

Effects of climate change on the elevational distribution of bumble bees near Crested Butte, CO:
comparing data across 47 years

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Abstract

As climate change continues to alter the abiotic environment, many organisms must adapt to survive. In montane systems where changes in elevation can present noticeable changes in temperature and moisture, many organisms may adapt to climate change by migrating to higher elevations. Bumble bees, which are diverse and abundant in temperate montane ecosystems, may be vulnerable to climate change as changing environments alter the composition of plants. However, it's unclear whether the elevational ranges of bumble bees have shifted over time. Here, we analyze a new survey in the context of a long-term project monitoring the elevational distributions of bumble bee communities near Crested Butte, Colorado. Our findings suggest that some species may be shifting to higher elevation, but many appear to be stable.

Introduction

Mountain ecosystems are among the most threatened by climate change (Seddon et al. 2016; Viterbi et al. 2020), yet they contain many unique features that may facilitate resilience and create opportunities for adaptation to increasing temperature (Anthelme 2014; García et al. 2020). Organisms can adapt to a changing climate through adaptive or plastic alterations to their physiology, behavior, or phenology (reviewed in Maebe et al. 2021 Jun 12).

Bumble bees are most diverse in temperate and montane environments, where they perform important ecosystem services as generalist pollinators (Williams et al. 2014). Please understand that this paper is a very rough draft. In montane systems where elevation can change

by thousands of meters in a small area, bumble bees have the potential to migrate to higher elevations as climate change makes their original ranges less hospitable.

Bumble bee responses to climate change will not be uniform, as physiological and environmental contexts will impact the ability of different species and populations to adapt (Grabherr et al. 2010; Kerr et al. 2015; Inouye 2020). Populations of *Bombus vosnesenskii* exhibit local adaptation to cold temperatures, but the species appears to be constrained in its ability to tolerate high temperatures (Pimsler et al. 2020). The alpine bumble bee *Bombus alpinus* experienced an upward range contraction in the Swiss Alps (Biella et al. 2017). An analysis of museum specimens for four North American *Bombus* species found evidence of significant elevational shifts over 125 years for all four species, however, such results should be treated with caution as historic sampling may be biased to recording outliers (Nooten and Rehan 2020). A comparison with historic bumble bee samples suggests that bumble bees in the Pyrenees have shifted to higher elevation and have changed their diets accordingly (Marshall et al. 2020). Small mammals in the Rocky Mountains displayed variable responses to climate change: most shifted or expanded upwards in elevation, but some did not change in elevation and some shifted their ranges to lower elevation (McCain et al. 2021). I hope to make this a lot more coherent in the manuscript.

Montane ecosystems are ideal systems for studying how climate variation will affect organisms, due to the naturally broad variation in climatic conditions across elevational gradients (Tito et al. 2020). Long-term studies with a variety of field sites that include diverse microhabitats are best suited to document the effects of climate change on organisms, especially in alpine ecosystems, where temporal and spatial heterogeneity can limit the ability of short-term

research to pick up on broad patterns (Inouye 2020; Shah et al. 2020). A total of fifteen species of bumblebees have been recorded in the study sites (Pyke 1982; Pyke et al. 2016; Zung et al. 2014 unpublished), although the seven most common species account for roughly 96% of observations (Pyke 1982).

Previous research in our study area (Ogilvie et al. 2017) and in alpine Japan (Kudo 2014) indicates that climate has a significant indirect effect on the abundance of bumble bees, with bumble bee abundance increasing with floral resource availability, and floral resources being more abundant in years with more summer rain and later snowmelt days. A long-term study in our study area suggested that floral resource abundance over the growing season is beginning to show a mid-summer decline in flowering density with increasing temperatures and drought (Aldridge et al. 2011).

