LETTER

Local bumble bee decline linked to recovery of honey bees, drought effects on floral resources

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Abstract

Time series of abundances are critical for understanding how abiotic factors and species interactions affect population dynamics, but are rarely linked with experiments and also scarce for bee pollinators. This gap is important given concerns about declines in some bee species. I monitored honey bee (*Apis mellifera*) and bumble bee (*Bombus* spp.) foragers in coastal California from 1999, when feral *A. mellifera* populations were low due to *Varroa destructor*, until 2014. *Apis mellifera* increased substantially, except between 2006 and 2011, coinciding with declines in managed populations. Increases in *A. mellifera* strongly correlated with declines in *Bombus* and reduced diet overlap between them, suggesting resource competition consistent with past experimental results. Lower *Bombus* numbers also correlated with diminished floral resources. Declines in floral abundances were associated with drought and reduced spring rainfall. These results illustrate how competition with an introduced species may interact with climate to drive local decline of native pollinators.

Keywords

Apis mellifera, *Bombus*, bumble bee, climate, competition, drought, floral resources, honey bee, pollinator declines, population trends.

Ecology Letters (2016)

INTRODUCTION

Time series of abundances are critical for evaluating mechanistic hypotheses about how both abiotic factors like climate and biotic ones such as competition interact to shape population dynamics. Recent studies have used long-term abundance records to explore the dual effects of climate variation and interspecific competition in a range of organisms, including birds (Woehler *et al*. 2014) and fish (Helland *et al*. 2011). Yet, there are few such data for bees (Roubik 2001; LeBuhn *et al*. 2013). This is a key gap, given the ecological importance of bees as mutualists and concerns about potential declines in some populations and species of pollinators (Goulson *et al*. 2015).

Two groups of bees have captured much of the recent attention about potential pollinator declines: the European honey bee, *Apis mellifera*, and bumble bees (*Bombus* spp.). During the 1990s, mortality rates for managed *A. mellifera* colonies in many parts of the world went up in association with the spread of a parasitic mite, *Varroa destructor* (Watanabe 1994). In the winter of 2006, North American bee keepers reported another large increase in winter colony losses linked with a new syndrome of symptoms, colony collapse disorder (CCD) (Steinhauer *et al*. 2014). Likewise, several recent landscape-scale studies show evidence of declines in range and abundance for some North American *Bombus* (Cameron *et al*. 2011; Colla *et al*. 2012; Kerr *et al*. 2015), although many species appear stable or lack adequate data to evaluate status. Much about the extent and causes of these changes remains unknown, and one major source of uncertainty is the scarcity of long-term data sets for bee abundances (LeBuhn *et al*. 2013; Goulson *et al*. 2015). Most evidence comes from broad-scale comparisons of recent collections with historic museum specimens (Cameron *et al*. 2011; Colla *et al*. 2012; Szabo *et al*. 2012; Bartomeus *et al*. 2013). Moreover, bee populations can fluctuate strongly over time and the effects of different environmental factors in driving variation are not well understood (LeBuhn *et al*. 2013).

Many classic studies have used bumble bees to test hypotheses about competitive interactions and coexistence, for example based on niche differentiation in tongue length and flower use (Inouye 1980; Pyke 1982). Recent work has revisited some of these systems with new results, suggesting that competition interacts with abiotic factors such as elevation to shape community structure in more complex ways than previously thought (Pyke *et al*. 2012; Miller-Struttmann & Galen 2014). Understanding such interactions is important to predicting the consequences of climate change, but potential effects of variation over time have often by necessity been assessed through spatial proxies, like elevational gradients (Miller-Struttmann & Galen 2014).

Introduced bees, such as *A. mellifera* in North America, also have long been thought to compete with some native pollinators, including *Bombus* (Goulson 2003; Goulson *et al*. 2008). Many short-term observational studies show that *A. mellifera* can overlap substantially in plant use with native bees and displace them from the richest floral resources (Goulson 2003), but the strength of competition may vary substantially within and across seasons (Tepedino & Stanton 1981). Only a few long-term studies have tried to link population dynamics of native bees with those of *A. mellifera*, primarily in the neotropics (Roubik & Wolda 2001; Roubik & Villanueva-Gutierrez 2009), with high variability due to other factors complicating detection of any signal from competition.

In this study, I monitored forager abundances of *A. mellifera* and two *Bombus* species (*B. vosnesenskii* and *B. caliginosus*) in a California coastal scrub community over 15 years. Neither of the *Bombus* species previously has been identified as declining by landscape assessments. Populations of feral *A. mellifera* were low in central California when the study began, likely because of *V. destructor* (Kraus & Page 1995). Experimental work at the study site from 1998 to 2000 found that raising local densities of *A. mellifera* through temporary colony introductions reduced *Bombus* forager numbers in nearby flower patches (Thomson 2006). Foraging and reproductive success for *Bombus* colonies in artificial nest boxes also increased with greater distance from *A. mellifera* introductions (Thomson 2004). I subsequently monitored *A. mellifera* and *Bombus* forager numbers from 2003 to 2014, creating a unique pairing between manipulative competition experiments and long-term monitoring data. Changes in abundances of introduced species can provide powerful natural experiments for understanding interspecific competition (Cooper *et al.* 2007); I hypothesised that feral *A. mellifera* might recover from low levels observed in the late 1990s and generate such an experiment.

