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Bee species richness through time in an urbanizing landscape of the southeastern United States

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Abstract

Compared to non-urban environments, cities host ecological communities with altered taxonomic diversity and functional trait composition. However, we know little about how these urban changes take shape over time. Using historical bee (Apoidea: Anthophila) museum specimens supplemented with online repositories and researcher collections, we investigated whether bee species richness tracked urban and human population growth over the past 118 years. We also determined which species were no longer collected, whether those species shared certain traits, and if collector behavior changed over time. We focused on Wake County, North Carolina, United States where human population size has increased over 16 times over the last century along with the urban area within its largest city, Raleigh, which has increased over four times. We estimated bee species richness with occupancy models, and rarefaction and extrapolation curves to account for imperfect detection and sample coverage. To determine if bee traits correlated with when species were collected, we compiled information on native status, nesting habits, diet breadth, and sociality. We used non-metric multidimensional scaling to determine if individual collectors contributed different bee assemblages over time. In total, there were 328 species collected in Wake County. We found that although bee species richness varied, there was no clear trend in bee species richness over time. However, recent collections (since 2003) were missing 195 species, and there was a shift in trait composition, particularly lost species were below-ground nesters. The top collectors in the dataset differed in how often they collected bee species, but this was not consistent between historic and contemporary time periods; some contemporary collectors grouped closer together than others, potentially due to focusing on urban habitats. Use of historical collections and complimentary analyses can fill knowledge gaps to help understand temporal patterns of species richness in taxonomic groups that may not have planned long-term data.

KEYWORDS
extrapolation, museum collections, occupancy models, pollinators, rarefaction, urbanization, Wake County, North Carolina

1 | INTRODUCTION

Understanding the drivers of changes in species composition and distribution is a cornerstone of ecological research. Interest in these drivers has become increasingly important as the rise of the Anthropocene has led to a massive defaunation (Dirzo et al., 2014; the Anthropocene is used here to indicate a time period when human activities have significant effects on the global environment as there is no current formal status, Orndorff et al., 2018) of both vertebrates (Ceballos et al., 2017; Pimm et al., 2006; Schipper et al., 2008; Stuart et al., 2004; Wake & Vredenburg, 2008) and invertebrates (reviewed for terrestrial insects by Wagner, 2020). Within invertebrates, bees (Hymenoptera: Apoidea: Anthophila) are a part of this larger pattern of insect decline (Wagner, 2020). Bees are a taxonomically well resolved group that collectively provide the essential ecosystem service of pollination. More than 87% of flowering plant species (Ollerton et al., 2011) and many food crops (Klein et al., 2007; Lorenzo-Felipe et al., 2020) benefit from animal pollinators. In most systems, bees are the most abundant and efficient pollinators (Rader et al., 2016), and this service is stabilized by bee diversity (Bartomeus, Park, et al., 2013; Rader et al., 2013; Winfree et al., 2018). Several studies provide evidence of declines or changes in bee health (Cameron et al., 2016), distribution (Cameron et al., 2011; Kerr et al., 2015), and diversity (Bartomeus, Ascher, et al., 2013; Zattara & Aizen, 2021) over the past 150 years (Goulson et al., 2015), though these trends vary by bee species (e.g., Cameron et al., 2011) and study (e.g., Senapathi et al., 2015 vs. Van Dooren, 2019).

