# Resource diversity and landscape-level homogeneity drive native bee foraging

Shalene Jha[a,b,1] and Claire Kremen[c]

[a]Integrative Biology and [b]Environmental Science Institute, University of Texas at Austin, Austin, TX 78712; and [c]Environmental Sciences, Policy and Management, University of California, Berkeley, CA 94720

Given widespread declines in pollinator communities and increasing global reliance on pollinator-dependent crops, there is an acute need to develop a mechanistic understanding of native pollinator population and foraging biology. Using a population genetics approach, we determine the impact of habitat and floral resource distributions on nesting and foraging patterns of a critical native pollinator, *Bombus vosnesenskii*. Our findings demonstrate that native bee foraging is far more plastic and extensive than previously believed and does not follow a simple optimal foraging strategy. Rather, bumble bees forage further in pursuit of species-rich floral patches and in landscapes where patch-to-patch variation in floral resources is less, regardless of habitat composition. Thus, our results reveal extreme foraging plasticity and demonstrate that floral diversity, not density, drives bee foraging distance. Furthermore, we find a negative impact of paved habitat and a positive impact of natural woodland on bumble bee nesting densities. Overall, this study reveals that natural and human-altered landscapes can be managed for increased native bee nesting and extended foraging, dually enhancing biodiversity and the spatial extent of pollination services.

dispersal | ecosystem services | resource dynamics | spatial ecology | urban

Over the last two decades, evidence of native pollinator decline has grown dramatically worldwide (1, 2). These declines are of critical concern for humanity, given that pollinators are responsible for the increased quantity, quality, and stability of over 60% of world crops (3), worth an estimated 200 billion dollars per year (4). Recent losses in managed honey bee populations have drawn further attention to the importance of native pollinator communities and their ability to provide effective and sufficient pollination services in certain landscapes (5). However, despite human dependence on native pollinators, and growing evidence that agricultural management can negatively impact colony growth (6), the mechanism behind how human-altered landscapes impact native pollinator foraging patterns and population densities remains unclear.

In this study, we use a population genetics approach to investigate the foraging and nesting dynamics of bumble bees across natural and human-dominated landscapes. Bumble bees (*Bombus* spp.) are among the most effective native pollinators (7) but are often the first bee species to be extirpated with land use intensification (8), exhibiting declines across a wide range of geographic regions (9). Although habitat and floral resource composition may influence native bee colony productivity (7) and foraging duration (8), it is not known how these factors impact foraging distance, which is critical for predicting the spatial extent of pollination services. Understanding the factors that mediate pollinator foraging distance could provide essential insight into the management practices that simultaneously provision native pollinators and extend their foraging patterns.

Specifically, we examine the utility of optimal foraging theory, a foundational concept in the field of foraging biology, to predict wild bumble bee foraging patterns. Optimal foraging is supported by substantial empirical and theoretical work (9, 10) and suggests that organisms should forage to maximize energy gain and minimize energy loss. This is often achieved by using "marginal foraging behavior" where the distance and duration spent foraging in a patch depend on the relative advantage of leaving and foraging elsewhere (11). Laboratory experiments with floral arrays have provided evidence that bumble bees may use previously gathered knowledge of resource distributions to inform their foraging decisions (12), yet it remains unknown how resource and habitat composition impact wild pollinator foraging at landscape scales. Given that foraging patterns determine the spatial extent of pollination services, and that global food security depends on effective pollination (3), it is essential to quantify the impact of habitat and resource composition on wild pollinator foraging.

In this study, we investigated the foraging and nesting dynamics of *Bombus vosnesenskii*, a critical crop pollinator (13) that is not believed to be exhibiting population declines (14), but that shares many life history features with declining *Bombus* species, such as a univoltine reproductive cycle, high foraging demands, and subterranean nesting. Due to bumble bee sociality, past abundance-based surveys have not been able to provide insight into nesting densities; however, molecular techniques allowing for colony assignment (e.g., ref. 15) permit the quantification of nesting densities and colony-level foraging patterns. In this study, a mean of 104.3 (±2.8) *B. vosnesenskii* worker bees were sampled in each of eight study regions (separated by more than 3 km) across the Bay and Delta bioregions of California, areas including extensive agriculture and moderate urbanization. The study regions varied in the proportion of human-altered and natural habitat within a 2-km radius (ranging from 5 to 95% natural habitat cover). Within each study region, we caught a mean of 20.8 (±2.2) bees at each of five equidistant sites on a 1.2-km transect. DNA was extracted from the tarsal segment of each individual, and screened at 13 microsatellite loci (16) to assign individuals to colonies. Nesting densities were estimated from the distribution of resampled colonies per site using mark-recapture methods, where sampling of each additional colony mate is treated as a "recapture" event (17). At the study region level, maximum foraging distance was estimated by fitting a logarithmic curve to the relative frequency of sister pairs across geographic space, and halving the distance to assume central colony location (18). At the colony level, the mean foraging distance was calculated as the distance that all sister pairs were found away from one another within a site, halved (*Materials and Methods*). Floral resource surveys were conducted within 250 m of each sampling site (five patches) and between sampling sites (four patches) to assess mean and coefficient of variation (CV) of both floral cover and species richness. Habitat composition for all sampling sites was characterized at 250-m and 2-km scales using