Rainfall plays a strong role in annual variation of California coastal scrub plant cover and flowering (Keeley *et al.* 2005; Pratt & Mooney 2013), and also potentially bee populations. During the original study, floral abundances were progressively lower from 1998 to 2000, as spring (March to May) precipitation declined each year (Thomson 2006). This shift was associated with lower floral diversity and greater plant use overlap between *A. mellifera* and *Bombus* (Thomson 2006), and also some evidence for reduced foraging and reproductive success in *Bombus* colonies (Thomson 2004). The presence of a clear potential climate driver makes this system a good one for exploring how climate variability and competition together influence changes in abundance over time. The longer term monitoring from 2003 to 2014 captured substantial variation in annual weather conditions, including a major drought.

I used these data to ask: (1) Did feral *A. mellifera* or native *Bombus* forager abundances show trends over the 15 years observed? (2) Was there an inverse relationship between changes in *A. mellifera* and *Bombus*? (3) Was annual variation in either *A. mellifera* or *Bombus* forager numbers related to abundances of the most visited plant species? (4) Was annual variation in floral and bee abundances related to weather patterns, especially in precipitation?

MATERIALS AND METHODS

Study system and data collection

Apis and *Bombus* forager densities were monitored near peak summer flowering (late June to early July) in patches of coastal scrub at 180–340 m elevation in the Landels-Hill Big Creek Reserve (Lucia, CA, USA, 36°4′14″ N, 121°35′25″ W). The study site is embedded within the 970 km^2 Ventana Wilderness, distant from developed and agricultural areas, and therefore buffered against anthropogenic effects such as pesticides and managed *A. mellifera* colonies. Central California coastal scrub consists of shrubs mixed with primarily

perennial but also some annual herbaceous species (Thomson 2006). Summer flowering is limited to a narrow elevation band where moisture levels are enhanced by coastal fog. While floral resources can reach high densities, plant diversity is relatively low. Four plant species (*Eriophyllum staechadifolium*, *Scrophularia californica*, *Stachys bullata*, and *Phacelia malvifolia*) accounted for 94.0% (*n* = 17 037) of all *A. mellifera* and 94.6% (*n* = 5431) of all *Bombus* observations.

Patches were selected and bee densities first measured in 1999–2000 as part of an experiment to test the effects of *A. mellifera* on *Bombus* (Thomson 2004, 2006). Additional data were collected in 10 of these original patches from 2003–2007 and 2009–2014; 2008 was missed because road closures prevented access to the site (Table S1). The monitored patches are each on the order of several hundred m^2 in size. Distance to the nearest adjacent patch ranged from 100 to 500 m because of high spatial heterogeneity in plant community types (Fig. S1). An eleventh patch was also monitored, but excluded from the final analysis because the nearest-neighbouring patch was < 50 m away.

Almost all recorded *Bombus* foragers were either *B. caliginosus* or *B. vosnesenskii*. These species are in the same colour complex and cannot be distinguished in visual counts, so were treated as a single group. *B. melanopygus* and *B. sitkensis* are found at the site but rarely observed during monitoring (< 0.10% of foragers). Specimens collected in 1996–1998, 2004–2007 and 2011–2015 were used to quantify the relative abundances of *B. caliginosus* and *B. vosnesenskii*. Queens were never observed in transect counts during the monitoring period. Workers and males cannot be differentiated readily on flowers, but 82% of individuals (*n* = 55) collected during July were workers; collection of potential gynes was avoided to minimise possible effects on populations. During 1999–2000, newly emerged queens for this colour morph were observed through late May, and workers until September. *Bombus* forager abundances in both years peaked between July 1 and July 14 and remained at 60–80% of maximum through the end of July. *Apis* forager numbers showed less distinct peaks, but reached their highest abundances by early (1999) or mid (2000) July and sustained them into August.

The original study introduced both *A. mellifera* and *B. occidentalis* colonies to the site. The data from 1999 to 2000 included in the analysis presented here were collected with 6–9 managed *A. mellifera* hives present (Thomson 2004, 2006). Introduced *A. mellifera* colonies were removed when the experiment ended in fall of 2000. In addition, nine *Bombus occidentalis* colonies in artificial nest boxes were present both in 1999 and 2000. Since no *B. occidentalis* were recorded in the forager counts, the presence of these additional *Bombus* colonies did not affect estimates of forager density.

Data collection

Data were collected in four of the 10 focal patches for all 13 years of the study, and a fifth patch in 11 years (Table S1). Limiting the analysis to these five most sampled patches did not change the qualitative results. I included other patches for less frequent monitoring, to better capture spatial variation and characterise plant species use by *A. mellifera* and *Bombus*.

Three such patches were initially monitored prior to 2007, but not after because of successional changes in the plant community. Two nearby alternative patches from the original study replaced these (Table S1). For the 2003–2014 monitoring, data were collected over 5–6 consecutive days each year with the start date varying between June 28 and July 8. Data from 1999 to 2000 were drawn from those collected for the original study during a comparable time window (Thomson 2006; see Supplementary Methods for details).

