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Honey bee success predicted by landscape composition in Ohio, USA

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Foraging honey bees (*Apis mellifera* L.) routinely travel as far as several kilometers from their hive in the process of collecting nectar and pollen from floral patches within the surrounding landscape. Since the availability of floral resources at the landscape scale is a function of landscape composition, apiculturists have long recognized that landscape composition is a critical determinant of honey bee colony success. Nevertheless, we are aware of no published studies that present quantitative data relating colony success metrics to local landscape composition. We employed a beekeeper survey in conjunction with GIS-based landscape analysis to model colony success as a function of landscape composition in the State of Ohio, USA, a region characterized by intensive cropland, urban development, deciduous forest, and grassland. We found that colony food accumulation and wax production were positively related to cropland and negatively related to forest and grassland, a pattern that may be driven by the abundance of dandelion and clovers in agricultural areas compared to forest or mature grassland. Colony food accumulation was also negatively correlated with the ratio of urban:crop area in sites dominated by urban and agricultural land cover, which does not support the popular opinion that the urban environment is more favorable to honey bees than cropland.

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Honey bee success predicted by landscape composition in Ohio, USA.

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Introduction

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Honey bees (*Apis mellifera*, L.) exist in large, eusocial colonies that require massive and sustained inputs of floral nectar and pollen. They meet this demand by foraging at an extremely large spatial scale and with rapid responsiveness to changes in the surrounding floral community (Visscher & Seeley, 1982; Seeley, 1995). Depending on local floral availability, colonies may routinely forage over an area of more than 100 km2 (Seeley, 1995), and much larger ranges have been reported under extreme conditions (Eckert, 1931; Beekman & Ratnieks, 2001).

Because honey bee foraging is a decidedly landscape-scale process, one should expect landscape composition to interact meaningfully with colony nutrition and overall colony success. While the plausibility of such a relationship is widely acknowledged (Steffan-Dewenter & Kuhn, 2003; Naug, 2009; vanEngelsdorp & Meixner, 2010; Härtel & Steffan-Dewenter, 2014), and the importance of apiary location is axiomatic among practicing beekeepers, we are aware of no published studies that quantitatively measure colony success in response to local landscape variables. As rapid landscape conversion continues as a global phenomenon, and beekeepers in many regions continue to suffer unsustainable losses, the task of refining and expanding our knowledge of honey bee landscape ecology takes on obvious urgency.

Several studies have indirectly explored the relationship between landscape and colony success by analyzing the spatial information encoded in the honey bee dance language (von Frisch, 1967). Waddington et al. (1994) found that colonies located in two suburban landscapes tended to forage over a smaller area and with a less clumped distribution than a previously studied colony located in a temperate deciduous forest (Visscher and Seeley, 1982), suggesting that suburban landscapes provide richer and more evenly distributed resource patches. Conversely, Beekman and Ratnieks (2001) observed remarkably long-distance foraging under conditions of apparently scarce local resources in a suburban landscape and highly rewarding resources in outlying seminatural heather moors. In agricultural landscapes, honey bee foraging patterns suggest that pollen sources can be scarcer and floral patches less spatially and temporally variable in highly simplified cropping systems compared to more structurally complex habitats (Steffan-Dewenter & Kuhn, 2003), while conservation management within farmlands can increase the availability of bee-attractive flora (Couvillon, Schürch & Ratnieks, 2014).

Among non-peer-reviewed sources, there is a widely circulated opinion that honey bee success is favored by urban/suburban landscapes, especially in comparison to cropland (Graham, 1992; New York Times, 2008; Wilson-Rich, 2012). These claims remain unsubstantiated but plausible given the ostensibly positive effects of suburban land use suggested by Waddington et al. (1994) and the more direct evidence supporting the favorability of suburban land use for bumble bees (Hymenoptera: *Bombus,* Latreille) living in predominantly agricultural areas (Goulson et al., 2002; 2010).

Here, we present a quantitative study of honey bee colony success in relation to landscape composition in the State of Ohio, USA, a region characterized by a mixture of intensive cropland, deciduous forest, grassland, and urban development. Using a citizen-science survey, we investigate the relationship between colony success and the landscape as a whole, accounting for all major land cover types and also for the potential influence of hive management variables that vary between beekeepers. Then, we specifically evaluate the putative favorability of urban landscapes relative to agricultural ones using a subset of sites dominated by crop and/or urban development.

Materials and Methods

Survey Design. In 2012 and 2013, we used a survey-based, citizen-science approach to measure the productivity of honey bee colonies in the state of Ohio, USA. All participants were beekeepers whose hives were registered with the Ohio Department of Agriculture and who volunteered to participate in our study. Our survey was conducted with written exemption from

IRB review by the Ohio State University Office of Responsible Research Practices (Protocol # 2012E0136 and # 2013E0012).

In order to standardize the initial strength of the colonies in our study (hereafter “study colonies”) and minimize the influence of parasites and pathogens, we restricted our study to colonies that had been started from artificial swarms, known as “package bees”, in the spring of each study year. Honey bee packages are created by combining a standard quantity of worker bees (usually 1.36 kg) with a newly mated queen. The initial strength of colonies started from package bees is, therefore, less variable than that of over-wintered colonies. Moreover, because they are sold without comb or brood, they tend to have reduced parasite and pathogen loads.

