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Forests do not limit bumble bee foraging movements in a montane meadow complex

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Abstract. 1. Understanding the roles of habitat fragmentation and resource availability in shaping animal movement are integral for promoting species persistence and conservation. For insects such as bumble bees, their movement patterns affect the survival and reproductive potential of their colonies, as well as the pollen flow of plant species. However, the understanding of their mobility or the impact of putative barriers in natural environments is limited due to the technical difficulties of studying wild populations.

2. Genetic mark–recapture was used to estimate the foraging distance, resource use, and site connectivity of two bumble bee species in a montane meadow complex composed of open meadows within a matrix of forest.

3. There was no evidence that forests or changes in landcover function as barriers to the fine-scale movement for either species. Substantially greater colony-specific foraging distances were found for *Bombus vosnesenskii* (maximum: 1867 m) compared to *Bombus bifarius* (maximum: 362 m). Despite this difference in absolute range, both species were detected across putative forest barriers at frequencies expected by uninhibited movement. Siblings separated by greater distances were more likely to be foraging on different floral species, potentially suggesting a resource-based motivation for movement.

4. These results suggest that bumble bee foraging patterns are influenced by species-specific differences in movement capacity, with little influence of matrix composition between resource patches. They also support the perspective that habitat conservation for bumble bees should prioritise providing abundant and diverse patches of resources within species-specific movement radii with less emphasis on matrix composition.

Key words. Central place foraging, foraging range, genetic mark–recapture, habitat connectivity, movement ecology, pollinators.

Introduction

The influence of landscape structure and habitat composition on organismal movement is a major focus of ecological research and is critical for conservation planning (Taylor *et al.*, 1993; Fahrig, 2003; Allen & Singh, 2016). Patterns of movement can vary substantially across context, ontogeny, and among closely related species (Ricketts, 2001; Nathan *et al.*, 2008). Species-specific movement and the effects of habitat structure on movement processes are key influences on population dynamics, as well as on the composition of ecological communities across space and time (e.g. beta diversity; Cadotte, 2006; Grainger & Gilbert, 2016). Individuals may respond to different landscape features by altering their rate of movement (Van Dyck & Baguette, 2005; Brown *et al.*, 2017), changing their directionality or path of travel (Mader *et al.*, 1990; Bartomeus & Winfree, 2011; Brittain *et al.*, 2013), or avoiding certain features altogether (Shepard *et al.*, 2008; Kuefler *et al.*, 2010). As such,

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landscape connectivity for a given species is determined by a combination of the arrangement of resource patches, the composition of the matrix, and the suite of species-specific behaviours that determine the necessity and ability to move between differing landcovers.

For highly mobile pollinating insects such as bumble bees, their movement patterns affect not only the survival and reproductive potential of their colonies but also the patterns of pollen flow and landscape connectivity for plant species with which they interact (Kremen *et al.*, 2007; Cranmer *et al.*, 2012). Bumble bees are important pollinators of wildland plants and domesticated crops within temperate regions (Free & Butler, 1959; Goulson, 2009). Recent worldwide declines in their populations (Grixti *et al.*, 2009; Williams & Osborne, 2009) have sparked intense interest in understanding the role habitat structure, floral resource distribution, and species-specific differences in movement capacity may play in their persistence (Westphal *et al.*, 2006; Redhead *et al.*, 2016). However, the difficulty of studying small, fast-flying organisms with cryptic nesting habits has limited our understanding of large-scale bumble bee movement, especially with regard to landscape context (Mola & Williams, 2019).

Bumble bees are central-place foragers that establish colonies early in the spring with fixed locations for the remainder of the season. Therefore, the scale over which individuals and their colonies can forage determines how they will respond to resources that vary spatially and temporally over the season (Knight *et al.*, 2005). Resource-economic foraging models show that flight distances of several kilometres can be profitable (Dukas & Edelstein-Keshet, 1998; Cresswell *et al.*, 2000). Empirical studies demonstrate great plasticity of worker foraging movements and offer some explanation for differences observed among species and landscapes (Knight *et al.*, 2005; Wood *et al.*, 2015; Redhead *et al.*, 2016). Nonetheless, comparatively few estimates of bumble bee movement exist in naturally fragmented habitat landscapes, especially in forested or high-elevation environments.

There are conflicting reports about the scale of bumble bee movement and sensitivity to habitat fragmentation. Early studies suggested that workers were unable to move through forests, restricting the foraging area of colonies to the meadow immediately around their nest (Bowers, 1985). Others suggest that foraging range may be reduced in high-elevation environments due to the dense and short-lived blooming period typical of these habitats (Elliott, 2009; Geib *et al.*, 2015). However, these findings may be artefacts of low sample abundance and the tendency of bumble bee workers to exhibit high site fidelity (Manning, 1956; Comba, 1999; Ogilvie & Thomson, 2016), both of which can reduce the estimated range of bumble bee foraging and overestimate the influence of putative barriers (Mola & Williams, 2019). Furthermore, even if individuals exhibit strong site fidelity or are limited by barriers, there may be strong motivation for siblings to forage widely separated from each other to gain access to complementary food resources for the colony (Mandelik *et al.*, 2012). In at least one study, foragers were observed to cross forested areas of up to 600 m (Kreyer *et al.*, 2004). Similarly, a recent investigation using experimentally placed bumble bee colonies in a fragmented forest found that habitat connectivity was not indicative of colony reproductive success (Herrmann *et al.*, 2017), suggesting fragmentation did not limit profitable movement. These conflicting results suggest the need for further study of the scale of foraging and the sensitivity of movement to putative barriers such as forests, especially with naturally foraging bees.