The influence of human disturbance on biodiversity can be studied in multiple ways, including examining spatial or temporal gradients. Spatial gradients use different locations with different land uses to provide cross-sectional understanding of the effects of disturbance, but do not aid in understanding longitudinal effects. Urbanization is one key form of ecological disturbance that is known to affect bee abundance (e.g., Carper et al., 2014; Fortel et al., 2014), diversity (e.g., Fortel et al., 2014; Villalta et al., 2022; Wenzel et al., 2020), and pollination services (e.g., Carper et al., 2022). However, as with many studies on human disturbance, urban research rarely addresses the influence of time (Szulkin et al., 2020), despite the possibility that current land use patterns are influenced by temporal processes. For example, habitat quality, which may not have been homogeneous throughout the pre-urban landscape, can change over time because of surrounding land use change (ecosystem decay hypothesis, Chase et al., 2020). It is also likely that locations were chosen to have their land use altered in nonrandom ways. How species and communities respond to these land use changes may not be instantaneous (discussed in Szulkin et al., 2020); instead, there can be a time lag where previous land use better explains current species richness and species traits than more recent land use (e.g., Alberti et al., 2017; Krauss et al., 2010) indicating that there could be a delay in species extinction (extinction debt, Kuussaari et al., 2009). In these situations, spatial urban gradients likely provide an incomplete view of the effects of urbanization, and temporal datasets–repeatedly

sampling the same location through time–may reveal how temporal processes influence species richness patterns. As long-term studies are rare or lacking for most systems, museum collections can fill these data gaps, providing a historical baseline and sampling through time for long-term ecological research (Boakes et al., 2010; Suarez & Tsutsui, 2004).

Museum collections provide unique snapshots of the past by preserving collections of Earth's biodiversity as well as organisms that are now extinct. For example, museums have provided the most comprehensive historical data on the distribution of ground-feeding birds at a broad spatial scale compared to information gathered from other sources (e.g., literature, atlases, and citizen science reports, Boakes et al., 2010). However, due to the opportunistic nature of the data, datasets drawn from historical collections have various limitations that arise from unknown sampling effort and unplanned spatial and temporal sampling (e.g., Bartomeus, Ascher, et al., 2013; Van Dooren, 2019). Additionally, surveys of biodiversity rarely achieve complete censuses of the entire community due to imperfect detectability; yet, imperfect detectability is rarely considered in analyses of species (Benoit et al., 2018; Guillera-Arroita, 2017).

To overcome these limitations, potential biases in datasets need to be explored and, when possible, explicitly accounted for (e.g., Davis et al., 2023). For example, restricting analyses to a certain method of capture (e.g., Bartomeus, Ascher, et al., 2013), reducing the dataset to a single record per species per collecting event (e.g., Bartomeus, Ascher, et al., 2013), analyzing presence/non-detection instead of abundance (e.g., Zattara & Aizen, 2021), incorporating imperfect detection (Guillera-Arroita, 2017), and including sampling effort in analyses can help account for some biases. Multiple analytical methods may be used to assess species diversity trends, each with distinct advantages and disadvantages. For example, occupancy models are based on detection/non-detection data and allow for explicit modeling of occupancy and detection probabilities along with other community dynamics such as local colonization and extinction (MacKenzie et al., 2018). Additionally, they allow for the inclusion of rare species which otherwise tend to be removed from trend datasets for lack of sample size (Benoit et al., 2018). However, occupancy models do not assess sample completeness. In contrast, rarefaction and extrapolation techniques can assess sample size, sample completeness, provide estimates of asymptotic species richness, and allow for easy comparison among communities by estimating diversity to a shared sample size or completeness (e.g., Chao et al., 2014; Gotelli & Colwell, 2011).

Here, we use extensive historical bee collections as well as contemporary researcher collections to evaluate trends in species richness through time and increasing urbanization using presence/non-presence data. We focus on bees in Wake County, North Carolina, United States; this area has extensive collections of bees that are taxonomically resolved dating back to 1900, as well as numerous recent collections. In addition, the area has experienced rapid human population growth, increasing 16-fold over the last 100 years (Forstall, 1996; US Census Bureau, 2021). Specifically, we investigated the following two questions: (1) Is there a trend in bee

richness over time in this rapidly urbanizing area, and (2) are there bee species no longer found in contemporary compared to historical collections? If the answer to (2) is yes, are these species no longer collected because they share particular traits or trait combinations, or is their absence in collections associated with changes in collector behavior? Taken together, these results provide insights into the use of museum specimens in understanding temporal trends in species richness.

