RESEARCH ARTICLE

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Long-term organic farming and floral diversity promotes stability of bee communities in agroecosystems

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Abstract

1. Increasing bee diversity promotes pollination services on farms. Yet, given the high turnover in pollinator communities, without knowledge of how pollinator communities assemble, it is difficult to conserve or increase bee diversity. Thus, a mechanistic understanding of factors mediating pollinator community assembly could promote pollinator conservation measures.

2. To assess the determinants of pollinator community assembly and structure, we surveyed bee communities and floral resources on 36 farms ranging from 0 to 43 years in organic production. We used niche-based and stochastic species abundance models to characterise the mechanisms driving community assembly, and an additive partition of beta diversity to evaluate resource and species turnover (i.e. community structure). We then used statistical models to assess whether resource turnover or time in organic production altered community assembly and beta diversity, and a jackknife analysis to assess the sensitivity of top models to resource and species identity.

3. We show that bee communities on farms that practiced organic methods for longer assembled by niche-based rather than stochastic processes and had less turnover in bee species across years. Because our model of niche-based processes assumes resource use, these results indicate bee communities reflect underlying species-specific resource preferences (e.g. floral and/or nesting resources) and that longer periods of organic management reduced dissimilarity mediated by species replacement. Our jackknife approach then examined the role of species identity effects in beta diversity, showing changes in floral resources increased dissimilarity driven by bee species loss, but only in landscapes simplified by urbanisation. This jackknife analysis then indicated that landscape resource replacement which was not driven by particular landscape classes, mediated bee species replacement

wherein dissimilarity was driven by a generalist native bee, suggesting bee life history (e.g. flexibility in resource use) and landscape complementarity, rather than identity, underlie patterns identified using the beta diversity equations.

4. Our results show bee communities assemble by niche-based processes, evidenced by collinearity in resource and bee species turnover. Because niche-based assembly indicates ecosystem health, farmers who adopt crop diversification and practice organic methods for longer may promote pollinator diversity and stability leading to improved pollination in farms.

1 | INTRODUCTION

Conventional farming tends to simplify plant communities and homogenise landscapes, reducing bee biodiversity and pollination services (Koh et al., 2016). Compared to conventional farms, organic farms trade short-term yield increases for long-term sustainability and ecosystem services (Bennett et al., 2012). Organic farms are more likely to be diversified than conventional counterparts, with multiple crops grown in a field. Crop diversification supports yields (Ponisio et al., 2015), which are enhanced by diverse pollinator communities (Garibaldi et al., 2019; Kennedy et al., 2013; Lichtenberg et al., 2017). Taken together, crop diversification and organic production may promote long term productivity, pollinator biodiversity and pollination services (Lichtenberg et al., 2017; Ponisio et al., 2015; Tamburini et al., 2020). However, the ecology of diversified and long-term organic farming systems is poorly understood, apart from a handful of correlative studies (Kennedy et al., 2013; Sciligo et al., 2022). This results in a lack of mechanistic theory describing the benefits of these farming approaches for bee pollinators that can be applied to agroecosystems for promoting pollinator conservation and ecosystem services.

Analyses of pollinator networks show that bee communities generally comprise species ranging in preferences for different pollen and nectar resources (Burkle et al., 2013; Kremen et al., 2018; Potts et al., 2003). Resource specialisation, for example, is known to mediate changes in bee identities driving dynamic species-specific responses to changes in resource composition across natural and managed landscapes (Burkle et al., 2013; Forrest et al., 2015; Winfree et al., 2018). However, most research in farming systems to date simply focuses on broad patterns between pollinators and plant richness, which do not use approaches that parse species identity effects (e.g. Lichtenberg et al., 2017), or focuses only on a small group of economically important species (e.g. honey bees; Guzman et al., 2019; Wintermantel et al., 2019). The dynamics of interactions between pollinators and floral resources is further complicated by the ephemeral nature of local resources, such as flower availability, relative to more stable resources like habitat availability at landscape scales. Indeed, the benefits of bee richness for pollination at greater spatiotemporal scales, for example, was only recently revealed (Winfree et al., 2018).

Underlying changes in bee diversity, functional traits and phylogeny can mediate identity, where sampling across a changing landscape can yield minimal changes in alpha diversity ignoring turnover (beta diversity) of species across bee populations (but see Harrison et al., 2018a, 2018b). Similarly, at the local level, communities can have zero sum changes in alpha diversity over time (Jonason et al., 2011), obscuring not only turnover in species but the rate of turnover with potentially stabilizing parameters such as time in organic management. However, the relationship between beta diversity and theoretical models of community assembly explaining the mechanisms driving variation in bee identity, such as changes in the identity of plants and landscape level resources, remain under-addressed (but see Tucker et al., 2016). We suggest developing these models is critical for promoting general theory inclusive of bees that can be applied to a range of systems and used to infer ecosystem health (Kevan, 1999).

Here, we pair two complementary analyses to better understand the impacts of resource variability and organic farming on bee pollinators. First, we assessed mechanisms mediating bee community assembly by comparing species abundance models that account for bee species resource-use (niche-based processes) as compared to models that account for stochastic variation (neutral processes; Connolly et al., 2014; Table 1). The application of species abundance models to farming systems is sparse, but Kevan (1999) proposed that bee populations fitting niche-based models indicate ecosystem health and pollination services. However, these models do not consider species abundance fluctuations; thus, we link assembly mechanisms to spatiotemporal variability (turnover) in local and landscape-level resources using beta diversity equations (Baselga, 2010). We then question: (Q1) assuming agroecosystems are highly disturbed (Murdoch et al., 2006), does variability in resources at local and landscape scales and the amount of time in organic production mediate assembly of bee populations by niche-based processes? Finally, evidence for niche-based processes assumes interactions between species and resources alter bee populations (Connolly et al., 2014) but provide little empirical proof. Thus, we next link resource change to turnover in bee species (Winfree et al., 2018) and question: (Q2) can variability in floral and landscape level resources and time in organic management predictably alter bee community

TABLE 1 Descriptions of links between mechanisms, statistical models, theory and agroecological interpretations for species abundance distributions.

Mechanism	Statistical model	Theory	Agroecological implications
Niche-based processes	Poisson-lognormal	Bee abundance reflects the underlying structure of niches (resources) and the availability of each niche. Species interactions (e.g. between plants and bee pollinators) structure the bee species abundance distribution	Reduced disturbances such as those caused by insecticide treatments reduce stochastic effects, allowing for bee populations to respond to available niches, leading to relative abundances characterised by the Poisson-lognormal model
Neutral processes	Poisson-gamma	Variation in resource-use patterns across bee communities is trivial, and bee species abundances primarily arise from stochastic events. Birth, death, immigration, emigration and local extinction events, rather than species interactions, structure the species abundance distribution	Stochastic processes, potentially driven by disruptive management practices reduce the effects of plant-pollinator interactions and lead to relative abundances characterised by the Poisson-gamma model
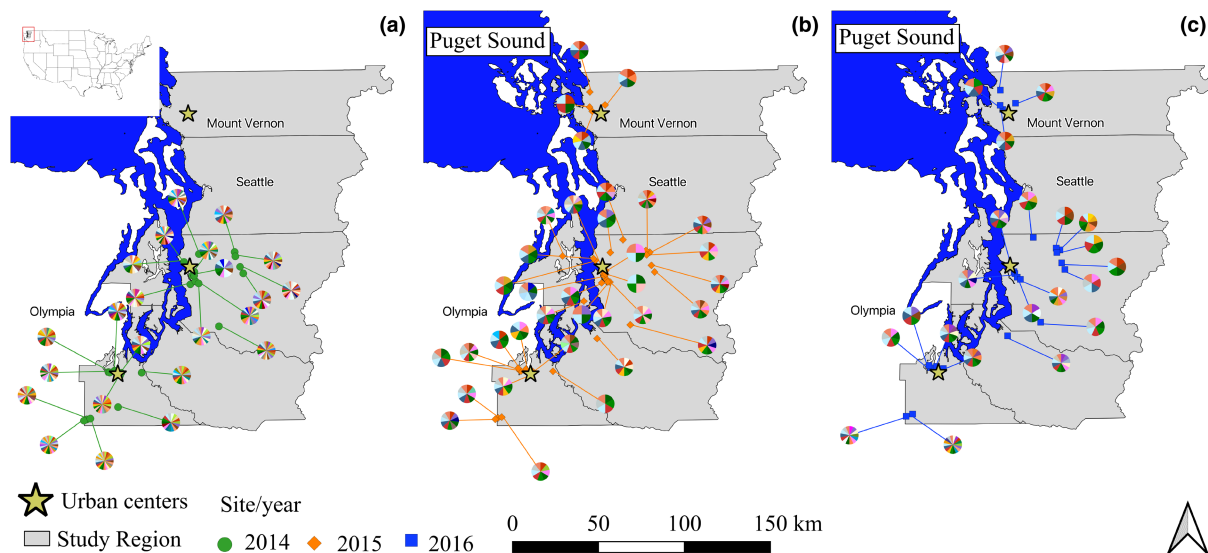
FIGURE 1 Sampling sites throughout the Puget Lowlands of Washington State, USA. Sites were sampled for bee pollinators in (a) 2014 (green dots; $n=23$), (b) 2015 (orange diamond; $n=35$) and (c) 2016 (blue square; $n=22$). Pie charts give bee species composition of each site during each year. Each section of the pie represents one species (see Appendix S1, Figure S1). Grey areas are counties included in the analysis of our study region.