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geographic information system (GIS) at 5-m resolution (*Materials and Methods*).

## Results

Across individuals at the study region level, the extrapolated maximum foraging estimate varied by more than 30 times, from 82 to 2,783 m. At the colony level, the mean empirically measured foraging distance between colony mates ranged from 13 to 600 m. Using these colony-level distances, we examined how resource levels and habitat composition at local scales (250 m) and landscape scales (2 km) impacted mean foraging (Fig. 1). Because habitat composition variables (listed in Fig. 2) were correlated, we individually investigated the role of each habitat composition variable at both spatial scales and found that landscape-scale riparian forest habitat was most predictive, but that no habitat composition variable significantly explained colony mean foraging distance given correction for multiple comparisons (Table S1). Instead, we documented significantly longer mean foraging distances at patches with greater flowering plant species richness and in landscapes with lower variability (more among-patch homogeneity) in floral cover (Table 1 and Fig. 1). Finally, variation in nest density among study regions was significantly explained by the proportion of paved surface in a 250-m radius (Fig. 2*A*) and the proportion of oak woodland–chaparral in a 2 km radius (Fig. 2*B*).

## Discussion

Results from this research reveal extreme plasticity in the estimated maximum foraging distance and mean foraging distance of wild bumble bees. We use a well-established technique to estimate maximum foraging distance for wild bumble bees and show that this value varied by more than 30 times within our study system and exceeded those distances measured via radio tagging (2.5 km; ref. 19), colony displacement (1.5 km; ref. 20), and previous molecular studies using the same technique (449–758 m; ref. 18).

This high level of variation in pollinator foraging distance indicates that pollinators are capable of shifting foraging patterns dramatically across landscapes and emphasizes that a single maximum foraging distance, often used to describe pollinator species (21), is a highly simplified measure of pollinator movement. More importantly, our empirical measures of colony foraging distance indicate that bumble bee mean foraging distances are not shorter in landscapes with higher floral cover, as suggested by the simplest optimal foraging assumptions. Rather, bees forage further for species-rich patches within landscapes where floral cover is more homogenous from patch to patch. In other words, in support of the marginal value theorem and accumulated foraging knowledge, bumble bees are more likely to "give up" on patch-level resources in search of others when the level of rewards among patches are relatively consistent (12). Therefore, our results suggest that bumble bees perceive and consider both landscape-scale and patch-scale resources, using sensory cues and past foraging trips (individual level or colony level) to build an understanding of resource quality and quantity across spatial scales.