2 | METHODS

2.1 | Study site and species

The human population of Wake County, North Carolina, which contains the urban center of Raleigh and other municipalities, has increased 16-fold from 1900 to 2010 (Forstall, 1996; US Census Bureau, 2021). This area has comprehensive geospatial records for how urbanization has occurred over time (Brown et al., 2005) and how it is projected to occur in the future (Terando et al., 2014), which demonstrate that time and amount of urbanization in this region are correlated. If current rates continue, urbanization in the Southeastern United States is projected to double or triple in area between 2010 and 2060, with urban centers becoming more connected and natural or semi-natural habitats becoming more fragmented (Terando et al., 2014).

Bees are a diverse clade within the insect order Hymenoptera, consisting of about 4000 described species in North America, of which approx. 560 are recorded in North Carolina (Ascher & Pickering, 2019; Youngsteadt et al., 2021). Bee species can respond differently to anthropogenic disturbances, including urbanization, based on differences in their functional traits (e.g., Hamblin et al., 2017; Harrison et al., 2018; Wenzel et al., 2020; Williams et al., 2010). Bee species found in North Carolina exhibit trait variation in social status, nesting habits, and diet specialization.

2.2 | Dataset compilation and processing

Physical museum specimen records were primarily collated from the North Carolina State University (NC State) Insect Museum, which has over 47,000 bee specimens (Youngsteadt et al., 2016). Specific to Wake County, North Carolina, the NC State Insect Museum includes 7240 pinned and identified bee specimens spanning six families (Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae, and Melittidae) collected from 1900 to 2009, including specimens from T.B. Mitchell's extensive and well-resolved bee collection (NCSU Insect Museum, 2020). An additional identified 1194 (1900 to 2018) Wake County specimens are available in online repositories (Global Biodiversity Information Facility-GBIF, Biodiversity Information Serving Our Nation-BISON, Symbiota Collections of Arthropods Network-SCAN) and 2797 specimens are available from individual researcher collections.

From this specimen list, we removed any specimens that could not be assigned a collection year, were collected by methods other than hand netting, or belonged to species whose range does not include Wake County (see Data S5 for more information). Specimen records that did not have a collection method provided were assumed to be netted, as the use of pan traps or bee bowls is a more recent sampling method, with its first formal assessment for bees in approximately 1999 (Leong & Thorp, 1999). We did not include specimens collected by methods other than netting as this could introduce a potential confounding variable. For example, although pan traps were the second most common sampling method to netting in recent studies, they sample a different subset of the community than does netting (reviewed in Prendergast et al., 2020), and including them would have introduced unique biases to the last ~20 years of our time series. To reduce the influence of multiple specimens per collection event on biodiversity estimates, we collapsed the dataset to one specimen per species per collection event. Collection event was defined as unique combinations of collector, collection date, and spatial coordinates. Additionally, we checked all scientific names using both ITIS (Integrated Taxonomic Information System, www.itis.gov) and Discover Life (www.discoverlife.org). Names that were not valid were updated to valid scientific names. For a detailed description of specimen data sources, the breakdown of records across data sources, and data processing, see Data S5.

2.3 | Statistical analyses

All analyses were conducted in R (version 3.6.1, R Core Team, 2019) using RStudio (version 1.2.5019 for desktop, RStudio Team, 2019) unless otherwise noted. All graphing was conducted in R and RStudio, using the *ggplot2* package (version 3.2.1, Wickham, 2016).

In analyses, time was our proxy for human modification from increasing human population size, urban land development, and climate change, among others. To assess whether human population size and year were correlated, we conducted a Spearman correlation using US Census Bureau data and US Census year (data from Forstall, 1996; US Census Bureau, 2021) and the *cor.test* function in R. Additionally, we estimated the urban extent of Raleigh using the global urban dynamics product developed by Li et al. (2021) by determining the number of urban pixels and converting this to extent of urban area based on pixel size (height and width = 1831.53 m) in ArcMap (version 10.7.1.11595). To determine if the extent of urban area (in square kilometers) was correlated with time, we conducted a Spearman correlation using the *cor.test* function.