In 1974, Graham Pyke conducted a survey documenting the identities, phenology, and plant visitation of bumblebees along transects of varying elevations near Crested Butte, Colorado (Pyke 1982; Pyke et al. 2011; Pyke et al. 2012). The objective of this survey was to test the hypothesis that resource partitioning and competition determines the spatial distributions of bumble bees. It is known that bumble bees are best suited to take advantage of floral resources that correspond to the length of their proboscis, i.e. short tongued bees maximize their net rate of energy intake while feeding on flowers with short corollas, and likewise for medium and long tongued bees. Thus, Pyke expected that distributions of bumblebees should be driven largely by competition for resources, with any given site having no more than one species of each tongue length present, independent of the elevation or environment of the site. To test this, Pyke and several assistants surveyed 36 sites ranging in elevation from 9000 to 11,000 ft at multiple

timepoints between late June and early September, 1974. In total, the survey recorded 13,136 observations of bumble bees, including data on the caste, sex, and identity of the bee; the site, elevation, time, and date at which it was observed; the flower it was observed feeding on; and a list of the plants flowering at each visit to a site.

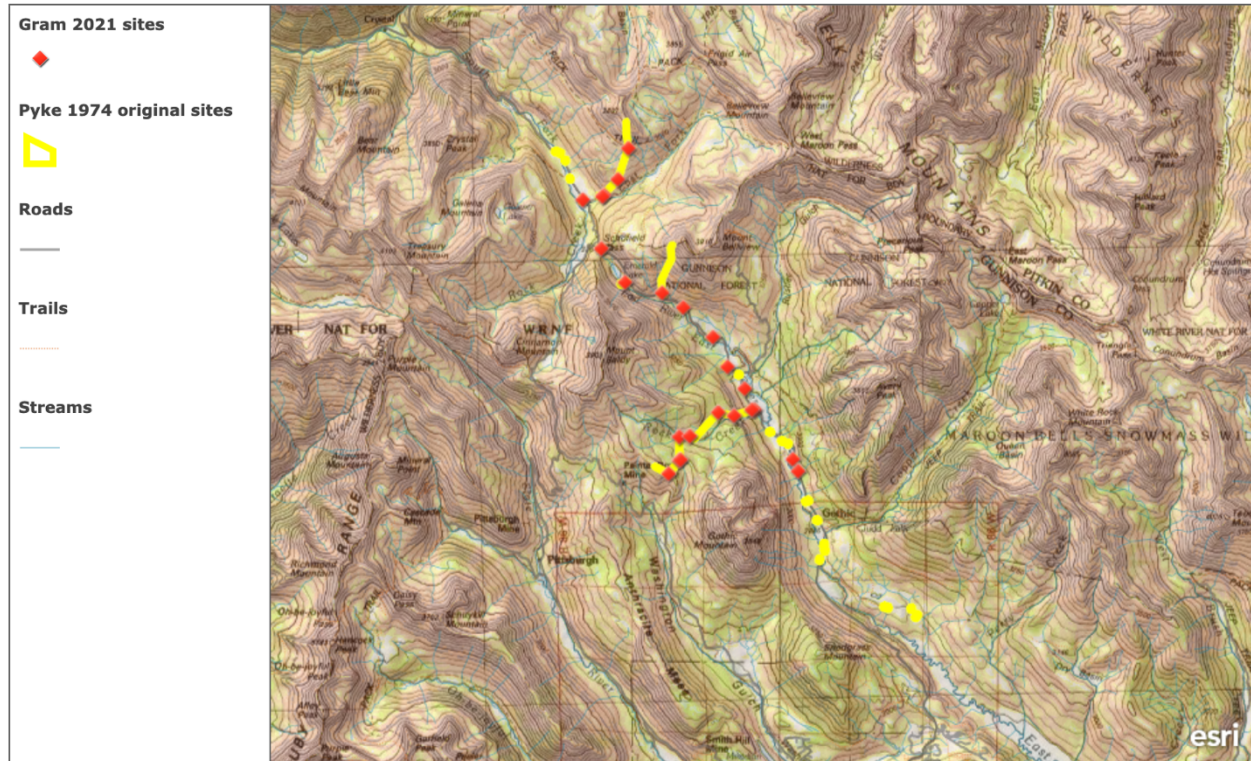
Although the goal of Pyke's 1974 survey was not to initiate any sort of long-term monitoring project, the repeatability of Pyke's methods, combined with ecologists' growing interest in the altitudinal shifts, has led to contemporary efforts to re-survey Pyke's sites. The first such re-survey took place in 2007, led by Tim Miller, and an analysis of elevational shifts between 1974 and 2007 was published in 2016 (Pyke et al. 2016). A second survey was conducted in 2014, led by Jessica Zung (unpublished). This survey, conducted in 2021, will be the third re-survey of Pyke's original transects.