structure? We hypothesise that if community assembly is driven by niche-based processes (Q1), then bee identity should shift with resources and management (Q2).

We focused our analyses of bee populations on a cluster of 36 diversified organic farming systems in the Puget Lowland region of Washington State, USA, an area under rapid urbanisation driven by the expanding metropolitan area of Seattle (USDA-NASS, 2014, 2015, 2016; Figure 1, Figure S1). While organic farms are more bio-diverse than conventional counterparts (Reganold & Wachter, 2016) less is known about the benefits of long-term organic management. To address our questions (Q1-2) and guide conservation of bee pollinators via theory in agroecosystems, we apply species abun-dance models (Connolly et al., 2014) and beta diversity equations (Baselga, 2010) to 3 years of data on bee populations from the 36 farms which varied in the amount of time in organic management, plant and landscape composition.

2 | MATERIALS AND METHODS

2.1 | Study location

Our study was conducted on 36 organic farms in the Puget Low-land of western Washington, USA, across an extent of >7000 km^2 (Figure 1a–c). Farms in the region typically have less than 13 ha of production area (Kirby & Granatstein, 2017). All farm sites were polycultures growing diverse mixtures of pollinator dependent fruits and vegetables, with a minimum floral diversity of five or more unique flowering crops (Table 2). Twenty five percent of Washing-ton State organic farms are found in the Puget Lowland, which has a maritime climate and is bound by the Cascade Range and Puget Sound to the east and west, respectively. Urban expansion (human development) over the last half century has modified the Puget Low-land from landscapes dominated by forest to urban (city) landscapes,

TABLE 2 Characteristics of 36 farm sites included in study of bee populations in the Puget Lowlands of Washington State, USA.

Farm	Latitude[a]	Longitude[a]	Years organic	Area (m²)	Perimeter (m)	Years sampled	Bees[b]	Plants[b]	Landscape[b,c]	Urbanisation (%)
Site 1	47.75	−122.154	6	11,870	616	2	10; 256	57; 680	26; 6,251,400	65.7
Site 2	47.662	−122.639	12	22,188	657	1	10; 172	14; 702	14; 3,118,500	35.2
Site 3	47.57	−122.316	3	5782	324	3	27; 268	99; 1278	14; 9,401,400	95.5
Site 4	47.589	−122.291	30	2650	272	2	23; 180	90; 1517	13; 6,262,200	90.1
Site 5	47.057	−122.97	7	29,664	804	3	22; 240	56; 3350	15; 9,371,700	59.6
Site 6	47.678	−121.949	9	19,207	706	2	14; 220	58; 1329	23; 6,215,400	9.6
Site 7	47.063	−122.926	21	5109	363	3	25; 133	71; 3841	17; 8,545,500	66.8
Site 8	48.543	−122.413	6	18,571	861	2	11; 186	36; 537	37; 6,255,000	5.81
Site 9	46.801	−123.145	19	139,384	1987	2	22; 187	49; 2937	18; 6,258,600	8.04
Site 10	48.471	−122.286	9	25,852	719	2	10; 166	25; 920	37; 6,256,800	3.31
Site 11	47.642	−122.379	43	5036	317	2	19; 131	116; 2123	13; 6,253,200	99.4
Site 12	47.056	−122.96	27	3428	264	2	24; 130	49; 2471	15; 6,235,200	64.3
Site 13	47.562	−122.303	35	6341	392	2	11; 212	28; 461	12; 6,251,400	96.4
Site 14	47.654	−122.393	4	1701	174	1	6; 83	43; 261	6; 3,108,600	99.5
Site 15	47.688	−122.254	40	4628	307	2	25; 163	103; 1616	16; 6,262,200	75
Site 16	47.526	−122.333	20	2968	289	2	24; 213	42; 1335	14; 6,258,600	88.1
Site 17	46.874	−122.901	1	298	331	1	18; 78	24; 1398	12; 3,131,100	10.7
Site 18	47.543	−122.287	14	1396	193	3	27; 197	58; 1444	9; 9,369,000	98.8
Site 19	47.039	−122.886	30	1661	163	2	25; 140	66; 838	14; 6,231,600	81.9
Site 20	47.686	−121.972	17	222,538	3461	3	22; 245	42; 28,610	28; 9,347,400	7.06
Site 21	47.05	−122.71	23	30,406	758	2	20; 129	50; 4712	22; 6,231,600	27.7
Site 22	47.422	−122.468	5	5069	389	1	9; 80	32; 677	14; 3,123,000	37.2
Site 23	47.671	−121.976	16	21,809	704	3	24; 276	58; 7181	22; 9,355,500	10.9
Site 24	47.522	−122.259	5	1247	159	3	23; 213	50; 1042	13; 9,336,600	57.5
Site 25	46.801	−123.159	23	85,458	1222	3	31; 443	36; 19,048	21; 9,350,100	11.1
Site 26	48.435	−122.394	12	27,477	816	2	10; 127	26; 3079	39; 6,238,800	11.8
Site 27	47.57	−122.294	8	1010	178	2	13; 92	50; 885	15; 6,238,800	93.5
Site 28	47.301	−122.102	2	39,072	802	3	26; 254	68; 9944	14; 9,363,600	47.6
Site 29	47.611	−121.937	2	18,448	766	3	28; 351	37; 1825	25; 9,320,400	5.45
Site 30	47.583	−121.916	6	10,087	402	3	20; 348	55; 3374	28; 9,398,700	27
Site 31	47.065	−122.984	17	9377	493	2	9; 132	34; 815	15; 6,249,600	22
Site 32	47.531	−122.283	43	7988	419	1	4; 81	22; 401	9; 3,128,400	93.4

TABLE 2 (Continued)

Farm	Latitude[a]	Longitude[a]	Years organic	Area (m²)	Perimeter (m)	Years sampled	Bees[b]	Plants[b]	Landscape[b,c]	Urbanisation (%)
Site 33	48.461	−122.411	0	115,349	1884	2	7; 64	32; 950	41; 6,242,400	13.7
Site 34	47.049	−122.872	2	998	195	3	21; 240	67; 2370	17; 9,369,000	82
Site 35	47.225	−122.367	2	72,892	1093	2	15; 259	33; 1353	33; 6,228,000	47.3
Site 36	46.807	−123.11	9	58,155	1296	3	30; 266	47; 6976	24; 9,328,500	13.6

[a]Latitude and longitude of sites have been jittered to protect the identity of project stakeholders.

[b]Richness and abundance values are separated by a ";" in these columns.

[c]Abundance values are summed counts of 30×30 m grid cells within 1 km of the sampling site.

particularly the urban centres stretching from Mount Vernon, WA in the north to Seattle and Olympia, WA in the south (Bloom, Oeller, et al., 2022) (Figure 1a–c). Approximately 34.5% of the Puget Lowland landscape is dominated by human development (urbanisation; USDA-NASS, 2014, 2015, 2016). Our sites were imbedded within the development matrix as urban gardens and farms, and in remaining rural regions outside of urban centres. Our site selection focused on identifying farms varying in floral diversity, along urbanisation and time in organic management gradients. Farm sites differed in the length of time under organic management (mean = 14.67, median = 10.5, range = 0 to 43 years), percent urbanisation surrounding the site (mean = 49.02, median = 47.52, range = 3.14%–99.51% development) and production area (mean = 2.88, median = 0.97, range = 0.03–22.25 ha; Table 2). Crops produced served farmers markets, community supported agriculture programs (CSA), high-end restaurants and household consumption. Bloom, Oeller, et al. (2022) discussed site selection and evaluation in greater detail and is open access providing all raw data used in this analysis. No licences or permits were required to carry out this field work.

