

# Six years of wild bee monitoring shows dramatic seasonal shifts in biodiversity and species declines

Nash Turley<sup>1</sup>, Neelendra Joshi<sup>2</sup>, David Biddinger<sup>3</sup>, and Margarita López-Uribe<sup>1</sup>

<sup>1</sup>The Pennsylvania State University Department of Entomology

<sup>2</sup>University of Arkansas Department of Entomology

<sup>3</sup>The Pennsylvania State University

March 28, 2022

## Abstract

Wild bees form diverse communities that pollinate plants in both native and agricultural ecosystems making them both ecologically and economically important. The growing evidence of bee declines has sparked increased interest in monitoring bee community and population dynamics using standardized methods. Here, we studied the dynamics of bee biodiversity within and across years by monitoring wild bees adjacent to four apple orchard locations in Southern Pennsylvania, USA. We collected bees using passive Blue Vane traps continuously from April to October for six years amassing over 26,000 bees representing 144 species. We quantified total abundance, richness, diversity, composition, and phylogenetic structure. There were large seasonal changes in all measures of biodiversity with month explaining an average of 72% of the variation in our models. Changes over time were less dramatic with years explaining an average of 44% of the variation in biodiversity metrics. We found declines in all measures of biodiversity especially in the last 3 years. Analyses of population trends over time for the 40 most abundant species indicate that about one third of species showed at least some evidence for declines in abundance. Bee family explained variation in species-level seasonal patterns but we found no consistent family-level patterns in declines, though bumble bees and sweat bees were groups that declined the most. Overall, our results show that season-wide standardized sampling across multiple years can reveal nuanced patterns in bee biodiversity, phenological patterns of bees, and population trends over time of many co-occurring species. These datasets could be used to quantify the relative effects that different aspects of environmental change have on bee communities and to help prioritize conservation efforts.

## Introduction

Pollinators facilitate reproduction for over 80% of flowering plants (Ollerton et al. 2011) and increase the yield, to varying extent, of 75% of crop species (Klein et al., 2007). Bees are the single most important group of pollinators (Neff and Simpson, 1993) thus detecting changes in bee biodiversity is important for developing pollinator management plans to sustain wild plant communities while maximizing crop yields (Garibaldi et al., 2013, Winfree et al., 2018). A variety of bee monitoring efforts have found troubling declines among wild bees (Koh et al., 2016). For example, some species have had substantial range contractions and declines in abundance, especially bumble bees in North America and Europe (Beiseijer et al., 2006, Williams and Osborne. 2009, Cameron et al, 2011, Bartomeus et al., 2013). Overall wild bee abundance is falling in over 23% of the United States land area (Koh et al., 2016). And the number of bee species observed around the world in museum collections and from community science observations has dropped by 25% from 1990 to 2015 (Zattara and Aizen, 2021). Because of their importance and growing evidence of declines, bee monitoring efforts that build a better understanding of the dynamics of bee biodiversity are important for developing

plans that can lead to conserving and restoring wild bee populations (Winfree, 2010, LeBuhn et al., 2013, Woodard et al., 2020).

Bee biodiversity can be measured in a variety of ways, all of which can give unique insights into the dynamic of populations and communities within and across years. The simplest component of biodiversity is the total abundance (e.g. total number of bees) and the abundance of individual species measured over a given period. Total abundance can provide information on the times within years that are most favorable for most species. Data on the abundance of individual species across years is critical for understanding if species population trends are stable, increasing, or declining over time. For bees, these types of abundance data are often not available because of a lack of repeated and standardized sampling over time (Portman et al., 2020). Richness, or the number of species, is another metric of interest in biodiversity studies, particularly from a restoration and conservation perspective. However, richness can sometimes provide limited unique information because the detection of species is highly dependent on sample sizes as more individuals counted tend to lead to higher species detection. Diversity metrics help solve these limitations by summarizing aspects of richness and relative abundance among species (evenness) in a single estimator. For example, measures like inverse Simpson's and rarefied richness represent the effective number of species and provide biodiversity measures that are independent of abundance-driven changes in richness (Jost, 2006). Diversity can also be measured in a way that incorporates information about the evolutionary distance that is present among all species in a community using tools from the field of community phylogenetics (Webb et al., 2002). A community with many closely related species is more clustered, while a community populated with distantly related species is more even (also called overdispersed). Finally, measures of community composition are among the most information-rich measures of biodiversity because they can incorporate the relative abundances of all species to determine how similar communities are. The multivariate nature of these measures means it is possible to detect changes among communities even if overall richness, abundance, and diversity are the same. For this reason, community composition measures can be particularly powerful in detecting changes over time or responses of communities to environmental degradation or restoration (Nerlekar and Veldman, 2020).

Adult bee communities are highly dynamic within years making standardized and season-long sampling necessary to accurately characterize seasonal variations in biodiversity (Leong et al, 2016). In temperate climates, bees overwinter as larvae, pupae, or adults and then emerge in spring or summer in response to a variety of environmental cues (Cane, 2021). But the time of the year in which bees are active (seasonality) and the duration of their period of activity (phenological breadth) vary greatly among species, resulting in ever-shifting communities within each year (Ogilvie and Forrest, 2017, Kammerer et al., 2021). Some studies have investigated changes in bee community composition using continuous standardized sampling across the entire period of adult bee activity (e.g., Heithaus, 1979, Wilson et al., 2008, Joshi et al., 2015, Kammerer et al., 2016, Leong et al., 2016, Naeve et al., 2020, Stenkovski et al. 2020, Roubik et al., 2021) However, for many bee communities, we still lack a detailed understanding of how community biodiversity and composition change from month to month. Relatively fewer studies have compared the phenological patterns, both seasonality, and phenological breadth, for many co-occurring species (but see: Stenkovski et al. 2020). One reason for this is that the focus of many bee community studies are in agricultural settings where the blooming period of crops is only over a small period of time (e.g. Russo et al., 2015, Grab et al., 2019, Graham et al., 2021).

Bee abundance and richness can also change greatly across years (Ogilvie et al., 2017, Graham et al., 2021). One method for studying changes in bee species over time is to compare historical records with more recent collections (Cameron et al, 2011, Bartomeus et al., 2013, Burkle et al., 2013, Mathiasson et al., 2019, Wood et al., 2019). This approach is typically only able to test for changes in a small number of species that are popular among collectors (like bumble bees) and is most informative to detect changes in species geographic distribution (Cameron et al, 2011, Mathiasson et al., 2019, Wood et al., 2019). The lack of standardized collection methods between historical and current records means it is difficult to separate if the changes in abundance are the result of changes in population size or changes in sampling efforts (Portman et al., 2020). An alternative approach is to conduct standardized sampling, often using passive traps, in the same locations across multiple years (Iserbyt and Rasmont, 2012, Martins et al. 2013, Gezon et al., 2015, Onuferko et al.,

2018, Graham et al., 2021). These types of long-term longitudinal studies of bee communities are rare but the existing ones have reported a mix of species that are stable, increasing, and decreasing over time (e.g. Graham et al., 2021, Roubik et al., 2021). These sampling approaches can give more explicit insight into the changes in relative abundance in a wide variety of species. Jointly, these studies have increased the need and interest in formal monitoring of bee biodiversity to assess if there are declines and potential links to decreasing pollination services (Woodard et al., 2020).

In this study, we conducted standardized bee collections across 6 years in Southern Pennsylvania, USA to characterize changes in bee community biodiversity and changes in abundance of specific species. Specifically, we quantified abundance, richness, diversity, phylogenetic structure, and composition of bee communities between months and years. We collected bees continuously from April through October using passive Blue Vane traps. With this, we asked the following specific research questions:

1. How does bee biodiversity change within-years?
2. How does bee biodiversity change across years?
3. How do seasonal patterns differ among bee families and species?
4. Do bee families and species differ in their changes in abundance over time?

