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Non-native plants affect generalist pollinator diet overlap and foraging behavior indirectly, via impacts on native plant abundance

Sandra Gillespie (iD) · **Elizabeth Elle**

Abstract Flowering invasive plants can have dramatic effects on the resource landscape available to pollinators. Because many pollinators exhibit behavioral plasticity in response to competitor or resource density, this in turn can result in impacts on ecological processes such as pollination and plant reproduction. We examine how interactions between five common generalist eusocial bees change across an invasion gradient by examining how bee abundance and diet overlap changed with variation in both invasive plant abundance and competitor abundance in a temperate oak-savannah ecosystem. Specifically we focus on the bumblebees *Bombus bifarius*, *B. mixtus*, *B. melanopygus* and *B. vosnesenskii*, as well as the non-native honeybee *Apis mellifera*, and their interactions with the native flowering plants *Camassia quamash*, *Camassia liechtlinii*, and the invasive shrub *Cytisus scoparius*. We further examine whether changes in pollinator visits to the invasive and two common native plants can explain changes in diet overlap. Abundance of the invasive plant and other common floral resources had strong impacts on focal bee abundance, with certain species more likely to be present at highly invaded sites. This may be because highly invaded sites tended to be embedded in forested landscapes where those bees are common. Diet overlap was most affected by abundance of a common native plant, rather than the invasive plant, with diet overlap increasing non-linearly with abundance of the native plant. Furthermore, *Apis mellifera*, did not appear to have direct competitive effects on native bumblebees in this habitat. However, visit patterns suggest that bees most abundant at highly invaded sites may compete for access to native resources. Thus the impacts of this invasive plant on our focal bee species may be primarily indirect, via its' competitive effects on native plants.

S. Gillespie (✉)
University of the Fraser Valley, 33844 King Rd.,
Abbotsford, BC V2S 7M8, Canada
e-mail: Sandra.Gillespie@ufv.ca

E. Elle
Evolutionary and Behavioural Ecology Research Group,
Department of Biological Sciences, Simon Fraser
University, Burnaby, BC V5A 1S6, Canada
e-mail: eelle@sfu.ca

Introduction

Changes in local resource density driven by invasive plants can affect community composition at multiple

trophic levels leading to emergent impacts on species interactions (Bezemer et al. 2014; McCary et al. 2016). For example, within fragmented ecosystems, invasive plants can have dramatic impacts on plant community composition (Pysek et al. 2012) that can in turn affect both plant-pollinator interactions by changing resource availability (Albrecht et al. 2016; Brown et al. 2002; Herron-Sweet et al. 2016) and potentially interactions between the pollinators themselves. This is because bees are known to modify their foraging behavior in response to resource abundance, resource quality (Robertson et al. 1999), competitor density (Brosi and Briggs 2013) and opportunity costs for foraging on complex flowers (Muth et al. 2015), all of which may be affected by an invasive plant.

Furthermore, resource quality can be a function of competitor abundance. Competing pollinators may deplete floral nectar or pollen and thus reduce resource quality (Heinrich 1976a; Robertson et al. 1999). As an invasive plant increases in density, it may reduce native plant abundance via resource competition (Jauni and Ramula 2015), increasing competition among pollinators for resources provided by native plants. However, a flowering invasive plant may provide an alternative resource for outcompeted pollinators (Harmon-Threatt and Kremen 2015), if they are capable of foraging on the invasive. This means the impact of competitors in invaded communities may depend on the foraging flexibility of pollinators, and whether they vary in ability to use the non-native resource.

These context-dependent foraging shifts have been studied extensively in bumblebees, where worker foraging behavior is a model system for optimal foraging and decision making. Some of the earliest studies of resource partitioning examined resource use relative to tongue length in bumblebees (Heinrich 1976b; Ranta and Lundberg 1980). Current research has demonstrated that bumblebees are responsive to both competitor density (Brosi and Briggs 2013) and resource abundance (Cartar 2009).

Our project focuses on interactions among five common generalist social pollinator species in the Oak Savannah of Southern Vancouver Island, a highly fragmented ecosystem spread across multiple urban parks and conservation areas. For pollinators, we focus on four native, short tongued bumblebee species: *Bombus bifarius* (Cresson)*, Bombus mixtus* Cresson*, Bombus melanopygus* Nylander and *Bombus*

vosnesenskii Radoszkowski. These species are the most abundant bumblebees at our sites, and have similar (short) tongue lengths and a high degree of overlap in floral resource use (Wray et al. 2014). We also include the non-native honeybee, *Apis mellifera* Linnaeus, because it is a common floral visitor with high resource use overlap with our focal bumblebee species. Furthermore, some evidence suggests that non-native honeybees may compete with wild pollinators for resources (Dohzono and Yokoyama 2010).

We examine pollinator foraging behavior and the potential for competition for resources, using two focal native plant species, as well as the introduced *Cytisus scoparius* (L.) Link (Fabaceae, scotch broom). These include two native perennials, *Camassia quamash* (Pursh) Greene, and *Camassia leichtlinii* (Baker) S. Watson (Asparagaceae). Both *Camassia* species produce multiple blue to purple flowers on a single stem with pollen and nectar rewards that are easily accessible to all species of bees as well as other floral visitors that are not the focus of this paper (solitary bees, flies, wasps). *Cytisus scoparius* has hundreds of nectarless yellow pea-shaped flowers on a single bush with access to rewards limited to large bodied bees that can open, or "trip" the flowers (Knuth 1906; Parker 1997; Traveset and Richardson 2014). Our pollinator species vary in their collection of *C. scoparius* pollen, potentially due to differences in worker body size (Gillespie et al. 2017), thus we may expect them to differ in their responses to *C. scoparius* density. We focus on *Camassia* as native species because they are extremely common, have easily accessible flowers, and are likely important resources for a diversity of floral visitors. They are also the most highly visited native plants by our focal bees, which may be competing for access to floral rewards (Based on data from Wray et al. 2014). *Cytisus scoparius* is a highly disruptive non-native plant in this ecosystem, capable of completely replacing the native flora in the absence of active management (Shaben and Myers 2010). It is also pollinator dependent, but limits its floral visitors to large-bodied bees due to flower morphology: larger bodied bees are most efficient at 'tripping' the flower keel and accessing pollen rewards (Parker 1997). At our sites, *C. scoparius* and both *Camassia* spp. have coinciding blooms occurring in late spring to early summer. *Cytisus scoparius* density varies across sites primarily due to removal efforts by volunteers.

We examine how variation in non-native plant density and abundance of other pollinator species affect interactions among these potential competitors, and interactions between pollinators and plant species. Specifically, we ask (1) How does bee abundance vary with invasive plant abundance and other site characteristics; (2) how does bee diet overlap change with focal plant and competitor abundance and (3) how do visit rates by bees to focal plants change with plant and competitor abundance?