2.2 | Bee community structure

Approximately 63 bee genera with 600 to 900 species are recognised to occur in the Northwestern US. The majority (≈80%) of these bees are solitary in life-history (Stephen et al., 1969). While arid regions are the most bee biodiverse, climate only partially explains bee biodiversity patterns, with soil types, pithy-stems and entomophilous vegetation further regulating niches for bees in the Northwest. Features of the Puget Lowland, including high rainfall and humidity, low temperatures and densely forested canopy cover, are generally unfavourable for most bee species (Stephen et al., 1969). Few bee species are actively managed in farming systems, thus most species found in farms are likely wild bees adapted to the Puget Lowland, but a systematic study of habitat types including farming systems is lacking, and a synthesis for each bee species of the Puget Lowland in terms of niche is needed.

For our study, we measured bee richness and abundance three times (May, July, September) at the 36 farm sites in our network across 3 years, with 23, 35 and 22 of 36 sites sampled in 2014, 2015 and 2016, respectively (23 sites × 3 sampling events [2014] + 35 sites × 3 sampling events [2015] + 22 sites × 3 sampling events [2016] = 240 samples total; Figure 1a–c; Appendix S1; Figure S1). Thus, not all sites were measured each year due to logistical issues. To sample bee communities, bees were trapped from 07:00 to 17:00 at temperatures above 12°C with minimal cloud cover and wind. Three blue vane traps (SpringStar LLC) and 15 bee bowls (5 blue, 5 yellow and 5 white) were placed along a linear 50-m transect, with ≈3.3-m between each trap (Droege, 2015). The transect began 5-m from the field margin with a blue vane trap, proceeding linearly toward the interior of the field. Five randomly selected bee bowls from the pool of 15 bowls (5 of each colour) were placed individually after each blue vane trap, with the bowls placed ≈3.3-m from each other.

Therefore, all traps were evenly spaced linearly along the 50-m transect, with ≈3.3-m between each trap, terminating at 50-m with a linear placement of five random bee bowls. Bees were netted in two 15-min bouts: 09:00–11:00 and 14:00–16:00. All bee specimens collected were identified to species or morphospecies (see Appendix S1 for additional details) and pooled across time points within years ($n=80$ sites).

2.3 | Floral community structure

To assess effects of floral communities on bee communities, floral abundance and richness were measured on each farm in a 1-h serpentine transect with a 1-m^2 polyvinyl chloride plot (Bloom et al., 2019). Measures of floral communities were taken on the same dates as samples of the bee populations (see Bee community structure). Serpentine transects beginning 5-m from the field margin were used to infer responses of bees to plants within the farm's production area. Then, every 5 m, the richness and abundance of plants in anthesis within the 1-m^2 plot were recorded. Moving down the production row, these measurements were repeated until reaching the row end. Walking along the margin of the farm, we then moved over 5-m and again measured the richness and abundance of plants in anthesis in the opposite direction. We continued this measurement process, moving up and down production rows in a serpentine fashion until the end of the 1-h measurement period (Bloom et al., 2019; Bloom, Oeller, et al., 2022). Abundance and richness of flowering plants were pooled by site across time points within year ($n=80$ sites). Flowering plants were identified to species. However, we were unable to identify ≈6% of the plants at each site, and these plants were excluded from the analyses.

2.4 | Landscape context and duration in organic production

To determine effects of landscapes on bee communities, we obtained data on abundance and richness of landscape classes within 1 km of each farm, for each year from Cropland Data Layers (USDA-NASS, 2014, 2015, 2016). These layers classify single habitat types within 30×30 m grid cells on an annual basis. All sites were located a minimum of 1 km apart to promote spatial independence. While some species of bees forage distances beyond 1 km, most bees are small bodied, and forage preferentially in the vicinity of nesting locations (e.g. 250-m of nest; Gathmann & Tscharntke, 2002; Greenleaf et al., 2007; Hofmann et al., 2020). The length of time each farm had been managed organically was determined from site operators and certifiers. For statistical purposes, farms with less than 1 year in organic production were given a value of 0, and the time in organic management variable was treated as an integer (0–30+ years). Not all farmers in our network were certified organic; however, we refer to farms on the low (0–3 years) and high (30+ years) ends of the time in organic management spectrum as transitional, and long

term organic, respectively. Additional details on determinations for time in organic management were documented by Bloom, Oeller, et al. (2022), and summaries of site characterisations are in Table 2. Some characteristics (e.g. farm size), were not included in our analysis because we focus on variables farmers can influence through practices or policy to support bees rather than variables, such as farm size, that farmers perceive as fixed. For example, changes in landscape management of floral resources are negotiated every 5 years via the Farm Bill mediating millions of acres in floral resources in farming landscapes (Bloom et al., 2021).

2.5 | Bee community species abundance models

We next addressed Q1 by examining the assembly of bee populations. Connolly et al. (2014) demonstrated that communities arising entirely from stochastic processes according to neutral theory leads to a species abundance distribution well described by a gamma distribution. This work built on analyses by Pueyo (2006) and others using niche theory showing that natural community assembly leads to a species abundance distribution that "for practical purposes… is a lognormal" distribution. The identification of these two species abundance models describing ecological communities assembled along the lines of neutral and niche theory, respectively, allows for a comparison of the two models to evaluate the relative importance of neutral versus niche theory for community assembly (Connolly et al., 2014; Table 1). Because empirical species abundance distributions are inherently discrete, and species with abundances of zero are not observed (e.g. it is not feasible to determine which out of all possible species could have been observed but were not), in practice this evaluation can be accomplished by comparing the fits of a zero-truncated Poisson-gamma (neutral theory) or a zero-truncated Poisson-lognormal to species abundance distributions. Using our trapping and netting data, we applied this approach by comparing the fit of observed bee species abundance distributions to those expected from niche-based (Poisson-lognormal) or neutral (Poisson-gamma) models, testing whether communities were structured primarily by niche-based or stochastic processes (Connolly et al., 2014). The Poisson-lognormal (niche-based) model assumes that unique bee species interact with different resources, and that the relative abundances of these resources are key determinants of bee species abundances. In theory, bee abundance on a farm should reflect the underlying structure of niches, and the availability of each niche, which in turn drives plant-bee interactions (Fründ et al., 2013; Kevan, 1999; Waser et al., 1996). In contrast, the Poisson-gamma (neutral) model assumes that variation in resource-use patterns across bee communities is trivial, and variation in bee species abundances primarily arise from stochastic events (Connolly et al., 2014; Table 1). In practical terms, this approach can infer species interactions at the scale of populations, which is exceptionally difficult in the field where bees are often grouped to morphological species (e.g. Kremen et al., 2002). Moreover, fits

to species abundance distributions can be used by managers as a proxy for agroecosystem health (Kevan, 1999).