## Methods

### Study site

Our study sites were located in-and-around the Pennsylvania State Fruit Research and Extension Center in Adams County, Pennsylvania, USA (39.935226, -77.254530). The area has an average yearly rainfall of 112 cm, average summer temperature ranging from 16 °C to 28 °C, and average winter temperatures of -5 °C to 5 °C (Biddinger et al., 2018). This landscape is hilly with well-drained soils and the broader area is approximately 56% broadleaf forest fragments, 25% pastureland, 9% developed areas, and 8% commercial orchards (Biddinger et al., 2018). All orchards were managed under growers' choice conventional pest management programs that use pesticide classes including insect growth regulators, anthranilic diamide, tetramic acid, microbials, and neonicotinoid insecticides (Biddinger et al., 2018). We sampled bees at 8 locations adjacent to 4 different active apple orchards. Sampling locations were within 150 m of orchards and 250 m of a forest fragment (Figure 1) which have diverse plant and pollinator communities (Kammerer et al., 2016). Often orchards rely, in part, on managed honey bee colonies for pollination, which have the potential to negatively impact native bee populations (Mallinger et al., 2017). However, our sampling sites did not have managed honey bee hives within 2 km and growers managing the adjacent orchards had not rented honey bees for at least 15 years.

Our bee monitoring traps were located within perennial wildflower strips approximately 50 m x 10 m in size that were sown between 2-3 years before the beginning of our study. Wildflower sites used in this study were established and managed using the specific planting guidelines developed by the Pennsylvania USDA-NRCS and the Xerces Society for Invertebrate Conservation (NRCS, 2011). They were sown with 21 species of native forbs and grasses sourced from a local native seed supplier (Ernst Conservation Seed, Meadville, PA 16335). All wildflower sites were mowed once a year and received spot sprays of common selective herbicides as needed.

### Bee collections

We trapped bees continuously from April to October from 2014 to 2019 using Blue Vane traps (BanfieldBio Inc., Woodinville WA). A previous study in this region showed that Blue Vane traps collect a higher abundance and total richness of bees than colored bowl traps, also called pan traps (Joshi et al., 2015). Although the overall community composition of bees captured in Blue Vane traps was different from bowl traps, nearly

all species were more likely to be captured in Blue Vane traps over bowls, except some *Andrena* and *Lasio-glossum* species (Joshi et al., 2015). In our study, Blue Vane traps were filled with about 7 cm of 60% ethylene glycol (Supertech® Wal-Mart Stores, Inc., Bentonville, AR), hung from posts about 1.5 m off the ground. At each of our 8 locations, we placed 2 traps 25 m apart (Figure 1). Traps were left outside continuously from April to October every year and traps were replaced each year in case wear over time decreases their attractiveness. Each week, all specimens were removed and the ethylene glycol was replaced. Bee specimens were separated from other insects collected in the traps and stored in 70% alcohol until they were washed, pinned, and labeled. All bees were identified to the species level except 14 individuals were removed because of uncertain species-level identification. For bee identification, we used published dichotomous keys (Mitchell, 1960, 1962; Michener et al., 1994, Michener, 2000) and various interactive bee identification guides available at Discover Life (<http://www.discoverlife.org>). Species identifications were conducted by David Biddinger (Pennsylvania State University), Robert Jean (Senior Entomologist, Environmental Solutions and Innovations, Inc.), Jason Gibbs (University of Manitoba), and Sam Droege (United States Geological Survey). All specimens from this study are stored at the Pennsylvania State Fruit Research and Extension Center, Biglerville, PA, or the Frost Insect Museum at Pennsylvania State University, University Park, PA.

## Data and statistical analyses

All analyses were conducted with R version 4.0.3. To explore how thorough our sampling of bee biodiversity was we created a species accumulation curve based on the number of individuals sampled. We did this using the ‘specaccum’ function in the vegan package (Oksanen et al., 2013).

We calculated biodiversity metrics for each of our 8 sampling locations using the combined data from both traps at each site. For month analyses (within years) we calculated biodiversity metrics for each month and then averaged across all years. We then averaged together sites closer than 900 m resulting in 4 replicates. Therefore, the interpretation of each replicate is the average biodiversity value per site for a single month. For year analyses (across years), we first summed data across all months and then calculated metrics for each year and then averaged to get 4 replicates per year. The interpretation of these data is then the total biodiversity value per site for a single year.

Using community abundance data, we measured total abundance, richness, and diversity (inverse Simpson’s) within and across years using the ‘specnumber’ and ‘diversity’ functions in the vegan package (Oksanen et al., 2013). We also used community abundance data to measure differences in community composition using a Bray-Curtis dissimilarity matrix. To measure phylogenetic structure, we use a genus-level molecular phylogeny from Hedtke et al. (2013). We made the phylogeny ultrametric with the ‘force.ultrametric’ function in the phytools package (Revel, 2012) using the non-Negative Least-squares method. We then amended our species below the genus-level using the ‘genus.to.species.tree’ function which creates bifurcating subtrees among species in each genus and then binds them at a random place along the terminal edge. With this approach, the relationships among species below the genus level are created at random. We only had to drop 2 species from these analyses because their genera (*Cemolobus*, *Triepeolus*) were not in the tree, which only had 7 and 2 individuals in the dataset, respectively.

Using the community data and this phylogeny, we calculated mean pairwise distance (MPD) among all taxa. This metric is a measure of the average evolutionary distance between all pairs of species in a community and was calculated with the ‘mpd.query’ function in the PhyloMeasures package (Tsirogiannis and Sandel, 2016). Because raw values of MPD can be impacted by species richness of samples, we used a standardized effect size of MPD that is based on the difference between the observed measure of MPD and a random null model of a community with the same number of species (Tsirogiannis and Sandel, 2016). This value is also standardized by variance making the metric an effect size in standard deviation units. Negative values of this metric indicate a community is more clustered (less average evolutionary distance among pairs of species) than a random community with the same richness, and positive values indicate a more even community, also known as overdispersed. The resolution of phylogenies below the species level has little-to-no impact on MPD calculations. Qian and Jin (2021) found that MPD values are nearly identical when calculated with

a genus-level phylogeny with species amended (like ours) compared to a fully resolved phylogenetic tree. And in our case, repeating the process of randomly adding species below the genus level resulted in nearly perfectly correlated measures of MPD ( $r = 0.99$ ). However, trees without species-level resolution do not provide reliable estimates of phylogenetic signals of species' traits (Davies and Kraft, 2012), so we did not include those analyses in the current study.

We modeled the changes in bee biodiversity within and across years by fitting general additive models using the 'gam' function in the mgcv package (Wood, 2017). These allowed for non-linear fits to the data. For all tests, we used 5 knots which allowed for sufficient curviness to represent observed patterns and to produce linear relationships between observed and fitted values. The amount of variation explained by these models was typically similar to ANOVA models fit to the same data. We report percent change effect sizes among extreme values of months and years as the difference in means between a pair of values (e.g. the mean from April minus the mean for August) then divided that difference by the overall mean for that variable. This gives a standardized effect size that can be compared among variables. We used perMANOVA to test differences in composition among groups using the 'escalc' function and visualized results with non-metric multidimensional scaling fit with the 'metaMDS' function, both from the vegan package (Oksanen et al., 2013).