Materials and methods

Field sites

Sites comprised 18 oak-savannah fragments in the greater Victoria area, British Columbia, Canada, 1.75 km or more apart (Supplemental Table 1). At each site, we delineated a 1 ha focal area, encompassing populations of all our focal plant species, where present. At several sites this was split into two 1/2 ha patches, due to the steep rocky nature of the habitat. Sites varied in *C. scoparius* density primarily due to removal efforts by local volunteers and land managers (S. Gillespie, pers. obs).

We divided sampling periods within a day into morning (10–12), mid-day (12–2), and afternoon (2–4) periods. Each site was sampled at least twice for each period (morning, mid and afternoon) in 2014 and 2015, for a total of 6 or more samples for each site for each year collected over the course of focal species bloom. We sampled only during pollinator appropriate weather (temperatures above 15 °C and low winds).

Plant community sampling

On each sampling date, we quantified the flowering community using four 50 m transects spaced 50 meters apart throughout the sampling area. We sampled 10, 0.25 × 2.0 m quadrats per transect, perpendicular to the transect at random distances ranging from 1 to 5 m. Within each quadrat we counted the number of flowering units of each plant species in bloom. For herbaceous plants, a flowering unit was defined as an individual stem, flower or inflorescence to which a bee must fly to access resources. A flowering unit for both *Camassia* spp. was defined as a single inflorescence (*C. quamash*: average 1.97 open flowers, range 1–10;

C. leichtlinii: average 2.45 open flowers, range 1–11). For *C. scoparius*, a flowering unit was an individual branch on a bush with no further flowering branches arising from it (Average 2.29 open flowers, range 1–10). To estimate the density of our focal plants at the site by year level, we first summed the number of flowering units across plots for each sampling day, and then averaged the number of flowering units across sampling days for each site. Thus plant density is measured as flowering stems/40 m². Due to time constraints, we estimate resource availability as the number of flowering stems, rather than nectar or pollen resources explicitly.

Pollinator community sampling

The pollinator community was quantified during each sampling date by two people netting insects directly off of flowers, each for 20 min, for a total of 40 min sampled per site on each sampling date (over 120 min of sampling each year). While processing insects, the timer was stopped. Netters sampled throughout the 1 ha area on all plant species with open flowers. We collected all flower visitors—defined as any insect that was contacting the sexual parts of the plant. Butterflies, queen bumblebees, and honeybees were netted, identified, noted, and released. Insects were pinned and identified to species, or genera or morphospecies where species identification was not possible (Supplemental Table 2); however only focal bee identity was relevant to our analysis. To calculate the site-level abundance of each bumblebee species we averaged the number collected across sampling dates, for each site in each year.

Observations of visiting pollinators

To quantify visits by our focal pollinators independently of netting, we observed pollinator visits to our focal plants for two 10 min periods per focal plant species per sampling date for a total of at least 120 min of observation per plant species per site per year. For *C. leichtlinii* and *C. quamash*, we watched up to 20 flowering units of each plant, depending on the numbers present at locations chosen haphazardly for observation. For *C. scoparius*, because of its structure and very low visit rates, we observed up to 40 flowering units (branches) on an individual shrub. We identified bumblebees and honeybees to species on the

wing, and other visitors to morphospecies groups (Supplemental Table 2). For each insect that visited flowers within our patch, we counted the number of stems visited and the number of flowers visited per stem. From this data, for each sample date, we calculated the number of individuals of each focal pollinator seen per flowering unit observed. This accounts for variable numbers of flowering units observed across some samples. We then averaged this value for each observation date, then across observation dates for each site in each year.

Analysis

All analyses were conducted in R. We examined explanatory variables using variance inflation factors (VIF). Unless otherwise stated, VIF were all less than 3.0, indicating that covariance is not sufficient to confound our analysis (Zuur et al. 2007). In all analyses, focal plant densities were log transformed to improve normality. Response variables were log transformed when necessary, as indicated in statistical tables. All variables were calculated at the site-by-year level to account for variable sample sizes among sites and years. One site had to be discarded for 2015 (Little Saanich Mountain), due to highly disruptive invasive species control efforts. Data is averaged within site and year by necessity, as individual dates may have low numbers of observations of our focal insects. Our study spans a 1 month period in early spring. While the plants are highly structured in their phenology, all of our focal insects are all social insects that have long-lived colonies that should be common within the landscape during that time, though their local abundance may change in response to resource availability.

Bumblebee site abundance

We used general linear mixed models to examine which site characteristics explained the abundance of each focal bee species (Bates et al. 2015). Our model examined what effect *C. scoparius*, *C. leichtlinii,* and *C. quamash* density and year had on relative focal bee abundance, with site included as a random variable. For all analyses, type 3 sums of squares were calculated using the "Anova" function in the car package (Fox and Weisber 2011), while the slope of each linear relationship was extracted using the summary function (R-Development-Core-Team 2009).

Diet overlap

Diet overlap was calculated using the Morista Index (Krebs 1999) for each focal bee combination at each site. For example, we calculated the diet overlap of *B. bifarius* with *B. melanopygus* at each site, based on the resource use they have in common, and then similarly calculated overlap of *B. bifarius* with all other focal bee species at that site. We used our netting data to approximate resource use as it estimates the proportion of bees at a site that are using each visited flowering plant. Low values of the Morista index indicate that two bee species are using disparate resources, while high values indicate use of similar resources. The Morista index was chosen specifically because it handles smaller, and unbalanced sample sizes with low bias (Smith and Zaret 1982); however to be conservative we removed any samples with fewer than 5 individual bees in a combination at that specific site.

For each focal bee species, we asked whether its' diet overlap with competitors changed with any site characteristics. To test this, we asked whether *C. scoparius*, *C. leichtlinii,* or *C. quamash* density, partner identity, year, total pollinator abundance at that site, and the partner bee-by-plant interactions, affected the Morista index for each focal bee species, with site included as a random effect. Non-significant interactions were dropped from the final model.

Focal pollinator visit patterns

To analyze the effects of site characteristics on visit patterns to focal plants, we subdivided data by whether we observed a focal species in bloom on a given observation date. Then, to calculate focal pollinator and plant density for analyses of focal pollinator visit patterns, we only included those observations where the focal plant in question was blooming. Thus, calculations for *C. quamash* analyses only include those dates where we could observe pollinator visits to *C. quamash*. This means for example that the flowering community during *C. quamash* bloom will be different than that for *C. scoparius*, as they do not have perfect overlap in flowering time.

When examining VIF for these subdivided data, we find that they are greater 3.0 for focal plant densities in the *C. leichtlinii* and *C. scoparius* samples, suggesting that plant densities were more correlated in these slightly later-flowering plant samples. To address this covariance, we summarized focal plant densities into a single gradient using principal component analysis. For both *C. leichtlinii* and *C. scoparius* visit rates, PC1 represents a gradient from high *C. scoparius* (negative values) to high *Camassia* density (positive values), and we refer to it as the *C. scoparius* to *Camassia* gradient. This gradient (PC1) explains ~ 57% of the variation in the variables included in the analysis. Other PCs explain 20% or less additional variation each, and examination of scree plots shows that only PC1 explains sufficient variation to be retained in further analyses (Supplemental Table 3).