For each patch, I estimated *A. mellifera* and *Bombus* forager and also floral densities on a single 5 m wide belt transect running 25–100 m along the edge. Transect lengths and exact locations changed slightly between years in response to vegetation shifts, but for a given patch varied by < 60 m over the study. The protocol for counting foragers was the same in all years. During approximately 35–40 min observation periods, I walked a transect from start to end three separate times. Transect counts were started 15 min apart within an observation period. For every transect count, I recorded all *A. mellifera* and *Bombus* foragers in a 5 m band extending into the patch and the first plant species visited by each forager (Thomson 2006). I measured air temperature and relative humidity with a sling psychrometer at the beginning and end of every observation period. Observation periods were evenly divided among morning (9 : 00–12 : 00), midday (12 : 00–15 : 00) and afternoon (15 : 00 to dusk). From 2003 to 2014, at least one observation period a year was completed in each of these three time categories (morning, midday and afternoon) per sampled patch, for a minimum of nine total transect counts in a patch. In eight of these 11 years, additional counts were done in some patches following the same protocol, to better ensure sampling effectiveness (Table S1; Supporting Information I). Data from each year were combined into a single value per patch prior to statistical analysis (see *Data analysis*).

Numbers of flowering stems were counted by species for each patch along the same 5 m wide belt transect as for bees (Thomson 2006). Since floral densities were high, I subsampled this belt transect in 0.2 m long by 5 m wide sections, spaced evenly at 1 m intervals. The number of open flowers was recorded for one stem per species in each subsampled area of transect, to a minimum of 10 replicate stems per species per transect. I calculated the patch density of flowers for each species as the product of mean flowering stem density per metre and mean number of open flowers per stem. To ensure that the density of rarer plants was estimated accurately, I counted the total number of flowering inflorescences on the whole transect for any visited plant species not found in at least 10% of the subsamples. Species found in more than 40% of subsamples were counted at 2 m rather than 1 m intervals.

Data analysis

I addressed the research questions with general linear mixed models that tested relationships between *A. mellifera* and *Bombus* abundances, as the two response variables, and year, temperature and time of day during sampling, annual weather variation, and floral abundances as fixed effects. In addition, I included variables to account for potential changes in *A. mellifera* during the period associated with colony collapse and effects of competition from *A. mellifera* on *Bombus* (see below). All models were fit using the lme4 package version 1.1-7 (Bates *et al.* 2014) in R (version 3.1.2) with patch as a random effect. I developed best fit models through sequential forward addition of the candidate variables that most improved AIC, first main effects and then all potential two-way interactions. Once no additional variables improved the fit with ΔAIC > 2, I verified the best model had been obtained by removing variables or substituting ecologically similar ones (61 total candidate models compared for *A. mellifera*, 55 for *Bombus*). Significance of fixed effects was then assessed with bootstrapped likelihood ratio tests comparing the best fit model with ones where single variables were removed ($n = 10\ 000$ replicates), along with delta AICs (Faraway 2005).

I aggregated observations for a given patch and year, so each replicate represents mean annual density for one patch (91 total patch × year replicates). All bee and floral abundances were analysed as densities per metre of transect. Data were log transformed to correct for skew, and subsequently met assumptions. Best fit model residuals showed no spatial autocorrelation, indicating patches were statistically independent (Figs S2–S5, Tables S2–S3). There was no evidence of temporal autocorrelation in residuals for either *A. mellifera* (Box-Ljung test, lag = 1, $\chi^2 = 0.09$, d.f. = 1, $P = 0.77$) or *Bombus* ($\chi^2 = 0.67$, d.f. = 1, $P = 0.42$). Automatically adding the year variable to all models for detrending did not change results, so year was included in the final reported models only when this significantly improved fit.

Three variables characterising annual weather were developed as candidate fixed effects (see Supporting Information II for details). One quantified the timing of rainfall within a year (hereafter Phenology). This measure correlated strongly with flowering phenology and helped control for differences that likely affected the timing of annual data collection relative to annual peaks in floral and bee abundances. I also used total rain year (September 1–August 31) precipitation (Total rainfall) as a candidate variable. Finally, I included the number of days with precipitation between March 15 and May 15 (Days spring rainfall) to capture differences in the number and length of spring storms; these have important rainfall and temperature effects that potentially influence not only floral abundance but also early season bee emergence and colony growth.

For *A. mellifera*, temporal changes appeared to shift from increasing to declining between 2006 and 2011, coinciding with the period when overwinter mortality rates for domesticated hives in the U.S. consistently exceeded 29% (Steinhauer *et al.* 2014). I created a categorical variable (Colony collapse), scored one for years from 2006 to 2011 and 0 otherwise, to test for differences in abundance during this period; an interaction term between year and colony collapse allowed the direction and magnitude of temporal trends to differ in 2006–2011 compared to other parts of the time series.

Bombus models also included competition with *A. mellifera*, quantified as the mean *A. mellifera* density observed across all transects in the previous year. For 1999, this value represented

A. mellifera density in a subset of four patches for which data were available in 1998; densities in these patches from 2003 to 2014 tightly correlated with those for the full data set (Spearman rank correlation, $r = 0.92$). Since no data could be taken in 2008, I used the average of 2007 and 2009 *A. mellifera* densities. The year 2003 was excluded from *Bombus* analyses because data were unavailable to estimate *A. mellifera* densities for two previous years; this reduced total n to 85 patch × year observations. Since the year variable did not enter the best fit model for *Bombus*, I carried out a *post hoc* model selection without the ecological predictors (*A. mellifera* and floral abundances). This additional analysis confirmed whether *Bombus* abundances followed a significant temporal trend during the study period.