Methods

Sites: The sites used in this study are identical to those utilized originally by Pyke (1982); however, a smaller number of sites (Figure 1) will be surveyed in 2021 compared to 1974 and previous re-surveys. Low-elevation sites near Crested Butte and some sites along Gothic Rd. are not included due to land use changes; the Mt. Bellview transect (except for the lowest site, which overlaps with the Gothic Rd. transect) will be omitted due to the small size of the sampling team; and the highest elevation site at the summit of Mt. Schofield will be omitted due to potential hazards. A summary of survey sites is presented in Table 1.

Sites range in elevation from 2900 m to 3600 m. Sampling sites consist of a mixture of transect and circular sites, depending on the local terrain. Circular plots are used in flat, even ground such as meadows, and such plots encompass everything within about 50 m of a central point. Elevational range plots encompass defined sections of trails, often through steep terrain, and the sampling area extends 25 m on either side of the path.

Gram2021 Bombus elevational transects



Historical sites sampled by Pyke 1974 overlaid with sites sampled by Gram 2021

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Figure 1 Topographical map of sampling. Selected sites for 2021 sampling are shown in red.

	Gothic Road transect			
	Latitude	Longitude	Elevation (m)	Site type
GOTH 3	38°58.19501'	-106°59.73042'	2906	point
GOTH 4	38°58.34186'	-106°59.80924'	2909	point

GOTH 5	38°58.93918'	-107°00.41508'	2924	point
GOTH 6	38°59.19830'	-107°00.56376'	2948	point
GOTH 7	38°59.46405'	-107°00.82889'	2975-3000	elevation range
GOTH 8	38°59.82252'	-107°01.06513'	3002	point
GOTH 9	39°00.17781'	-107°01.52490'	3074	point
GOTH 10	39°00.35989'	-107°01.85276'	3141	point
GOTH 11	39°00.48412'	-107°02.43157'	3177	point
GOTH 12	39°00.89394'	-107°02.80220'	3252	point
	Washington Gulch transect			
	Latitude	Longitude	Elevation (m)	Site type
WAGU 1	38°58.93786'	-107°00.45160'	2931-3086	elevation range
WAGU 2	38°58.86805'	-107°00.72873'	3086-3178	elevation range
WAGU 3	38°58.90780'	-107°00.98027'	3178-3243	elevation range
WAGU 4	38°58.62202'	-107°01.42404'	3251	point
WAGU 5	38°58.61442'	-107°01.58639'	3259-3333	elevation range
WAGU 6	38°58.33348'	-107°01.56429'	3333	point
WAGU 7	38°58.32040'	-107°01.59006'	3348-3388	elevation range
WAGU 8	38°58.16237'	-107°01.75291'	3388-3456	elevation range
	Mt. Schofield transect			
	Latitude	Longitude	Elevation (m)	Site type
SCHO 1	39°01.48943'	-107°03.09404'	3156	point
SCHO 2	39°01.52943'	-107°02.77836'	3193	point
SCHO 3	39°01.54554'	-107°02.76329'	3205-3322	elevation range
SCHO 4	39°01.73703'	-107°02.54087'	3322-3481	elevation range
SCHO 5	39°02.11276'	-107°02.38135'	3481-3640	elevation range

Table 1. Survey site locations. Point sites consist of open meadows and surveys are conducted within the meadow, typically within ~50 m of the central point. Elevation range sites are along trails and surveys are conducted within ~ 25 m of the trail.