For *C. scoparius* and *C. leichtlinii* samples, we asked whether the frequency of observation of each focal bee on each focal plant was affected by the *C. scoparius* to *Camassia* gradient (PC1), *B. mixtus*, *B. melanopygus*, *B. bifarius*, *A. mellifera* or *B. vosnesenskii* abundance, and sampling year, with site included as a random effect.

For bee visits to *C. quamash*, VIF values were less than 3 and focal plants were analyzed separately without using PCA. Thus for *C. quamash* our model examines whether visit patterns to each focal plant are affected by *C. scoparius*, *C. leichtlinii*, *C. quamash*, *B. mixtus*, *B. melanopygus*, *B. bifarius*, *Apis mellifera* or *B. vosnesenskii* abundance, and sampling year, with site included as a random effect.

Explanatory and response variables were transformed as necessary (Tables 1, 2, 3) to improve assumptions of normality. Where focal bee abundance data was sufficient for linear analysis, we used the lmer function with a logistic distribution (Bates et al. 2015). Where data were highly zero-skewed we used negative binomial models to examine whether explanatory variables affected the likelihood of observing a bee on a plant at a site. Then where there were sufficient numerical data (> 10 positive observations) we used general linear mixed models on the non-zero observations to test for an impact of site characteristics and focal bee abundance on the number of bees observed. To visualize significant effects, we used the Effect package in R (Fox and Hong 2009) to plot partial regressions with 95% confidence limits. Partial regression plots show the effect of adding the variable of interest to a model.

Results

Bumblebee site abundance and plant community patterns

We netted a total of 2840 focal pollinators across both years. Of these, 1355 were *A. mellifera*, 672 were *B. mixtus*, 296 were *B. melanopygus,* 294 *B. vosnesenskii* and 223 were *B bifarius*. *Camassia quamash* density varied from an average of 0.04–6 stems per m^2; *C. leichtlinii* varied from zero to 5.1 stems per m^2, while *C. scoparius* varied from zero to 25.7 stems per m^2.

While not sufficiently correlated to confound most analyses, sites with high *C. scoparius* have lower densities of both *Camassia* species (spearman correlation coefficient: − 0.43 for *C. leichtlinii*, − 0.50 for *C. quamash*), likely due to physical displacement, particularly at high *C. scoparius* densities. This pattern was stronger during observations of *C. leictlinii* (i.e.

Table 1 Impacts of focal plant abundance on focal bee abundance

Focal bee	*C. leichtlinii*	*C. quamash*	*C. scoparius*	Year
Bombus bifarius	0.62 (− 0.06)	0.58 (− 0.09)	**0.007** (0.20)	**0.05** (2014)
Bombus mixtus	**0.02** (0.80)	0.77 (− 0.13)	0.36 (− 0.19)	0.13
Bombus melanopygus	0.67 (− 0.9)	0.83 (− 0.5)	**0.04** (0.26)	**< 0.0001** (2015)
Bombus vosnesenskii	0.61 (0.09)	0.4 (0.18)	0.52 (0.07)	0.06
Apis mellifera	**0.01** (1.6)	**0.009** (2.0)	0.41 (0.35)	0.08

Values in table are *p* values, with values significant at *p* < 0.05 bolded, with the relationship slope in parentheses. Where year is significant, the year with more bees is in parentheses. Full statistical information in Supplemental Table 4

Table 2 Results of glm analysis of the impacts of focal plant abundance and partner bee identity on diet overlap as measured by the Morista index

Focal bee	Partner bee	C. quamash	C. leichtlinii	C. scoparius	Competitor density	Year	Partner bee × C. leichtlinii
Bombus bifarius	0.87	**0.0002** (0.08)	0.09 (0.04)	0.17 (− 0.02)	**0.01** (− **0.001**)	0.61	ns
Bombus mixtus	0.28	**< 0.0001** (edf = 3.3)	0.67 (0.013)	0.52 (− 0.003)	0.23 (7×10^{-5})	0.11	ns
Bombus melanopygus	0.002	**0.002** (edf = 2.1)	0.48 (0.017)	0.07 (− 0.018)	0.98 (5×10^{-6})	0.74	**0.005**
Bombus vosnesenskii	0.31	**0.00005** (0.06)	0.94 (0.001)	0.81 (− 0.002)	0.46 (0.0003)	**0.03** (2015)	ns
Apis mellifera	0.51	**0.0001** (edf = 2.2)	0.45 (0.01)	**0.02** (− 0.017)	0.59 (− 0.0002)	0.50	ns

Values in table are p values, with values significant at $p < 0.05$ bolded, with the relationship slope in parentheses. Where year is significant, the year with more bees is in parentheses. Where the relationship was non-linear, we include edf (estimated degrees of freedom), which indicates the number of nodes in the fit model (i.e. the shape of the curve). Full statistical information in Supplemental Table 5

later in the season when more *C. scoparius* was in flower).

Bombus bifarius and *B. melanopygus* both increased in abundance with *C. scoparius* abundance. *Bombus mixtus* was more common at sites with more *C. leichtlinii*, and *A. mellifera* increased with both *Camassia* species. *Bombus melanopygus* and *A. mellifera* were more common in 2015, while *B. bifarius* and *B. vosnesenskii* were more common in 2014 (Figs. 1, 2; Table 1; full statistics in Supplemental Table 4).

Diet overlap

Diet overlap increased with *C. quamash* density for all focal bees. This relationship was significantly non-linear for *B. mixtus*, *B. melanopygus* and *A. mellifera*, saturating at high *C. quamash* abundance (Table 2, Fig. 3a, Supplemental Table 5). For *B. vosnesenskii* diet overlap was also higher in 2015. Finally, for *B. melanopygus*, diet overlap was lower with *B. vosnesenskii* than with other partners (Table 2, Supplemental Table 5). There was also a significant interaction between partner bee identity and *C. leichtlinii* density for *B. melanopygus.* Diet overlap between *B. melanopygus* and *B. bifarius* declined with *C. leichtlinii* abundance while overlap with other partner bees was stable (Fig. 3b). Diet overlap declined with competitor abundance for *B. bifarius* only (Table 2).

Finally, diet overlap for *A. mellifera* declined with *C. scoparius* density (Fig. 3c).

Visit patterns

There was no effect of either floral resource or competitor abundance on visit rates of *B. bifarius* to *C. quamash* in the binomial model. For those sites where we observed *B. bifarius* visiting *C. quamash*, observations increased at sites with more *C. leichtlinii* (Fig. 4a). For *B. bifarius* visiting *C. leichtlinii* nothing was significant in the binomial model; however, for those sites where we observed *B. bifarius*, observations decreased with *B. melanopygus* site abundance (Fig. 4b). There was no effect of either floral resource or competitor abundance on observations of *B. bifarius* visiting *C. scoparius* (Table 3A, Supplemental Table 6).