Data for each study colony were gathered using a two-part survey consisting of spring and fall components (hereafter “spring survey” and “fall survey”). The spring survey was made available beginning in early March, and participants were instructed to complete the survey immediately after installing their honey bee packages. In the spring survey, we gathered the geographic location of each study colony and the years of experience of each participating beekeeper (see S1 for full spring survey questionnaire). The fall survey was made available in mid-September and completed by mid-October. To complete the fall survey, each participant performed a frame-by-frame hive inspection and reported the number of frames in the study hive belonging to the following categories: (1) more than half honey/nectar, (2) more than half pollen, (3) more than half brood, (4) more than half empty wax comb, (5) more than half bare foundation (no wax comb). Participants also reported the quantity of sugar syrup that had been given to their hives as supplemental feeding, a common beekeeping practice that could be affect colony success. See S2 for full fall survey questionnaire.

Survey Processing. Each beekeeper was instructed to submit data for only one study hive at one apiary site. The data quality of all surveys was carefully vetted prior to analysis, and surveys missing critical data or having irreconcilable inconsistencies were discarded. Fall surveys reporting hives that had died since spring installation were also discarded. The final numbers of surveys included in analyses for 2012 and 2013 were 32 and 18, respectively; these were selected from a pre-processing total of 55 surveys in 2012 and 33 in 2013.

From our survey data, we derived four metrics to represent colony success: *net food accumulation*, *net wax production*, *adult population*, and *brood population*. For consistency, all metrics were recorded in units of standard deep frames.

Net food accumulation:

$$Food = H + H_{harv} - H_{add} + P$$

where H = honey/nectar frames in hive at time of inspection, H_{harv} = honey frames harvested prior to inspection, H_{add} = honey frames added to the hive prior to inspection, and P = frames of pollen in hive at time of inspection. This variable will hereafter be abbreviated *Food*.

Net wax production:

$$Wax = H + H_{harv} + P + B + B_{rm} + D - H_{add} + B_{add} + D_{add}$$

where B = brood frames in hive at time of inspection, B_{rm} = brood frames removed prior to inspection, D = drawn but mostly empty frames in hive at time of inspection, B_{add} = brood frames added to the hive prior to inspection, and D_{add} = drawn but mostly empty frames added to hive prior to inspection. This variable will hereafter be abbreviated *Wax*.

Adult population (hereafter, *AdultPop*) was measured as the number of frames “more than half covered” with adult bees at time of inspection. *Brood population* (hereafter, *BroodPop*) was simply the number of “mostly brood” frames reported by the inspecting beekeeper.

We also measured two hive management variables: years of beekeeping experience of the participating beekeeper (*years*) and quantity of sugar syrup fed to the study hive since its installation (*syrup*).

Landscape Analysis. Geographic coordinates for each study hive were determined and mapped using QGIS v. 2.1 (QGIS Development Team, 2014). To encompass a range of spatial scales at which landscape effects on colony success might be seen, we defined the landscape of each hive using six nested buffers having radii of 0.5, 1, 2, 3, 4, and 5 km, respectively. Land cover data for the State of Ohio were obtained from the 2006 dataset provided by the National Land Cover Database (NLCD 2006) (Fry et al., 2011). The NLCD 2006 land cover layer for Ohio is comprised primarily of seven land cover classes: *cultivated crops*, *pasture/hay*, *deciduous forest*, and four levels of urban development (*open space*, *low intensity*, *medium intensity*, *high intensity*). Minor classes, present only at very low abundance, include *evergreen forest*, *mixed forest*, *woody wetland*, *herbaceous wetland*, *grassland/herbaceous*, *shrub/scrub*, *barren land*, and *open water*. To simplify our analysis of landscape composition, we condensed the non-crop land cover classes (ignoring *barren land* and *open water*) into three aggregate classes: Forest (*deciduous* + *evergreen* + *mixed* + *woody wetland* + *shrub/scrub*), Grassland (*pasture/hay* + *grassland/herbaceous* + *herbaceous wetland*), and Urban (*open space* + *low intensity* + *medium intensity* + *high intensity*). The landscape composition of each study site, measured in terms of the total land cover of Crop (*cultivated crop*) and each aggregate class, was determined at each spatial scale using LECOS (Jung, 2013), a QGIS plugin for calculating patch-based landscape metrics. As a measure of overall landscape heterogeneity, we also calculated Simpson's Diversity Index (D) based on the original, non-aggregated land cover classes.

Data Analysis. We first reduced the dimensionality of our landscape data using principal components analysis (PCA) based on the covariance between the variables *Crop*, *Forest*, *Grassland*, and *Urban*. This step was repeated for each spatial scale. For all scales, the first two principal components (*PC 1* and *PC 2*) explained > 96% of total variance.