Furthermore, our results highlight the unique finding that floral species diversity, not density, is most predictive of foraging distance. Although the need to forage for multiple resources is evident across animal taxa and can alter foraging strategies (22), this pattern has never been documented to influence the spatial foraging patterns of wild pollinators. As generalists, bumble bees often visit several floral species for pollen and nectar within a single foraging bout (23). The act of foraging to maximize floral species richness may provide bumble bees with more stable food sources across temporal and spatial scales and more diverse nutrient intake. This behavior may be particularly advantageous given that the nutrition content of pollen and nectar varies substantially between plant species (24, 25) and that multiple pollen species are essential for optimal bee larval growth (26, 27).
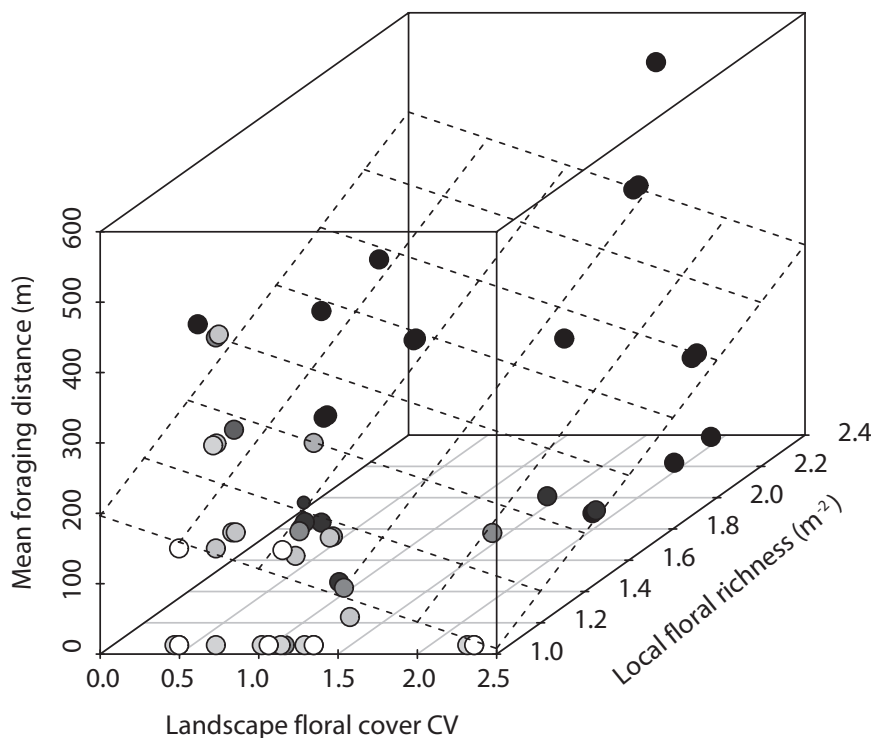


**Fig. 1.** Colony-level mean foraging distances with respect to local floral species richness (within patch) and landscape floral cover CV (among patches). The lighter-colored dots represent graphical foreground. Data are untransformed, and overlapping points have been jittered horizontally for clarity. The plane illustrates the significant variables of the LME model (Table 1).
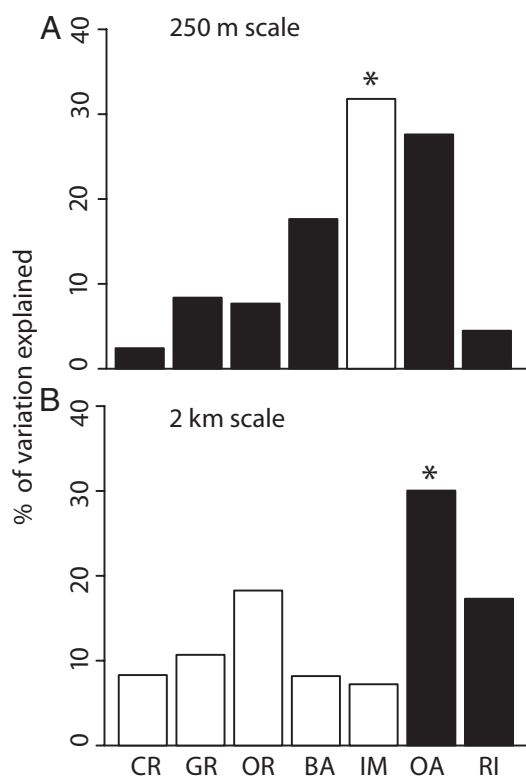
**Fig. 2.** Hierarchical partitioning showing independent effects of habitat composition variables on nesting density, expressed as the percentage of the total variance explained. Percentage of variation explained at the (*A*) 250-m and (*B*) 2-km spatial scales. The black bars indicate a positive effect, and the white bars indicate a negative effect based on linear regression. CR, crop; GR, grassland; OR, orchard; BA, bare ground; IM, impervious (concrete); OA, oak woodland–chaparral; RI, riparian forest. The asterisk denotes significance at the *P* < 0.05 level.