For three of the most visited plant species (*E. staechadifolium*, *S. californica*, and *S. bullata*), I fit separate mixed models to test for temporal trends in density and fixed effects of the candidate weather variables (Table S6). *Phacelia malvifolia* was not found in enough patches to include in these analyses. Yearly changes in bee relative plant use and diet overlap were assessed with Moritsa's index of similarity (Krebs 2014). To test a *post hoc* hypothesis that *Bombus* shifted plant use in response to *A. mellifera*, I also quantified yearly *Bombus* preference for *E. staechadifolium* relative to other food sources as the proportion of total *Bombus* foragers that were observed on *E. staechadifolium* divided by the fraction of all flowers consisting of *E. staechadifolium*.

RESULTS

Model results for *A. mellifera* showed strong support for a positive effect of year and negative year by colony collapse interaction (Fig. 1, Table 1); *A. mellifera* abundances overall increased except during the time period associated with CCD in managed colonies (2006–2011), when they declined (Fig. 1a, Figs S6–S7). These patterns were not explained by variation in the precipitation variables or floral abundances, although both evidenced significant relationships with *A. mellifera* density. *Apis mellifera* were strongly reduced in years with more days of spring rainfall, and significantly increased with air temperature during data collection; there was a marginal relationship with later phenology (Table 1). The best fit model also included a strong positive effect of flowering *E. staechadifolium* density (Table 1). None of the other candidate variables significantly improved the *A. mellifera* model (marginal $r^2 = 0.65$) (Figs S6–S7, Table S4).

Results for *Bombus* supported a very strong negative relationship with *A. mellifera* density in the previous year (Fig. 2, Table 1), even controlling for annual variation due to other factors. *Bombus* numbers were also lower in years with later phenology (Table 1). *Bombus* density positively related to floral abundance for two plants, *P. malvifolia* and *S. californica* (Table 1). The best fit model included an interaction effect between *S. californica* and *A. mellifera*; the relationship between *S. californica* and *Bombus* was stronger with greater competition from *A. mellifera* (Table 1). No other climate or floral resource variables significantly improved the *Bombus* model (marginal $r^2 = 0.55$) (Table S5, Figs S8–S9). Year did not enter any models that included ecological factors (*A. mellifera* and floral abundances), but was the only significant predictor when these variables were excluded, confirming a strong negative temporal trend in *Bombus* abundances (estimate = −0.12, ΔAIC = 15.66; Fig 1b). Relative abundance of *B. vosnesenskii* and *B. caliginosus* also shifted significantly over time (Fisher's Exact Test, $P < 0.0001$). From 1996 to 2007, 64.1% ($n = 39$; Table S7) of specimens from this colour morph were *B. vosnesenskii*, compared to only 15.4% of those collected since ($n = 52$; Table S8).
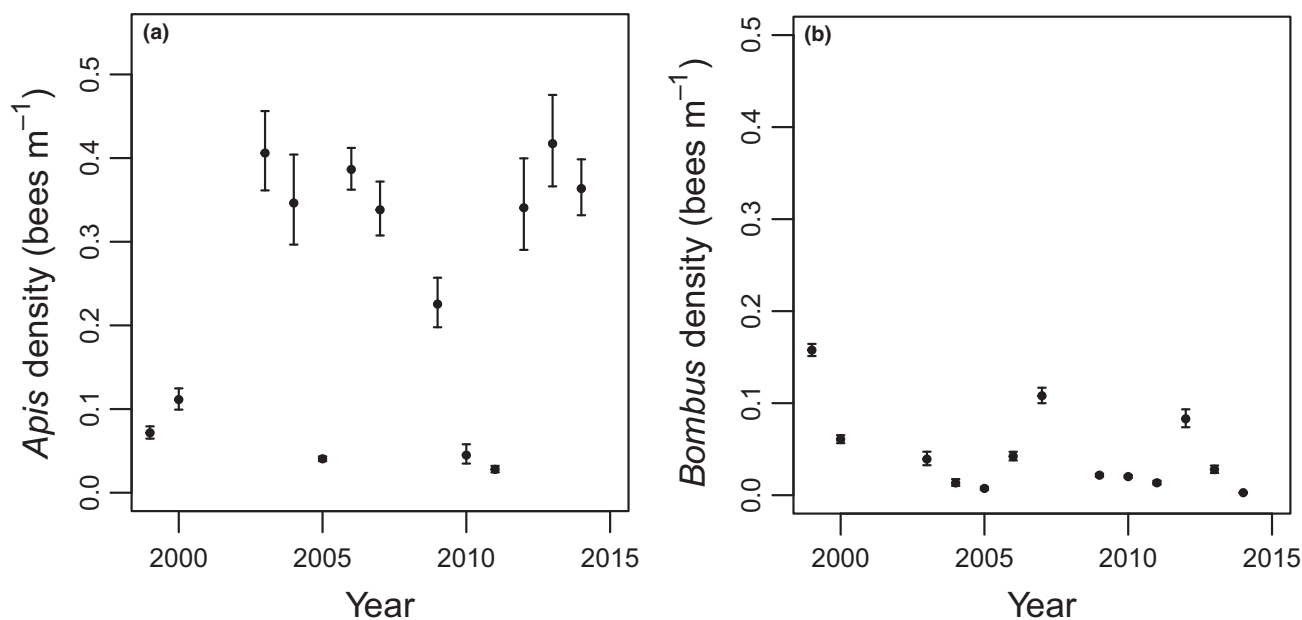