To model the relationship between landscape composition and colony success, accounting also for the management variables *years* and *syrup*, we conducted model selection using Akaike's Information Criterion corrected for small sample size (AIC_c) (Burnham & Anderson, 2002). Each success metric--*Food*, *Wax*, *AdultPop*, and *BroodPop*--was modeled separately. Fourteen candidate linear models were constructed for each success metric at each spatial scale; these included all combinations of the landscape variables (*PC 1*, *PC 2*, *D*) and the coupled management variables *years* and *syrup*, a year-only model, and an intercept-only model. For each success metric, we present the candidate model having the lowest AICc score at each scale along with any competing models having an AIC_c difference of < 2 (Table 1) (Burnham & Anderson, 2002). We then selected a single best model for each success metric by choosing the model with the lowest AIC_c score across all spatial scales.

To evaluate the prediction that urban land cover favors honey bee success relative to agricultural land cover, we first extracted the subset of our sites for which *Urban* + *Crop* was greater than 50% of total landcover; then, we calculated the ratio of *Urban* : *Crop* for each of these sites, thus representing the relative dominance of *Urban* vs. *Crop* in sites dominated by some combination of the two. To avoid infinite or undefined results for sites having a value of zero for either *Urban* or *Crop*, a constant of 0.001 (i.e. 0.1% land cover) was added to each value. We then set up separate linear regression models for *Food* and *Wax* with the log-transformed ratio of *Urban* : *Crop* as the explanatory variable Only *Food* and *Wax* were analyzed because the results of the PCA described above indicated that only these two success metrics should be expected to respond to landscape variables. We did not use *years* and *syrup* as covariates because previous analysis showed they were not predictive of *Food* or *Wax*. Regression analysis was repeated for each spatial scale.

All analysis was performed in R statistical software (R Core Team, 2014). AIC_c model selection used the package `AICcmodavg` (Mazerolle, 2014).

Results

Landscape analysis. The landscapes surrounding the colonies in our survey represented a broad range of landscape composition in terms of the major land cover classes *Crop*, *Forest*, *Grassland*, and *Urban* (Fig. 1) . Principal components analysis of these four variables yielded two readily interpretable axes that explained greater than 96% of total variance (Fig. 2). *PC 1* was essentially an urban-rural axis, with sites dominated by *Urban* scoring low and sites dominated by combinations of *Crop*, *Forest*, and/or *Grassland* scoring high. *PC 2* partitioned non-urban landscapes into those characterized by *Crop* and those characterized by *Forest* and, to a lesser extent, *Grassland*.

Modeling colony success metrics by landscape principal components. *Food* and *Wax* were best modeled with *PC 2* as the only explanatory variable. Almost all competing models ($\Delta AIC_c < 2$) included *PC 2* alongside other explanatory variables, further supporting the conclusion that *PC 2* was the single most important predictor (Table 1). For *Food*, the optimal spatial scale was a 1 km radius, while *Wax* was best predicted at a 2 km radius. In both cases, the relationship was negative and the linear regression models were statistically significant (*Food*: $p = 0.033$, *Wax*: $p = 0.016$) (Fig. 3). *AdultPop* was best modeled with the coupled management variables *years* and *syrup* as the only explanatory variables. The relationship was positive and the linear regression model was significant ($p = 0.004$), with significant contributions from both *years* ($p = 0.005$) and *syrup* ($p = 0.017$) (Fig. 4). *BroodPop* was best predicted by the intercept-only model, indicating that none of our measured explanatory variables were good predictors of this success metric.

Modeling colony success metrics by *Urban* : *Crop* ratio. We found a significant ($p < 0.05$) negative relationship between *Food* and the log-transformed *Urban* : *Crop* ratio (Fig. 5) at the 1 km ($p = 0.005$) and 2 km ($p = 0.030$) scales. No other success metrics were significantly ($p < 0.05$) related to the *Urban* : *Crop* ratio.

Discussion

The negative responses of *Food* and *Wax* to *PC 2* indicate that food accumulation and wax production increase with surrounding cropland and decrease with forest/grassland. This finding seems to contradict the conventional wisdom that agricultural land conversion threatens honey bee nutrition through the depauperation of floral resources relative to semi-natural environments (De La Rúa et al., 2009), but is consistent with studies that have found honey bees to be notably resilient to natural habitat loss compared to other bee taxa (Ricketts et al., 2008; Winfree et al., 2009). The productivity of honey bees does not depend so much on the presence of undisturbed natural floral communities as it does on the availability of rich resources that can be exploited efficiently by cooperative foraging (Visscher & Seeley, 1982). In Ohio, the largest honey yield is believed to come from non-native clovers (*Trifolium* spp. L.) (Pellett, 1920; Bailey, 1955; Goltz, 1975); these plants grow abundantly along roadsides, in field margins, and in grassy yards, but they are scarce in habitats shaded by forest canopy or dominated by the dense herbaceous vegetation of unmowed grassland. In addition to the clovers, Erickson (Erickson, 1984) observed that, under some conditions, honey bees will forage very productively on soybean (*Glycine max* (L.) Merr.), and corn/soybean rotations comprise the vast majority of Ohio cropland. Dandelion (*Taraxacum officinale* F. H. Wigg.), one of the most important spring flora for honey bees in the Midwest (Jaycox, 1976) during the period of peak wax production, is distributed in much the same pattern as the clovers, thus favoring wax production in cropland over seminatural forest and grassland.