We used differences in model fit for each of these distributions (ΔAIC = AIC Poisson-gamma model − AIC Poisson-lognormal model) to address Q1 by drawing inferences about processes governing the assembly of bee pollinator communities at each farm site (Figure 1a–c) and for use in our regression analysis (see Model selection). Negative and positive ΔAIC values indicate support for the Poisson-gamma (stochastic) and Poisson-lognormal (niche-based) models, respectively. Prior to model fitting, observations of bee species richness and abundance found via trapping and netting were pooled across the three sampling periods (May, July, and September) by site and year ($n = 80$) and zeros were removed from our data (zero truncated) for each site year^{-1} combination to model distributions of observed species (Connolly et al., 2014). Therefore, zero truncation accounts for species that are seen in our sample because the species that are not represented are unknown (Fisher et al., 1943). After model fitting, the ΔAIC values were used in pairwise comparisons between sites as the response variable to time in organic management and resource variability (see Preparing covariates for modelling) to answer Q1. As an additional test, we grouped observations by year to enhance our ability to detect differences in predictions given by the Poisson-gamma and Poisson-lognormal models. Moreover, honey bees generally had high abundance, and while they likely interact with other species, their abundance may be affected by other factors, such as beekeeping activities. Thus, we modelled distributions both with and without honey bees to determine their relative effects on results of these analyses. We fit models using the *dpoilog* and *dpoig* functions in the R package *sads* (Prado et al., 2018), with a number of starting values for each parameter to avoid local, rather than global, maximum likelihood values. We used the lowest AIC value for each site year^{-1} model^{-1} combination to calculate ΔAIC values that compared fits of each model. We interpreted ΔAIC values greater than 2 to indicate a better fit to a specific model (Burnham & Anderson, 2002). Burnham and Anderson (2002) suggest a "rule of thumb" where ΔAIC values greater than 4 and 10 indicate models explaining considerably less and essentially no variation, respectively. Therefore, we use ΔAIC to estimate relative fit between the Poisson-gamma and Poisson-lognormal models, and picked a ΔAIC of greater than 2, due to its simplicity to interpret, dependence on robust statistical foundations like model likelihood, and independence from the assumptions of a normal distribution (Burnham & Anderson, 2002). Here, however, we are not using ΔAIC for model building (but see Model selection), rather we use ΔAIC as a relative metric to quantify the differences we observe graphically between our two statistical distributions.

2.6 | Beta diversity of bee communities and resources

While landscape, floral diversity and farming practices affect bee richness (Kennedy et al., 2013; Lichtenberg et al., 2017), resource beta diversity and changes in farming practices may also affect the identity of bees found on farms without changing richness (Gossner et al., 2016; Jonason et al., 2011). Thus, to address Q2, we expected changes in resources would drive bee community change (turnover) through variation in bee species identities, because sites with a longer history of organic management would be less variable and stochastic and thus have greater effects of niche processes on bee communities (Q1) (Smith et al., 2019). In other terms, Smith et al. (2019) found lower biotic variability in organic compared to conventional farming systems, particularly for plants. We extend on the findings of Smith et al. (2019), by suggesting that variability in floral resources lessens over time as farmers gain experience with local conditions and organic standards, refining their farming practices which reduces biotic variation.

To assess changes in resources and bee species across our sites, we used the multi-site additive partition of Sørenson's beta diversity (Baselga, 2010), where Sørenson dissimilarity was equal to species replacement + species loss (Figure 2). Importantly, we assume that alpha and beta diversity for bee species is independent (Chase et al., 2011) as described by Baselga (2010), and modelling confirmed this (Figure 3a–d). Each additive portion of beta diversity was calculated as:

$$\text{Species replacement} = \frac{\left[\sum_{i<j}\min(b_{ij}, b_{ji})\right]}{\left[\sum_i S_i - S_T\right] + \left[\sum_{i<j}\min(b_{ij}, b_{ji})\right]} \quad (1)$$

$$\text{Species loss} = \frac{\left[\sum_{i<j}\max(b_{ij}, b_{ji})\right] - \left[\sum_{i<j}\min(b_{ij}, b_{ji})\right]}{2\left[\sum_i S_i - S_T\right] + \left[\sum_{i<j}\min(b_{ij}, b_{ji})\right] + \left[\sum_{i<j}\max(b_{ij}, b_{ji})\right]}$$
$$\times \frac{\left[\sum_i S_i - S_T\right]}{\left[\sum_i S_i - S_T\right] + \left[\sum_{i<j}\min(b_{ij}, b_{ji})\right]} \quad (2)$$

where S_i is the number of species at site i and S_T is the species richness of the site pool (Baselga, 2010; Baselga & Orme, 2012). These values (S_i and S_T) calculate the number of species common to the pool of sites being compared. The numbers of species appearing only in sites i and j are b_i and b_j, respectively, giving the unique number of species at each site. Therefore, in a pairwise site comparison, b_{ij} and b_{ji} are the number of species that occur in the first site but not the second (Baselga, 2010) and vice versa, respectively. The remaining terms, $\min(b_{ij}, b_{ji})$ and $\max(b_{ij}, b_{ji})$ gives the minimum and maximum number of species not shared across site pairs, respectively, for all sites in the pool being compared. Values for Equations 1 and 2 are bound between 0 and 1, with greater values indicating more variation in the species composition of assemblages.

The two components (species loss and replacement) of the multi-site additive partition of Sørenson's beta diversity measure changes in the identity of species across communities. Species replacement occurs when the identity of a species changes over space or time (Figure 2). Two sites can have equal richness but different species (Figure 2). The magnitude of this term is greatest when many species are unique to each site. When species richness decreases, species loss occurs, but the identity of species in the less rich community are a subset of those in the richer community (Figure 2). Sites that have large differences in the number of shared

FIGURE 2 Graphical example of terms in Sørenson's beta diversity, where each bee species is represented by a different colour. Species replacement occurs when bee species at one time or site are replaced by new species. Even if two sites have equal richness, they can be different in species. This underscores the importance of measuring species replacement when comparing bee richness across communities. Species loss occurs when a subset of bees is found at one time point or site compared to another. This is assumed to occur in most pollinator studies, whereby pollinator richness is lumped into a single term, and fewer pollinator species at one site are assumed to be a subset of a richer community. Species loss and replacement can occur simultaneously with richness remaining constant, underscoring the importance of tracking species identity in studies of pollinator communities. Values for species replacement and species loss sum to the value for Sørenson's beta diversity when two sites or time points are compared.
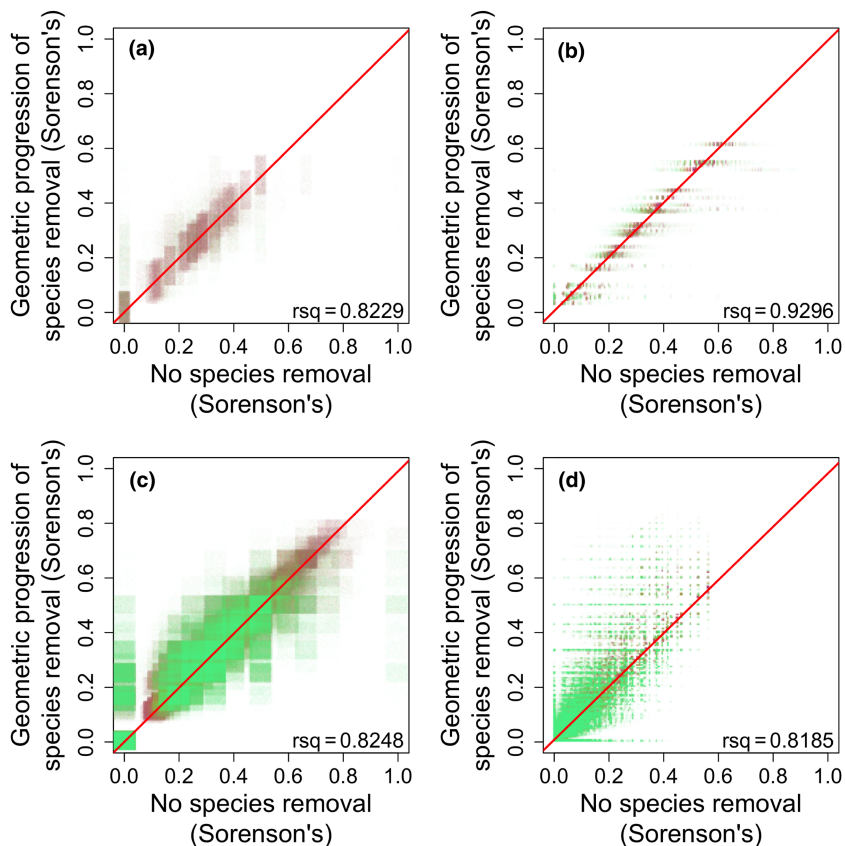
FIGURE 3 Geometric progression of random bee species removal at the (a, b) local and (c, d) landscape levels for the (a, c) loss and (b, d) replacement beta diversity terms. Colours indicate number of bee species removed (red = 1 species; dark green = 2; pink = 4; purple = 8; orange = 16; light green = 32). Points have been jittered and transparency added for visualisation, however overlapping points are common due to point density, thus all points are plotted but random geometric removal of lower species numbers (e.g. 1 species red points) are often hidden. Red lines are estimates (regression coefficients) from linear models.

species maximise the species loss term. The species loss term should not, however, be equivocated with species richness decline, as this is a relativistic measure. Species loss and replacement can occur simultaneously (Figure 2). Thus, communities can have both similar and dissimilar species while being equally rich. The balance of each term in the additive partition indicates the impact of species loss and replacement on variation in the composition of assemblages (Baselga, 2010).