Figure 1 Mean annual (a) *Apis mellifera* and (b) *Bombus* density (foraging bees/metre of transect) from 1999 to 2014. Points and error bars represent back transformed values of the mean ± 1 SE for log transformed data.

Table 1 Results of linear mixed effects models for *Apis mellifera* and *Bombus* forager densities. Parameter estimates for fixed effects are from the best fit model. Statistics were derived using likelihood ratio tests that compared models with a single factor removed to the best fit model; *P* values were calculated by bootstrapping (*n* = 10 000 replicates). *P* values significant at a *P* < 0.05 level are bolded. Changes in AIC resulting from removal of a given parameter relative to the best fit model are also shown. All models included patch as a random effect. All species densities are expressed as numbers per m of transect; the phenology measure is in units of cm days (see Methods, Tables S4–S5).

| Response	Factor	Estimate	SE	χ^2	d.f.	*P*	ΔAIC
A. mellifera density	Year	0.07	0.02	69.15	2	**< 0.0001**	65.15
	Colony collapse	6.75	0.76	66.48	2	**< 0.0001**	62.48
	Temperature	0.11	0.03	11.98	1	**0.001**	9.98
	Days spring rainfall	−0.08	0.01	26.66	1	**< 0.0001**	24.66
	Eriophyllum density	0.007	0.0009	44.91	1	**< 0.0001**	42.91
	Year × Colony collapse	−0.68	0.07	65.99	1	**< 0.0001**	63.99
	Phenology (later)	0.07	0.03	4.64	1	**0.04**	2.64
Bombus density	*Apis* density previous year	−4.33	0.67	36.49	2	**< 0.0001**	32.49
	Scrophularia density	−0.008	0.008	12.02	2	**0.0044**	8.02
	Phacelia density	0.14	0.04	11.58	1	**0.0011**	9.58
	Phenology (later)	−0.17	0.03	28.35	1	**< 0.0001**	26.35
	Apis × *Scrophularia*	0.22	0.07	9.09	1	**0.0035**	7.09
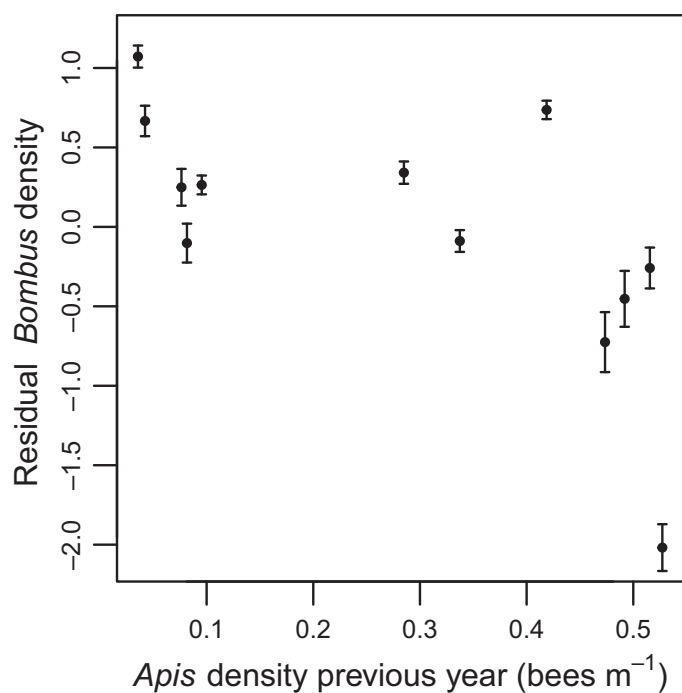
Figure 2 Relationship between *Apis mellifera* density in the previous year and mean (± 1 SE) *Bombus* density across all transects. *Bombus* density is shown as the residual variation from the best fit model that did not include *A. mellifera* density as a predictor, to account for variation explained by other factors (see Table 1).

Patterns of floral use showed that diet niche overlap between *A. mellifera* and *Bombus* decreased with higher *A. mellifera* densities, consistent with the hypothesis that they were competing more intensely for resources (Fig. 3, linear regression, $F_{1,11} = 24.5$, *P* < 0.001). A shift in *Bombus* visitation away from *E. staechadifolium*, the plant most used by *A. mellifera*, shaped much of this pattern. During the 7 years when *A. mellifera* densities on *E. staechadifolium* were below the study mean, *Bombus* relative preference for *E. staechadifolium* averaged 0.25 ± 0.091 (mean ± 1 SE) and 22.0% of

Bombus foragers were found on this plant species. In contrast, *Bombus* preference for *E. staechadifolium* fell to 0.039 ± 0.011 during the 6 years when *A. mellifera* densities on this plant were above the study average, and only 3.74% of all *Bombus* were recorded visiting *E. staechadifolium*.