Interestingly, our finding that colony productivity is favored by cropland relative to forest/grassland is strikingly consistent with an anecdotal description of regional honey production in Ohio published nearly forty years ago (Goltz, 1975). In Goltz' account, the areas of "primary" and "secondary" importance for honey production are in the heavily cultivated glacial plains that comprise most of the state, while the forest-dominated Appalachian Plateaus in the southeast are described as only "marginally" productive.

The positive response of *AdultPop* to the management variables *years* and *syrup* is difficult to interpret. In early spring, when new colonies are very small and limited in their foraging ability, it is standard practice to supplement colony nutrition with sugar syrup. All workers produced during the period of spring build-up, though, died long before colonies were inspected in the fall, so any positive effect of the springtime management on *AdultPop* at time of inspection would have to be mediated by factors that allow colonies to increase reproduction later in the year. An alternative interpretation is plausible if we allow that significant feeding may have occurred later in the year. While supplemental feeding is normally concentrated in early spring, some Ohio beekeepers also feed their colonies in mid-late summer, a period of perceived dearth in natural forage. Feeding during the summer dearth period might trigger a population increase that would persist until fall inspection. Our survey did not distinguish between feeding at different times during the season.

By late September and early October, when beekeepers were inspecting their colonies for the fall survey, the bees had likely already begun to reduce brood rearing in preparation for winter (Graham, 1992). This would explain the failure of both landscape and management variables in predicting *BroodPop*.

The negative relationship observed between *Food* and the ratio of *Urban* : *Crop* does not support the popular opinion that urban landscapes favor honey bee success relative to agricultural landscapes. At least in Ohio, the relationship appears to be the opposite, and the fact that *Food* was the only success metric to respond to *Urban* : *Crop* ratio suggests a likely mechanism. The last major nectar and pollen flow in Ohio is usually from goldenrod (*Solidago* spp. L.) (Morse, 1972; D. B. Sponsler, unpublished data), which blooms prolifically from late summer into fall, roughly the same period during which beekeepers in our study were conducting fall hive inspections and filling out the fall survey. At this time of year, honey bees rarely produce additional wax (Lee & Winston, 1985), and brood rearing has begun to slow down in preparation for winter (Graham, 1992), so incoming food is stored rather than being invested in brood or wax production. Goldenrod occurs abundantly in uncultivated fields and conservation strips throughout agricultural landscapes, but it is relatively scarce in developed areas where vegetation is more often subject to mowing and weed control. This is consistent with the anecdotal observation of Burgett et al. (1978) that urban hives tend to have poor late-season honey production, which he attributes to scarcity of late-blooming "weeds", including goldenrod.

We conclude that both landscape composition and colony management contribute to the success of nascent honey bee colonies in our study region. Due to complexities not explored in this study, the prediction of colony success was partitioned such that landscape predicted food accumulation and wax production, while colony management predicted only adult worker population. We find no support for the opinion that honey bees in urban landscapes are more successful than those in cropland. To the contrary, we find that colony food accumulation responds positively to cropland relative to urban land, a pattern that we attribute to the influence of late-season floral availability, particularly goldenrod.

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Table 1(on next page)

AIC_c model selection table

Table 1: Summary of model selection statistics for each colony success metric. Only models with $\Delta\text{AIC}_c < 2$ are presented a competing models. Models within each spatial scale are listed in order of increasing AIC_c value. The best model for each success metric is depicted in bold.