Bombus mixtus visits to *C. leichtlinii* and *C. quamash* increased with *B. mixtus* site abundance. There was insufficient data to analyze *B. mixtus* visits to *C. scoparius* (Table 3B).

Nothing significantly affected *B. melanopygus* visits to *C. leichtlinii* or *C. quamash*. For visits to *C. scoparius*, nothing was significant in the binomial model, and there was insufficient data to apply a linear model (n = 8 observations; Table 3C).

Nothing affected *B. vosnesenskii* visits to *C. quamash* or *C. scoparius*. We were more likely to observe *B. vosnesenskii* visiting *C. lelichtinii* at sites

Table 3 Results of glm analysis of the impacts of focal plant and competitor abundance on the number focal bees per stem observed on each focal plant for (A) *B. bifarius*; (B) *B. mixtus*; (C) *B. melanopygus*; (D) *B. vosnesenskii*; (E) *A. mellifera*

Focal plant	Model type	n	C. leicht.	C. quam.	C. scop.	PC1
(A) B. bifarius						
C. quam.	Binary model	35	0.39 (0.46)	0.68 (0.33)	0.55 (0.23)	–
	Linear on non zero	15	**0.03** (0.02)	0.23 (− 0.01)	0.81 (0.001)	–
C. leicht.	Binary model	35	–	–	–	0.97 (0.02)
	Linear on non zero	16	–	–	–	0.26(− 0.003)
C. scop.	Binary model	21	–	–	–	0.98 (− 0.01)
(B) B. mix.						
C. quam.	Linear model	35	0.91 (− 3e−4)	0.69 (− 1.8e−3)	0.98 (− 5e−5)	–
C. leicht.	Linear model	35	–	–	–	0.84(0.0006)
(C) B. mel.						
C. quam.	Binary model	35	0.28 (1.0)	0.63 (1.96)	0.10 (− 0.35)	–
C. leicht.	Linear model	35	–	–	–	0.57 (− 0.001)
C. scop.	Binary model	21	–	–	–	0.51 (− 0.32)
(D) B. vos.						
C. quam.	Linear model	35	0.38 (− 1e−3)	0.35 (1.5e−3)	0.71 (2.7e−4)	–
C. leicht.	Binary model	35	–	–	–	0.11 (− 0.21)
C. scop.	Binary model	21	–	–	–	0.42 (− 0.4)
(E) A. mell.						
C. quam.	Linear model	35	0.61 (− 0.003)	0.87 (0.002)	**0.03** (− 0.001)	–
C. leicht.	Linear model	35	–	–	–	0.42 (0.008)
C. scop.	Binary model	21	–	–	–	0.28 (− 2.9)
	Linear on non zero	12	–	–	–	**0.004** (− 0.008)

Focal plant	B. mix.	B. mel.	B. bif.	B. vos.	A. mell.	Year
(A) B. bifarius						
C. quam.	0.50 (0.19)	0.15 (2.48)	0.16 (2.23)	0.57 (0.33)	0.20 (− 0.19)	0.96
	0.28 (− 0.002)	0.07 (0.02)	0.08 (0.03)	0.29 (− 0.004)	0.26 (0.002)	0.64
C. leicht.	0.65 (− 0.1)	0.84 (− 0.31)	0.30 (1.47)	0.13 (1.12)	0.74 (− 0.32)	0.28
	0.45 (− 0.001)	**0.01** (− 0.02)	0.09 (0.01)	0.75 (0.0006)	0.21 (− 0.001)	0.18
C. scop.	0.84 (0.07)	0.89 (− 0.25)	0.42 (1.5)	0.35 (0.53)	0.95 (− 0.01)	0.52
(B) B. mix.						
C. quam.	**0.008** (0.003)	0.21 (− 1.1e−3)	0.31 (7e−3)	0.54 (1.6e−3)	0.72 (− 2.1e−4)	0.31
C. leicht.	**0.0002** (0.004)	0.44 (0.007)	0.92 (− 0.001)	0.48 (− 0.002)	0.73 (0.0002)	0.31
(C) B. mel.						
C. quam.	0.20 (0.72)	0.12 (− 2.26)	0.79 (0.3)	0.31 (0.3)	0.06 (− 0.5)	–
C. leicht.	0.46 (0.001)	0.21 (0.01)	0.99 (− 8e−5)	0.83 (− 5e−4)	0.7 (− 3e−4)	0.5
C. scop.	0.28 (0.39)	0.25 (1.8)	0.89 (− 0.22)	0.70 (0.21)	0.81 (0.03)	0.84
(D) B. vos.						
C. quam.	0.62 (− 2.1e−2)	0.44 (2.5e−3)	0.75 (8e−4)	0.32 (9.2e−4)	0.90 (− 2.5e−5)	0.80
C. leicht.	0.95 (0.05)	0.49 (− 0.17)	0.27 (− 0.59)	**0.02** (1.69)	0.97 (− 0.03)	
C. scop.	0.17 (0.58)	0.52 (− 0.6)	0.32 (− 1.6)	0.54 (0.34)	0.94 (0.01)	–
(E) A. mell.						

Table 3 continued

Focal plant	B. mix.	B. mel.	B. bif.	B. vos.	A. mell.	Year
C. quam.	0.63 (− 0.001)	0.33 (− 0.02)	**0.002** (0.05)	0.80 (0.002)	**0.0003** (0.005)	− 0.28
C. leicht.	0.78 (− 0.0004)	**0.02** (− 0.04)	0.57 (0.009)	0.39 (0.005)	0.15 (0.002)	> 0.001 (2015)
C. scop.	0.87 (− 0.01)	0.31 (9.9)	0.71 (1.8)	0.30 (1.8)	0.20 (1.6)	0.33
	0.07 (0.001)	0.07 (− 0.01)	**0.004** (− 0.01)	**0.03** (0.006)	0.28 (0.0005)	0.06

Values in table are *p* values, with values significant at $p < 0.05$ bolded, with the relationship slope in parentheses. Where year is significant, the year with more bees is in parentheses. (Abbreviations: *B. mix.* = *B. mixtus*; *B. mel.* = *B. melanopygus*; *B. bif.* = *B. bifarius*; *B. vos.* = *B. vosnesenskii*; *A. mell.* = *A. mellifera*; *C quam.* = *C. quamash*; *C. leicht.* = *C. leichtlinii*; *C. scop.* = *C scoparius*). Full statistical information in Supplemental Table 6