Model results for floral resources also support a connection between *Bombus* decline, lowered availability of key plant species and dry conditions. Flower densities were significantly, positively linked to days of spring rainfall for *Scrophularia californica* and *Stachys bullata*, but not *E. staechadifolium* (Fig. 4, Table 2). Long-term precipitation data for Big Sur Station, CA (1915–2014) include only 7 years (*n* = 82 years with complete records) when five or fewer days of rainfall occurred between March 15 and May 15; three of these fell after 2003 (2004, 2008 and 2013). In addition to a strong negative relationship with dry springs, models for *S. californica* and *E. staechadifolium* showed a separate significant year effect, indicating declining trends; this pattern was stronger for *S. californica* (Table 2). Model results for *Bombus* suggest that reduced *S. californica* abundances during periods of higher *A. mellifera* density were significantly associated with *Bombus* declines (Table 1). Averaged across all years, 60.5% of *Bombus* were recorded visiting either *S. californica* or *S. bullata*, further reinforcing the importance of changes in these resources for *Bombus*. In contrast, on average 71.8% of *A. mellifera* were recorded visiting *E. staechadifolium*, the only plant species significantly associated with *A. mellifera* density (Table 1) and also the one most buffered against dry conditions (Fig. 4, Table 2).

DISCUSSION

These results document a substantial local decline in the abundance of two native *Bombus* species over the last 15 years, at a site buffered from direct anthropogenic effects. They also support the conclusion that two main factors and their interaction were associated with this decline: first and most strongly, increases in feral *A. mellifera* populations that intensified competition for floral resources, and second, reductions in the abundance of a key forage plant, *S. californica*. Finally,

I found evidence for indirect negative effects of dry spring conditions on *Bombus*, mediated by interactions with *S. californica* and *A. mellifera*. This suggests that increased drought
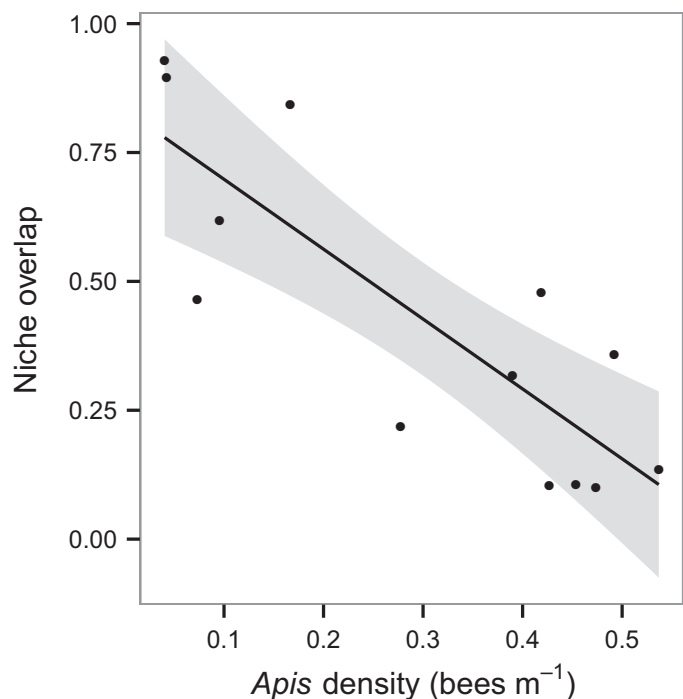

Figure 3 Relationship between *Apis mellifera* density and niche overlap between *A. mellifera* and *Bombus*, measured as a similarity index for plant visitation; a value of one indicates perfect overlap ($F_{1,11}$ = 24.5, $P < 0.001$, r^2 = 0.69). Each data point represents pooled observations for a single year. The grey area shows 95% confidence bounds.

might further promote a shift from *Bombus* to feral *A. mellifera* in the local pollinator community.

Directly linking the observed growth in *A. mellifera* abundances between 2000 and 2014 to recovery from *V. destructor* is not possible without data on colony infection and mortality rates. However, feral *A. mellifera* in Louisiana showed a strong negative effect of *V. destructor* in the first five years, followed by recovery to pre-*Varroa* levels (Villa *et al.* 2008). At my site, *A. mellifera* likewise sharply increased between 5 and 8 years after high levels of feral colony morality were documented in central California (Kraus & Page 1995). The timing of *A. mellifera* declines between 2006 and 2011 (Fig. 1a) raises interesting questions, given that managed *Apis* hives in North America were experiencing elevated mortality rates during this period (Steinhauer *et al.* 2014). There are few data on disease or abundance trends in feral *Apis* to compare with these results or evaluate potential explanations, though, highlighting a need for further research.