To assess how phenological patterns differ among bee families and species, we calculated a metric for seasonality (time of year when the species showed the highest abundance) and phenological breadth (a measure of the amount of time bees are active as adults). Phenology measures were calculated for species with 30 or more individuals (a total of 40 species) as this is enough to reliably estimate phenological breadth (Bartomeus et al., 2013). We measured seasonality as the median day of year (Julian date) of capture across individuals collected for a species. Our measure of breadth was the difference between the 10th and 90th percentile of capture dates. To control for the different numbers of individuals across species, we randomly drew 30 data points for each species repeated 500 times. For each of these subsamples, we calculated the seasonality and breadth statistics and then averaged those 500 values to get our final statistics (Bartomeus et al., 2013).

To evaluate how bee families and species differ in their changes in abundance over time, we calculated a metric of change over time for each species as the slope of the linear relationship between abundance and year. We standardized abundance data for each species to have a mean of 0 and a standard deviation of 1 to allow comparisons across species. We multiplied the model coefficients by five (the change in years in our sampling) to get a predicted level of change in standard deviation units over the course of the study.

## Results

### Description of biodiversity

Our final dataset included 26,716 individual bees representing 5 bee families, 30 genera, and 144 species. See [CITATION FOR DRYAD SUBMISSION] for the complete dataset and list of species. We collected 33% of the total number of bee species that have been found in Pennsylvania (Kilpatrick et al., 2020). The species accumulation curve for these data shows a leveling off pattern but did not reach an asymptote (Figure 2A). The abundances among species show a typical rank abundance curve with a small number of very abundant species and many rare species (Figure 2B). Ten species had over 1,000 individuals while over half of the species had 5 or fewer individuals. We captured by far the most individuals and species from the family Apidae (19,870 individuals and 47 species) followed by Halictidae (5,942 and 33), Andrenidae (477 and 28), Megachilidae (383 and 30), and Colletidae (44 and 6).

### Biodiversity changes within years

We found very strong evidence for seasonal changes in all measures of biodiversity and on average month explained an average of 74% of the variation in our models (Figure 3, Table 1). Abundance and richness

showed a hump-shaped pattern peaking in July. In our models, month explained nearly 90% of variation in abundance and richness. The number of bees captured per site increased by 193% between April and August, which were the lowest and highest values we observed (Figure 3A). Similarly, average richness increased by 89% between April and July (Figure 3B). Diversity also increased and decreased across the seasons, but less sharply than in richness, and peaked in August instead of July (Figure 3C). Diversity increased by 41% between May and August and decreased by 60% from August to October (Figure 3C). Because diversity incorporates both richness and evenness, the weaker pattern in diversity compared to richness is a consequence of evenness having a pattern nearly opposite that seen in richness ( $P < 0.0001$ ,  $R^2 = 0.68$ ), highest in spring and fall and lowest in July.

Phylogenetic structure also varied between months. Mean pairwise distance dropped (becoming more clustered) by 1.9 standard deviations between May and July and then increased (becoming more even) by 1.1 standard deviations between July and October. The months of April, June, August, and September had intermediate values (Figure 3D). We observed limited variation in phylogenetic structure between sites resulting in our model explaining 87% of the total variation (Table 1). Community composition varied substantially among months with our multivariate model explaining 64% of the variation in bee communities (Figure 4A, Table 1). Spring months (April-June) all had distinct bee communities. July through September had similar compositions which were themselves distinct from spring months and October (Figure 4A).

## Biodiversity change across years

We found very strong evidence for biodiversity change over time between 2014 and 2019 with year explaining an average of 42% of variation across all biodiversity metrics (Figure 3, Table 1). Abundance of bees captured declined by 48% between 2014 and 2019 (Figure 3E). Richness declined by 41% between the peak in 2016 and the lowest point in 2019 (Figure 3F). Similar to richness, diversity also declined after 2016, dropping by 59% between 2016 and 2019 (Figure 3G), though the model for diversity explained about half as much variation as the model for richness (Table 1).

Phylogenetic structure increased and decreased over time with the most clustered communities in 2014 and 2019, and the most even communities in 2016 (Figure 3H). Mean pairwise distance increased (became more even) by 1.8 standard deviations between 2014 and 2016, and then decreased (becoming more clustered) by 1.6 standard deviations between 2016 and 2019. Bee communities were quite stable across the first three years though they shifted slightly over time in the last three years (Figure 4B). Year explained about 36% of the variation in community composition.

## Species patterns in seasonality, phenological breadth, and change over time

Looking across the 40 species for which we collected 30 or more individuals (Table A1), bee families varied significantly in seasonality (Figure 5, Figure 6,  $F_{3,36} = 10.91$ ,  $P < 0.001$ ). Species in the families Megachilidae and Andrenidae were collected an average of 54 days earlier than species in the families Apidae and Halictidae (Tukey tests,  $P < 0.006$ ). In the family Megachilidae, *Osmia* species and *Hoplitis pilosifrons* were among the earliest emerging species, but *Megachile mendica* was most active in July and August (Figure 5). In the Andrenidae, all *Andrena* species are most active in April and May, but *Calliopsis andreniformis* was most abundant in July. Among species in the family Apidae, *Eucera hamata* was the only species with peak abundance in May. Species in the genera *Anthophora*, *Ceratina*, and *Bombus* were most active in June, though there is some variation among species within those genera. Other species in the family Apidae, including *Ptilothrix*, *Melitoma*, and *Melissodes*, as well as *Eucera (Peponapis) pruinosa*, peaked in July and August (Figure 5). Most species in the family Halictidae were most abundant in July and August, though two *Agapostemon* species were active earlier (Figure 5, Figure 6).

Phenological breadth varied among families (Figure 5, Figure 6,  $F_{3,36} = 3.896$ ,  $P = 0.02$ ) with two families that were significantly different. Species in the family Andrenidae had the narrowest breadth at 35 days on average, and species in the Halictidae were active the longest at 89 days on average (Tukey test,  $P = 0.02$ ).

The families Megachilidae (49 days) and Apidae (66 days) showed intermediate breadth. In the Andrenidae, all *Andrena* species had a breadth of less than 42 days, but *Calliopsis andreniformis* had a breadth of 79 days. In the Megachilidae, *Osmia* species' breadths range from 21 to 58 days while *Megachile mendica* had a breadth of 71 days. Species in the Halictidae consistently had a wide phenological breadth, greater than 75 days, though *Halictus ligatus* had a relatively narrow window of 55 days. We split species in the Apidae into two groups, each consisting of related clades, that varied significantly in phenological breadth (t-test,  $t = -3.7$ ,  $df = 18.3$ ,  $P = 0.002$ ). Species in the genera *Bombus*, *Apis*, *Ceratina*, and *Xylocopa* had an average breadth of 85 days, while species in the genera *Eucera*, *Melissodes*, *Ptilothrix*, *Melitoma*, and *Anthophora* had an average breadth of 44 days (Figure 5, Figure 6).

We observed substantial species-level variation in the changes in abundance across years (Figure 5, Table A1). We detected no little-to no change in abundance for 26 species ( $P > 0.1$ ), 8 species showed moderate to strong evidence for decline ( $P < 0.05$ ), 5 more showed weak evidence for decline ( $P < 0.1$ ), and we found strong evidence for increase in 1 species ( $P < 0.01$ ). While bee family was not a significant predictor of changes in abundance ( $F_{3,36} = 1.813$ ,  $P = 0.16$ ), we observed some patterns among families and genera. Species in the families Megachilidae and Andrenidae were all stable. Other families showed mixed trends. For example, among species in the family Apidae, all carpenter bee species in the genera *Xylocopa* and *Ceratina* were stable except for *Ceratina mikmaqi* which declined by 1 standard deviation unit (SD) between 2014 and 2019. Six out of eight species in the Halictidae showed evidence for declines, most species by about 1 SD, but *Agapostemon virescens* declined by 1.7 SD. Four species in the genus *Bombus* showed pronounced declines ranging between 1.2 and 1.8 SD while two *Bombus* species were stable. Similarly, *Melitoma taurea* declined by 1.3 SD. We saw radical variation among species in tribe Eucerini (Apidae): some species stable over time (*Eucera* and some *Melissodes*), *Melissodes desponsa* had the biggest decline we observed (1.8 SD), and *Melissodes bimaculatus* increased by 2.2 SD, which was the only significant increase and also the largest magnitude of change we found.