To help build our understanding of bumble bee movement ecology in heterogenous environments, we sought to answer three main questions. (1) What is the scale of foraging movement in a montane meadow complex?; (2) Do forests act as barriers to movement, limiting the connectivity of flower-rich meadows?; and (3) Are there species-specific differences in foraging distance or sensitivity to forest 'barriers'? To address these questions, we use a genetic mark–recapture sampling scheme to estimate the landscape-scale movements of two bumble bee species within a montane meadow complex. We further inform the questions by examining patterns of resource use across siblings and colonies and use community dissimilarity metrics to explore the role of land cover in structuring habitat connectivity.

Methods

Study region and sampling locations

The study was carried out in the summers of 2015 and 2018 within the Tahoe National Forest North of Truckee, California, U.S.A. The region is characterised by mixed conifer forests (predominantly *Pinus contorta*, *Pinus jeffreyi*, and *Abies concolor*) interspersed with open meadows and gaps in the forest canopy, allowing for the growth of understorey flowering herbs and shrubs. We centred our study around a focal meadow ('Secret Meadow', 39.4608157 N, −120.2734177 W) and adjacent forest gaps (we refer to the focal meadow and nearby forest gaps together as the 'core sites'). Forest gaps differed from meadow sites in that they contained mature, overstory trees within the boundaries of the collecting area (Fig. 1). In addition, we collected from four distant meadows within 1.5–3.5 km from the focal meadow (Fig. 1). In 2015, we established 10 core sampling sites (six meadows, four forest gaps) and two distant meadows. In 2018, when collecting only *Bombus bifarius* (see below), we obtained samples at four core sites (two large meadows and two large forest gaps) and three distant patches in order to ensure the collection of enough genetic material at each site. Sampling in core sites occurred within a 50-m radius of a central point. The distant meadows had no *a priori* boundaries and simply reflected the availability of resources within a given area. Bees captured at the distant meadows were excluded from site-level analyses and were only used for their individual capture points, so differences in the sizes of distant meadows should not influence our results.

Study species and captures of specimens

To determine foraging range, we used a genetic mark–recapture framework focusing on two common species within the study region, *Bombus vosnesenskii* (Radoszkowski, 1862) and *B. bifarius* (Cresson, 1878; Hatfield & Lebuhn, 2007). In 2015, we captured both species, and in 2018, we

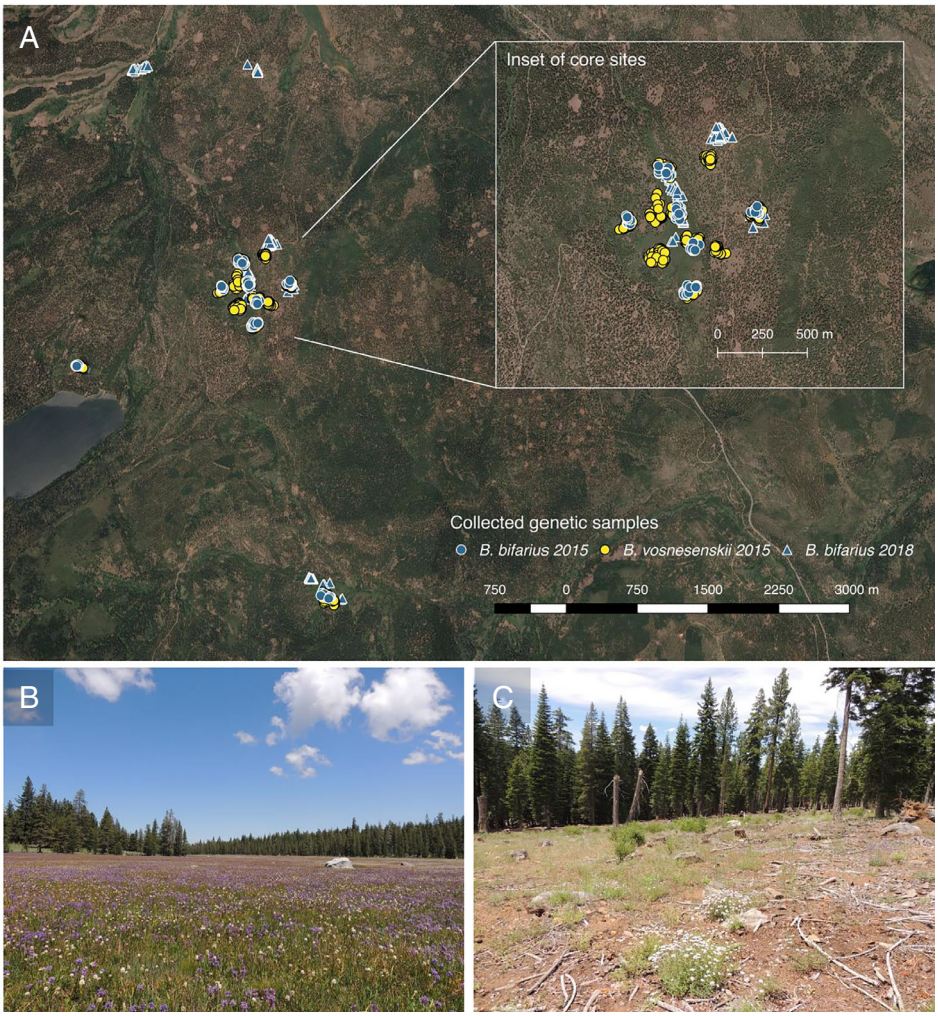

Fig. 1. (a) Map of study area and collections. Inset shows the core meadow and core forest gap collection locations. (b) Core meadow with forest edge visible in background. (c) A core forest gap site east of the focal meadow. [Colour figure can be viewed at wileyonlinelibrary.com].