2.3.1 | Question 1: Is there a trend in bee richness over time?

We used two methods to estimate species richness for different time intervals: occupancy models and rarefaction. Given the opportunistic nature of the data, we used both methods to address

both imperfect detection (occupancy models) and sampling effort (rarefaction).

Occupancy models: We used multi-season occupancy models to assess bee species richness over time using the program PRESENCE (Hines, 2006), with time as a proxy for increasing anthropogenic disturbance. To interface with PRESENCE, we used the *RPresence* package (version 2.13.10, Mackenzie & Hines, 2021) in R. A multi-season modeling framework is based on Pollock's robust design (Pollock, 1982). This design involves sampling over two temporal scales: primary and secondary periods. Primary periods (henceforth seasons) are sampling occasions over which changes in community composition can occur. That is, the population is open to changes owing to the time elapsed between seasons. Note that in this study, 'seasons' do not correspond to meteorological seasons, but refer to longer, multi-year periods. Secondary periods are nested within seasons and consist of shorter sampling occasions over which there are no significant changes in the community (i.e., closure). This sampling framework yields estimates of several parameters, namely, probabilities of initial occupancy (ψ_1), local seasonal colonization (γ), and local seasonal extinction (ε) (MacKenzie et al., 2006, 2018). Initial local occupancy was defined as the probability that Wake County was occupied by a species in the initial season of the time series being assessed. This parameter is estimated using data from the sampling occasions within the first season. When there is a series of primary sampling periods or seasons, as in this study, then two other parameters can be estimated relative to the first or previous season. Local seasonal extinction probability (ε_t) is the probability that a species occupying Wake County at season t is no longer occupying the county in season $t+1$. Local seasonal colonization probability (γ_t) is the probability that Wake County was unoccupied by a species at season t and becomes occupied at season $t+1$. In the multi-season occupancy framework, parameters are adjusted by detection probability, or the probability that at least one individual of a species is detected in season t, provided the individuals are available to be detected. We note that estimates of occupancy for every season in the time series are estimable as derived parameters or obtained using appropriate model parameterizations (MacKenzie et al., 2006). Before running the multi-season model, survey (captures) data were converted into an encounter history of presence (1), non-presence (0), or missed (–). Non-presence was assumed if specimens of other species were captured that same year (defined as pseudo-absences in Davis et al., 2023). In years where there were no specimens of any species captured, missed was entered. Missing data appear as NAs within occupancy models and do not contribute to likelihood estimations, though they can make standard errors for estimated variables larger.

As the multi-season occupancy model did not estimate species richness directly, we estimated species richness ($\hat{S}$) within each season using Equation (1),
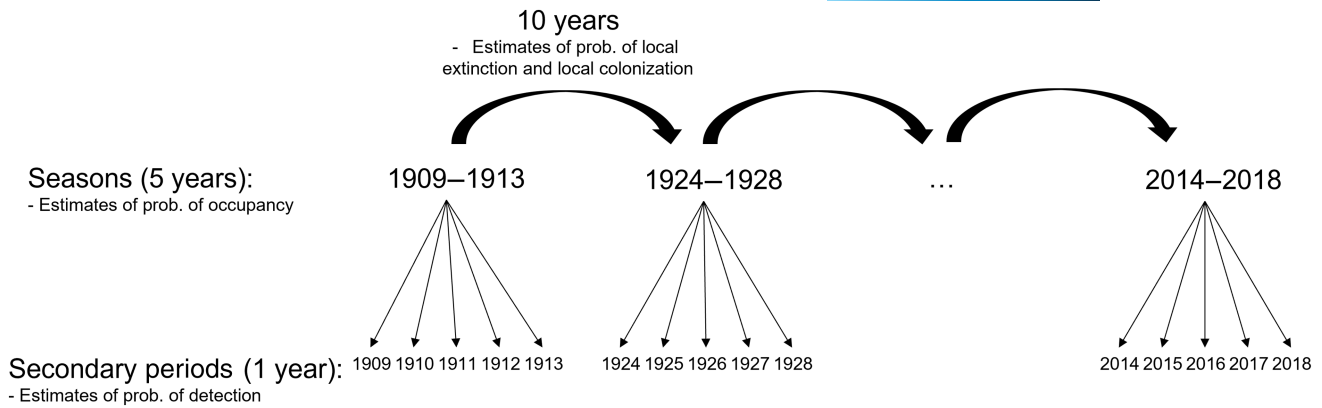
$$\hat{S} = M\hat{\psi}, \tag{1}$$