We calculated loss and replacement of bee species, floral species, and landscape classes at local ($n = 31$; *turnover at sites over time*) and landscape levels ($n = 1079$; *turnover across sites within year*). Local beta diversity was calculated across years by site, with 31 sites sampled in more than 1 year. Landscape beta diversity was calculated pairwise across sites within year (Gossner et al., 2016) (2014: $22 + 21 + 20 + \ldots 1 = 235$; 2015: $34 + 33 + 32 + \ldots 1 = 595$; 2016: $21 + 20 + 19 + \ldots 1 = 231$; Total = 1079 *pairwise comparisons*). For

landscape beta diversity and instances of local turnover with sites sampled for 2 years, calculations for the multi-site additive partition (Equations 1 and 2) reduce to the pairwise measure. Differences between species loss and replacement for bees, plants, and landscape classes at the local and landscape-scale were examined with two sample *t*-tests; a summary of these statistics are in the Supporting Information (Table S1, Figure S2).

We also evaluated the partial contribution of each bee species, floral species and landscape class to beta diversity at the local ($n=31$) and landscape level ($n=1079$) by applying a jackknife approach (Benito & Birks, 2020; Bloom, Constancio, et al., 2022). This approach consists of removing one bee species, floral species and landscape class at a time and recomputing the partial turnover value for each term in the additive partition of Sørenson's beta diversity (Equations 1 and 2; Baselga, 2010), at both scales (local and landscape level). Partial terms were then used in sensitivity tests of our top models (see below). This approach also supports the independence of species richness from our beta diversity terms (Baselga, 2010; Chase et al., 2011), which we further confirmed through modelling (see Appendix S1 for additional details; Figure 3a–d).

2.7 | Preparing covariates for modelling

To address Q1-2, we created a set of linear models. In models addressing Q1, which used ∆AIC values as a response variable characterizing fit to the Poisson-lognormal model compared to the Poisson-gamma ($n=80$), values were averaged across years at sites sampled in more than 1 year (31 out of 36) to determine changes in community assembly to resource variation over time within a site ($n=31$). At the landscape-level ($n=1079$), the ∆AIC value used as the response was found as the pairwise site to site difference between the values within year to match with resource beta diversity. In models addressing Q2, that included beta diversity as a predictor (local floral resources and landscape classes) or response (bees) either focused on change over time within each site ($n=31$) or across sites within year ($n=1079$). We used the number of years a site had practiced organic methods at the start of our study as a predictor variable that we refer to as an organic management predictor. For comparisons across sites ($n=1079$), we used the difference in the number of years each site was in organic management as the predictor variable. Regarding interpretation of the organic predictor variable, for pairwise comparisons across sites ($n=1079$), values for sites practicing organic methods for equal amounts of time were zero, whereas negative and positive values indicated comparisons between sites practicing organic methods for shorter and longer periods of time, respectively. However, in models focused on change over time within each site ($n=31$), the organic predictor value is years the site had practiced organic management at the beginning of our study. To improve model stability, the organic production predictor variables were standardised by calculating the mean and standard deviation of the entire vector, then subtracting each element of the vector by the mean and dividing by the standard deviation. Values

for all other explanatory factors and parameters were found with Sørenson's index and did not need scaling because values were bound between 0 and 1 and thus were identical in scale.

2.8 | Model selection

Linear models had five covariates: (i) plant species loss, (ii) landscape class loss, (iii) plant species replacement, (iv) landscape class replacement, (v) time in organic management, and all two-way interactions among these factors (15 parameters total). We fit all parameters in models describing three unique response variables: (i) the ∆AIC values comparing the Poisson-lognormal and Poisson-gamma models (to assess mechanisms of bee community assembly), (ii) bee species loss, and (iii) bee species replacement. All variable combinations (15 parameters × 3 response variables = 45 models) were assessed at two scales, local ($n=31$; *turnover at sites over time*) and landscape ($n=1079$; *turnover across sites within year*) (90 models total). We then use an information theoretic (IT) approach designed for model selection in ecology (see Grueber et al., 2011; Kennedy et al., 2013). In brief, models for each response were first ranked using AICc with the top models having the lowest AICc scores (∆AICc < 2.0; Grueber et al., 2011). We then calculated Akaike weights (ω) and conditional model-averaged partial regression coefficients for each model based on the 95% confidence set. Factors were considered significant if they appeared in the top models, had a high ω (>0.6), and included unconditional confidence intervals that did not cross zero (Grueber et al., 2011; Kennedy et al., 2013). To avoid confusion, above we use ∆AIC values to compare relative fit between the Poisson-gamma and Poisson-lognormal models (see Bee community species abundance models). These relative fit values were used as a response variable in our regression models and should not be confused with the ∆AICc values used for model selection in our IT approach. To assess the sensitivity of our results for the top IT-selected models using beta diversity terms as predictor or response variables, we then used a permutation (jackknife) approach. These top models were refit with partial beta diversity terms for bee species, floral species and landscape classes. Estimated *p*-values for the partial model were visually inspected via histograms and statistically with Shapiro–Wilk normality tests. Model estimated *p*-values were determined to be not normal for all predictor and response variables in top models. Thus, we used one sample Wilcoxon signed rank tests with continuity correction where the p-value from the top model was set as mu. In other terms, we used these tests to determine if the vector of partial estimated *p*-values were different from those found with the top model. In cases where we established statistical differences existed between the top and partial *p*-values, we again visually examined our data to determine which bee species, floral species, and landscape classes mediated these patterns. Otherwise, we surmised that specific bee species, floral species, and landscape classes did not contribute to the overall term used in the top model, and the permutation approach indicated models were not sensitive to compositional changes in our dataset. Our permutation

approach is analogous to the distance decay method used by Baselga et al. (2022); however, we use a linear, rather than exponential curve, and the jackknife as our permutation, because it evaluates the effects of bee species, floral species and landscape class identity. Additionally, we used a jackknife approach (see Appendix S1) where we performed geometric species removal on our dataset to determine the independence of our beta diversity terms from changes in bee species richness (Chase et al., 2011; Figure 3a–d). All analyses were performed in R v. 4.0.2 with the packages 'bbmle' and 'MuMln' (Bolker & R Development Core Team, 2017; Bartoń, 2018; R Core Team, 2017).

3 | RESULTS

Across 3 years, 36 farms, and 240 sampling events we captured 6955 bees from 95 species and morphospecies. Blue vane traps, bee bowls, and netting captured 2121, 1175 and 3649 specimens, respectively. Identification of specimens was primarily assigned using taxonomic approaches (>95%; $n = 6654$), and <5% of bees ($n = 301$) were identified to species or morphospecies using DNA barcoding (see Appendix S1 for details). Bees were collected from five families (Andrenidae, Apidae, Colletidae, Halictidae, and Megachilidae). Dominant species were bees from the genera *Apis* and *Bombus*, composing ≈70% of the specimens in our collection. Species level determinations for approximately 9% of specimens was unresolved.

3.1 | Factors driving bee community assembly

For our question regarding the mechanisms driving bee community assembly (Q1), when we fit species abundance models separately for each site and year combination ($n = 80$), we found 88.75% support for the Poisson-lognormal model, which arises from niche-based rather than neutral (Poisson-gamma) community assembly. When we grouped all bees within each year ($n = 3$), the Poisson-lognormal model fit better than the Poisson-gamma for each year (ΔAIC values >2; Figure 4), indicating the importance of sampling effort and scale for detecting the mechanisms of community assembly. The Poisson-lognormal model was effective at characterizing bee species of

moderate abundance, while both models characterised species of high and low abundance (Figure 4). The exclusion of honey bees did not qualitatively affect our results (Figure S3).