collected only *B. bifarius* due to low captures in the first season. We captured wild-foraging workers, obtained genetic samples from them, and assigned individuals to sibling groups (colonies) using pedigree reconstruction software (*detailed below*). We visited each site every 7–10 days from June to August in full or partial sun and sustained winds of less than 10 mph. We netted foraging workers for approximately 2 h per site per visit. Each site was visited at least thrice per season. For each bee, we recorded its location with a global positioning system (GPS), noted the plant species it was captured from, and then chilled the specimen on ice. Within the core sampling sites, specimens were sampled non-lethally by clipping the distal two to three segments of a mid-tarsus (Holehouse *et al.*, 2003). *Bombus vosnesenskii* individuals were tagged on the thorax with a small, uniquely numbered disc and released. We tagged only *B. vosnesenskii* because of time constraints. For distant sites, we sampled lethally by capturing specimens, chilling them to confirm species identity, and then storing them in 95% ethanol. Due to the low recapture rate of individuals (see below), lethal sampling should not substantially impact our estimates of movement distances between core and distant sites. All samples were stored in 95% ethanol in a −20 °C freezer until subsequent laboratory analysis.

DNA extraction and restriction site-associated DNA library preparation

DNA was extracted, and restriction site-associated DNA (RAD) libraries were produced from all specimens following a bead-based extraction procedure detailed in Mola (2019). Samples were placed into 80 µl of Lifton's buffer and macerated. Plates were stored at −20 °C until further extraction. DNA yields were variable but usually between 0.2 and 2 $ng \cdot \mu l^{-1}$ following the extraction procedure described by Ali *et al.* (2016). RAD libraries were produced by transferring 10 µl of DNA to a new plate and cleaving with *PstI* (New England Biolabs [NEB]). Unique barcodes were then attached to the cleaved DNA via a

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biotinylated adapter. Samples were then pooled for each plate, and the pooled DNA was sheared and purified with magnetic streptavidin beads. *SbfI-HF* (NEB) was used to remove DNA from the beads. Each plate library received a unique barcode using a NEBNext Ultra DNA Library Prep Kit for Illumina. Finally, libraries from each plate were pooled in an equimolar ratio and sequenced at the UC Davis Genome Center on an Illumina HiSeq 4000 using paired-end 150 bp reads. Libraries were submitted for resequencing a second time to yield sufficient reads for subsequent analysis (see below).

Genotyping

RAD analysis was performed as described in Prince *et al.* (2017). Sequence data were demultiplexed and aligned to the *Bombus impatiens* genome (Sadd *et al.*, 2015) using the backtrack algorithm of the software burrows-wheeler aligner (bwa) with default parameters (Li & Durbin, 2009). We used SAMtools to sort and filter for proper pairs (Li *et al.*, 2009). We merged multiple libraries of sequencing of matched samples before removing PCR duplicates and indexing Binary Alignment Map (BAM) files as necessary. Only samples containing at least 100 000 aligned reads were retained as preliminary tests showed that genotype calls for lower thresholds yielded inconsistent sibship assignment. To call genotypes, we used Analysis of Next Generation Sequencing Data (ANGSD; Korneliussen *et al.*, 2014) with a minimum mapping quality (−minMapQ) of 20, a minimum base quality score (−minQ) of 20, a minimum of 50% of individuals having data per site (−minInd), and the SAMtools genotype likelihood model.

Sibship assignment

To assign individuals to sibling groups, we used COLONY version 2 (Wang, 2004) on called genotypes. To reduce computing time and to ensure that markers used in COLONY analyses were informative, we selected three batches of 5000 anonymous single nucleotide polymorphisms (SNPs). We filtered SNPs by selecting the first 5000 random markers with a minor allele frequency greater than 0.05, at least 1000 bp from other selected SNPs, and conforming to Hardy–Weinberg Equilibrium as calculated from allele frequencies. COLONY was run using mostly default settings, assuming monogamous breeding for males and females (Goulson, 2009; Owen & Whidden, 2013), and using the full pairwise-likelihood score setting to improve computing speed. We ran COLONY for five runs on medium length and compared the results of all three SNP batches used. Only sibling groups that were confirmed by all three SNP batches were retained, ensuring high reliability of our putative family assignments.

Colony abundance estimation

After obtaining our sibship pedigrees, we conducted all subsequent analyses in R version 3.6.0 (R Core Team, 2016). To understand the completeness of our sampling for each species and year, we estimated total colony abundance and compared it to the raw number of colonies detected from sibship assignment. We estimated undetected colony abundance using the mark–recapture package CapWire (Pennell *et al.*, 2013). We obtained the maximum likelihood estimate of colony abundance and 95% CI using the two-innate rates model (TIRM), which assumes heterogeneity of capture probability among colonies (Goulson *et al.*, 2010; Wood *et al.*, 2015).

Sibling separation distances and colony-specific foraging range

To understand the frequency of long-distance movements and compare the scale of foraging for the two species, we estimated sibling separation distance and colony-specific foraging distances. We assessed the expected distribution of sibling separation distances in two ways. First, we calculated the relative frequency of sibling separation distances adjusted for varying numbers of captures across all pairwise distances (Darvill *et al.*, 2004; Jha & Kremen, 2013):

$$\text{Relative frequency} = \frac{n_i}{m_i}$$

Here, n_i represents the observed number of pairwise sibling separation distances within the ith 100 m bin, and m_i is the total number of possible pairwise captures within each bin. Second, because each bin i represents a 100 m sampling annulus, the amount of unsampled habitat within annulus $i+1$ will increase with square of the radius, making distant captures probabilistically rare if individuals are moving away from their colonies randomly. To explore this possibility, we calculated an area-adjusted relative frequency (Sivakoff *et al.*, 2012):

$$\text{Area – adjusted relative frequency} = \frac{n_i}{m_i}(r_{2i}^2 - r_{1i}^2) \Big/ \sum_i \frac{n_i}{m_i}(r_{2i}^2 - r_{1i}^2)$$

where r_{2i}^2 is the outer radius of annulus i, and r_{1i}^2 is the inner radius. To estimate the slope of relative frequency and area-adjusted relative frequency as a function of binned separation distances, we fit generalised linear models (GLMs) with a binomial error term for each species and their interaction. Comparison of the slopes of the two metrics allows us to examine potential explanations for the commonality of large separation distances. Specifically, if the relative frequency of distant captures is low in the effort-only estimate but high in the area-adjusted estimate, it suggests that foragers were captured at those distances much more than expected under random dispersion from a nest site alone given the large potential search area at distant annuli. This would suggest that we are observing directed foraging events rather than simple distance-decay functions (Fig. 2).