Metric	Radius (km)	Model	Log-likelihood	*K*	*AIC*	*ΔAIC*	*W*	Adjusted r	Coefficients
Food	0.5	PC2	-165.808	3	338.138	0.00	0.233	0.047	-5.9142
"	0.5	PC1 + PC2	-165.060	4	339.008	0.87	0.151	0.055	PC2 = -5.9142, PC1 = 2.5032
"	1	PC2*	**-165.134**	**3**	**336.791**	**0.00**	**0.260**	**0.072**	**-7.3139**
"	1	PC1 + PC2*	-164.175	4	337.240	0.45	0.208	0.088	PC2 = -7.3139, PC1 = 2.9608
"	2	PC2	-165.686	3	337.894	0.00	0.197	0.051	-6.541
"	2	PC1 + PC2	-164.553	4	337.995	0.10	0.187	0.074	PC2 = -6.5409, PC1 = 3.5536
"	2	PC1 + PC2 + D	-163.990	5	339.343	1.45	0.095	0.075	PC2 = -7.529, PC1 = 5.195, D = 7.674
"	2	PC1	-166.464	3	339.450	1.56	0.090	0.021	3.5536
"	3	PC2	-165.871	3	338.265	0.00	0.183	0.044	-6.0981
"	3	PC1 + PC2	-164.733	4	338.355	0.09	0.175	0.067	PC2 = -6.0981, PC1 = 3.7970
"	3	PC1	-166.451	3	339.424	1.16	0.103	0.022	3.7970
"	3	PC1 + PC2 + D	-164.247	5	339.858	1.59	0.083	0.065	PC2 = -6.554, PC1 = 5.729, D = 7.200
"	4	PC2	-166.135	3	338.791	0.00	0.179	0.034	-5.5831
"	4	PC1 + PC2	-165.202	4	339.293	0.50	0.139	0.050	PC2 = -5.5831, PC1 = 3.5906
"	4	PC1	-166.634	3	339.789	1.00	0.109	0.015	3.5906
"	5	PC2	-166.203	3	338.928	0.00	0.174	0.031	-5.378
"	5	PC1 + PC2	-165.269	4	339.428	0.50	0.135	0.047	PC2 = -5.3783, PC1 = 3.6745
"	5	PC1	-166.630	3	339.782	0.85	0.113	0.015	3.6745
"	NA	intercept	-167.515	2	339.286	1.15	0.131		
Wax	0.5	PC2	-180.163	3	366.848	0.00	0.242	0.041	-7.525
"	1	PC2*	-179.240	3	365.001	0.00	0.299	0.076	-9.917
"	1	PC2 + D	-178.958	4	366.804	1.80	0.122	0.067	PC2 = -8.892, D = -6.540
"	2	PC2*	**-178.695**	**3**	**363.911**	**0.00**	**0.341**	**0.096**	**-11.053**
"	2	PC2 + D*	-178.388	4	365.665	1.75	0.142	0.088	PC2 = -10.247, D = -6.265
"	2	PC2 + years + syrup*	-177.249	5	365.862	1.95	0.129	0.109	PC2 = -11.8583, years = 0.1252, syrup = 0.2578
"	3	PC2*	-179.076	3	364.673	0.00	0.278	0.082	-10.183
"	3	PC2 + D*	-178.374	4	365.636	0.96	0.172	0.088	PC2 = -9.611, D = -9.020
"	3	PC2 + years + syrup*	-177.453	5	366.270	1.60	0.125	0.102	PC2 = -11.4033, years = 0.1346, syrup = 0.2765
"	4	PC2*	-179.411	3	365.344	0.00	0.260	0.069	-9.514
"	4	PC2 + D	-178.721	4	366.331	0.99	0.159	0.075	PC2 = -9.281, D = -8.998
"	4	PC2 + years + syrup	-177.827	5	367.017	1.67	0.113	0.089	PC2 = -10.7781, years = 0.1244, syrup = 0.2762
"	5	PC2*	-179.465	3	365.451	0.00	0.255	0.067	-9.290
"	5	PC2 + D	-178.750	4	366.389	0.94	0.159	0.074	PC2 = -9.253, D = -9.112
"	5	PC2 + years + syrup	-177.865	5	367.095	1.64	0.112	0.087	PC2 = -10.5842, years = 0.1317, syrup = 0.2776
"	NA	Year	-180.538	3	367.598	0.75	0.167	0.026	-4.111
"	NA	intercept	-181.724	2	367.704	0.86	0.158		
BroodPop	1	D	-134.504	3	275.529	1.99	0.090	-0.015	-1.782
“	2	PC1	-134.457	3	275.435	1.90	0.091	-0.013	-0.7763
“	2	D	-134.500	3	275.521	1.99	0.087	-0.015	-1.714
“	3	PC1	-134.438	3	275.399	1.86	0.093	-0.013	-0.8642
“	4	PC1	-134.440	3	275.401	1.87	0.093	-0.013	-0.8934
“	5	PC1	-134.437	3	275.397	1.86	0.093	-0.013	-0.9176
“	NA	Year	-133.708	3	273.938	0.40	0.208	0.017	-1.425
“	NA	years + syrup	-133.237	4	275.363	1.83	0.102	0.014	years = 0.11618, syrup = 0.08545
“	NA	intercept	**-134.640**	**2**	**273.536**	**0.00**	**0.254**		
AdultPop	2	PC2 + years + syrup**	-160.864	5	333.092	1.47	0.205	0.172	PC2 = -3.0878, years = 0.4904, syrup = 0.2896
"	3	PC2 + years + syrup**	-160.590	5	332.544	0.92	0.247	0.181	PC2: -3.7837, years: 0.4939, syrup: 0.2991
"	4	PC2 + years + syrup**	-160.652	5	332.668	1.05	0.235	0.179	PC2 = -3.6243, years = 0.4906, syrup = 0.2993
"	4	D + years + syrup*	-161.090	5	333.544	1.92	0.151	0.164	D: 4.2943, years: 0.5219, syrup: 0.3059
"	5	PC2 + years + syrup**	-160.634	5	332.631	1.01	0.234	0.180	PC2 = -3.6267, years = 0.4931, syrup = 0.3002
"	5	D + years + syrup**	-161.002	5	333.367	1.75	0.162	0.167	D = 4.9270, years = 0.5308, syrup = 0.3094
"	NA	**years + syrup****	**-161.365**	**4**	**331.620**	**0.00**	**0.475**	**0.173**	**years = 0.4887, syrup = 0.2774**

*p < 0.05, **p < 0.01; **bold** = best model for given success metric

Figure 1(on next page)

Landscape composition of study sites at 2 km radius

Figure 1: Landscape composition of study sites at 2 km radius. Sites are depicted in order of increasing urban (red) land cover. Other major land cover classes include crop (gold), forest (dark green), and grassland (light green). Remaining land cover (grey) consisted of barren land and open water.