For local (within site) bee communities, we observed no effect of the variation in resources (i.e. plant and landscape turnover) or the amount of time the site has been in organic management ($n = 31$; *turnover at sites over time*) on the fit to the Poisson-lognormal (niche-based) relative to the Poisson-gamma (stochastic) models (Table S2). At the landscape level ($n = 1079$; *turnover across sites within year*), comparisons between sites showed that increasing time in organic production supported bee communities that were better described by Poisson-lognormal model suggesting longer periods of organic management allow for variation in species specific niches (Figure 5a, Figure S4a; Table S3) ($\omega = 1$; $\beta = -0.21$; CI = −0.36, −0.056; $p = 0.0070$). Conversely, pairwise comparisons between sites yielding negative values for the time in organic management parameter, were better described by the Poisson-gamma model (Figure 5a, Figure S4a; Table S3). This finding shows that compared to long term organic sites, those transitioning to organic methods (e.g. 0–3 years along the time in organic management continuum) had stronger impacts of stochastic events on bee community assembly. This is notable because organic farms are required to undergo a 3-year transition period before receiving certification.

3.2 | Factors altering bee community structure

Because our results indicate that resource availability (niche-based processes) structures the composition of bee communities (Q1), we next considered how time in organic management and variation in resources at the local and landscape levels affected the variability in bee communities, as described by beta diversity (Q2). In our evaluation of beta diversity, we found that farms practicing organic methods for longer periods of time retained more of the same bee species. This result was indicated by a negative relationship between the time in organic management parameter and lower dissimilarity driven by the bee species replacement term calculated locally ($n = 31$; *turnover at sites over time*; Figure 5b, Figure S4b; Table S4; $\omega = 0.68$; $\beta = -0.081$; CI = −0.15, −0.012; $p = 0.022$). In other terms, farms practicing organic methods for longer had more similar bee
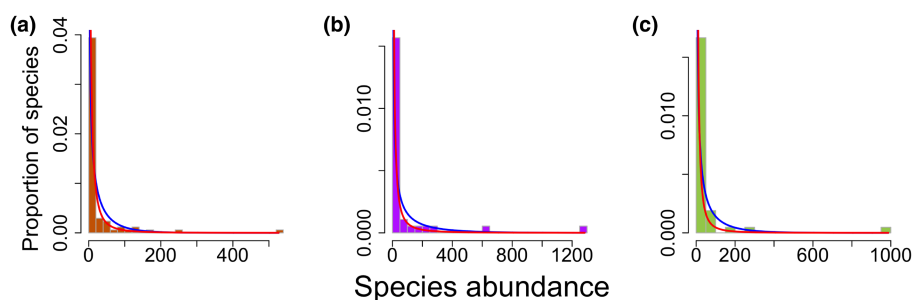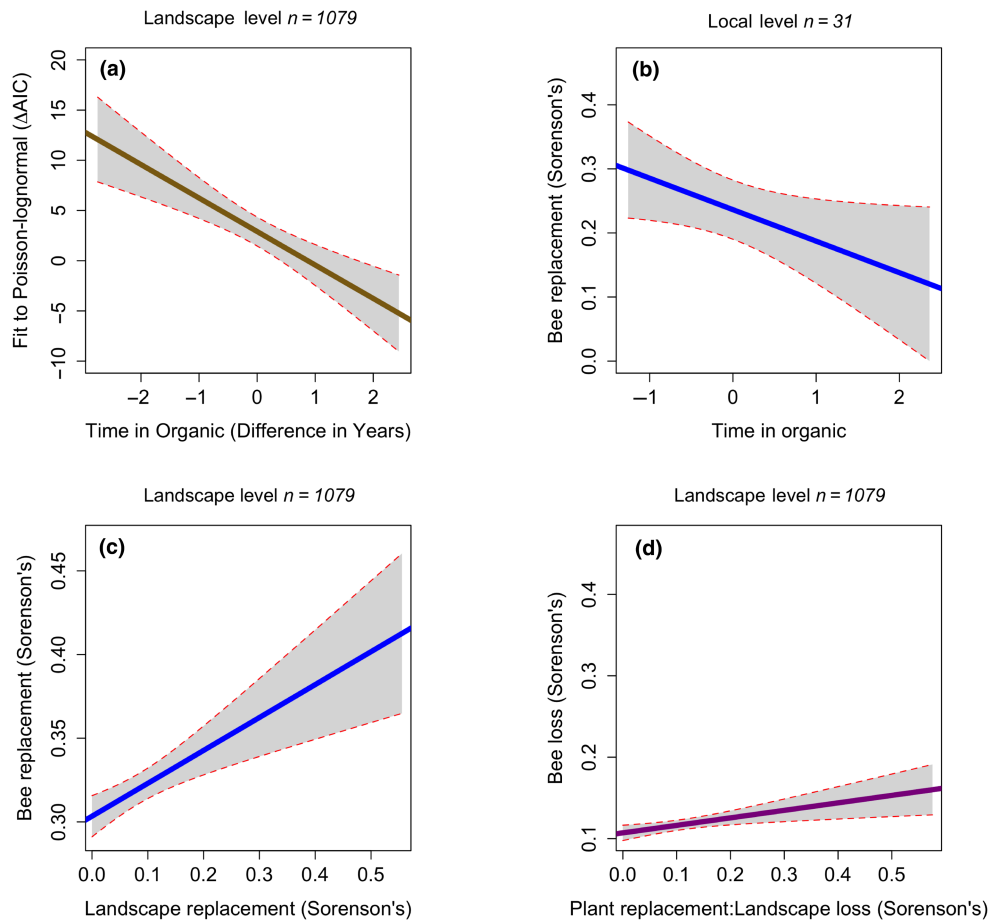

FIGURE 4 Fit of observed data to species abundance models for three study years: (a) 2014; (b) 2015; and (c) 2016. Support for the Poisson-lognormal (red lines) was 100% when compared to the Poisson-gamma (blue lines) by year. The Poisson-lognormal model better predicts bee species of moderate abundance, particularly in 2014 and 2015.

FIGURE 5 (a) Site comparisons indicating increasing time in organic management (a) better fit the Poisson-lognormal (niche-based) model and (b) sites practicing organic methods for longer had less bee species replacement across years (Tables S3 and S4). Values for time in organic management were standardised (see Methods). (c) Bee species replacement increased with the replacement of landscape classes (Table S5). (d) Bee species loss increases when plant species were replaced and landscapes simplified (Table S5). In "d" the terms for plant replacement and landscape loss were multiplied for the purpose of plotting the interaction in one dimension. The time in organic management variables in "a" and "b" were scaled to enhance model stability.

communities across the 3 years (2014–2016) of our study. Biologically, this may indicate older organic farms have more stability in bee community structure compared to those with less time in organic production, driven by lower dissimilarity in the replacement term (Figure 5b, Figure S4b; Table S4).

The replacement of landscape classes across sites ($n=1079$; *turnover across sites within year*) was positively associated with bee species dissimilarity as measured by the replacement term (Figure 5c, Figure S4c; Table S5) ($\omega=1$; $\beta=0.24$; CI=0.05, 0.42; $p=0.013$). Therefore, landscape-level resources appeared to provide habitat for particular bee species, which we analysed further with our jackknife approach (see below). Dissimilarity mediated by landscape class loss between sites, and comparisons with higher plant species replacement, were associated with increasing values for the bee species loss term at the landscape scale ($n=1079$; *turnover across sites within year*; Table S5). Thus, increasing values for the plant species replacement term, was correlated with increases in the loss, rather than replacement, term for bee species. In addition, we found the impacts of plant species change were magnified by landscape loss (Figure 5d, Figure S4d; Table S5; $\omega=0.79$; $\beta=-0.49$;

CI=−0.84, −0.14; $p=0.0059$), suggesting that changes in bee species driven by the loss term were not offset by increases in the bee species replacement term, due to changes in the plant community, particularly for comparisons between sites indicating a shift to simpler landscapes. Again, our jackknife approach (see below) describes which landscape classes may drive this simplification and changes in the bee species loss term.