Fig. 1 Impacts of site characteristics on focal bee abundance. **a** *Bombus bifarius* abundance increased with *Cytisus scoparius* density (stems/m²); **b** *Bombus mixtus* abundance increased with *Camassia leichtlinii* density (stems/m²); **c** *Bombus melanopygus* density increased with *C. scoparius* density (stems/m²); **d** *Apis mellifera* abundance increased with both *Camassia quamash* and *C. leichtlinii* density (stems/m²)
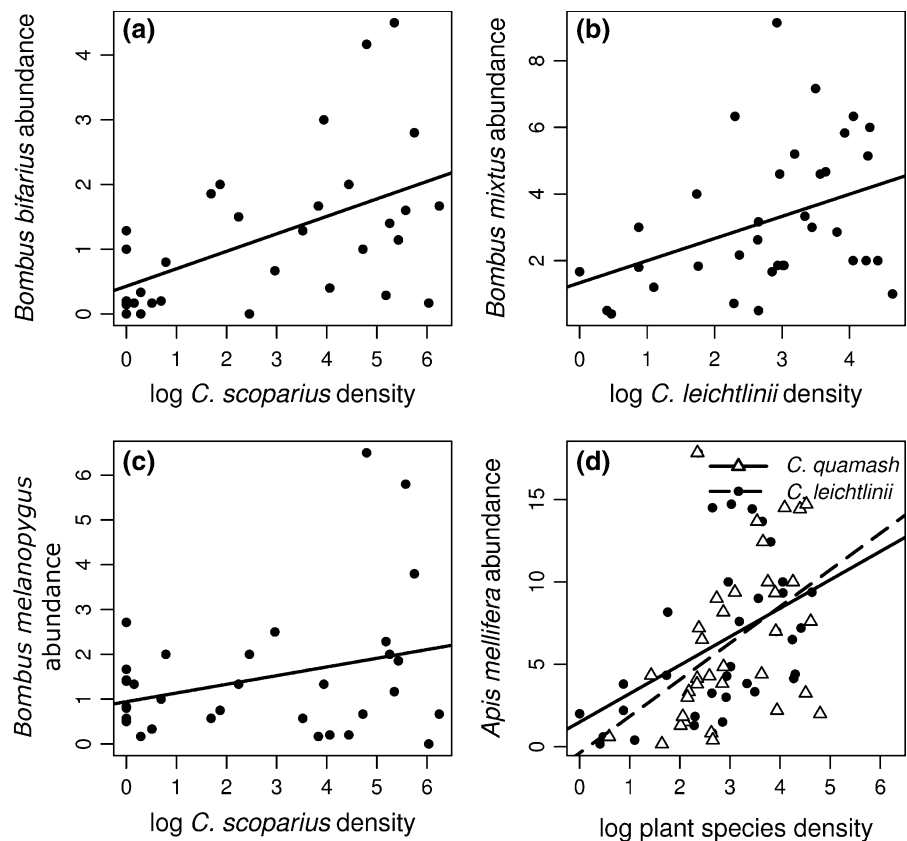
with more *B. vosnesenskii* overall (binary model) (Table 3D).

We observed more *A. mellifera* visiting *C. quamash* at sites with less *C. scoparius*, more *B. bifarius* and more *A. mellifera* (Fig. 5). More *A. mellifera* visited *C. leichtlinii* in 2015 and at sites with less *B. melanopygus*. For *A. mellifera* visits to *C. scoparius*, nothing was significant in the binomial model. When we examined patterns in *A. mellifera* at sites where it was present on *C. scoparius*, we saw more *A. mellifera* at sites with more *B. vosnesenskii*, and higher values of PC1 (less *C. scoparius* and more *Camassia*; Fig. 6). We observed *Apis mellifera* less frequently on *C. scoparius* at sites with more *B. bifarius*, and more frequently in 2014 (Table 3E).
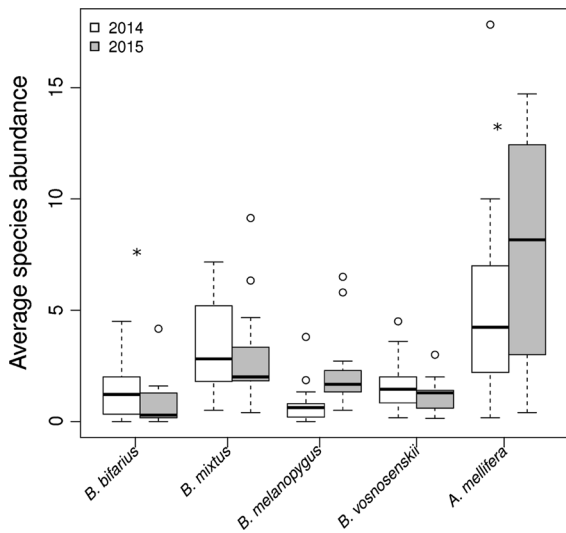
Fig. 2 Variation in focal pollinator abundance by year. An asterisk indicates a significant difference in bee abundance across years

Discussion

Focal bee abundance

Focal plant density was associated with variable changes in focal bee abundance. *Bombus bifarius* and *B. melanopygus* were both associated with sites with higher *C. scoparius* abundance, whereas *B. mixtus* and *A. mellifera* were more abundant at sites with more *C. leichtlinii,* and more *C. quamash* in the case of *A. mellifera. Apis mellifera* was also the most abundant of our focal bees and several species varied in abundance across years (Fig. 2). Year to year variation in focal bee abundance is likely related to changes in spring weather. The months preceding bloom in 2015 were considerably warmer and dryer than in 2014, with higher average temperatures and far fewer days without precipitation in February and March (mean temperature in February, March: 3.6, 7.4 °C in 2014; 8.3, 8.9 °C in 2015, Environment Canada, http://climate.weather.gc.ca/historical_data/search_historic_data_e.html). This may favor colony growth of different species, or cause shifts in bee phenology relative to flower phenology.