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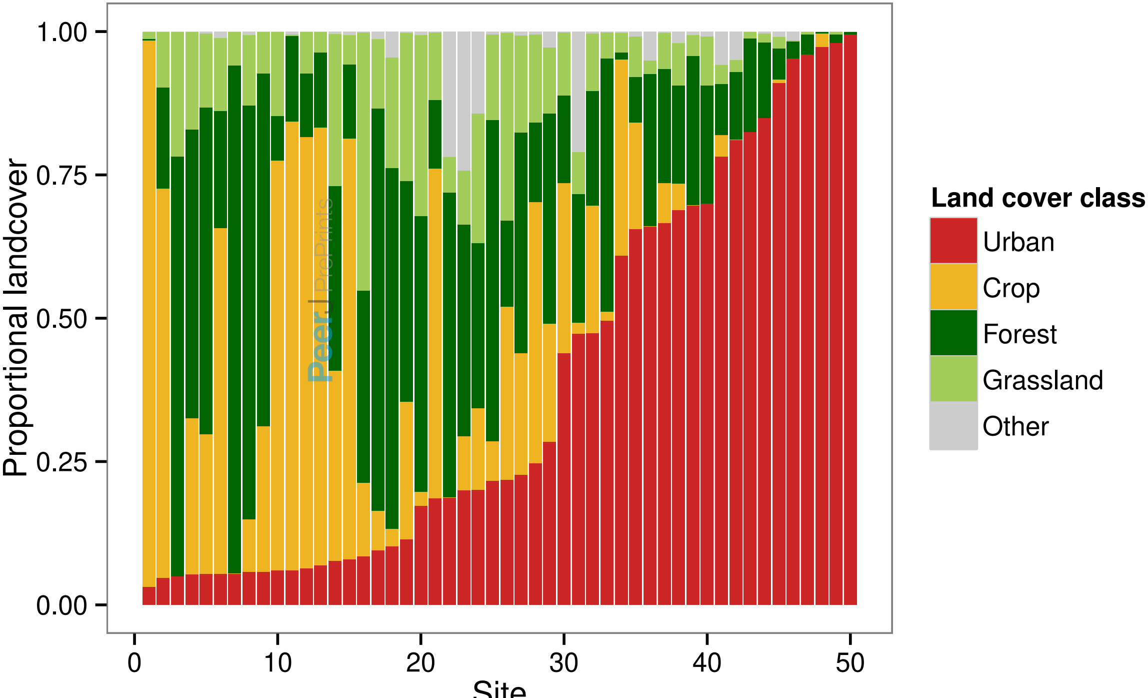
1.00
0.75
0.50
0.25
0.00
Proportional landcover
0
10
20
30
40
50
Site
Land cover class
Urban
Crop
Forest
Grassland
Other

Figure 2(on next page)

Principal components biplot of major land cover classes at a radius of 2 km

Figure 2: Principal components biplot of major land cover classes at a radius of 2 km. Principal component 1 (PC 1) comprises an urban-rural axis, with lower scores corresponding to higher urbanness. Principal component 2 (PC 2) forms an axis that separates sites characterized by forest/grassland from those characterized by cropland. This pattern was consistent at all spatial scales with only minor variation.