The identity of bee species, floral species and landscape classes, as described by our jackknife approach (sensitivity analysis), rarely mediated statistical changes in beta diversity terms, indicating the general robustness of our analysis (Figure 6a–f). However, at the landscape scale ($n=1079$; *turnover across sites within year*), the response of bees to landscape class replacement (Figures 5b and 6b) was mediated by specific bees. For example, the removal of *Andrena candida* from calculating the replacement term (see extreme positive value Figure 6b) indicated the sensitivity of the overall term to compositional changes, and the importance of *A. candida* for replacing other bee species across sites. However, the replacement of bee species was not tied to the replacement of specific landscape classes, which may indicate the habitat generality of *A. candida*
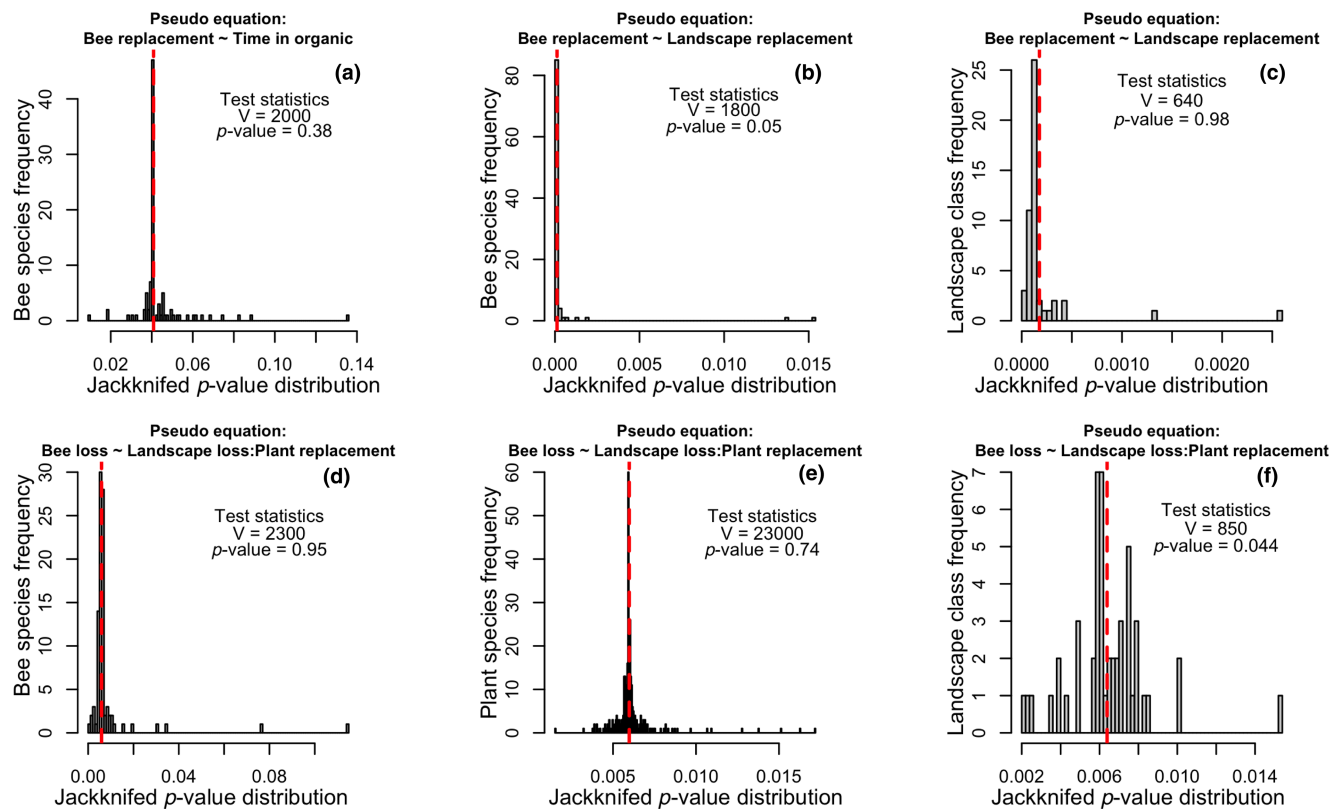
FIGURE 6 Jackknifed p-value distributions showing sensitivity of top models (see Figure 5) which used terms of the additive partition of Sørenson's beta diversity as either response (a, b, d) or predictor variables (c, e, f). Distributions (a–f) were determined to be non-normal using Shapiro–Wilk normality test. Test statistics are given on plots (a–f) for one sample Wilcoxon signed rank test with continuity correction where "mu" was the p-value estimate from the top model. Red lines are the estimated pseudo-median values. Jackknifed top models shown in "b" and "f" were sensitive to the removal of bee species and landscape classes, respectively. Specifically, in "b" a wild bee species (*Andrena candida*) contributed positively to bee species replacement at the landscape scale ($n = 1079$). Whereas, in "f" bee species loss, was driven by high intensity development (urbanisation). For "a, c, d, e" test statistics show low sensitivity to changes in the composition of beta diversity values used in the top models (see Figure 5b–d), indicating that identity did not contribute to the correlations observed when using the overall term value.

(Figure 6c). Similarly, the loss of bee species across landscapes ($n = 1079$; *turnover across sites within year*) was tied to the loss of a specific landscape class, high intensity development (Figures 5d and 6f). This result shows the loss of urbanisation as a statistically important variable for mediating bee species loss in general, particularly when accounting for replacement in the plant community (but not particular plant species) across sites (Figure 6d–f).

4 | DISCUSSION

Pivotal research suggests pollinator diversity promotes pollination services (Garibaldi et al., 2013; Winfree et al., 2018). However, a mechanistic understanding of processes driving these findings that also accounts for the dynamic nature of pollinator and flower abundances is lacking. Here we hypothesised if community assembly is driven by niche-based processes (Q1), then bee identity should shift with resources and management (Q2). Using species abundance distributions to address Q1, we inferred based on model assumptions that bee communities assembled by the availability of resources

(niche partitioning), rather than stochastic processes, particularly when comparing farms with a long history of organic farming to those in the transition period. This is notable because organic farms are not static; they exist along temporal gradients which we show shape benefits for bee pollinator conservation, an encouraging result for farmers seeking to undergo the regulated 3-year transition from conventional farming. These findings were further supported by our beta diversity analyses addressing Q2, which suggested changes in resource availability led to changes in bee species composition, especially on farms with more time in organic production. Taken together, our modelling approach allowed us to confirm our hypothesis by determining that increases in variability of landscape or plant resources alters bee communities by indirectly altering the abundances of bees that depend on the particular resources gained or lost. Our study thus confirms an underlying theoretical basis regarding the importance of resource preferences for pollinator conservation in farms.

Our analysis which used comparisons between farms practicing organic methods for different periods of time along a continuum (0–30+ years), indicated long term organic production

promoted pollinator communities more likely to be assembled by niche-based processes and suggests that bee communities may be impacted by more stochastic events during the organic transition period. In addition to altering the relative importance of stochastic processes in community assembly, the amount of time a farm had been in organic production at the beginning of our study affected changes in pollinator species identity over our 3-year course of observations. Taken together, these results shed light on an important axiom in ecology. Namely, our findings indicate that long-term organic production (30+ years) promotes pollinator community stability, exemplified by lack of species change over time, and proxied by the species replacement term in Sørenson's additive partition of beta diversity (Baselga, 2010). Evidence suggests that reducing the amount of disturbance on farms will allow community structure to be governed more by species interactions and less by stochastic processes (Connell, 1978). We agree with Connell (1978) and suggest that species interactions and stability likely is mediated by the refinement of practices over time within farms, which selects for particular bee species yielding niche saturation, lower species turnover, and elevated plant-pollinator interactions, however these conclusions likely need further empirical testing. Similarly, previous research has highlighted the capacity of farm management practices to disrupt equilibriums, leading to less stable communities that respond to stochastic processes (Murdoch et al., 2006). Indeed, ~10% of the farms in our study were better characterised by stochastic processes, indicating parameters attributed to birth and death of individuals, and colonisation and extinction of bee species, rather than species interactions, dominate these systems (Hubbell, 2001). In terms of farm management, Kremen et al. (2018) found the maturation of floral resources (hedgerows) on the margins of agroecosystems saturated community assembly processes over time, indicating farming practices disrupt equilibriums and induce instability, with pollinator communities eventually attaining stable states over time (e.g. >8 years). Here, we build on these findings to show that disruptions from transitioning to organic farming methods exacerbate the role of stochasticity on community assembly. In practical terms, we propose bee communities that reflect the underlying niches like those identified in our long-term organic farms indicate lower disturbances from the introduction of new practices that disrupt relationships between pollinators and their resources, and the saturation of niches by bee species over time. Moving forward, we propose that organic farms function similarly to ecosystems undergoing successions, with species composition changing over time and eventually reaching stable states with low species replacement (Clements, 1916; Pickett, 1976). For example, changes in management (e.g. reduced pesticide use) may encourage species replacement, where bee species tolerant of conventional practices are replaced by species more suited to organic production (Russo et al., 2020). Then, over time species replacement slows and the community stabilises. However, our findings should not be equivocated with time since disturbance (e.g. a pesticide application) because farms are highly managed, rather, we suggest organic

farming practices can reduce species replacement thereby selecting for specific species via the stabilisation of niche space over time leading to population equilibriums.