## Discussion

With 6 years of continuous sampling with passive traps we collected over 26,000 bees and 144 species. The leveling off of the species accumulation curve suggests we captured most, but not all, of bee biodiversity in the system (Figure 2A). The inability to fully document biodiversity (i.e., reach an asymptote in the species accumulation curve) is typical for other extensive bee monitoring efforts (Wilson et al., 2008, Russo et al., 2015) and species-rich invertebrate communities more generally (Gotelli and Colwell, 2001).

We found that all measures of community biodiversity varied dramatically within years and across years (Figure 3, Figure 4). Abundance, richness, and diversity all peaked in summer, though diversity to a lesser extent. By contrast, phylogenetic structure was most even in spring (May) and became most clustered in summer. Community composition also varied greatly within years with communities changing quickly early then becoming much more stable between July and September (Figure 4). This high-level of variation in species-level phenological patterns (Figure 6) resulted in the dramatic turnover of communities between seasons.

All measures of biodiversity also changed across years (Figure 3, Figure 4). The magnitude of changes within years was about twice as large for abundance, richness, and community composition than it was for changes across years. However, for diversity and phylogenetic structure, the changes within and across years were of similar magnitude. After 2016, all measures of biodiversity declined. Community composition also shifted in that time, but not dramatically (Figure 4). These changes in diversity metrics and composition were the result of, in part, 13 species that declined in abundance over time, which were dispersed across the bee evolutionary tree (Figure 5).

## Insights from species-level changes in abundance

Species across the bee evolutionary tree showed a wide variety of phenological patterns (changes in abundance within years). Among the 40 species for which we had sufficient data for, we observed three general patterns, which could be called “phenological syndromes” illustrated in Figure 6. First, *Andrena* and *Osmia* species emerged early in the year and had narrow breadth. Second, species in the tribe Eucerini, (*Melissodes* and *Eucera*), and other sister clades had narrow breadth but, in the summer, rather than in spring. The third group was composed of species with wide phenological breadth including the social and multivoltine species in the genera *Bombus*, *Apis*, *Xylocopa* and *Ceratina*, and nearly all the sweat bees (family Halictidae). Monitoring of species that represent these different phenological syndromes is important because they provide unique ecological functions (Ogilvie and Forrest, 2017). For example, many of the early emerging bee species are of critical importance for early flowering plants such as spring ephemeral wildflowers, and these interactions may be particularly sensitive to disruptions from climate change (Kudo and Ida, 2013). And many crops such as apples and blueberries rely on pollination by early emerging wild bees (Isaacs and Kirk, 2010, Biddinger et al., 2018, Grab et al., 2019, Reilly et al., 2020).

We found that 33% of species had at least some evidence of declines while only 3% increased, and 65% percent showed no changes over time. For comparison, a study using museum records of 187 bee species in eastern North America found significant decreases in the relative number of samples in collections for 29% of species and increases for 27% of species (Bartomeus et al., 2013). Similarly, 38% of non-parasitic bumble-bee species in the UK show clear signs of decline (Williams and Osborne, 2009). While it is possible that we could have had more power to detect changes in rare species with more thorough sampling, we found significant changes among species with a wide variety of abundance (min = 37, max = 3774, mean = 894) and there was no correlation between species’ total abundance and amount of predicted change ( $r = 0.18$ ,  $P = 0.26$ ). Therefore, our finding of 65% of species being stable is robust and comparable to studies in North America and Europe. We did not find that bee family was a significant predictor of which bees are stable or declining. But, there were some clades that were more prone to declines than others, notably bumble bees (*Bombus*) and sweat bees (Halictidae). In another case, 2 closely related longhorn bees (genus *Melissodes*) showed large changes in abundance in opposite directions. More generally, this suggests that phylogenetic relationships are not a good predictor of species changes over time. Understanding which adaptations or life history traits are associated with population increases or decreases over time is likely to be a better approach (Williams et al., 2009). The great variation in species’ changes in abundance is also aligned with van Klink et al. (2022) who found that, on average, different insect species’ population trends are only weakly correlated.

## Insights from multiple measures of community biodiversity

Our thorough collections of bees throughout the seasons, and measurements of communities using a variety of metrics, highlighted the unique biodiversity of bee communities in the spring. Measures of abundance and richness suggested that biodiversity in the spring is low. However, diversity was similar in April and May as it was in July and August despite huge differences in richness. This relative elevation of diversity in the spring was a consequence of greater evenness, or more equal abundances among species. The total amount of spring species captured across all sites and years was also high despite the low abundances. Using rarefaction to standardize the number of individuals collected, we detected 58 species per 900 individuals in April compared to 40 in July. The month of May was also the time with the most phylogenetically even (overdispersed) communities. A non-mechanistic interpretation is that in May, spring bees (largely from Andrenidae and Megachilidae) and some summer bees (mostly in Apidae and Halictidae; Figure 5) were both active resulting in long branch lengths between pairs of species. This parallels results by Ramirez et al (2015) who found that orchid bee communities in Colombia were much more phylogenetically even in the transition period between wet and dry seasons. Composition of bees also shows great uniqueness of spring bee communities and the fast turnover communities resulting in totally unique communities in April, May, and June. These unique aspects of spring biodiversity would be completely missed by looking at only abundance and richness measures and not diversity, phylogenetic structure, and composition. This suggests that studies

seeking to understand the phenological changes of bee communities and the impacts of environmental change on spring bees, need to have robust sampling and multiple measure bee biodiversity.

Repeated measures of bee communities across years suggested a loss of community biodiversity over time, though the patterns of declines depend on which metric you look at (Figure 3). Total abundance showed a linear decline over time which mirrors the patterns we observed for many individual species (Figure 3E, Figure 5). The reasons for these changes over time are not clear. While habitat loss, land-use changes, and pesticide use all likely impacts bee communities in this system, these were all relatively unchanging over the course of this study (Biddinger et al., 2018). Changes in the floral resources of the flower strips where we sampled could have been a factor since they likely experience a reduction of plant diversity over time, as is typical in restored grasslands (Sluis et al., 2002). Climate could also be a driver of population declines, though longer-term data would be needed to test the effect of climate on bee abundance declines (Ogilvie et al., 2017, Kammerer et al., 2021). Other biodiversity metrics showed similar, but more nuanced patterns than abundance. Richness, diversity, and phylogenetic structure were steady or increasing for the first three years, and then declined for the last three (Figure 3). Similarly, community composition also shifted but primarily in the last three years (Figure 4B). Longer-term monitoring is needed to see if these declines are part of an ongoing trend or a result of year-to-year fluctuations.

From a bee monitoring and conservation perspective, changes in abundance, richness, and diversity are easy to interpret. In most cases, decreases in these metrics are problematic and suggest some environmental degradation is causing losses of biodiversity. However, metrics like composition, and phylogenetic structure are harder to interpret without a reference point but can reveal changes not seen in simpler measures (Tucker et al., 2017, Nerlekar & Veldman, 2020). For example, Tonietto et al. (2017) found that old fields, restored prairies, and remnant prairies all had the same abundance and diversity of bees but community compositions were different. And similarly, Frishkoff et al. (2014) found that one type of agricultural land-use did not change bird richness, but it did lead to more phylogenetically clustered communities compared to forest reserves. Going forward, more long-term bee monitoring studies are needed to determine if biodiversity measures like composition and phylogenetic structure provide unique and useful information for conservation efforts.

