8.

Boone CG, Cook E, Hall SJ et al. (2012) A comparative gradient approach as a tool for understanding and managing urban ecosystems. Urban Ecosystems, 15, 795–807.

Both C, Van Asch M, Bijlsma RG, Van Den Burg AB, Visser ME (2009) Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? Journal of Animal Ecology, 78, 73–83.

Burkle LA, Marlin JC, Knight TM (2013) Plant-pollinator interactions over 120 Years: loss of species, co-occurrence, and function. Science, 339, 1611–1615.

Cane JK, Minckley RL, Kervin LJ (2000) Sampling bees (Hymenoptera: Apiformes) for pollinator community studies: pitfalls of pan-trapping. Journal of the Kansas Entomological Society, 73, 225–231.

Carper AL, Adler LS, Warren PS, Irwin RE (2014) Effects of suburbanization on forest bee communities. Environmental Entomology, 43, 253–262.

Chao A, Chazdon RL, Colwell RK, Shen TJ (2005) A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecology Letters, 8, 148–159.

Chiariello NR (1989) Phenology of California Grasslands. In: *Grassland Structure and Function* (eds Huenneke LF, Mooney H), pp. 47–58. Springer, The Netherlands..

Driscoll DA, Banks SC, Barton PS, Lindenmayer DB, Smith AL (2013) Conceptual domain of the matrix in fragmented landscapes. *Trends in Ecology & Evolution*, **28**, 605–613.

Eilers EJ, Kremen C, Greenleaf SS, Garber AK, Klein A-M (2011) Contribution of pollinator-mediated crops to nutrients in the human food supply. *PLoS One*, **6**, e21363.

Gallai N, Salles JM, Settele J, Vaissiere BE (2009) Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecological Economics*, **68**, 810–821.

Gathmann A, Tscharntke T (2002) Foraging ranges of solitary bees. *Journal of Animal Ecology*, **71**, 757–764.

Gezon ZJ, Wyman ES, Ascher SA, Inouye DW, Irwin RE (2015) The effect of repeated, lethal sampling on wild bee abundance and diversity. *Methods in Ecology and Evolution*, **6**, 1044–1054.

Gill SE, Handley JF, Ennos AR, Pauleit S (2007) Adapting cities for climate change: the role of the green infrastructure. *Built Environment*, **33**, 115–133.

Greenleaf SS, Williams NM, Winfree R, Kremen C (2007) Bee foraging ranges and their relationship to body size. *Oecologia*, **153**, 589–596.

Grimm NB, Faeth SH, Golubiewski NE, Redman CL (2008) Global change and the ecology of cities. *Science*, **319**, 756–760.

Groom MJ, Meffe GK, Carroll CR (2006) *Principles of Conservation Biology*, 3rd edn. Sinauer, Sunderland, Massachusetts.

Guise V (2011) Annual Crop and Livestock Report for Contra Costa County. Concord, CA, Director of Agriculture.

Hannon LE, Sisk TD (2009) Hedgerows in an agri-natural landscape: potential habitat value for native bees. *Biological Conservation*, **142**, 2140–2154.

Hart M, Sailor D (2009) Quantifying the influence of land-use and surface characteristics on spatial variability in the urban heat island. *Theoretical and Applied Climatology*, **95**, 397–406.

Irwin R, Warren P, Carper A, Adler L (2013) Plant–animal interactions in suburban environments: implications for floral evolution. *Oecologia*, **174**, 1–13.

Kollin C (1991) On Balance: Weighing the Benefits and Costs of Urban Trees. (ed Station USFSNFE), Syracuse, NY.

Kudo G, Ida TY (2013) Early onset of spring increases the phenological mismatch between plants and pollinators. *Ecology*, **94**, 2311–2320.

Lebuhn G, Griswold T, Minckley R *et al.* (2003) A Standardized Method of Monitoring Bee Populations—The Bee Inventory (BI) Plot. Available at: http://online.sfsu.edu/beeplot/pdfs/Bee%20Plot%202003.pdf. Last accessed 22 APRIL 2015.

Leong M, Roderick GK (2015) Remote sensing captures varying temporal patterns of vegetation between human-altered and natural landscapes. *PeerJ*, **3**, e1141.

Leong M, Kremen C, Roderick GK (2014) Pollinator Interactions with Yellow Starthistle (*Centaurea solstitialis*) across Urban, Agricultural, and Natural Landscapes. *PLoS One*, **9**, e86357.

Mandelik Y, Winfree R, Neeson T, Kremen C (2012) Complementary habitat use by wild bees in agro-natural landscapes. *Ecological Applications*, **22**, 1535–1546.

Mckinney ML (2008) Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosystems*, **11**, 161–176.

Menz MH, Philips RD, Winfree R, Kremen C, Aizen MS, Johnson SD, Dixon KW (2011) Reconnecting plants and pollinators: challenges in the restoration of pollination mutualisms. *Trends in Plant Science*, **16**, 4–12.