We estimated colony-specific foraging distances by calculating the mean of linear distances between each colony member and their shared centroid. Although this estimate is likely an underestimate of a colony's true foraging range, it represents a reliable estimator for relative comparisons between species

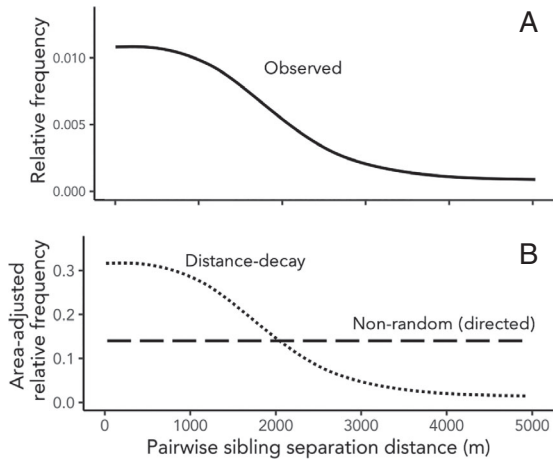

Fig. 2. Conceptual diagram demonstrating how the expected distribution of sibling separation distances should change under a distance-decay versus non-random (i.e. directed) foraging strategy. (a) In either case, our observed frequency of sibling separation distance should decline at larger distances. (b) In a distance-decay scenario, the area adjustment has no influence on the shape of the distribution as individuals are detected infrequently at long distances even when correcting for area sampled (dotted line). In a non-random, directed foraging distribution, the distribution is uniform as sibling pairs are detected frequently at long distances relative to the sampling area (dashed line). The shape of the non-random distribution may be positive, negative, or uniform as shown, but the key feature is that it strays substantially from the effort-only adjusted estimate given in panel A.

within a common landscape (Pope & Jha, 2017; Mola & Williams, 2019). We tested for statistically significant differences in colony-specific foraging distances between species using a Wilcoxon Rank-Sum test to account for non-normally distributed estimates.

Plant use across distance

Because colonies benefit from diverse pollen diets (Vaudo *et al.*, 2015), siblings may separate in space to have access to complementary floral sources. To determine if siblings separated by longer distances are more likely to be foraging on different plant species, we assigned a value of 0 (both siblings foraging on the same plant species) or 1 (siblings foraging on different plant species) to all sibling pairs. We then fit a GLM with the binomial outcome as the function of separation distance for both species. We conducted this analysis at two levels: (1) *B. vosnesenskii* and *B. bifarius* siblings (pooled) within 1000 m and (2) *B. vosnesenskii* across all distances. The latter analysis was used to account for the fact that no *B. bifarius* siblings were observed beyond 726 meters (see results) and because the relationship may differ across scale.

Habitat connectivity

We investigated the influence of forests as barriers and site-level habitat connectivity in two ways. First, we calculated the number of colonies with at least one pair of siblings in a core forest and core meadow site against a null expectation. Any colonies detected within both forest and meadow would necessitate at least one sibling crossing between the two vegetation types. To generate our null expectation, we randomly reassigned individuals to families 1000 times by shuffling family membership to preserve the number and size distribution of families but randomise individual identity. For *B. bifarius*, we generated the null expectation for each year separately before summing. For each iteration, we totalled the number of families detected within at least one forest and one meadow site. If the observed number of colonies falls within the null expectation, it implies that colonies are using both forest and meadow resources at frequencies expected, with free movement between sites and without specialisation in one habitat type or the other.

Second, to determine if connectivity between sites is affected by the differences in habitat composition between them, we calculated the Jaccard dissimilarity index between sites, treating unique colonies as 'species'. If siblings were detected in two sites, they subtract from the dissimilarity of those sites, and if siblings are not detected between the two sites, they add to their dissimilarity. For every pairwise combination of core sites, we calculated dissimilarity in the package Vegan using the 'jaccard' option (Oksanen *et al.*, 2007). We classified each site pair according to the vegetation type between their shortest path by walking the length between each pair of sites and confirming with Google Earth imagery. If two meadow sites were separated by continuous meadow or two forest sites were separated by forest, they were categorised as homogenous. If they were separated by a contrasting habitat type (e.g. two meadow sites separated by forest), the pair was classified as heterogenous. Necessarily, any pairwise comparisons of a forested site and a meadow site were classified as heterogenous. Because we restricted our analysis to the core sites, the range of separation distances between the centres of heterogenous (105–745 m) and homogenous (174–696 m) site pairs were roughly similar. To test if landcover restricted site connectivity, we fit a generalised linear regression model with our sibling-based dissimilarity metric as a function of linear distance and heterogenous or homogenous vegetation type between sites as a categorical covariate. We tested both the main effects and their interaction.

Results

Captures and colony abundance

We captured and successfully genotyped 332 *B. vosnesenskii* and 401 *B. bifarius* (*B. bifarius*: 161 in 2015, 240 in 2018; Table 1). We detected approximately 46% of the estimated *B. vosnesenskii* colonies. Detection of *B. bifarius* colonies was lower, with 14% and 21% of the estimated colony abundance captured in 2015 and 2018, respectively. Because there was no detectable difference in *B. bifarius* foraging distance between years ($W = 192$, $P = 0.5076$), and no changes in landscape configuration, we conducted all subsequent analyses on the combined *B. bifarius* data.