## Implications for bee monitoring

There are a variety of bee monitoring approaches that range from standardized and repeated collections of bees with detailed taxonomic identification to visual observations of broad taxonomic groups that involve participation from the public. There are pros and cons to studies using methods on both ends of this spectrum (Woodard et al., 2020). Our approach involved continuous collecting using passive Blue Vane traps and species-level identification of all bees. The sampling throughout the year gave us the ability to quantify seasonal changes in biodiversity with fine resolution. The huge number of bees collected means we had 40 species with sufficient data to characterize phenological patterns. And the standardized sampling over many years allowed us to quantify changes in abundance over time, something many most studies have limitations with (Portman et al., 2020). However, it is important to highlight that studies using passive trapping need to be interpreted with caution as the data do not reflect true population sizes (Portman et al., 2020, Briggs et al., 2022). This is because some species are more attracted to traps than others and because trapping results are impacted by context (Kuhlman et al., 2021). While our data may not reflect the absolute abundance of species in the wild, it does show that standardized passive trapping is effective at measuring relative changes within and across years. Overall, the intensive type of monitoring of our study is a good approach to answer questions about community biodiversity change and the unique population dynamics across many co-occurring species.

Our sampling approach and experimental design have several constraints for its implementation on large-scale monitoring projects that aim to detect bee declines. First, collecting, processing, and databasing large numbers of bees is labor-intensive and taxonomic identification requires specialized skills and expertise. This makes specimen curation and identification untenable and impractical for large-scale projects. Second, tens of thousands of bees were killed in the sampling. Concerns have been raised that sampling many bees with

Blue Vane traps could cause declines in some species (Gibbs et al., 2017). While we did not estimate how our collections impacted populations, the lack of correlation between the number of individuals captured and that species change over time ( $r = 0.18$ ,  $P = 0.26$ ) provides at least some evidence that this was not the case in our study. Third, implementing passive traps exclusively have inherent biases in the species they collect and these biases impact biodiversity metrics. While collections with other techniques would have resulted in different biodiversity measures, we know from our system that Blue Vane traps provide the most thorough sample of the whole bee community (Joshi et al., 2015). And finally, our collections are only from one relatively small area (Figure 1). Given the local nature of our dataset, the observed changes within and across years could be unique to our study area. However, similar phenological patterns and declines have been found in other studies (Bartomeus et al., 2013, Leong et al., 2016, Graham et al., 2021, Kammerer et al., 2021).

## Conclusions

Concerns about the ecological consequences of changes in bee biodiversity are leading to increased recognition of the importance of wild bee conservation and promoting wild bees in agricultural systems (Isaacs and Kirk, 2010, Biddinger et al., 2018, Reilly et al. 2020). But wild bee communities are diverse and dynamic, and little is known about what species or groups have the greatest conservation needs. Our intensive sampling across six years shows that bee communities vary greatly from month to month for all measures of biodiversity. For monitoring efforts to capture the full breadth of bee biodiversity, it is important to sample bees across all seasons, especially during spring when communities turnover rapidly. Biodiversity changes across the six years of our study were less dramatic than seasonal changes, but we found evidence of biodiversity loss over time with declines in abundance in 33% of the species. Notably, our results indicate that bee family is not a good predictor of changes over time, and in some cases, closely related species showed very different patterns. This suggests that species-specific traits may be more important predictors of long-term population dynamics than shared evolutionary history. We recommend that future monitoring efforts that seek to understand species-level dynamics for multiple co-occurring species, and whole-community patterns in biodiversity, utilize standardized collection methods repeated over multiple years. Longer-term and species-specific data on wild bee dynamics could provide greater insight into which species need targeted conservation efforts (Woodard et al., 2020).

## Acknowledgments

We thank the orchard fruit grower Scott Slaybaugh, Jim Lerew, Bill Pulig, and Barry Rice for allowing us to conduct studies on their land and to Jim Gillis and Mace Vaughan for their support in establishing the USDA-NRCS wildflower strips. Thank you to Kathryn Wholaver, Lolita Miller, Sarah Heller, and many others at the Pennsylvania State Fruit Research and Extension Center. Jason Gibbs, Robert Jean, and Sam Droege identified bees and the members of the López-Urbe Lab provided helpful feedback on the previous versions of the manuscript. This research was supported by a Pennsylvania Department of Agriculture Grant number C940000555, and USDA-NIFA-AFRI Specialty Crop Research Initiative, Project 2012-51181-20105. DJB was funded through the USDA NIFA Appropriations under Project PEN04620. MML-U was funded through the USDA NIFA Appropriations under Projects PEN04716 and PEN04620.

## Conflicts of interest

The authors declare no conflicts of interest.

## Data availability statement

The data used in this study will be posted on Dryad after the paper is accepted for publication.

## Author contributions

Nash E. Turley: Formal analysis (lead); Visualization (lead); Writing – original draft (lead); Writing – review & editing (equal)

David J. Biddinger: Conceptualization (equal); Funding acquisition (equal); Investigation (lead); Methodology (equal); Writing – review & editing (equal)

Neelendra K. Joshi: Conceptualization (equal); Investigation (equal); Methodology (equal); Writing – review & editing (equal)

Margarita M. López-Urbe: Conceptualization (equal), Funding acquisition (lead); Writing – review & editing (lead)

## References

- Bartomeus, I., Ascher, J.S., Gibbs, J., Danforth, B.N., Wagner, D.L., Hedtke, S.M. and Winfree, R., 2013. Historical changes in northeastern US bee pollinators related to shared ecological traits. *Proceedings of the National Academy of Sciences*, 110(12), pp.4656-4660.
- Biddinger, D.J., Rajotte, E.G., and Joshi, N.K. 2018. Integrating pollinator health into tree fruit IPM - A case study of Pennsylvania apple production, in and Roubik, D.W., (ed). *The pollination of cultivated plants: a compendium for practitioners*. Vol. 1. Food and Agricultural Organization of the United Nations. pp. 69-83.
- Biesmeijer, J.C., Roberts, S.P., Reemer, M., Ohlemuller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R.J.M.C., Thomas, C.D. and Settele, J., 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, 313(5785), pp.351-354.
- Briggs, E.L., Baranski, C., Münzer Schaetz, O., Garrison, G., Collazo, J.A. and Youngsteadt, E., 2022. Estimating bee abundance: can mark-recapture methods validate common sampling protocols? *Apidologie*, 53(1), pp.1-24.
- Burkle, L.A., Marlin, J.C., and Knight, T.M., 2013. Plant-pollinator interactions over 120 years: loss of species, co-occurrence, and function. *Science*, 339(6127), pp.1611-1615.
- Cameron, S.A., Lozier, J.D., Strange, J.P., Koch, J.B., Cordes, N., Solter, L.F. and Griswold, T.L., 2011. Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences*, 108(2), pp.662-667.
- Cane, J., 2021. Global warming, advancing bloom and evidence for pollinator plasticity from long-term bee emergence monitoring. *Insects*, 12(5), p.457.
- Davies, T.J., Kraft, N.J., Salamin, N. and Wolkovich, E.M., 2012. Incompletely resolved phylogenetic trees inflate estimates of phylogenetic conservatism. *Ecology*, 93(2), pp.242-247.
- Frishkoff, L.O., Karp, D.S., M'Gonigle, L.K., Mendenhall, C.D., Zook, J., Kremen, C., Hadly, E.A. and Daily, G.C., 2014. Loss of avian phylogenetic diversity in neotropical agricultural systems. *science*, 345(6202), pp.1343-1346.
- Gallai, N., Salles, J.M., Settele, J. and Vaissière, B.E., 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecological economics*, 68(3), pp.810-821.
- Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A., Kremen, C., Carvalheiro, L.G., Harder, L.D., Afik, O. and Bartomeus, I., 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *science*, 339(6127), pp.1608-1611.