Previous work in our lab showed that *B. bifarius* and *B. melanopygus* are both associated with forested sites (Wray et al. 2014). In our data, high broom sites tended to be more highly forested in the surrounding
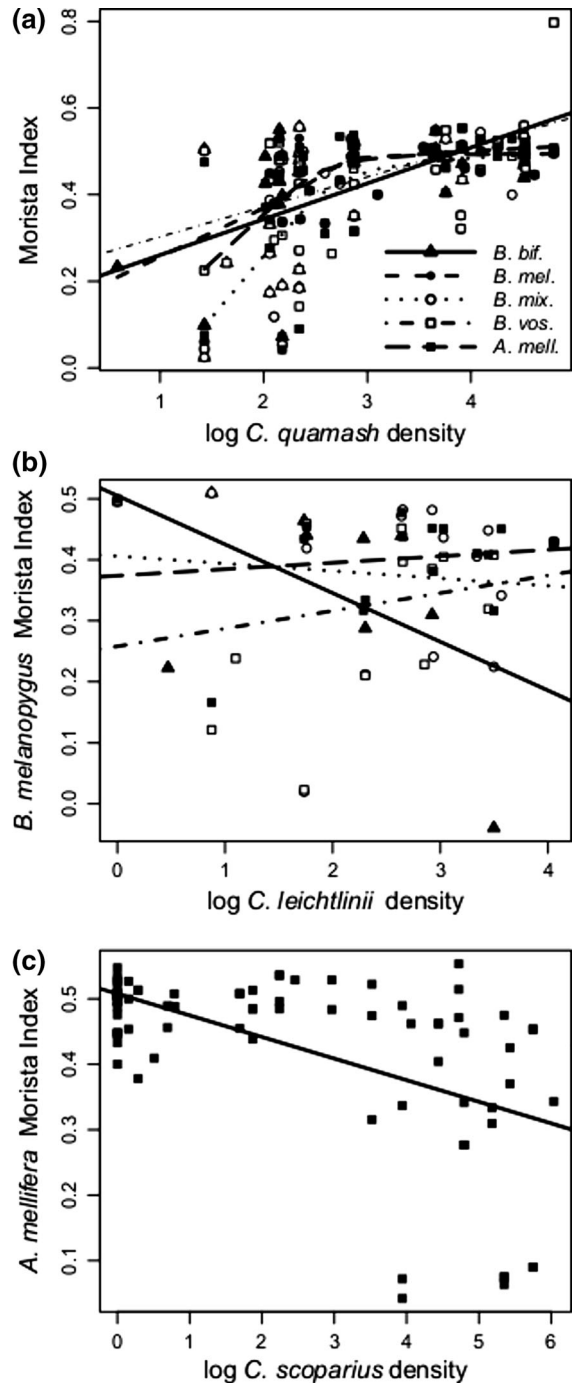

matrix, while lower broom sites are surrounded by other habitat types, mostly urban areas (correlation between forest cover within 400 m buffer, and log *C. scoparius* density: Pearson coefficient = 0.57; $p < 0.001$). This correlation may help to explain the pattern of *B. bifarius* and *B. melanopygus* co-

◄ **Fig. 3** Factors affecting resource overlap between different bee species. Higher values on the Y axis indicate more diet overlap. **a** Diet overlap for all species increased with *Camassia quamash* density (stems/m²), but the increase was non-linear for *Bombus mixtus, Bombus melanopygus* and *Apis mellifera*; **b** residual *B. melanopygus* diet overlap with *Bombus bifarius* declined with *Camassia leichtlinii* density (stems/m²), but did not change with other partner bees **c** *A. mellifera* diet overlap declined with *Cytisus scoparius* abundance (stems/m²). Residuals for **b** were calculated using a model fit with all model variables except partner bee identity and *C. leichtlinii* abundance (stems/m²)
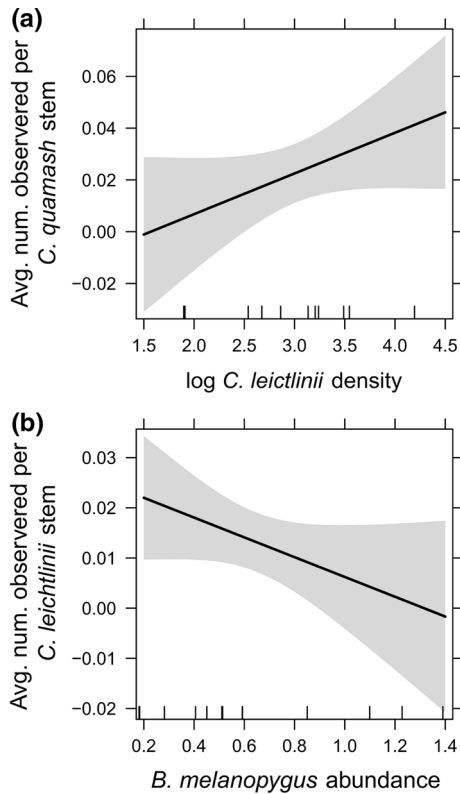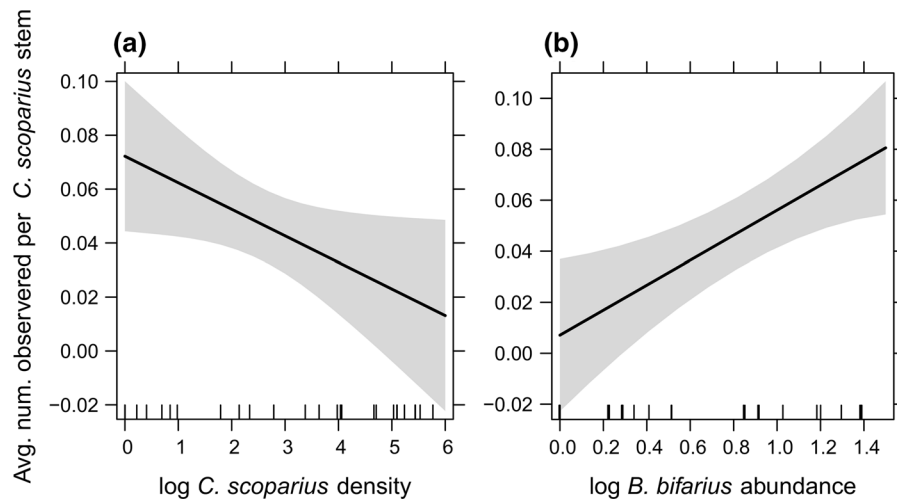

Fig. 4 Partial regressions showing factors significantly related to visit rates of *Bombs bifarius* to focal plant species. Grey bars represent upper and lower 95% confidence limits. **a** Observations of *B. bifarius* on *Camassia quamash* increased with log *Camassia leichtlinii* density (stems/m²). Model: *B. bifarius* observations ~ *Camassia leichtlinii* density + *C. quamash* density + *C. scoparius* density+ *B. mixtus* abundance + *B. melanopygus* abundance + *B. bifarius* abundance + *A. mellifera* abundance + *B. vosnesenskii* abundance, + sampling year + site (random effect). **b** observations of *B. bifarius* on *C. leichtlinii* decreased with *Bombus melanopygus* abundance. Model: *B. bifarius* observations ~ PC1 + *B. mixtus* abundance + *B. melanopygus* abundance + *B. bifarius* abundance + *A. mellifera* abundance + *B. vosnesenskii* abundance, + sampling year + site (random effect)
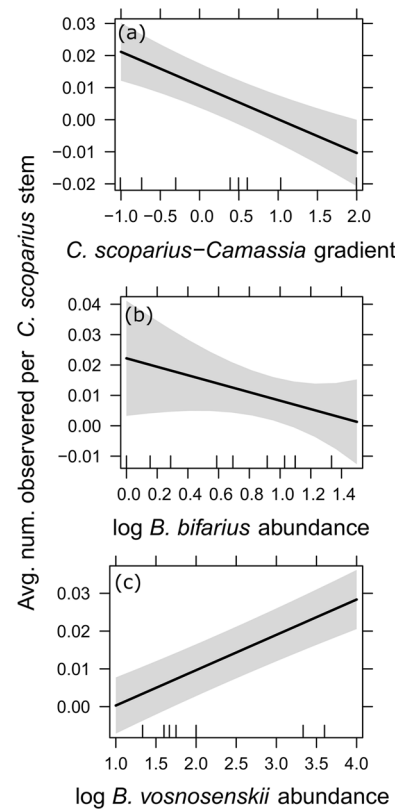
Fig. 5 Partial regressions showing variables significantly related to visit rates of *Apis mellifera* to *Camassia quamash*. Grey bars represent upper and lower 95% confidence limits. **a** Observations of *A. mellifera* declined with *Cytisus scoparius* density (stems/m²). and **b** increased with *Bombus bifarius* abundance and **c** increased with *B. vosnesenskii* abundance. Model: *A. mellifera* observations ~ *Camassia leichtlinii* density + *C. quamash* density + *C. scoparius* density+ *B. mixtus* abundance + *B. melanopygus* abundance + *B. bifarius* abundance + *A. mellifera* abundance +*B. vosnesenskii* abundance, + sampling year + site (random effect)