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Table 1. Captures of bumble bee workers, raw colony abundance from COLONY pedigree reconstruction software, and maximum likelihood estimate of total colony abundance from the program CapWire.

Species	Year	Individuals genotyped	Raw colonies	ML estimate (95% CI) of total colonies	% detected (raw/estimated)
Bombus bifarius	2015	161	148	1007 (712–2175)	14.70
	2018	240	207	975 (816–1535)	21.23
Bombus vosnesenskii	2015	332	192	413 (406–539)	46.49

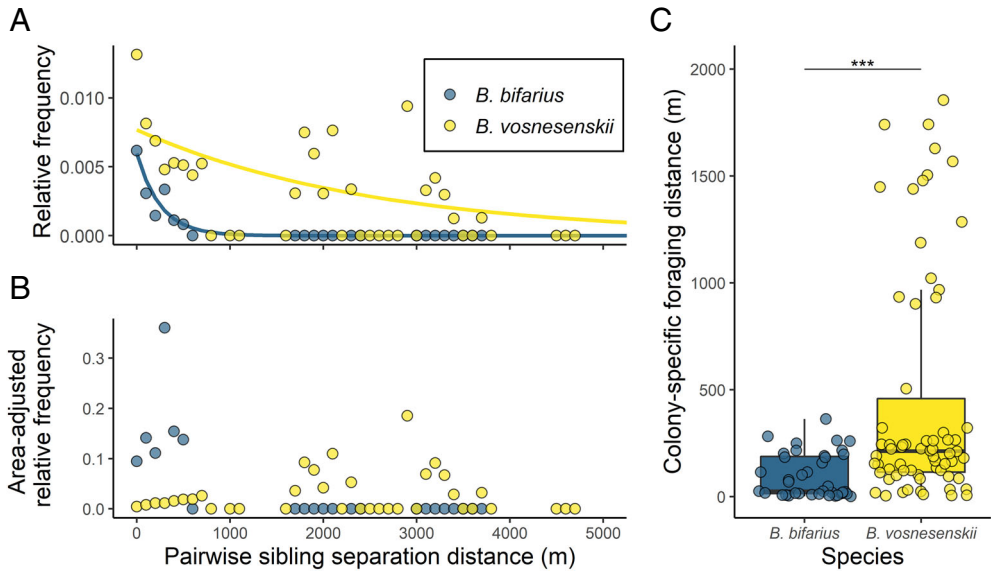

Fig. 3. Sibling separation and colony-specific foraging range. (a) Points represent the number of observed sibling pairs divided by the number of possible pairs from all genotyped specimens sampled within a given distance range. Fitted lines are predicted values from binomial GLM. (b) Values are the relative frequency of sibling capture adjusted for the area represented by the separation distance in 100 m annuli. (c) Boxplot with overlaid observations of colony-specific foraging distance for each species. [Colour figure can be viewed at wileyonlinelibrary.com].

Sibling separation distance and colony-specific foraging range

We tagged 275 *B. vosnesenskii* but only re-observed three of them at a site different from their original marking location (318, 535, 3406 m). The individuals re-observed at 318 and 535 m were each marked in a forest site and then re-observed within the focal meadow. The individual re-observed at 3406 m was marked at a core forest site and recaptured at a distant meadow (furthest south points in Fig. 1a) in flight.

Siblings of *B. vosnesenskii* were detected at distances substantially greater than *B. bifarius* (*B. vosnesenskii*, median = 334, $Q_1 = 170$, $Q_3 = 577$; *B. bifarius*, median = 49.5, $Q_1 = 23.4$, $Q_3 = 366$; $W = 4318$, $P < 0.001$). Colony-specific foraging distance also differed significantly between species (Fig. 3; *B. vosnesenskii*, median = 213, $Q_1 = 114$, $Q_3 = 459$; *B. bifarius*, median = 25.3, $Q_1 = 13.5$, $Q_3 = 187$; $W = 620$, $P < 0.001$), with *B. vosnesenskii* sibling pairs commonly detected between the core and distant sites (Fig. 3). The relative frequency of sibling pair samples for both species decreased with separation distance (*B. vosnesenskii*, $\beta = -3.9\text{x}10^{-4} \pm 6.4 \times 10^{-5}$, $P < 0.001$; *B. bifarius*, $\beta = -3.97 \times 10^{-3} \pm 7.9 \times 10^{-4}$, $P < 0.001$). The relationship between sibling separation distances and area-adjusted relative frequency was non-significant (*B. vosnesenskii*, $\beta = 8.15 \times 10^{-5} \pm 7.6 \times 10^{-4}$, $P = 0.91$; *B. bifarius*, $\beta = -2.2 \times 10^{-3} \pm 2.9 \times 10^{-3}$, $P = 0.45$). Because we captured a smaller proportion of the estimated number of colonies for *B. bifarius* compared *to B. vosnesenskii*, we recalculated mean *B. vosnesenskii* colony-specific foraging distances after sub-sampling to the detection rate of *B. bifarius* in 2018. This approach allows us to determine if the differences observed between species were due to the low detection of sibling pairs for *B. bifarius*. Sub-sampling of *B. vosnesenskii* reduced the estimate of colony-specific foraging distance by 14% (Observed median: 213 m, Mean of 10 000 estimates of the median: 185 m), but this is still substantially larger than observed values for *B. bifarius* (Observed median: 25 m; Appendix S1).