where M is the number of all species collected in Wake County (328 for this dataset) and $\hat{\psi}$ is the probability of occupancy for a given season.

Multi-season models assume that populations are closed within secondary periods (MacKenzie et al., 2018). In our study, this meant that we assumed there were no substantial losses or gains of bee species in Wake County during each secondary period. Thus, to select seasons and secondary periods that met model assumptions, we first estimated species richness by year using program SPECRICH2 (Hines, 2016; Rexstad & Burnham, 1991; White et al., 1982). This analytical approach also requires closure, but we used the shortest time interval available given the data (a year), which makes this assumption more likely to be met. The added benefit of this approach is that its estimates provided a separate basis to evaluate inferences on species richness obtained from our multi-season model. Species richness estimates are generated using model M(h) from program CAPTURE (Otis et al., 1978; Rexstad & Burnham, 1991; White et al., 1978, 1982). Model M(h) allows for detectability to vary by species and is often used when estimating species richness (e.g., Boulinier et al., 1998). For our analyses, the model takes the number of species collected in one, two, three, ... and so forth, surveys as an input, estimating the number of species never detected, and allowing the model to estimate the total number of species present. For our input, we treated collection date (day, month, year) as a survey and estimated species richness annually for every year that had at least three collection dates. Program SPECRICH2 also takes the number of species captured during each survey as inputs to calculate a goodness-of-fit (GOF) test, determining whether the M(h) model is appropriate for the data. We note that we ran analyses for each spring, summer, and fall within a year because M(h) assumes no seasonality and therefore GOF tests may be rejected (see Data S5 for more information). SPECRICH2 cannot be interfaced with R; instead, we ran the program directly through its URL (https://www.mbr-pwrc.usgs.gov/software/specrich2.html).

We used the SPECRICH2 output and a sliding frame to select our focal seasons (i.e., primary periods) to analyze with our multi-season models in PRESENCE (see Data S5 for more information). From this assessment, our seasons were separated by 10 years, and each season was made up of five consecutive years (i.e., secondary sampling occasions; Figure 1). We focus on results from the multi-season model for the following reasons: (1) species richness estimates generated from SPECRICH2 and the multi-season model are strongly correlated (Spearman's rho = 0.93, $S = 4$, $p < .01$, see Data S5 for more information), (2) the multi-season model provides additional information on local community dynamics such as local colonization and extinction, and (3) the multi-season model allowed us to explicitly test for temporal trends within the model itself. Seasons chosen for these analyses and the years they represent are summarized in Table 1. We then ran multiple multi-season models where the probability of detection, local colonization and extinction was modeled as constant or time-variant (i.e., differed among seasons). To explicitly test for temporal trends, we also fitted a linear or quadratic term to local colonization and extinction probability.