- Gezon, Z.J., Wyman, E.S., Ascher, J.S., Inouye, D.W. and Irwin, R.E., 2015. The effect of repeated, lethal sampling on wild bee abundance and diversity. *Methods in Ecology and Evolution*, 6(9), pp.1044-1054.
- Gibbs, J., Joshi, N.K., Wilson, J.K., Rothwell, N.L., Powers, K., Haas, M., Gut, L., Biddinger, D.J. and Isaacs, R., 2017. Does passive sampling accurately reflect the bee (Apoidea: Anthophila) communities pollinating apple and sour cherry orchards? *Environmental Entomology*, 46(3), pp.579-588.
- Gotelli, N.J., and Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology letters*, 4(4), pp.379-391.
- Goulson, D., Nicholls, E., Botías, C. and Rotheray, E.L., 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*, 347(6229), p.1255957.
- Grab, H., Branstetter, M.G., Amon, N., Urban-Mead, K.R., Park, M.G., Gibbs, J., Blitzer, E.J., Poveda, K., Loeb, G. and Danforth, B.N., 2019. Agriculturally dominated landscapes reduce bee phylogenetic diversity and pollination services. *Science*, 363(6424), pp.282-284.
- Graham, K.K., Gibbs, J., Wilson, J., May, E. and Isaacs, R., 2021. Resampling of wild bees across fifteen years reveals variable species declines and recoveries after extreme weather. *Agriculture, Ecosystems & Environment*, 317, p.107470.
- Hedtke, S.M., Patiny, S. and Danforth, B.N., 2013. The bee tree of life: a supermatrix approach to apoid phylogeny and biogeography. *BMC evolutionary biology*, 13(1), pp.1-13.
- Heithaus, E.R., 1979. Community structure of neotropical flower visiting bees and wasps: diversity and phenology. *Ecology*, 60(1), pp.190-202.
- Isaacs, R. and Kirk, A.K., 2010. Pollination services provided to small and large highbush blueberry fields by wild and managed bees. *Journal of Applied Ecology*, 47(4), pp.841-849.
- Iserbyt, S. and Rasmont, P., 2012. The effect of climatic variation on abundance and diversity of bumblebees: a ten-year survey in a mountain hotspot. *Annales de la Société entomologique de France*. 48(3-4). pp. 261-273.
- Joshi, N.K., Leslie, T., Rajotte, E.G., Kammerer, M.A., Otieno, M. and Biddinger, D.J., 2015. Comparative trapping efficiency to characterize bee abundance, diversity, and community composition in apple orchards. *Annals of the Entomological Society of America*, 108(5), pp.785-799.
- Jost, L., 2006. Entropy and diversity. *Oikos*, 113(2), pp.363-375.
- Kammerer, M., Goslee, S.C., Douglas, M.R., Tooker, J.F. and Grozinger, C.M., 2021. Wild bees as winners and losers: Relative impacts of landscape composition, quality, and climate. *Global change biology*, 27(6), pp.1250-1265.
- Kammerer, M.A., Biddinger, D.J., Rajotte, E.G. and Mortensen, D.A., 2016. Local plant diversity across multiple habitats supports a diverse wild bee community in Pennsylvania apple orchards. *Environmental Entomology*, 45(1), pp.32-38.
- Kilpatrick, S.K., Gibbs, J., Mikulas, M.M., Spichiger, S.E., Ostiguy, N., Biddinger, D.J. and Lopez-Urbe, M.M., 2020. An updated checklist of the bees (Hymenoptera, Apoidea, Anthophila) of Pennsylvania, United States of America. *Journal of Hymenoptera Research*, 77, p.1.
- Klein, A.M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. and Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of the royal society B: biological sciences*, 274(1608), pp.303-313.
- Koh, I., Lonsdorf, E.V., Williams, N.M., Brittain, C., Isaacs, R., Gibbs, J., and Ricketts, T.H., 2016. Modeling the status, trends, and impacts of wild bee abundance in the United States. *Proceedings of the National Academy of Sciences*, 113(1), pp.140-145.

- Kudo, G., and Ida, T.Y., 2013. Early onset of spring increases the phenological mismatch between plants and pollinators. *Ecology*, 94(10), pp.2311-2320.
- Kuhlman, M.P., Burrows, S., Mummey, D.L., Ramsey, P.W. and Hahn, P.G., 2021. Relative bee abundance varies by collection method and flowering richness: Implications for understanding patterns in bee community data. *Ecological Solutions and Evidence*, 2(2), p.e12071.
- Lebuhn, G., Droege, S., Connor, E.F., Gemmill-Herren, B., Potts, S.G., Minckley, R.L., Griswold, T., Jean, R., Kula, E., Roubik, D.W. and Cane, J., 2013. Detecting insect pollinator declines on regional and global scales. *Conservation Biology*, 27(1), pp.113-120.
- Leong, M., Ponisio, L.C., Kremen, C., Thorp, R.W., and Roderick, G.K., 2016. Temporal dynamics influenced by global change: bee community phenology in urban, agricultural, and natural landscapes. *Global change biology*, 22(3), pp.1046-1053.
- Mallinger, R.E., Gaines-Day, H.R. and Gratton, C., 2017. Do managed bees have negative effects on wild bees? A systematic review of the literature. *PloS one*, 12(12), p.e0189268.
- Martins, A.C., Goncalves, R.B. and Melo, G.A., 2013. Changes in wild bee fauna of a grassland in Brazil reveal negative effects associated with growing urbanization during the last 40 years. *Zoologia (Curitiba)*, 30(2), pp.157-176.
- Mathiasson, M.E. and Rehan, S.M., 2019. Status changes in the wild bees of north-eastern North America over 125 years revealed through museum specimens. *Insect Conservation and Diversity*, 12(4), pp.278-288.
- Michener, C.D., 2000. *The bees of the world*. The John Hopkins University Press. Baltimore, MD
- Michener, C.D., McGinley, R.J., and Danforth, B.N., 1994. *The bee genera of North and Central America (Hymenoptera:Apoidea)*. Smithsonian Institution Press, Washington, DC.
- Mitchell, T.B., 1960. *Bees of the eastern United States Volume 1*. Technical bulletin North Carolina Agricultural Experiment Station. 141, pp. 1-538.
- Mitchell, T.B., 1962. *Bees of the eastern United States Volume 2*. Technical bulletin North Carolina Agricultural Experiment Station. 152, pp. 1-557.
- Neave, M.J., Brown, J., Batley, M., Rao, S. and Cunningham, S.A., 2020. Phenology of a bee (Hymenoptera: Apoidea) community over a 10 year period in south-eastern Australia. *Austral Entomology*, 59(3), pp.602-611.
- Neff, J.L. and Simpson, B.B., 1993. Bees, pollination systems and plant diversity. In LaSalle, J. and Gauld I.D. (Eds) *Hymenoptera and Biodiversity*. CAB International. Wallingford, UK. pp 143–167.
- Nerlekar, A.N. and Veldman, J.W., 2020. High plant diversity and slow assembly of old-growth grasslands. *Proceedings of the National Academy of Sciences*, 117(31), pp.18550-18556.
- NRCS, 2011. *Pollinator Habitat- Conservation Reserve Program Job Sheet, CP42. P1-5*. Available at: [https://www.nrcs.usda.gov/Internet/FSE\\_DOCUMENTS/nrcs142p2\\_017524.pdf](https://www.nrcs.usda.gov/Internet/FSE_DOCUMENTS/nrcs142p2_017524.pdf)
- Ogilvie, J.E. and Forrest, J.R., 2017. Interactions between bee foraging and floral resource phenology shape bee populations and communities. *Current opinion in insect science*, 21, pp.75-82.
- Ogilvie, J.E., Griffin, S.R., Gezon, Z.J., Inouye, B.D., Underwood, N., Inouye, D.W. and Irwin, R.E., 2017. Interannual bumble bee abundance is driven by indirect climate effects on floral resource phenology. *Ecology letters*, 20(12), pp.1507-1515.
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., 2013. *Community ecology package*. R package version, 2(0).