occurrence at high *C. scoparius* sites in our data. Sites with high *C. scoparius* density also tended to have less *Camassia*—likely due to competitive impacts of *C. scoparius* (Shaben and Myers 2010). Wray et al. (2014) also found that *C. quamash* was associated with urban sites. In our data, we find that *A. mellifera* is positively associated with *C. quamash*, perhaps driven by a higher abundance of both species in urban areas (due to urban beekeeping and volunteer *C. scoparius* control efforts, respectively).

Fig. 6 Partial regressions showing variables significantly related to visit rates of *Apis mellifera* to *Cytisus scoparius*. Grey bars represent upper and lower 95% confidence limits. **a** *A. mellifera* on *C. scoparius* declined with PC1 (*C. scoparius* to *Camassia* gradient); **b** declined with *Bombus bifarius* abundance and **c** increased with *Bombus vosnesenskii* abundance. Model: *A. mellifera* observations ~ PC1 + *B. mixtus* abundance + *B. melanopygus* abundance + *B. bifarius* abundance + *A. mellifera* abundance + *B. vosnesenskii* abundance, + sampling year + site (random effect)

Diet overlap and foraging behavior

Diet overlap increased with *C. quamash* density for all focal pollinators. However, this increase saturates at high *C. quamash* density for *B. mixtus*, *B. melanopygus* and *A. mellifera*. This pattern is not driven by changes in focal pollinator abundance, as only *A. mellifera* increases in site-level abundance with *C. quamash* density (Fig. 1d).

While high diet overlap was traditionally used as evidence for high levels of interspecific competition, real-world interpretation is more complex (Holt 1987). At the small spatial and temporal scales measured here, high overlap may indicate that specific floral resources are common enough for pollinators to share, while lower overlap may indicate that one species is unable to compete with another, and has thus shifted onto alternative resources to avoid competition (Brosi and Briggs 2013).

Given that *C. quamash* provides abundant nectar and pollen with no barriers to access these rewards, it seems likely that an increase in diet overlap reflects increased shared use of *C. quamash*. As *C. quamash* becomes more common, more and more individual foragers of different species may swap onto this resource, leading to high overlap at moderate densities. This would match the predictions of optimal diet models, which suggest that individual diets should

broaden in low quality environments, leading to lower diet overlap (MacArthur and Pianaka 1966). As *C. quamash* increases in density, more high quality resources are available, the environmental quality is increasing, and competition may be lower, allowing for higher diet overlap. However, if exploitation of *C. quamash* reaches some maximum level where its pollen or nectar are depleted, some pollinators may diversify their resource use, causing diet overlap to saturate or even decline. Previous research has shown that reward depletion can lead to pollinators foraging on lower quality resources. For example, when pollen is depleted on high quality *Mimulus guttatus* plants, pollinators will switch to the lower-quality pollen morph (Robertson et al. 1999).

Bombus melanopygus also had lower diet overlap with *B. vosnesenskii* and declining overlap with *B. bifarius* with increasing *C. leichtlinii* abundance (Fig. 3b). For *B. vosnesenskii,* a simple explanation may be that *B. melanopygus* and *B. vosnesenskii* differ in abundance across years, and are thus less likely to be caught on similar resources when measured at the site by year level.

The decline in diet overlap between *B. melanopygus* and *B. bifarius* as *C. leichtlinii* abundance declines is less likely to be explained by changes in site abundance of bees. Neither bee species changes in density with *C. leichtlinii* abundance. We also observe

B. bifarius less frequently on *C. leichtlinii* at sites with abundant *B. melanopygus* (Table 3A; Fig. 4b). This decline in diet overlap could partly be explained by the fact that *B. melanopygus* was more common in 2015, while *B. bifarius* was more common in 2014. However, we do not find a significant year effect for *B. bifarius* observations on *C. leichtlinii*, and *B. melanopygus* is actually less abundant on *C. leichtlinii* in 2015 when it is more common overall. Given that both *B. bifarius* and *B. melanopygus* are also more common at sites with more *C. scoparius* the decrease in overlap may be partially driven by competition for *C. leichtlinii*. This latter result may reflect interspecific interactions on *C. leichtlinii*, where the two bumblebees most common at sites invaded by *C. scoparius* may compete for resource.

Bombus bifarius and *B. melanopygus* are most common at forested sites (Wray et al. 2014), where *C. scoparius* is most abundant in our data. We have also observed that extensive *C. scoparius* removal efforts are more likely to occur at more urban sites that are accessible to volunteers (personal observation). Given the negative effects that *C. scoparius* has on native plant abundance (Shaben and Myers 2010), it seems likely that both *B. bifarius* and *B. melanopygus* may be more resource stressed than our other focal bee species because of their association with forested landscapes. That is, increased *C. scoparius* removal and control efforts in forested habitats further from the urban core may be beneficial to these pollinators in particular.

Despite being the most abundant of all focal pollinator species (Fig. 2), we find no evidence for unique direct impacts of non-native *A. mellifera* on bumblebees. Patterns in diet overlap were not different with *A. mellifera* versus other species (Table 2), nor did site-level *A. mellifera* abundance have significant impacts on visit rates by focal bees (Table 3). Rather, the strong bottom-up effects of *C. quamash* density on diet overlap suggests that the overall impacts of resource availability outweighs high *A. mellifera* abundance. However, the highest densities of *A. mellifera* occur at sites with the highest densities of *C. quamash*. Thus, high abundance of *A. mellifera* could contribute to resource depletion of *C. quamash* at high densities that could contribute to the saturation of diet overlap with *C. quamash* density (Fig. 3a). Overall, the landscape heterogeneity around our habitats may also buffer wild bees from competitive impacts of honeybees that have been documented in homogeneous mass-flowering crops (Lindstrom et al. 2016). These results suggests that maintaining floral diversity in these urban parks can help support local co-existence of urban beekeeping with wild pollinators.