We used the Akaike's information criterion (AIC) to evaluate the support in the data for multi-season models where probabilities of local colonization and extinction were modelled differently

10 years
- Estimates of prob. of local extinction and local colonization

Seasons (5 years):
- Estimates of prob. of occupancy

1909–1913   1924–1928   …   2014–2018

Secondary periods (1 year):
- Estimates of prob. of detection

1909 1910 1911 1912 1913   1924 1925 1926 1927 1928   2014 2015 2016 2017 2018

FIGURE 1 Multi-season model sampling design. Seasons (i.e., primary periods) consist of five consecutive years with each consecutive year called a secondary period. Seasons are separated by 10 years.

TABLE 1 Summary of seasons for the multi-season model sampling design.

Season	Years	Number unique collection events	Number unique specimen records
1	1909–1913	20	38
2	1924–1928	241	485
3	1939–1943	230	380
4	1954–1958	222	441
5	1969–1973	29	36
6	1984–1988	33	35
7	1999–2003	1	2
8	2014–2018	441	1340

Note: The years, number of unique collection events, and number of unique bee species specimen records across seasons.

(Burnham & Anderson, 2002). Models with ΔAIC ≤2 were considered to have substantial support in the data. A summary of the full model selection table with more information is available in Data S5. The effect of covariates (i.e., β coefficient) on a model parameter was considered to be strong if the 95% confidence interval (CI) did not overlap zero, and weak otherwise.

Rarefaction curves: We generated rarefaction curves with both interpolation and extrapolation to estimate species richness over time to account for sample size and sample coverage. We generated these using the *iNEXT* function in the *iNEXT* package (version 2.0.19, Chao et al., 2014; Hsieh et al., 2019). We used the same focal seasons used in the multi-season model (see Data S5 for additional analyses for comparison with SPECRICH2). Therefore, for each season, species richness and sample coverage were estimated using sample-based raw incidence data and the Chao2 estimator (Chao et al., 2014; Gotelli & Colwell, 2011). We defined a sample as a year (i.e., a secondary period). Based on this, the number of samples for each season was either four or five (as some years did not have any specimens collected). One season (season 7: 1993–2003) was removed from consideration for rarefaction as it only had 1 year of data. While our multi-season model could compute estimates for this season, rarefaction and extrapolation

require at least three samples to estimate asymptotic species richness (McCabe, 2011). Because samples can differ in the number of individuals collected, one community may have a higher sample coverage by having more specimens collected in that year than another that may have fewer specimens collected (Gotelli & Colwell, 2001, 2011); therefore, we standardized our comparisons to a common sample coverage rather than a common sample size. Specifically, we followed box 1 from Chao et al. (2014) to determine the base sample size and sample coverage to use to compare groups. Thus, our base sample size was eight (two times the smallest sample size). We then determined that the smallest sample coverage for an extrapolated sample size of eight was 0.544. However, the sample coverage used to estimate species richness was 0.8976, which was the highest sample coverage from the original data, so that no data would be removed from the estimates (see example in Chao et al., 2014). It is important to note that extrapolating estimates to this sample coverage will extend the estimate past two times the smallest sample size; therefore, the estimate may be biased for some seasons. However, the richness estimator is conservative as it is considered a lower bound estimator, and thus, actual species richness is probably higher than estimated for those seasons.

Species richness over time: We used species richness estimates and 99% confidence intervals from both the best supported multi-season model (PRESENCE) and extrapolation (*iNEXT*) to a shared sample coverage to determine which season had the greatest species richness and whether that richness significantly differed from other time periods.

2.3.2 | Question 2: Are there bee species that are no longer found in contemporary collections compared to historical collections?

We split species capture records into three time period categories (1900–1969, 1970–1997, 2003–2018) to see when species were collected, and whether there were any species that were not collected recently. We chose these time period categories based on the estimated species richness trends which generally had higher

estimated species richness pre-1970 and post-2002. We visualized patterns using a Venn diagram using the *draw.triple.venn* function in the *VennDiagram* package (version 1.6.20; Chen, 2018).