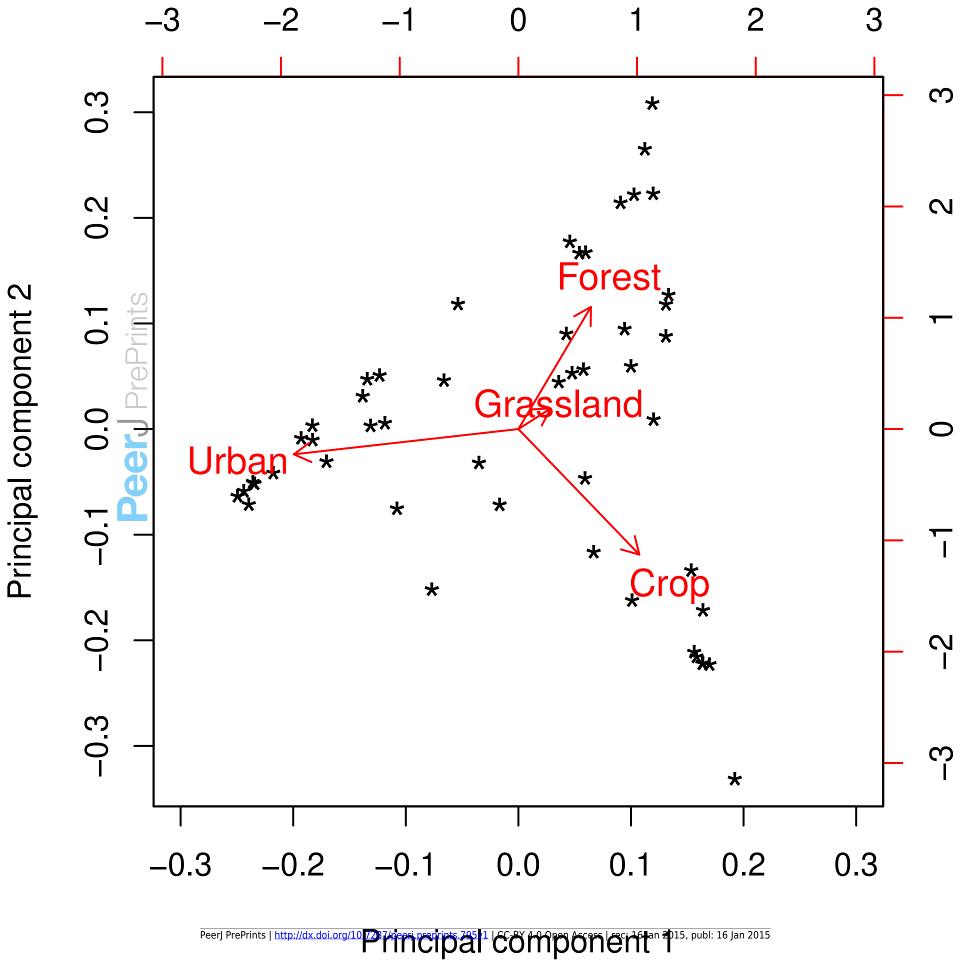

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Figure 3(on next page)

Food accumulation and wax production negatively correlated with PC 2

Figure 3: Food accumulation and wax production were negatively correlated with PC 2. This indicates that productivity in terms of food and wax increased in the direction of cropland and decreased in the direction of forest/grassland. This relationship was likely driven by the critical clover nectar flow, which is likely strongest in agricultural areas. A 95% confidence band is shaded in gray.

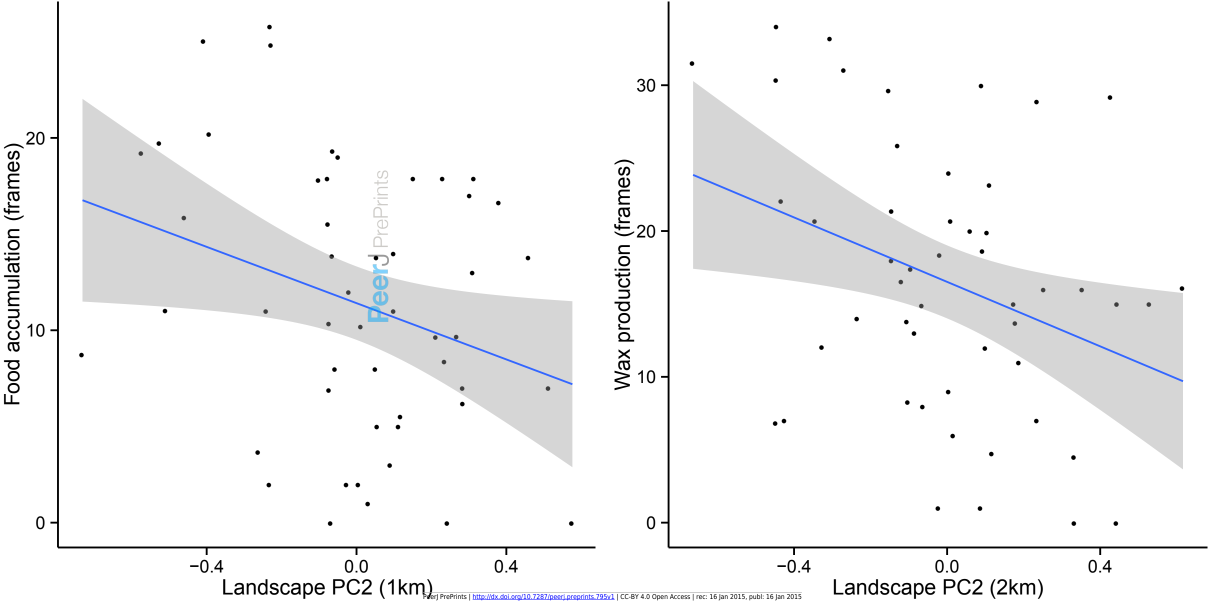

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Figure 4(on next page)

Adult population positively correlated with beekeeper years of experience and supplemental syrup feeding.

Figure 4: Adult population was positively correlated with beekeeper years of experience and supplemental syrup feeding. A 95% confidence band is shaded in gray.