Data collection: Each site will be surveyed for a minimum of 30 minutes weekly between June 28 and August 15, 2021. Bumblebees within the site will be netted and transferred to a “photo booth” imaging container to restrain bees while photo and video vouchers are being recorded. The photo booth is a version of the device described by Thompson and Zung (2015) that has been adapted for use with cell phone cameras. Metadata from each digital voucher, including the precise time of photographing and GPS coordinates will be compiled post-sampling. In addition to digital vouchers, field identifications for each bee will be recorded (based on Williams et al. 2014), along with caste and the identity of the flowering plant the bee was collected from. Bumble bees will be released without marking after digital vouchers and field identifications are recorded. Previous surveys have marked bees before releasing, but found that only an extremely small number of marked bees were observed again after releasing, and the extra time needed to mark bees hindered the sampling effort (Zung et al. 2014, unpublished). For each site visit, a list of the flowers in bloom will be compiled, and each flowering plant will be assigned a subjective rank of relative abundance as a floral resource (1, one or very few flowers blooming; 2, some blooms; 3, plant represents a substantial floral resource at the site; 4, plant is blooming and abundant or dominant at the site). Thus, for each bumble bee that is collected, we will have recorded: the species and caste (confirmed by digital voucher), the identity of the plant it was collected from, a list of floral resources available at the site and time of collection, the site location and elevation, date, and time. Starting on June 28, 2021, each of the three sites will be surveyed a minimum of once per week, with additional surveys depending on the weather and the availability of field assistants. Surveys will continue until mid-August.

Data analysis: Analyses will aim to determine whether bumble bee species are migrating up in elevation. Because no counts of absolute abundance of bumble bees at each site will be recorded, the dependent variable is the relative proportion of each bumble bee species observed at different elevational regions. Independent variables include *elevational region*, defined by Pyke et al. (2011) in 500 ft intervals, (i.e. region 1 is 8500–9000 ft; region 2 is 9000-9500 ft; region 3 is 9500-10,000 ft; region 4 is 10,000-10,500 ft; region 5 is 10,500-11,000 ft; region 6 is 11,000-11,500 ft; region 7 is 11,500-12,000 ft.); *site*, and year.

Bumble bees are rarely injured or killed during the process of netting and photographing, as opposed to lethal sampling (Zung J., *personal communication*). And given that a previous study in our survey area indicated that even repeated, lethal sampling did not have a significant impact on the abundance or community structure of bees (Gezon et al. 2015), it is unlikely that our method of catch-and-release will have significant effects on local bumble bee populations.

Results

A total of 2,722 bumble bees were recorded across all elevational transect sites between June 25 and August 15, 2021. Bees were identified to species in the field, and these IDs will be confirmed through photo vouchers. Because this study did not establish a method for reliably measuring and comparing the absolute abundances of different bumble bee species, we opted to instead analyze the shifts in relative proportions of species at different transects, both over time and across an elevational gradient. The relative proportions of each species at each site along the three elevational transects for all years sampled are summarized in Figure 2.