To determine whether species that disappeared from recent collections shared certain traits, we collated information on six categorical traits: native status (presumed native, ancient range expansion, or introduced); nesting level (above- or below-ground); whether they rent, build, or parasitize nests; nest substrate (wood, stem, soil, exposed, cavity); diet specialization (generalist, specialist, or parasite); and social category (parasite, social parasite, polymorphic, social, or solitary) (see Data S4 and sources within; Ruzi, 2023). These groupings are not mutually exclusive within a category. For example, some bee species use multiple substrates to build their nests. Thus, some species were scored as expressing multiple trait states in each category. To visualize what categorical traits were associated with bee species captured in different time frames, we used a heatmap to show the relative proportion of bee species with that trait within that time frame that also had trait information (i.e., trait information for that category was not left unknown). We limited the heatmap to bee species that were captured historically (1900–1969) and recently (2003–2018), categorizing a species as historic only, recent only, or both, depending on their occurrence records.

We investigated whether the composition of bee specimens contributed by top collectors in different time frames had changed using non-metric multidimensional scaling (NMDS) and the permutational multivariate analysis of variance (perMANOVA, with 999 permutations) using the *metaMDS* and *adonis2* functions in the *vegan* package, respectively (version 2.5–6, Oksanen et al., 2019). Top collectors were ones who contributed over 50 unique specimens to the dataset (i.e., unique combination of species and collection event) (Data S6 Table S2.1). Time was defined as historic (i.e., most of the specimens collected were 1980s and earlier) and contemporary (i.e., specimens collected in 2000s and 2010s). The distance matrix was compiled using frequency of detection/non-detection of species during unique collection events. The number of unique collection events differed among top collectors. The distance matrix was compiled using frequency of detection and the Bray-Curtis index. We used the *envfit* function in the *vegan* package to determine which bee species significantly separated collectors. For this analysis, we removed singletons, that is, species with only one collecting event in the top collector dataset. Differences in assemblages collected by top collectors could be due to collector behavior or to underlying community change. If differences are solely due to community change, we may expect collectors within the same timeframe to have similar communities.

Additionally, we investigated whether the collecting locations within Wake County were consistent over time. We conducted Spearman correlations with both decimal latitude and decimal longitude using the *cor.test* function in R. For this analysis, we removed specimens that were labelled as being collected in Wake County without any additional locality information (209 unique records removed). As many samples were collected within Raleigh city limits, we also subsampled the data to determine if trends were consistent between both Raleigh and Wake County samples (e.g., Davis et al., 2023). The results and interpretation were consistent whether we used Raleigh only or the entire Wake County dataset; we present results from the full dataset (see Data S5 for the comparison).

3 | RESULTS

3.1 | Time as a proxy for increasing human modification

Census year and the human population size of Wake County, North Carolina were positively correlated (Spearman's rho = 1, $S = 0$, $p < .001$; Figure 2a). Urban extent of Raleigh was positively correlated with year (Spearman's rho = 1.00, $S = 0.00$, $p < .0001$; Figure 2b).
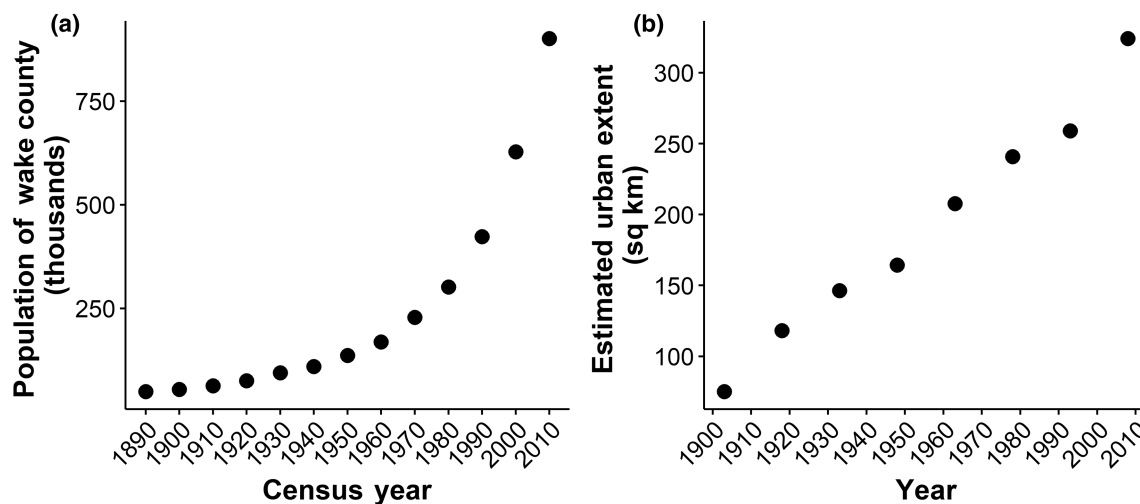