Results from this research also reveal a negative impact of paved habitat on native bee nesting densities. Although this finding is intuitive, our research provides previously unavailable empirical documentation. This pattern is visible at the smallest spatial scale investigated, likely due to the fact that paved surfaces primarily influence nearby nesting densities, whereas landscape-level nesting densities are more sensitive to natural habitat cover (15), specifically the cover of oak woodland–chaparral. Essentially, these results indicate that a simultaneous expansion of paved area and destruction of natural woodland could lead to substantially reduced

**Table 1. LME of mean foraging distance for individual colonies as a function of local (within patch) and landscape (among patches) floral resource levels and habitat composition (df = 60)**

| Fixed factors | Estimate | *t* value | *P* value |
|---|---|---|---|
| Local (within patch) scale | | | |
|   Mean floral cover | 0.471 | 1.177 | 0.244 |
|   CV floral cover | −6.958 | −0.621 | 0.537 |
|   Mean floral richness | 52.301 | 3.172 | 0.002* |
|   CV floral richness | −5.969 | −1.506 | 0.137 |
| Landscape (among patches) scale | | | |
|   Mean floral cover | 0.224 | 0.648 | 0.519 |
|   CV floral cover | −36.800 | −2.932 | 0.005* |
|   Mean floral richness | 11.719 | 1.429 | 0.158 |
|   CV floral richness | 16.344 | 1.017 | 0.313 |
|   Riparian forest cover in 2-km radius | 0.009 | 2.428 | 0.018 |

*Denotes significance at the *P* < 0.05 level given Bonferroni–Holm correction.

bumble bee nesting densities. This finding is especially alarming given that most native bees are soil nesting and that impervious surfaces are the most basic component of expanding urban areas.

Overall, our results have broad implications with respect to native bee conservation and pollination services. This study demonstrates empirically that native bee nesting densities are negatively impacted by pavement at the local scale; therefore, management strategies that reduce the local use of pavement and increase natural habitat within the landscape could improve nesting opportunities and/or reduce nesting disturbance for native bees at multiple spatial scales. Most importantly, this field study measures the impact of resource distributions and habitat composition on wild bee foraging distance, which is an essential step in the process of predicting and managing pollination services. Existing spatially explicit pollination models use static foraging distance to describe the extent of pollination services (e.g., refs. 28 and 29). Our research reveals the importance of dynamic foraging and highlights the potential role of flowering species richness and landscape homogeneity in predicting landscape-scale pollination services.

Specifically, our results provide insight into why bees exhibit long-distance foraging patterns, and how this information could be used to optimize the spatial extent of ecosystem services. We reveal that bumble bees forage longer distances for species-rich floral patches, particularly when landscape-scale floral resource levels are more consistent among patches. Floral diversity, not density, matters most for predicting long-distance pollinator foraging. These results suggest that increased availability of species-rich flowering patches (i.e., suburban and urban gardens, diversified farms, and restored habitat patches) and greater consistency among such patches at the landscape scale could provide pathways for bumble bee foraging and could improve the spatial extent of pollination services. Finally, our results demonstrate that bumble bee foraging distance is not significantly explained by any measure of habitat composition. Both natural and human-altered landscapes can be managed for improved bumble bee foraging, thus encouraging farmers, land managers, and urban dwellers to be involved in dually promoting biodiversity conservation and pollination service provision.

## Materials and Methods

**Floral Surveys and Habitat Composition.** Floral resource surveys were conducted in 12 randomly placed 1 × 1-m sampling quadrats located within 250 m of each sampling site (five patches) and between sampling sites at a distance of 300 m perpendicular to the transect (four patches). Floral cover was calculated based on inflorescence number of all flowering plant individuals, one of the best predictors of nectar and pollen resource availability, as documented within the bioregion (30). The 12 within-patch quadrats (250-m scale) were used to calculate the mean and CV of floral resources for area and richness at the patch scale. To quantify the amount of variation in floral resources among patches (2-km scale), all 108 quadrats were analyzed. Composition of flowering species (Table S2) varied substantially across patches and landscapes; thus, correlations between individual plant species and colony foraging distances were not possible. All land cover within 250-m and a 2-km radius of each sampling site was hand classified using ArcGIS at the 5-m scale, and land use classifications were confirmed with ground-truthing surveys at every site. None of the sites was sprayed with pesticides during the study.