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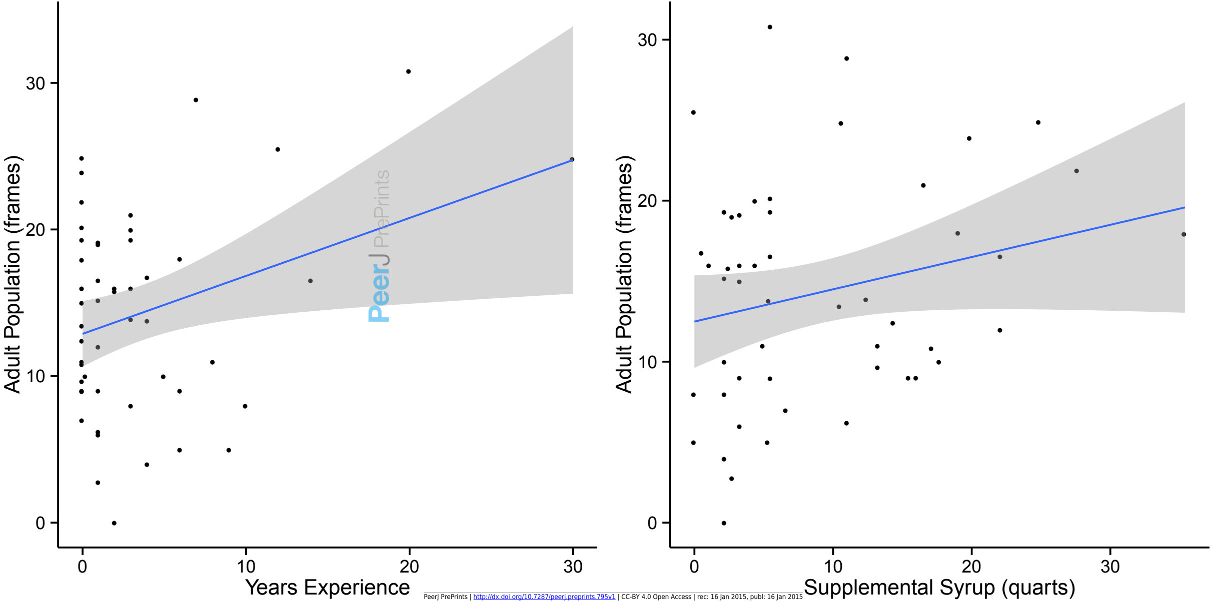

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Figure 5(on next page)

Colony food accumulation decreased significantly with increasing Urban : Crop ratio.

Figure 5: Colony food accumulation decreased significantly with increasing Urban : Crop ratio. This pattern was strongest at a 1 km radius (shown above), and may have been driven by the late-season goldenrod bloom that is often very strong agricultural areas but is typically weak in urban areas. A 95% confidence band is shaded in gray.

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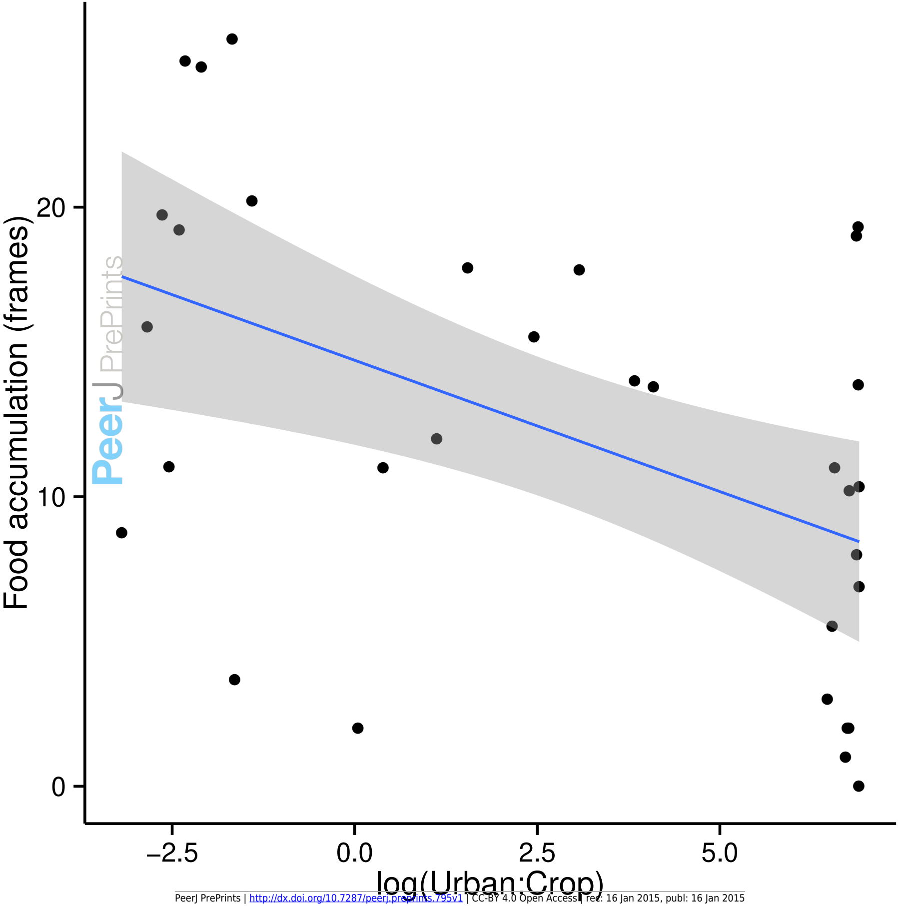

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