A second axiom highlighted by our research is fundamental to landscape ecology, namely landscape simplification as a driving factor behind species declines (Koh et al., 2016). We found bee species loss was only linked to plant species replacement in simplified landscapes, specifically landscapes simplified by urbanisation. This suggests that spillover of bees from landscapes mediates the benefits of local diversification (Bloom et al., 2019; Tscharntke et al., 2005), emphasizing the importance of landscape resources when introducing plant species. Indeed, our findings are consistent with the intermediate landscape complexity hypothesis (see Tscharntke et al., 2012) who suggested the benefits of local level diversification for bee pollinators are likely only realised in diverse landscapes. In practical terms, we find via our jackknife approach that urbanisation promoted the loss of bee species, via changes in the benefits of local plant populations. We suggest that this could be due to bee species isolation in simplified landscapes, which reduces the benefit of introducing new plant species (e.g. turnover) by land managers, leading to bee species loss because the pool of bees in the landscape is limited. Novel to our research though is the finding that landscape level resource replacement increases bee species replacement. Here, we found bee species identity was important, with a native bee species (*A. candida*) influencing the overall pattern of species replacement. *Andrena candida* is general in life history, inhabiting, coastal areas, agricultural landscapes, deserts and mountain environments in California, Oregon, Washington, Idaho, Utah and Colorado, with a broad range of floral hosts including trees and herbaceous plants (Youssef & Bohart, 1968). For this result, we suggest that bees with general life history strategies may fill a broad suite of niches vacated during species replacement, driven by non-specific landscape-level resource changes. In fact, we were unable to link replacement patterns of *A. candida* with specific landscape classes. This suggests processes such as landscape complementation (Dunning et al., 1992) or facilitation, rather than identity may be at play, and life histories likely underpin bee beta diversity patterns (Hann et al., 2020): two speculations needing further technical investigation. For example, a modification of the phylogenetic beta diversity measure proposed by Chao and Ricotta (2019) to a trait-based form could prove useful for identifying mechanisms driven by bee species life histories, underlying the patterns we observed. More broadly, we suggest that bees have a more complex relationship with landscape level resources than previously realised (Koh et al., 2016), where landscape-level resource turnover (e.g. changes in landscape identity) does not always cause bee species decline per se, highlighting the need for detailed investigations including species life history and landscape complementation (Dunning et al., 1992; Hann et al., 2020).

Some caveats apply to our research regarding our results on organic farming. For one, it is unclear if reverting to conventional practices (e.g. a disturbance) by organic farms with stable bee communities

would result in higher levels of species replacement and stochasticity, though, this would be an important follow-up study. Second, comparing farms ranging from 0 to 43 years in organic production provided greater power than evaluating changes in pollinator community assembly processes over the relatively short 3-year study period. While we were not surprised by the lack of evidence for lower stochastic impacts on community assembly over 1 or 2 years, this does mean that studies that track pollinators over long time periods on farms would provide further insights into our findings. On a technical level, our analysis also ignores the abundance of plant species and landscape classes via the use of presence and absence values in the additive partition of Sørenson's beta diversity (Baselga, 2010). Here, inclusion of not only identity but counts could yield additional insights, as for example, changes not only in the presence of landscape level resources but their abundance likely mediate pollinator populations. However, we caution the reader regarding the application of abundance-based beta diversity measures to managed landscapes and agroecosystems because these approaches are linked with neutral assembly, and the assemblage of landscape classes in human dominated landscapes could violate the deterministic assumptions of these equations (Chao & Ricotta, 2019; Hubbell, 2001).

Overall, our results suggest that organic practices, landscape context, and plant diversity affect pollinator community composition and stability by altering the resource niches available for specific pollinators in a community. By evaluating the factors that promote pollinator species loss and replacement, we found that long-term use of organic practices stabilises pollinator communities and reduces the impacts of stochastic events. Moreover, we found that changes in floral resources pose a threat to pollinator species loss, but only in landscapes simplified via urbanisation, and landscape change may influence bee communities through life history strategies. Overall, our findings using species abundance models and beta diversity show the importance of species-specific responses to resource niche availability for pollinator community assembly. Practically, we provide novel mechanistic evidence supporting the benefits of crop diversification and long-term organic farming for promoting wild and managed bee pollinators.

AUTHOR CONTRIBUTIONS

David W. Crowder and Elias H. Bloom conceived the study. Elias H. Bloom and Tobin D. Northfield performed analyses. All authors contributed critically to the drafts and gave final approval for publication.

CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

Data available from the Figshare Repository: https://doi.org/10.6084/m9.figshare.24057261 (Bloom et al., 2023).

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SUPPORTING INFORMATION

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

Figure S1. Legend for pie plots found in Figure 1. Each color represents one bee species, with 95 unique bee species in our study.

Figure S2. The additive partition of Sørenson's beta diversity for (a) bees, (b) flowering plants, and (c) landscape classes across years at each site ($n=31$) and across sites ($n=1079$). Values close to 1 indicate high dissimilarity. Total turnover is the summation of species loss and replacement. Welch two-sample t-tests indicate that the contributions of species loss and replacement to turnover were different for bees, plants and landscape classes at the landscape level ($n=1079$; see Table S1). At the local level ($n=31$), only plant species loss and plant species replacement were different, indicating that plant species loss contributed more to turnover than plant species replacement (see Table S1).

Figure S3. Fit of observed data to species abundance models without honey bees for three study years: "A" 2014; "B" 2015; and "C" 2016. See Figure 4 for comparison to fits with honey bees. Support for the Poisson-lognormal (red lines) was 100% when compared to the Poisson-gamma (blue lines) both with and without honey bees.

Figure S4. Scatter plots showing the effects of: organic management on (a) fit to the Poisson-lognormal (niche based) model and (b) bee species replacement; (c) landscape replacement on bee species replacement; and (d) the interaction between plant species replacement and landscape loss on bee species loss. Lines show predictions for linear models (Appendix S1, Tables S3–S5).

Table S1. Results of Welch two-sample t-tests. Contributions of loss and replacement to turnover are different for bees, plants and landscape classes at the landscape level ($n=1079$). Species loss contributed more than replacement for plant turnover at the local level ($n=31$).

Table S2. Model-averaged partial regression coefficients and unconditional 95% CIs for fit to Poisson-lognormal (ΔAIC values) across years ($n=31$) in relation to local and landscape factors. Akaike weights (ω) indicate relative importance of covariate based on summing weights across models where covariate occurs. Bold where $w>0.6$ and CIs do not include 0. Results indicate no context dependence of the niche-based model at the local scale.

Table S3. Model-averaged partial regression coefficients and unconditional 95% CIs for ΔAIC (fit to Poisson-lognormal) values across sites ($n=1079$) in relation to local and landscape factors. Akaike weights (ω) indicate relative importance of covariate based on summing weights across models where covariate occurs. Bold where $w>0.6$ and CIs do not include 0. Results indicate years in organic farming enhances fit to the niche-based model at landscape scale.

Table S4. Model-averaged partial regression coefficients and unconditional 95% CIs for bee species loss and replacement across years ($n=31$) in relation to local and landscape factors. Akaike weights (ω) indicate relative importance of covariate based on summing weights across models where covariate occurs. Bold where $w>0.6$ and CIs do not include 0. Sites which used organic methods longer had fewer bee species replaced across years.

Table S5. Model-averaged partial regression coefficients and unconditional 95% CIs for bee species loss and replacement across sites ($n=1079$) in relation to local and landscape factors. Akaike weights (ω) indicate relative importance of covariate based on summing weights across models where covariate occurs. Bold where $w>0.6$ and CIs do not include 0. Bee species replacement was enhanced by replacement of landscape classes. Bee species were lost with the replacement of plants, loss of landscape classes, and interactions among these covariates.