Plant use across distance

Within 1000 m, plant species use by siblings of both species was more dissimilar as separation distance increased (Fig. 4a; *B. vosnesenskii*, $\beta = 3.4\text{x}10^{-3} \pm 7.7 \times 10^{-4}$, $P < 0.001$; *B. bifarius*, $\beta = 4.5 \times 10^{-3} \pm 1.6 \times 10^{-3}$, $P = 0.005$). For *B. vosnesenskii* alone (with all distances included), there was no significant relationship with distance as the inclusion of distant captures meant that most pairs were found foraging at the flowers of

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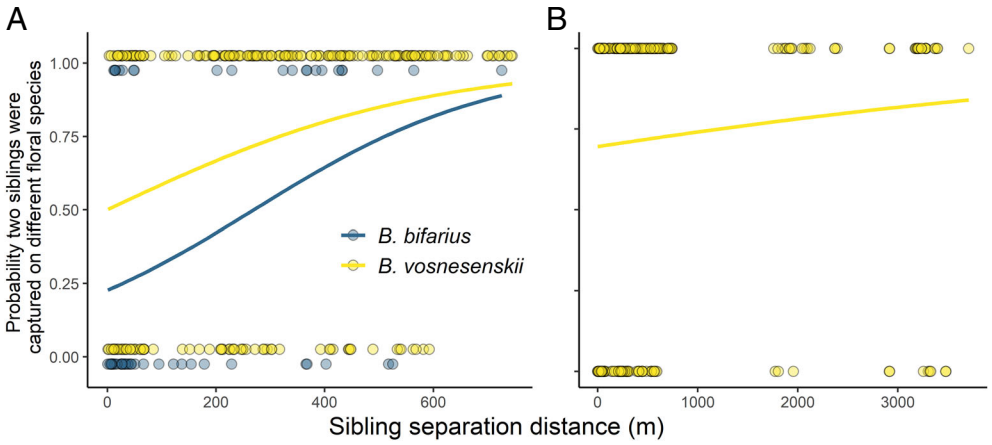

Fig. 4. Relationship between sibling separation distance and whether or not the pair was foraging on the same flower species. (a) For both species and for distances <1000 m, the probability that two siblings were captured on different flower species increases with separation between siblings. (b) For *B. vosnesenskii*, the inclusion of distant sibling captures results in most sibling pairs foraging on different plants and the loss of a relationship with distance. [Colour figure can be viewed at wileyonlinelibrary.com].

different plant species (Fig. 4b; $\beta = 2.2 \times 10^{-4} \pm 1.5 \times 10^{-4}$, $P = 0.145$). To explore the possibility that differences were due to turnover of plant species across time rather than space, we repeated the analyses including only siblings collected within 3 days of each other and found similar results (Within 1000 m: *B. vosnesenskii*, $\beta = 3.5 \times 10^{-3} \pm 1.2 \times 10^{-3}$, $P = 0.004$; *B. bifarius*, $\beta = 8.1 \times 10^{-3} \pm 3.1 \times 10^{-3}$, $P = 0.009$; All distances: $\beta = 1.2 \times 10^{-4} \pm 2.4 \times 10^{-4}$, $P = 0.628$). Repetition of this analysis at different thresholds (from 1 to 20 days) did not change the direction or significance of results.

Habitat connectivity

Workers from the same colonies were detected within both the forest and meadow, as expected based on randomisation of family assignment (Fig. 5, Mean ± SD of shuffled expectation *B. vosnesenskii*, 34.9 ± 3.54; *B. bifarius*, 4.50 ± 2.55. Observed *B. vosnesenskii*, 32; *B. bifarius*, 7). Visitation dissimilarity between sites increased significantly with linear distance for *B. vosnesenskii* (Fig. 6a; $\beta = 1.57 \times 10^{-4} \pm 5.5 \times 10^{-5}$, $P = 0.007$) but not for *B. bifarius* (Fig. 6b; $\beta = 3.2 \times 10^{-4} \pm 1.9 \times 10^{-4}$, $P = 0.124$), indicating that closer sites were more likely to share colonies, at least for *B. vosnesenskii*. Neither species showed an effect of vegetation heterogeneity on the visitation dissimilarity of sites with increased distance, suggesting that transitions between habitats do not create barriers to movement (*B. vosnesenskii*, $\beta = 0.055 \pm 0.051$, $P = 0.283$; *B. bifarius*, $\beta = -0.071 \pm 0.20$, $P = 0.73$).

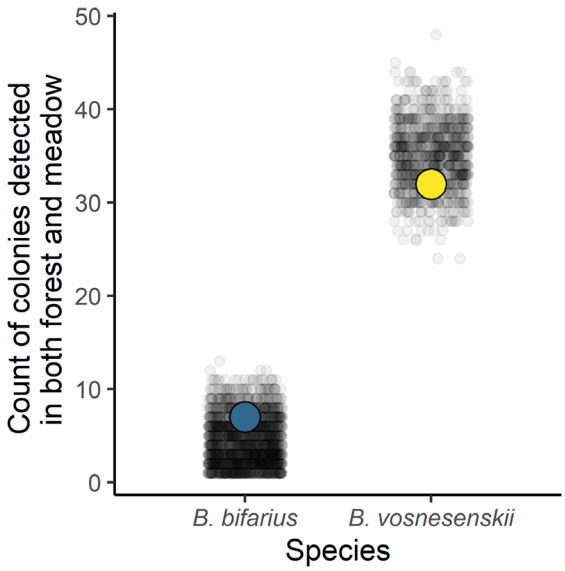

Fig. 5. Number of colonies observed foraging within both core forest and meadow patches (coloured points) compared to 1000 random draws (grey circles). [Colour figure can be viewed at wileyonlinelibrary.com].