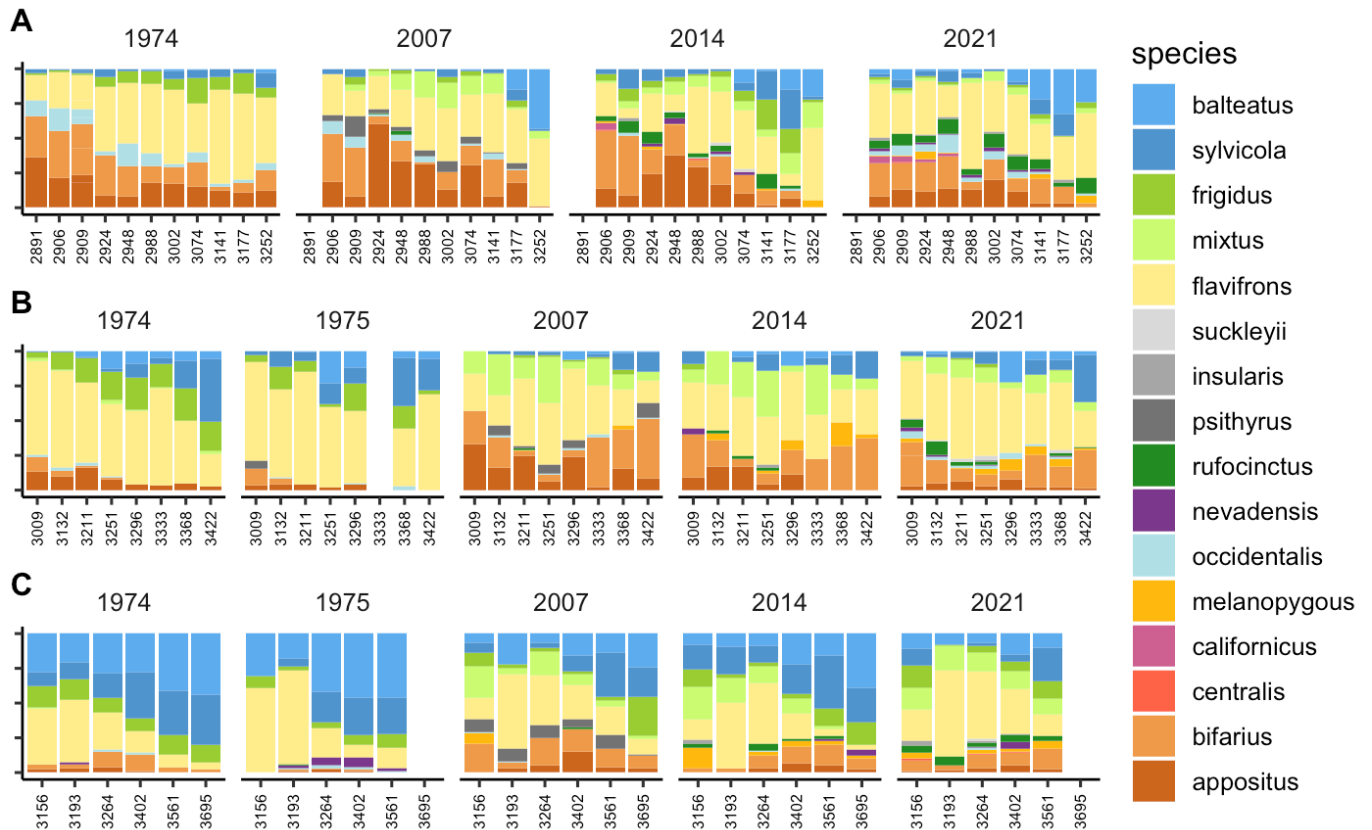


Figure 2. Relative proportions of each bumble bee species across elevational gradients along three surveyed transects. A, Gothic Road transect; B, Washington Gulch transect; C, Schofield transect.

In cases where niche partitioning has resulted in different bumble bee species with

similar dietary niches segregating to specific elevational ranges, we examined whether species typically found only at low-elevation are migrating to higher elevation by comparing the relative proportions of niche-matched low- and high-elevation species. *Bombus appositus* and *B. balteatus* are both large, long-tongued species that feed on similar plants, but *B. appositus* is generally observed to inhabit regions of lower elevation and *B. balteatus* is typically found only at high elevations. We find that over time, this general pattern of resource partitioning by elevation has not changed, i.e., *B. appositus* does not appear to be moving up in elevation in our sites (**Figure 3**). This is in contrast to the finding published by an earlier analysis of this data (Pyke et al. 2016) which compared only data from 1974 and 2007, and concluded that *B. appositus* was moving up in elevation. This difference in results when comparing just two years

of data versus five years, as in our analysis, highlights the importance of regular, repeated sampling across many years to avoid confounding interannual population dynamics variation