Our results show that *C. scoparius* differs from other commonly studied flowering invasive plants in its effects on the visit patterns of the local pollinator community. For example, many generalist, highly attractive flowering invasives can facilitate pollination of native plants by attracting more pollinators to a local area (Albrecht et al. 2016; Feldman et al. 2004). We see no evidence of higher visit rates by any focal pollinator to our native plants at sites with high *C. scoparius* density (Table 3). This may be because *C. scoparius* has specialized floral morphology, no nectar production, low overall visit rates and differs greatly in floral syndrome from both *Camassia* species. Indeed, invasive plants are more likely to affect natives pollinator visits directly when they share similar floral traits (Gibson et al. 2012).

Conclusions

Despite being a potential pollen resource, *C. scoparius* did not have strong direct impacts on diet overlap or foraging patterns among our focal pollinators. Rather, we find that variation in diet overlap among focal pollinator species is driven by abundance of native plant resources rather than non-native plant abundance. This suggests that any impacts of *C. scoparius* on diet overlap are indirect—via resource competition with and displacement of native species—rather than via direct interactions with pollinators (Stout and Morales 2009). However, competition for native resources may be occurring between pollinators that are more common at highly invaded sites, partly due to the landscape context in which the non-native is more common. Furthermore, at least in this habitat, we see no evidence for direct competitive effects between non-native honeybees and native bumblebees. Overall our findings indicate that both landscape context and local resources can affect diet overlap and foraging behavior by generalist pollinators, and that a major impact of non-native flowering plants on pollinators may be indirect, and driven by displacement of native floral resources.

References

Albrecht M, Ramis MR, Traveset A (2016) Pollinator-mediated impacts of alien invasive plants on the pollination of native plants: the role of spatial scale and distinct behaviour among pollinator guilds. Biol Invasions 18:1801–1812

Bates D, Maechler M, Bolker BM et al (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48

Bezemer TM, Harvey JA, Cronin JT (2014) Response of native insect communities to invasive plants. In: Berenbaum MR (ed) Annual review of entomology, vol 59. Annual Reviews, Palo Alto, p 119-U740

Brosi BJ, Briggs HM (2013) Single pollinator species losses reduce floral fidelity and plant reproductive function. Proc Natl Acad Sci U S A 110:13044–13048

Brown BJ, Mitchell RJ, Graham SA (2002) Competition for pollination between an invasive species (purple loosestrife) and a native congener. Ecology 83:2328–2336

Cartar RV (2009) Resource-tracking by bumble bees: What explains local responses to density of bergamot (*Monarda fistulosa*) flowers? Ecoscience 16:470–475

Dohzono I, Yokoyama J (2010) Impacts of alien bees on native plant-pollinator relationships: a review with special emphasis on plant reproduction. Appl Entomol Zool 45:37–47

Feldman TS, Morris WF, Wilson WG (2004) When can two plant species facilitate each other's pollination? Oikos 105:197–207

Fox J, Hong J (2009) Effect displays in R for multinomial and proportional-odds logit models: extensions to the effects package. J Stat Softw 32:1–24

Fox J, Weisber S (2011) An R companion to applied regression, 2nd edn. Sage, Thousand Oaks

Gibson MR, Richardson DM, Pauw A (2012) Can floral traits predict an invasive plant's impact on native plant-pollinator communities? J Ecol 100:1216–1223

Gillespie SD, Bayley J, Elle E (2017) Native bumble bee (Hymenoptera: Apidae) pollinators vary in floral resource use across an invasion gradient. Can Entomol 149:204–213

Harmon-Threatt AN, Kremen C (2015) Bumble bees selectively use native and exotic species to maintain nutritional intake across highly variable and invaded local floral resource pools. Ecol Entomol 40:471–478

Heinrich B (1976a) Foraging specializations of individual bumble-bees. Ecol Monogr 46:105–128

Heinrich B (1976b) Resource partitioning among some eusocial insects—bumblebees. Ecology 57:874–889

Herron-Sweet CR, Lehnhoff EA, Burkle LA et al (2016) Temporal- and density-dependent impacts of an invasive plant on pollinators and pollination services to a native plant. Ecosphere 7:1–13

Holt RD (1987) On the relationship between niche overlap and competition—the effect of incommensurable niche dimensions. Oikos 48:110–114

Jauni M, Ramula S (2015) Meta-analysis on the effects of exotic plants on the fitness of native plants. Perspect Plant Ecol Evol Syst 17:412–420

Knuth P (1906) Handbook of flower pollination based on Hermann Mueller's 'The fertilisation of flowers by insects'. Clarendon Press, Oxford

Krebs CJ (1999) Ecological methodology, 2nd edn. Addison-Wesley Educational Publishers Inc

Lindstrom SAM, Herbertsson L, Rundlof M et al (2016) Experimental evidence that honeybees depress wild insect densities in a flowering crop. Proc R Soc B Biol, Sci, p 283

MacArthur RH, Pianaka ER (1966) On optimal use of a patchy environment. Am Nat 100:603–609

McCary MA, Mores R, Farfan MA et al (2016) Invasive plants have different effects on trophic structure of green and brown food webs in terrestrial ecosystems: a meta-analysis. Ecol Lett 19:328–335

Muth F, Keasar T, Dornhaus A (2015) Trading off short-term costs for long-term gains: how do bumblebees decide to learn morphologically complex flowers? Anim Behav 101:191–199

Parker IM (1997) Pollinator limitation of *Cytisus scoparius* (Scotch broom), an invasive exotic shrub. Ecology 78:1457–1470

Pysek P, Jarosik V, Hulme PE et al (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. Glob Change Biol 18:1725–1737

R-Development-Core-Team (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Ranta E, Lundberg H (1980) Resource partitioning in bumblebees—the significance of differences in proboscis length. Oikos 35:298–302

Robertson AW, Mountjoy C, Faulkner BE et al (1999) Bumble bee selection of *Mimulus guttatus* flowers: the effects of pollen quality and reward depletion. Ecology 80:2594–2606

Shaben J, Myers JH (2010) Relationships between Scotch broom (*Cytisus scoparius*), soil nutrients, and plant diversity in the Garry oak savannah ecosystem. Plant Ecol 207:81–91

Smith EP, Zaret TM (1982) Bias in estimating niche overlap. Ecology 63:1248–1253

Stout JC, Morales CL (2009) Ecological impacts of invasive alien species on bees. Apidologie 40:388–409

Traveset A, Richardson DM (2014) Mutualistic interactions and biological invasions. Annu Rev Ecol Evol Syst 45:89–113

Wray JC, Neame LA, Elle E (2014) Floral resources, body size, and surrounding landscape influence bee community assemblages in oak-savannah fragments. Ecol Entomol 39:83–93

Zuur AF, Ieno EN, Smith GM (2007) Analysing ecological data. Springer, New York