Mimet A, Pellissier V, Quenol H, Aguejdad R, Dubreuil V, Roze F (2009) Urbanisation induces early flowering: evidence from *Platanus acerifolia* and *Prunus cerasus*. *International Journal of Biometeorology*, **53**, 287–298.

Okansen J, Blanchet FG, Kindt R *et al.* (2015) Vegan: Community Ecology Package. R package version 2.3-0.

Oke TR (1973) City size and the urban heat island. *Atmospheric Environment*, **7**, 769–779.

Ollerton J, Winfree R, Tarrant S (2011) How many flowering plants are pollinated by animals? *Oikos*, **120**, 321–326.

Post E, Pedersen C, Wilmers CC, Forchhammer MC (2008) Warming, plant phenology, and the spatial dimension of trophic mismatch for large herbivores. *Proceedings of the Royal Society B-Biological Sciences*, **275**, 2005–2013.

R Development Core Team (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Ramalho C, Hobbs R (2012) Time for a change: dynamic urban ecology. *Trends in Ecology and Evolution*, **27**, 179–188.

Riedinger V, Renner M, Rundlöf M, Steffan-Dewenter I, Holzschuh A (2014) Early mass-flowering crops mitigate pollinator dilution in late-flowering crops. *Landscape Ecology*, **29**, 425–435.

Roetzer T, Wittenzeller M, Haeckel H, Nekovar J (2000) Phenology in central Europe–differences and trends of spring phenophases in urban and rural areas. *International Journal of Biometeorology*, **44**, 60–66.

Rundlöf M, Persson AS, Smith HG, Bommarco R (2014) Late-season mass-flowering red clover increases bumble bee queen and male densities. *Biological Conservation*, **172**, 138–145.

Satterfield DA, Maerz JC, Altizer S (2015) Loss of migratory behaviour increases infection risk for a butterfly host. *Proceedings of the Royal Society B-Biological Sciences*, **282**, 20141734.

Shochat E, Lerman S, Anderies J, Warren P, Faeth S, Nilon C (2010) Invasion, competition, and biodiversity loss in urban ecosystems. *BioScience*, **60**, 199–208.

Smith B, Wilson JB (1996) A consumer's guide to evenness indices. *Oikos*, **76**, 70–82.

Thompson JD (2010) Flowering phenology, fruiting success and progressive deterioration of pollination in an early-flowering geophyte. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **365**, 3187–3199.

Tryjanowski P, Sparks TH, Kuźniak S, Czechowski P, Jerzak L (2013) Bird migration advances more strongly in urban environments. *PLoS One*, **8**, e63482.

Vanbergen AJ, Insect Pollinators Initiative (2013) Threats to an ecosystem service: pressures on pollinators. *Frontiers in Ecology and the Environment*, **11**, 251–259.

Visser ME (2008) Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proceedings of the Royal Society B-Biological Sciences*, **275**, 649–659.

Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of earth's ecosystems. *Science*, **277**, 494–499.

Williams PH, Osborne JL (2009) Bumblebee vulnerability and conservation worldwide. *Apidologie*, **40**, 367–387.

Winfree R, Bartomeus I, Cariveau DP (2011) Native pollinators in anthropogenic habitats. *Annual Review of Ecology, Evolution, and Systematics*, **42**, 1–22.

Wojcik VA, Frankie GW, Thorp RW, Hernandez JL (2008) Seasonality in bees and their floral resource plants at a constructed urban bee habitat in Berkeley, California. *Journal of the Kansas Entomological Society*, **81**, 15–28.

Zurbuchen A, Landert L, Klaiber J, Müller A, Hein S, Dorn S (2010) Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. *Biological Conservation*, **143**, 669–676.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Species accumulation curve. With 228 collecting events, the rarefaction curve flattens (shown with 95% confidence interval), with a Chao estimation of the species pool of 110.04 (SE = 11.54), suggesting that the sampling was sufficiently thorough.

Fig. S2. Raw data of plots for community metrics as a function of land use change and collecting ordinal day. Figure 2 is expanded here to view the raw data points by land use type. We overlay all points on the original Fig. 2, where the solid line is the mean and the shaded area is the 95% confidence interval.

Fig. S3. Rarified richness. Replicating the main analyses of species richness with rarified richness based on Chao estimates, shows similar, though slightly exaggerated patterns as those with species richness. All significant terms are the same relationships as found with non-rarified species richness. The equations that correspond to the figure are as follows (terms that are not significantly different from zero are not included, terms for urban and agricultural that are significantly different from natural are in bold, and standard errors are included in parentheses next to the term): Natural = 2.436 (0.090) + −0.123 (0.039) DAY + −0.091 (0.041) DAY^2; Urban = **1.920 (0.101)**; Agricultural = **2.110 (0.089)** + **0.206 (0.047) DAY** + −0.176 (0.051) DAY^2.