Discussion

Understanding organismal movement and the influence of landscape composition on it is critical for species ecology and conservation planning (Hamilton & May, 1977; Taylor *et al.*, 1993; Ricketts, 2001; Fahrig, 2003). Earlier work suggested that structurally dense habitats such as forests represent strong barriers to bumble bee movement (Bowers, 1985), but we found no support for this in two species of bumble bees in a montane forest–meadow landscape in the Sierra Nevada. Although the two species differed substantially in the scale of their foraging movements (Fig. 3), there was no evidence to suggest that forests or changes in landcover act as barriers to movement for either species (Figs. 5 and 6). Furthermore, we found no support for the contention that high-elevation bumble bees have a substantially reduced foraging range, in contrast to prior studies (Elliott, 2009; Geib *et al.*, 2015). We observed relatively long foraging distances for both species compared to prior investigations within high-elevation environments. Most colonies appear

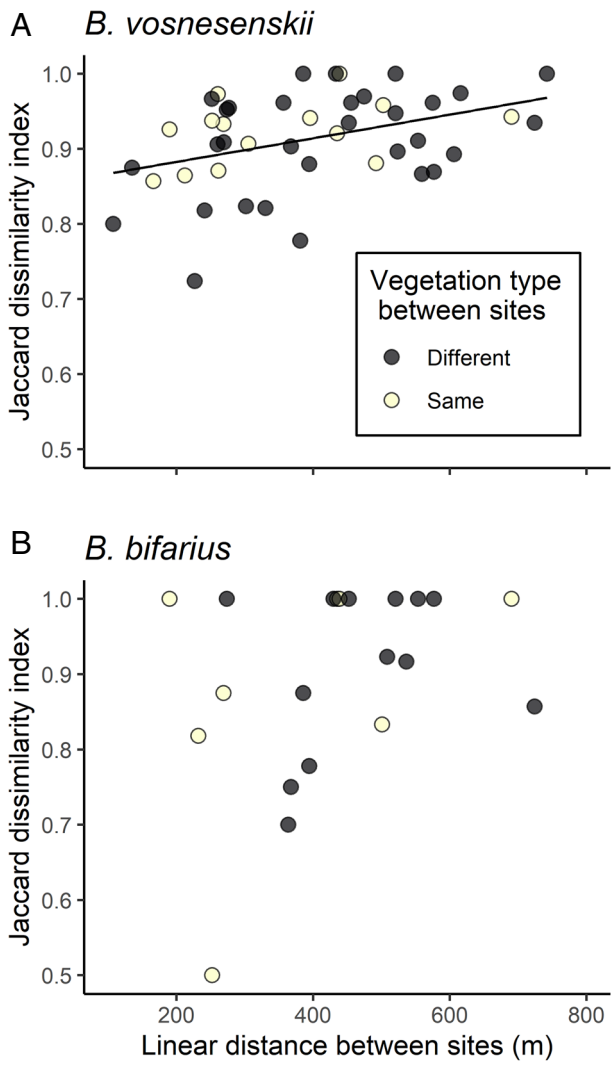

Fig. 6. Jaccard visitation dissimilarity between sites by geographic distance and vegetation type. (a) For *B. vosnesenskii*, visitation dissimilarity is positively related to the linear distance between sites. (b) No relationship between site-to-site distance and visitation dissimilarity was observed for *B. bifarius*. Neither species exhibited differences explained by the vegetation type between sites. [Colour figure can be viewed at wileyonlinelibrary.com].

to use directed movements to access a mix of floral species among forest gaps and open meadows (Fig. 5).

Our results support the idea that bumble bee foraging is plastic among different landscape contexts and that a heterogenous habitat can drive long-distance foraging if more distant patches are profitable (Jha & Kremen, 2013; Olsson *et al.*, 2015; Pope & Jha, 2018). Bumble bee movement is often modelled using a simple distance-decay function, with individuals dispersing from the central colony location with some declining probability (Lonsdorf *et al.*, 2009). This pattern was true for sibling separation distances within 1000 m (Fig. 3a); however, large separation distances occurred more frequently than would be expected by a simple distance-decay function. Because we observed no statistically clear relationship for the area-adjusted estimate of separation distances (Fig. 3b), it seems probable that we are observing the outcome of foraging behaviours, which respond to patchy resource environments. Much of the area in between the core sites and distant sampling patches are resource-poor conifer forests. Foragers encountering these low-quality habitats essentially have two choices: either return to the last known resource location or begin rapid movement towards distant foraging habitat, possibly using olfactory cues. Therefore, it seems likely that, as foragers encounter the low-resource conifer forests, they move in a directed fashion towards the next high-quality resource patch (Van Dyck & Baguette, 2005; Olsson *et al.*, 2015). In this case, simple distance-based corrections for an unsampled area (i.e. our area-adjusted relative frequency) overestimate the potential habitat available at greater distances and, also importantly, incorrectly represent foraging behaviour as a diffusive movement process rather than the result of learned routes and directed foraging behaviours (Woodgate *et al.*, 2016, 2017).

Large spatial gaps in resources or a suitable habitat may act as barriers to animal movement (Kuefler *et al.*, 2010; Krewenka *et al.*, 2011). Earlier work on bumble bees suggested that forests could constrain bumble bee workers in montane environments to forage only within the meadow nearest to their colony (Bowers, 1985). In contrast, we observed that intervening forests between meadows did not function as barriers for either bumble bee species. Instead, both species, and indeed different individuals from the same colony, used resources within both forest gaps and open meadows (Fig. 5), necessitating movement through forested areas. *Bombus vosnesenskii* foragers travelled over a kilometre through areas of unfavourable foraging habitat to reach flower-rich patches. Siblings foraging across these distances and across the potential forest barrier were less likely to be foraging on the same plant species (Fig. 4), suggesting that foraging among landcover types and among patches of the same habitat may give colonies access to diverse pollen sources. A prior study of *B. terrestris* and *B. pascuorum* in English forests similarly found little support for the idea that forests impede foraging movements (Kreyer *et al.*, 2004). Furthermore, when we estimated the visitation dissimilarity between sites in terms of their shared colonies, there was no statistically significant effect of vegetation type between sites on their dissimilarity (Fig. 6). This suggests that, if resources are within the flight range of a colony, individual foragers can and do access them regardless of the intervening landcover. Our result lends support to a recent study showing that resource abundance, not habitat connectivity, explained differences in the reproductive output of colonies placed within experimentally fragmented forests (Herrmann *et al.*, 2017). Further studies monitoring colonies within different habitat contexts could help to understand the generality of these findings. Currently, there seems to be little support for the prior suggestion that forests or resource-poor matrixes present a barrier to the movement of bumble bees so long as resources are available within economically profitable flight distances (Cresswell *et al.*, 2000; Olsson *et al.*, 2015).