Washington Gulch appositus vs balteatus proportion per site by year

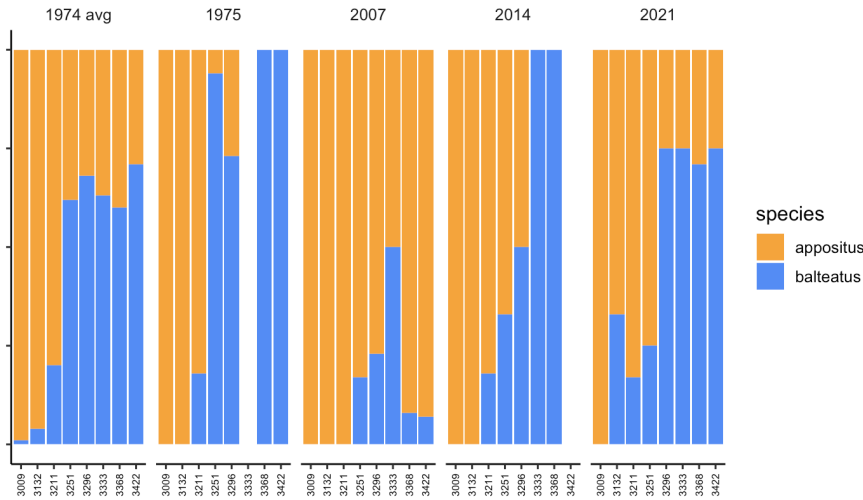


Figure 3. Relative proportions of *Bombus appositus*, a species typically seen at low elevation, and *B. balteatus*, a species typically seen at high elevation, at sites along an elevational gradient over time.

Washington Gulch bifarius vs sylvicola proportion per site by year

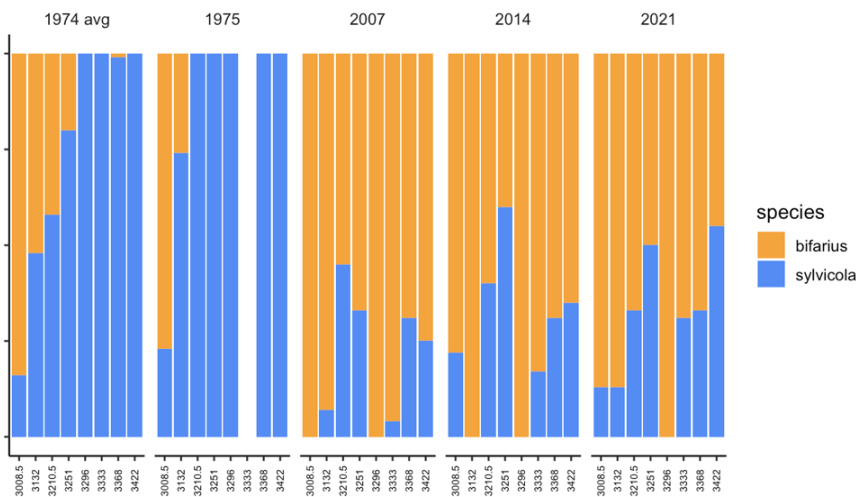


Figure 4. Relative proportions of *Bombus bifarius*, a species typically seen at low elevation, and *B. sylvicola*, a species typically seen at high elevation, at sites along an elevational gradient over time.

with actual migration omg this sentence is a monstrosity.

When comparing the relative proportions of two similarly matched short-tongued species, however, it does appear that elevational shifts are occurring (**Figure 4**).

Bombus bifarius, which was in the 70s the mainly present at lower elevation, has in the past three re-surveys been equally or more dominant than the “high-elevation” species *B. sylvicola*.

Bombus flavifrons is a medium-tongued species that has been reported as very common at nearly all sites in

this study. As a generalist

forager with a high degree of

interspecific variation in worker body size, we predicted that *B. flavifrons* is well-equipped to fill

into new niches that may be made available when other species contract or shift their range due to climate change. Comparing the relative proportions of *B. flavifrons* to all other species along an elevational gradient, however, shows no strong evidence that the proportion of *B. flavifrons* is increasing at any elevation (Figure 5).