- Ollerton, J., Winfree, R. and Tarrant, S., 2011. How many flowering plants are pollinated by animals? *Oikos*, 120(3), pp.321-326.
- Onuferko, T.M., Skandalis, D.A., Leon Cordero, R. and Richards, M.H., 2018. Rapid initial recovery and long-term persistence of a bee community in a former landfill. *Insect Conservation and Diversity*, 11(1), pp.88-99.
- Portman, Z.M., Bruninga-Socolar, B. and Cariveau, D.P., 2020. The state of bee monitoring in the United States: a call to refocus away from bowl traps and towards more effective methods. *Annals of the Entomological Society of America*, 113(5), pp.337-342.
- Qian, H. and Jin, Y., 2021. Are phylogenies resolved at the genus level appropriate for studies on phylogenetic structure of species assemblages? *Plant diversity*, 43(4), pp.255-263.
- Ramirez, S.R., Hernandez, C., Link, A. and Lopez-Uribe, M.M., 2015. Seasonal cycles, phylogenetic assembly, and functional diversity of orchid bee communities. *Ecology and evolution*, 5(9), pp.1896-1907.
- Reilly, J.R., Artz, D.R., Biddinger, D., Bobiwash, K., Boyle, N.K., Brittain, C., Brokaw, J., Campbell, J.W., Daniels, J., Elle, E. and Ellis, J.D., 2020. Crop production in the USA is frequently limited by a lack of pollinators. *Proceedings of the Royal Society B*, 287(1931), p.20200922.
- Revell, L. J., 2012. phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecology and Evolution*. 3, pp.217-223. doi:10.1111/j.2041-210X.2011.00169.x
- Roubik, D.W., Basset, Y., Lopez, Y., Bobadilla, R., Perez, F. and Ramirez S, J.A., 2021. Long-term (1979–2019) dynamics of protected orchid bees in Panama. *Conservation Science and Practice*, 3(12), p.e543.
- Russo, L., Park, M., Gibbs, J., & Danforth, B. (2015). The challenge of accurately documenting bee species richness in agroecosystems: bee diversity in eastern apple orchards. *Ecology and Evolution*, 5(17), 3531-3540.
- Sluis, W.J., 2002. Patterns of species richness and composition in re-created grassland. *Restoration Ecology*, 10(4), pp.677-684.
- Stemkovski, M., Pearse, W.D., Griffin, S.R., Pardee, G.L., Gibbs, J., Griswold, T., Neff, J.L., Oram, R., Rightmyer, M.G., Sheffield, C.S. and Wright, K., 2020. Bee phenology is predicted by climatic variation and functional traits. *Ecology Letters*, 23(11), pp.1589-1598.
- Tonietto, R.K., Ascher, J.S. and Larkin, D.J., 2017. Bee communities along a prairie restoration chronosequence: similar abundance and diversity, distinct composition. *Ecological Applications*, 27(3), pp.705-717.
- Tsirogiannis, C. and Sandel, B., 2016. PhyloMeasures: a package for computing phylogenetic biodiversity measures and their statistical moments. *Ecography*, 39(7), pp.709-714.
- Tucker, C.M., Cadotte, M.W., Carvalho, S.B., Davies, T.J., Ferrier, S., Fritz, S.A., Grenyer, R., Helmus, M.R., Jin, L.S., Mooers, A.O. and Pavoine, S., 2017. A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biological Reviews*, 92(2), pp.698-715.
- van Klink, R., Bowler, D.E., Gongalsky, K.B. and Chase, J.M., 2022. Long-term abundance trends of insect taxa are only weakly correlated. *Biology Letters*, 18(2), p.20210554.
- Webb, C.O., Ackerly, D.D., McPeck, M.A. and Donoghue, M.J., 2002. Phylogenies and community ecology. *Annual review of ecology and systematics*, 33(1), pp.475-505.
- Williams, P., Colla, S. and Xie, Z., 2009. Bumblebee vulnerability: common correlates of winners and losers across three continents. *Conservation Biology*, 23(4), pp.931-940.
- Williams, P.H. and Osborne, J.L., 2009. Bumblebee vulnerability and conservation world-wide. *Apidologie*, 40(3), pp.367-387.

Wilson, J.S., Griswold, T. and Messinger, O.J., 2008. Sampling bee communities (Hymenoptera: Apiformes) in a desert landscape: are pan traps sufficient? *Journal of the Kansas Entomological Society*, 81(3), pp.288-300.

Winfree, R., 2010. The conservation and restoration of wild bees. *Annals of the New York academy of sciences*, 1195(1), pp.169-197.

Winfree, R., Reilly, J.R., Bartomeus, I., Cariveau, D.P., Williams, N.M. and Gibbs, J., 2018. Species turnover promotes the importance of bee diversity for crop pollination at regional scales. *Science*, 359(6377), pp.791-793.

Wood, S.N. (2017) *Generalized Additive Models: An Introduction with R* (2nd edition). Chapman and Hall/CRC.

Wood, T.J., Gibbs, J., Graham, K.K. and Isaacs, R., 2019. Narrow pollen diets are associated with declining Midwestern bumble bee species. *Ecology*, 100(6), p.e02697.

Woodard, S.H., Federman, S., James, R.R., Danforth, B.N., Griswold, T.L., Inouye, D., McFrederick, Q.S., Morandin, L., Paul, D.L., Sellers, E., Strange, J.P., Vaughan, W., Branstetter, M.G., Burns, C.T., Cane, J., Cariveau, A.B., Cariveau, D.P., Childers, A., Childers, C., Cox-Foster, D.L., Evans, E.C., Graham, K.K., Hackett, K., Huntzinger, K., Irwin, R.E., Jha, S., Lawson, S., Liang, C., Lopez-Urbe, M.M., Melathopoulos, A., Moylett, H.M.C., Otto, C.R.V., Ponislo, L.C., Richardson, L.L., Rose, R., Singh, R. & Wehling, W. 2020. Towards a US national program for monitoring native bees. *Biological Conservation*, 252, p.108821.

Zattara, E.E. and Aizen, M.A., 2021. Worldwide occurrence records suggest a global decline in bee species richness. *One Earth*, 4(1), pp.114-123.

## Tables

**Table 1** . Model results for the effect of month (within year changes) and year (across year effects) on measures of biodiversity. Results for abundance, richness, diversity (inverse Simpson’s), and phylogenetic structure (mean pairwise distance) are from generalized additive models and the test statistics are t-values. Community composition results are from a perMANOVA and the test statistics are F-values.