In contrast, for *Bombus*, the likely causes of population trends at this site were much clearer. I found a strong relationship between *Bombus* declines and increases in *A. mellifera*. One potential explanation is apparent competition mediated by pathogen transmission from *A. mellifera* colonies (Furst *et al.* 2014), although neither of the two *Bombus* species in this study have been linked to pathogen spillover previously. The range of a historically co-occurring species, *B. occidentalis,* has contracted dramatically over the last 20 years, especially on the Pacific coast (Thorp & Shepherd 2005). *Bombus occidentalis* and several other North American species may have declined due to pathogen spillover from commercial *Bombus* colonies (Szabo *et al.* 2012). Use of commercial *Bombus* colonies in my original experiment could have introduced new pathogens to the site. However, comparisons of recent to historic *B. vosnesenskii* collections show stable
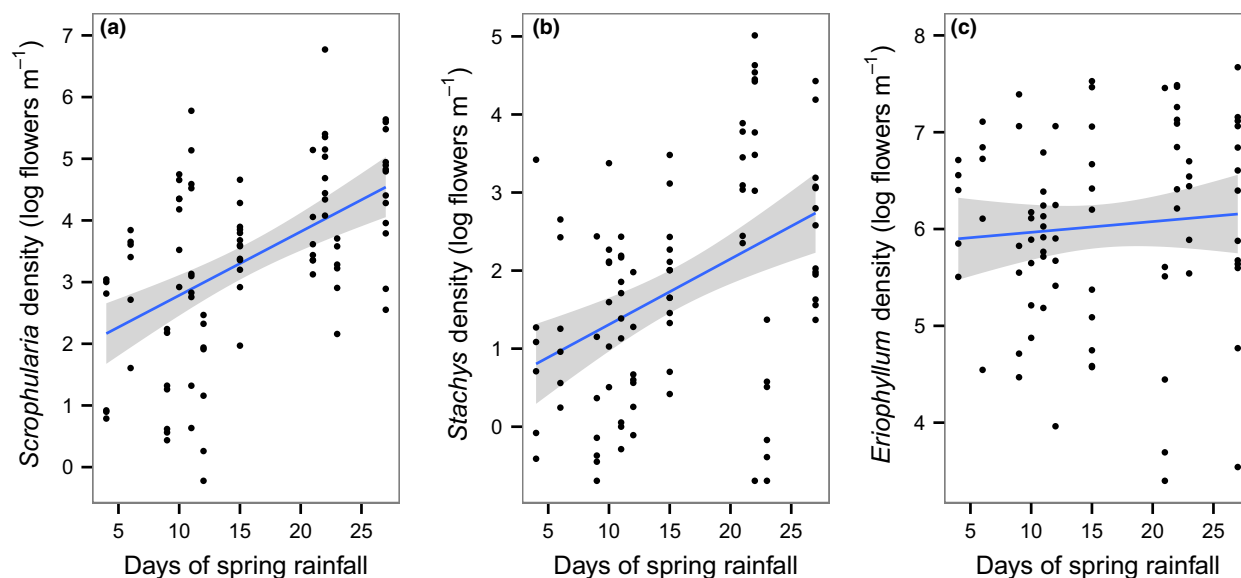

Figure 4 Relationship between days of spring (March 15–May 15) rainfall and mean floral abundance (flowers/m of transect, plotted on a log scale) for (a) *Scrophularia californica*, (b) *Stachys bullata* and (c) *Eriophyllum staechadifolium*. Best fit lines for simple linear regressions and 95% confidence bounds (grey area), are shown to aid in visualisation; see Table 2 for formal tests of effects using mixed models. Each data point represents a single transect.

and abundant occurrence records, with no evidence for elevated pathogen infection (Cameron *et al.* 2011). *Bombus occidentalis* was absent from this site by the beginning of the study. Nor were the timing and cyclical pattern of abundance changes I observed for *B. vosnesenskii/caliginosus* (Fig. 1b, Fig. S8) similar to the rapid crash without recovery documented for species such as *B. occidentalis* and *B. franklini* starting in the late 1990s (Thorp & Shepherd 2005).

Two compelling lines of evidence point instead to resource competition as the likely primary explanation. First, previous experiments at this site found that raising *A. mellifera* densities significantly reduced both *Bombus* colony reproductive success and forager abundances (Thomson 2004, 2006). Second, *Bombus* shifted plant use at higher *A. mellifera* densities in ways that significantly reduced diet niche overlap between the two. Some classic competition theory predicts that organisms with flexible foraging strategies should show narrower diet breadth and increased niche specialisation as resource scarcity and interspecific competition intensify; these predictions are at least partially supported by studies on a range of organisms (e.g. Correa & Winemiller 2014). In Colorado, increases in competitor abundance across elevational gradients have been shown to correlate with greater niche separation, as longer tongued *Bombus* specialise more on flowers with deeper corollas (Pyke *et al.* 2012; Miller-Struttmann & Galen 2014). Likewise, Brosi & Briggs (2013) found that experimentally removing the most abundant *Bombus* species from subalpine meadows led to reduced floral fidelity in the remaining *Bombus* foragers. Past studies document within season shifts in niche of some native bees with changes in *A. mellifera* densities (Goulson 2003), and a few connect these with changes in forager abundances (Pleasants 1981). Linking such short-term changes with population trends has proved challenging to date, though, illustrating the value of longer term data sets.