Gothic Rd. transect proportions occidentalis, flavifrons

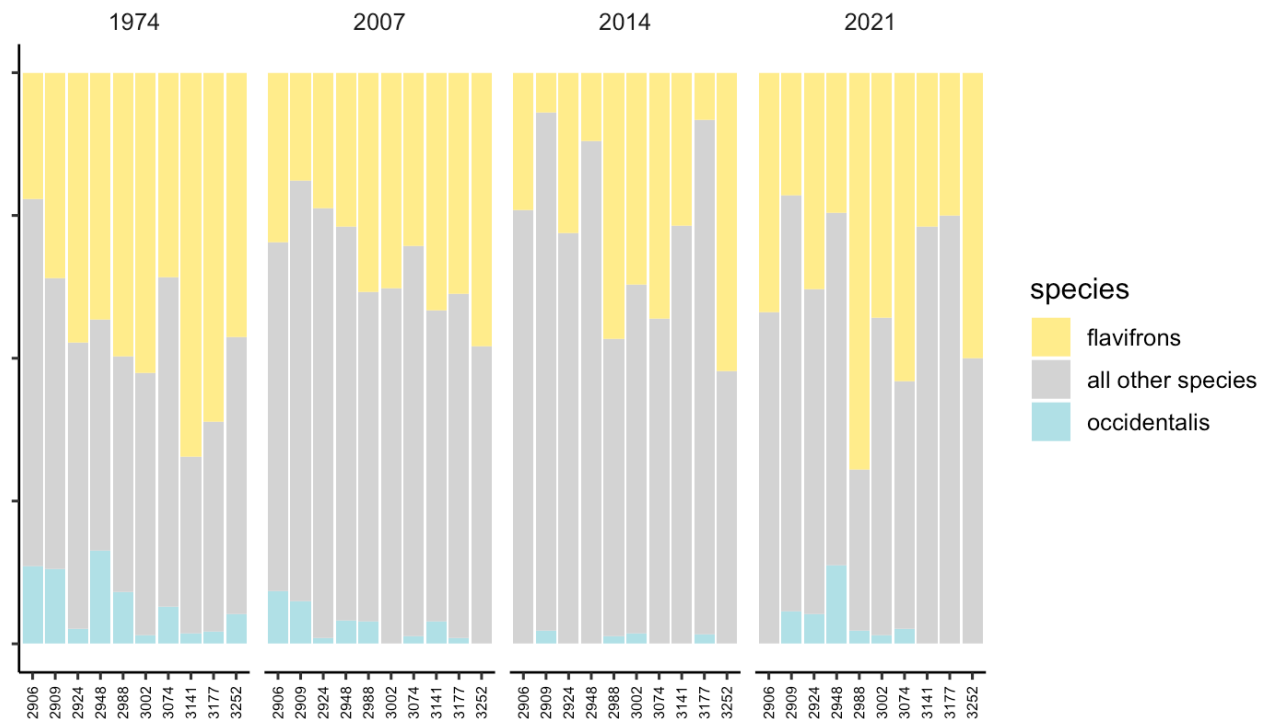


Figure 5. Change in relative proportions of *Bombus flavifrons* and *B. occidentalis* across an elevational gradient over time.

An additional species of interest is *B. occidentalis*, which is declining in most of its range. We compared the relative proportions of *B. occidentalis* in the overall community compositions of sites along an elevational gradient over time (Figure 5). There is no noticeable trend that would suggest *B. occidentalis* is declining in relative proportion in any of our study areas, despite its well-documented decline in nearby areas.

Discussion

This survey was the third such effort to re-survey the elevational transects first surveyed in 1974 by Pyke (1982). The addition of this third year of data has been helpful in distinguishing genuine elevational shifts from yearly variation.

One of the most striking results from comparison of species compositions across elevational gradients from all survey years is that *Bombus bifarius* appears to have shifted its range upward in elevation without any signs of contracting at its lower range. Continual monitoring of this species and similarly sized short-tongued bumble bees will be valuable for better understanding what this shift means. It is possible that by moving into higher elevations, *B. bifarius* will be more frequently competing with high-elevation species like *B. sylvicola* which tend to utilize the same resources. However, an alternate explanation for this trend is that *B. sylvicola* was misidentified in the 1974 surveys, causing it to be overrepresented in the dataset. Unfortunately, until the reference collection is found, it's not possible to verify any of the identifications made in the 1974 survey. However, the proportions of *B. sylvicola* recorded in 1974 are very similar to those recorded at the same sites in 1974 by Inouye, and in 1975 by Thomson. There is much more to discuss here, but I'm done writing this paper for now.

Acknowledgements

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