Month effects	Month effects	Month effects	Year effects	Year effects	Year effects		
<b>Response variable</b>	<b>Test stat.</b>	<b>P</b>	<b>R<sup>2</sup></b>	<b>Response variable</b>	<b>Test stat.</b>	<b>P</b>	<b>R<sup>2</sup></b>
Abundance	20.01	<0.001	0.88	Abundance	20.71	<0.001	0.25
Richness	38.70	<0.001	0.89	Richness	51.78	<0.001	0.61
Diversity	22.89	<0.001	0.34	Diversity	18.22	<0.001	0.35
Phylogenetic structure	14.16	<0.001	0.87	Phylogenetic structure	4.92	<0.001	0.62
Composition	6.21	<0.001	0.64	Composition	2.03	0.002	0.36

## Figure legends

**Figure 1.** Map of collection sites in Adams County, Pennsylvania, USA. Each yellow marker is the location of a single Blue Vane trap which was left out to capture bees from April to October for 6 years. The four shapes show the collection sites that were closer than 900 m and were lumped together for data analysis. The town of Biglerville is seen at the bottom right.

**Figure 2.** A) Species accumulation curve shows how the average number of species detected increases with the total number of bees collected. The flattening of the curve suggests that most, but not all, of bee biodiversity is represented in our collections. B) Rank abundance curve shows the number of individuals

collected for each species ranked from highest to lowest, note the log y-axis. In our dataset of over 26,000 bees, only 10 species had over 1000 individuals while over half of the species had 5 or fewer individuals.

**Figure 3.** Patterns of bee biodiversity across months, and changes across years. All model relationships were highly significant ( $P < 0.002$ ). Abundance (A, E) is the average number of bees collected per site. Richness (B, F) is the number of bee species per site. Diversity (C, G) is the inverse Simpson’s diversity index. Phylogenetic structure (D, H) is standardized effect size of mean pairwise distance (higher values are more even, and lower values are more clustered). Line fits and adjusted  $R^2$  values are from general additive models and the shading represents 95% confidence intervals of the models.

**Figure 4.** Effects of months (A) and years (B) on bee community composition. Both months and years have significant effects on bee composition but differences among months are larger than among years. Data are visualized using non-metric multidimensional scaling on a Bray-Curtis dissimilarity matrix which includes species abundances. The  $R^2$  values are the variance explained from perMANOVA models.

**Figure 5.** Species-level phenological patterns and changes in abundance over time for 40 species with at least 30 individuals collected. The colored heatmap shows the percentage of individuals captured for each species, therefore a value of 100% would mean all individuals of that species were captured in that one month. The black and gray points represent the positive or negative change in abundance over time. The size of the points are from coefficients from linear models (i.e. slope of the relationship between year and abundance using standardized data). The phylogeny has our focal species amended (see methods) to a genus-level tree by Hedtke et al (2013).

**Figure 6.** The distributions of both seasonality and phenological breadth among bee genera and families. Seasonality is the median Julian date in which each genus and species was captured across 6 years of continuous sampling. Phenological breadth is a measure of the length of time in which bees are active. Error bars show the highest and lowest values for species in each genus. Red dotted lines illustrate the conceptual idea of “phenological syndromes”. The bottom left quadrant are early emerging species with narrow phenological breadth. Species in the bottom right quadrant emerge in summer but still have narrow breadth. Species in the top right have wide phenological breadth and are most abundant in summer.

## Appendix

**Table A1.** Phenological and change over time data for 40 bee species which had 30 or more individuals captured. Seasonality represents the time of year a bee is most active and is calculated as the median Julian date that each species was captured. Phenological breadth, or the length of time a species is active, is the difference between the 10th and 90th percentile of Julian day of capture. Rate of change is a measure of how much the abundance of each species changed from 2014-2019. It is measured as the model coefficient for the linear regression between year and abundance, or the slope of that relationship. Data were standardized so the coefficient represents the change in standard deviation units in abundance per year. P-value is associated with that linear regression. Values with  $P < 0.1$  are bolded.

Species	Family	Seasonality (median Julian day)	Phenological breadth (days)	Rate
<i>Agapostemon texanus</i>	Halictidae	181.9	109.6	<b>-0.19</b>
<i>Agapostemon virescens</i>	Halictidae	178.2	93.9	<b>-0.35</b>
<i>Andrena imitatrix</i>	Andrenidae	106.4	19.5	-0.16
<i>Andrena miserabilis</i>	Andrenidae	105.0	17.9	-0.15
<i>Andrena perplexa</i>	Andrenidae	117.8	42.0	-0.13
<i>Andrena violae</i>	Andrenidae	130.5	19.9	0.14
<i>Anthophora bomboides</i>	Apidae	169.3	25.4	0.05
<i>Anthophora terminalis</i>	Apidae	173.8	93.1	-0.15
<i>Apis mellifera</i>	Apidae	178.2	147.1	-0.16

Species	Family	Seasonality (median Julian day)	Phenological breadth (days)	Rate
<i>Augochlora pura</i>	Halictidae	208.6	97.5	-0.10
<i>Augochlorella aurata</i>	Halictidae	193.8	73.6	-0.11
<i>Bombus bimaculatus</i>	Apidae	168.9	45.1	<b>-0.29</b>
<i>Bombus fervidus</i>	Apidae	176.8	116.5	<b>-0.31</b>
<i>Bombus griseocollis</i>	Apidae	194.4	61.7	0.16
<i>Bombus impatiens</i>	Apidae	210.9	80.6	<b>-0.23</b>
<i>Bombus perplexus</i>	Apidae	164.2	25.2	-0.15
<i>Bombus vagans</i>	Apidae	193.8	73.8	<b>-0.35</b>
<i>Calliopsis andreniformis</i>	Andrenidae	200.7	79.4	-0.13
<i>Ceratina calcarata</i>	Apidae	177.4	91.4	0.11
<i>Ceratina dupla</i>	Apidae	180.8	110.5	-0.07
<i>Ceratina mikmaqi</i>	Apidae	165.9	100.6	<b>-0.20</b>
<i>Ceratina strenua</i>	Apidae	167.3	76.1	0.12
<i>Eucera hamata</i>	Apidae	148.4	31.1	-0.12
<i>Eucera pruinosa</i>	Apidae	202.0	36.8	-0.09
<i>Halictus ligatus</i>	Halictidae	209.5	55.2	<b>-0.25</b>
<i>Hoplitis pilosifrons</i>	Megachilidae	147.2	36.4	0.02
<i>Lasioglossum hitchensi</i>	Halictidae	183.4	116.5	<b>-0.22</b>
<i>Lasioglossum pilosum</i>	Halictidae	204.0	68.7	<b>-0.20</b>
<i>Lasioglossum tegulare</i>	Halictidae	209.5	98.3	<b>-0.22</b>
<i>Megachile mendica</i>	Megachilidae	206.2	71.0	0.10
<i>Melissodes bimaculata</i>	Apidae	208.7	35.2	<b>0.44</b>
<i>Melissodes denticulata</i>	Apidae	220.7	36.7	-0.02
<i>Melissodes desponsa</i>	Apidae	230.9	47.5	<b>-0.36</b>
<i>Melissodes trinodis</i>	Apidae	212.8	43.2	0.14
<i>Melitoma taurea</i>	Apidae	212.4	55.1	<b>-0.25</b>
<i>Osmia bucephala</i>	Megachilidae	144.8	58.2	-0.04
<i>Osmia cornifrons</i>	Megachilidae	106.3	21.1	-0.10
<i>Osmia pumila</i>	Megachilidae	109.2	56.5	0.00
<i>Ptilothrix bombiformis</i>	Apidae	204.1	33.0	0.06
<i>Xylocopa virginica</i>	Apidae	188.9	88.8	0.16