Prior studies have suggested that the bumble bee foraging range is reduced in high-elevation habitats (Bowers, 1985; Elliott, 2009; Geib *et al.*, 2015). We found no support for

this contention. We observed colony-specific foraging distances of up to 1900 m (median = 213, $Q_1 = 114$, $Q_3 = 459$) and the recapture of a tagged individual at over 3000 m for *B. vosnesenskii*. At lower elevations, maximum colony-specific foraging distances for *B. vosnesenskii* range from 600 m (Jha & Kremen, 2013) to just over 3000 m (Mola, 2019). Substantially longer *maximum* distances (>10 km) were observed for sibling separation distances for *B. vosnesenskii* within an agricultural landscape (Rao & Strange, 2012), but *average* separation distance was much lower. In all cases, our results fall within the range of prior estimates of *B. vosnesenskii*'s foraging at lower elevations. Although the distances observed for *B. bifarius* were shorter, these appear to be species-specific differences and not a response of bumble bee foraging at high elevations. The explanation offered in prior studies, that foraging range is reduced as floral resource density increases, may be true, but we contend that the observed short foraging ranges in prior studies are likely artefacts of study design rather than bumble bee foraging patterns in high-elevation environments (reviewed in Mola & Williams, 2019). It seems likely that, as resource density increases, foraging range is reduced (Pope & Jha, 2018), which could occur in high-elevation environments with dense, co-flowering sub-alpine plant communities, but we do not think this occurs as a *de facto* consequence of foraging within high-elevation environments.

We observed a striking difference in the foraging distance of the two species, with *B. bifarius* siblings never observed more than 726 meters apart, whereas *B. vosnesenskii* siblings were frequently captured within both the core and distant sites (>1500 m apart). Species-specific movement differences among bumble bees are fairly well documented for European species (Knight *et al.*, 2005; Redhead *et al.*, 2016), but patterns are only beginning to emerge for North American species. Although it seems as if the absolute estimate of foraging distance is highly sensitive to a study's methodology or landscape, clear and consistent relative patterns of foraging distance emerge across studies (Mola & Williams, 2019). Our results support prior studies suggesting that *B. bifarius* has a relatively short foraging range (Geib *et al.*, 2015), whereas *B. vosnesenskii* is capable of much longer-distance flight (Rao & Strange, 2012; Jha & Kremen, 2013; Mola, 2019). Here, we demonstrate for the first time the differences in foraging distance for these species in a common landscape. In population genetic studies with these species, *B. bifarius* appears to have substantial genetic differentiation across its range, whereas *B. vosnesenskii* appears relatively panmictic (Lozier *et al.*, 2011; Jackson *et al.*, 2018). It is interesting to consider whether the relationship across movement scales, from foraging distance to genetic structure, is sufficiently consistent across bumble bee species to allow for the prediction of dispersal propensity and population structure from fine-scale foraging movements.

Our results suggest a few key points relevant for bumble bee conservation and habitat management. First, our study shows that forest or resource gaps do not significantly limit bumble bee movement, especially for far-ranging species such as *B. vosnesenskii*. It may be that, in systems with substantially more dense forest, landcover may act as a barrier, but no evidence yet supports this claim. Land managers seeking to provide habitat for bumble bees should therefore focus on providing adequate resources within ~1000 m of suspected nesting habitat, with less concern for the interceding landcover between resource patches. Second, our study demonstrates that not only are forests not barriers to movement but that forest understorey and gaps provide a key resource for bumble bees within our study area (Summary plant species list in Table S1). Prior studies in this region focused only on the meadow habitats (Hatfield & Lebuhn, 2007; VanWyk, 2018), but it is clear from our results that colonies use both forest and meadow resources at frequencies expected from a random resampling. Forest management practices targeting pollinators have generated much recent interest (Rivers *et al.*, 2018), and our study lends support to the idea that these habitats can provide key resources for bumble bees. Finally, we identified highly significant, species-specific differences in foraging distance, even for two bumble bees using a common landscape. When managing a particular species, it is important to determine the species-specific movement propensity as even closely related species may not be a good proxy. Relationships with body size or colony size may serve as appropriate proxies (Westphal *et al.*, 2006; Greenleaf *et al.*, 2007), but this remains to be verified for a wide range of species and contexts.

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Author Contributions

JMM and NMW designed the study. JMM collected the field data. SO performed DNA extractions and library prep. JMM and MM analysed the sequence data. JMM wrote the initial draft of the manuscript. NMW and JMM rewrote drafts together. All authors provided feedback and edits to the final draft of the manuscript.

Data Availability

Genetic data are available as BAM files in the NCBI Short Read Archive (accession no. PRJNA610901). Field-collected data and site metadata are available on Dryad (https://doi.org/10.25338/B86G7T). All scripts used to conduct analysis and generate figures are available on GitHub (https://github.com/John-Mola/bb-forage-mvmt-eco-ent).

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Full description of sub-sampling procedure to compare species with different sample sizes.

Table S1. Summary table of floral hosts for *Bombus vosnesenskii* and *Bombus bifarius*.

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