The results also support a role for reduced access to key food plants, particularly *S. californica*, in lower *Bombus* numbers over time. The importance of floral resources to *Bombus* colony growth and density has been demonstrated in multiple North American species (Pelletier & McNeil 2003; Knight *et al.* 2009). For *B. vosnesenskii*, male and forager production of colonies in a California agricultural landscape correlated with nearby resource density (Williams *et al.* 2012), while floral diversity predicted foraging distances (Jha & Kremen 2013). Lowered diversity and abundance of floral resources

are also thought to be important factors in some landscape scale changes, although much of the evidence is indirect. Narrow diet breadth was a significant predictor of decline for multiple bee species of the Northeastern U.S. (Bartomeus *et al.* 2013). Similarly, a recent general review of research on population limitation in bees showed that resource availability was the only factor consistently associated with abundance (Roulston & Goodell 2011).

Most research on diminishing floral resources for native bees in California has focused on loss of habitat in agricultural (Kremen *et al.* 2002) and urban (McFrederick & LeBuhn 2006) areas, as have many similar studies in Europe (Goulson *et al.* 2008). In the data presented here, a significant relationship between spring rainfall and *S. californica* flower density suggests that dry weather conditions are the cause. California is experiencing the worst drought in its recorded climate record, and potentially the last 1200 years (Griffin & Anchukaitis 2014). Recent research attributes the severity of this drought primarily to reduced precipitation independent of climate change, but identifies a major role for anthropogenic warming via increased potential evapotranspiration (Williams *et al.* 2015). *Apis mellifera* abundances were higher in years with fewer spring rainfall days (Table 1), and their primary forage plant (*E. staechadifolium*) more robust to such conditions than species preferred by *Bombus* (*S. californica* and *S. bullata*). As a result, future warming has the potential to further promote *A. mellifera* over *Bombus* in this habitat type. Comparable patterns have been documented recently in alpine systems, with reduced floral resources due to climate warming promoting generalist foragers over longer tongued specialists (Miller-Struttmann *et al.* 2015). More broadly, a number of North American and European *Bombus* appear to be undergoing range contractions at their southern distributions (Kerr *et al.* 2015). Narrow climatic distribution and proximity to range boundaries correlated with *Bombus* declines in several cross-species comparisons, and some authors have suggested the potential for interactions between climate shifts and food plant availability to drive this pattern (Fitzpatrick *et al.* 2007; Williams *et al.* 2007, 2009). My results document one potential mechanism for such an interaction.

There are important limitations to these data, suggesting avenues for future research. The 2003–2014 monitoring captured only one part of the summer flowering and flight seasons. The statistical models controlled for some variability in

Table 2 Results of linear mixed effects models for three of the most visited plant species. Parameter estimates for fixed effects are from the best fit model. Statistics were derived using likelihood ratio tests that compared models with each factor added to or removed from the best fit model; *P* values were calculated by bootstrapping (*n* = 10 000 replicates). *P* values significant at a *P* < 0.05 level are bolded. Changes in AIC resulting from addition or removal of a given parameter relative to the best fit model are also shown. All models included patch as a random effect. All species densities are expressed as numbers per m of transect; the later phenology measure is in units of cm days (see Methods, Table S6).

Response	Factor	Estimate	SE	χ^2	d.f.	*P*	ΔAIC
Scrophularia californica density	Days spring rainfall	0.09	0.02	22.91	1	**< 0.0001**	20.91
	Year	−0.10	0.03	13.78	1	**0.0002**	11.78
Stachys bullata density	Days spring rainfall	0.08	0.02	18.30	1	**0.0002**	16.30
	Year	−0.04	0.03	1.64	1	0.22	−0.36
Eriophyllum staechadifolium density	Total rainfall	−0.0207	0.009	5.30	1	**0.025**	3.30
	Phenology (later)	−0.01	0.05	0.04	1	0.84	−1.96
	Year	−0.09	0.02	15.46	1	**< 0.0001**	13.46

timing of peak abundances between years by including weather covariates, but the observed trends could still represent phenological shifts as well as changes in density or size of *A. mellifera* and *Bombus* colonies. Recent work in alpine communities demonstrates the complexity of community phenological responses to climate variation, with different species shifting flowering time independently (CaraDonna *et al.* 2014). Collections of *Bombus* specimens also showed a potential change in relative abundance of *B. caliginosus* relative to *B. vosnesenskii*, but sample sizes were small and the strength and potential causes of this result are unclear. Measuring *A. mellifera* and *Bombus* densities on the same suite of plant species both earlier in the summer flowering season and across the geographic range of coastal scrub in California is critical to assessing how these findings scale up temporally and spatially. Likewise, habitat mapping of the focal plants would better illuminate the role of precipitation relative to factors such as fire and successional changes in determining regional variation in floral abundances.

In summary, concern about local declines in *Bombus* may be warranted even for species that have not been identified as at risk based on regional collection records and sites that seem well protected from anthropogenic effects. Landscape scale studies of species distribution patterns may fail to detect important drivers of variation in local populations (Goulson *et al.* 2015). This study highlights the importance of mechanistic research on interactions between native and introduced bees, resource limitation and vegetation change linked with climate to our understanding of past and future shifts in pollinator communities. More broadly, there is a strong need to complement assessments at the species range scale with local ecological monitoring of populations, to build a more complete picture of how species interactions and abiotic factors will shape community responses to global change.

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