**Bee Collection, Molecular Techniques, and Colony Assignment.** Bees were collected and stored in 95% (vol/vol) ethanol at the University of Texas at Austin. DNA was extracted from the right hindmost leg and multiplex polymerase chain reactions (PCRs) were performed in a final volume of 20 µL, containing ~2 ng of DNA, 2 µL of 10× PCR buffer, 1.5 mM $MgCl_2$, 300 µM of each dNTP, 1 U of Taq polymerase, and 0.25 µM of each primer. The thermal cycle began with a 5-min denaturation step at 95 °C, and was followed by 37 cycles: 30 s at 94 °C, 60 s at the locus-specific annealing temperature, and 30 s at 72 °C, followed by a final extension at 72 °C for 20 min. One primer from each pair was labeled with FAM, HEX, or ROX, and genotyped on an ABI 3730 Sequencer. Alleles were scored manually using GENEMARKER (Softgenetics) and only samples with more than eight genotypes per individual were included in the analyses. All bees were genotyped and the probability of null alleles was calculated using the software Micro-

Checker (31). After removal of full sibs (described below), deviations from Hardy–Weinberg equilibrium (HWE) and linkage disequilibrium (LD) were tested in GenePop, version 4.0 (32), using the Markov chain method with 1,000 dememorizations, 100 batches, and 1,000 iterations per batch. A Bonferroni–Holm correction (33) for multiple comparisons was applied in all cases to a significance level of $P < 0.05$.

None of the loci exhibited signs of having null alleles. One locus (B136) was significantly out of HWE across all study regions; therefore, we chose to exclude it from the analysis. The remaining loci exhibited either no significant deviations from HWE in all study regions (BT65, BT33, BT43, B119, B132, B72, B131) or exhibited a significant deviation from HWE in only one study region (B125, B128, B96, B100, B124). Significant LD was detected for multiple loci, but only within single populations; therefore, we elected to retain all markers, except for B136, for the analyses.

Full sibs collected at each site were assigned to colonies using COLONY 2.0 (34), and only unique colonies were used for nesting density estimations. Nesting densities were estimated from the distribution of resampled colonies per site using the software Capwire (17), which uses the number of times an individual (or colony mate) is "recaptured" to estimate the population size. We used the Two Innate Rate Model (TIRM) mark-recapture approach because this has been shown to align best with the expected truncated Poisson distribution of nest densities (15). To assess the independent contributions of each habitat composition variable on nesting density per site, we used hierarchical partitioning using the hier.part package (35) of the R software (36).

**Foraging Distance Analysis.** At the site level, maximum worker foraging distances were estimated across the length of the transect by calculating relative frequency of *B. vosnesenskii* sister pairs divided by the total number of sister pairs possible, thus precluding biases due to transect "end effects" (37). A best-fit logarithmic curve was then plotted using all frequencies above the type II error value (0.001), and the resulting *x* value was halved, assuming central colony location (18). The sites closely matched the logarithmic dispersal function ($R^2 > 0.76$ for all sites) and the dispersal coefficient was not significantly explained by any habitat or floral resource variables ($P > 0.23$ for all variables). At the colony level, mean foraging distance was calculated

as the distance that all sister pairs were found away from one another within a site, halved. The sampling protocol of more than five bees per site has been deemed sufficient for dispersal analysis in previous work (37). Furthermore, to examine the persistence of patterns given smaller sample sizes, we randomly removed individuals from the dataset such that a maximum of 10 individuals were represented per site, and we still estimate similar overall foraging patterns (Table S3).

We used linear mixed-effects models (LMEs) fit by maximum likelihood to examine how local-scale and landscape-scale floral resources and habitat composition (fixed factors) and sampling location (random factor) impacted mean foraging distance (df = 60). Local- and landscape-scale floral resources were not correlated and therefore were explored simultaneously in each model. However, local and landscape habitat composition variables were often correlated (within and across scales); thus, they were independently examined and the LME with the lowest Akaike information criterion (AIC) score was selected (Table S1). Interaction effects were tested for all pairwise combinations of floral and habitat variables and none were significant ($P > 0.31$ for all variables). Furthermore, we conducted model selection using second-order information criterion (AICc) to penalize for smaller sample sizes (38), using the MuMIn R package (39), and we confirm that the top model ($\Delta$AICc greater than 1) includes only local floral species richness and landscape floral cover CV. The remaining top 10 models are the only models with $\Delta$AICc of <2 and all include local floral species richness and landscape floral cover CV as their only significant variables (Tables S4 and S5). All data were square-root transformed and all significance values were Bonferroni–Holm corrected for multiple comparisons, applied to a significance level of $P < 0.05$. All values in parentheses following means represent SE. Statistical analyses used to estimate nesting density, site-level foraging distance, and colony-level foraging distance were independent and unstacked.

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