FIGURE 2 Population of Wake County. (a) The population of Wake County, North Carolina is positively correlated with census year (Spearman's rho = 1, $S = 0$, $p < .001$). (b) The urban area within Raleigh city limits is positively correlated with time (Spearman's rho = 1.00, $S = 0.00$, $p < .001$).

3.2 | Dataset summary

The final dataset included 6080 unique records from 2949 unique collections from 1900 to 2018 (Data S1; Ruzi, 2023). These bee specimens represented 328 species in 47 genera and 6 families. These specimens were collected by 300 named collectors; only 660 specimens had no collector on record. The majority of collectors (293) contributed fewer than 50 unique occurrence records each, with 165 contributing only one unique occurrence record to the dataset. Only six collectors (not including unknown collectors) contributed over 50 unique occurrence records each. Most specimens were collected from 1920 to 1969 (4087 unique records; 67.2% of total unique records) and 2003 to 2018 (1501; 24.7%).

3.2.1 | Question 1: Is there a trend in bee richness over time?

We found no support for a directional trend in bee species richness over time. The model in which both local colonization and extinction probability was modeled as time-variant had the best predictive value (ΔAIC = 0; AICwt = 1.0) (see Data S5 Table S1.7). There were no competing models (ΔAIC >2). The effect of modeling colonization as time-variant was strong for most of the changes between seasons as β coefficients tended to not include zero in their 95% confidence intervals, but weak for modeling local extinction as time-variant (Data S6 Table S2.2). All methods estimated similar trends in species richness with higher estimated richness in the 1920s–1960s and 2010s than before 1920 or from the 1960s to early 2000s (Figure 3a). Only the annual extrapolation estimates were significantly correlated with time, albeit weakly (Table 2). None of the other estimations were correlated with time.

As estimates from all methods were highly correlated with each other (see Data S5), we focused on information gained using both the best supported multi-season and extrapolation models because both methods account for sources of uncertainty (e.g., detection probability) and coverage (i.e., sampling effort), and yield parameter rates that help quantify a dynamic process of species occurrence change over time. The multi-season model yielded estimates of higher probabilities of occupancy and detectability in seasons 2, 3, 4, and 8 (0.34 or higher) compared to other seasons (0.24 and lower) (Data S6 Table S2.3). The model also yielded a high probability of local colonization between the first and second seasons (i.e., before the mid-1920s at 0.39), and a high probability of local extinction between the fourth and fifth seasons (i.e., before the late-1960s at 0.73) (Data S6 Table S2.4, Data S6 Figure S2.1). Extrapolation demonstrated that seasons differed in sample coverage of the raw data (Figure 3b,c). Four of the eight seasons had raw sample coverage of 79% or higher. We focus on these, comparing the 99% confidence intervals of extrapolated values of only those four seasons to minimize the influence of extrapolating past two times the smallest sample size. Our top multi-season model identified season 2 as having the greatest species richness, which is not significantly different

from seasons 3, 4, or 8. Extrapolation also indicated that season 2 had the greatest species richness, though not significantly different from 4. Season 4 was marginally different from season 3, while season 8 had significantly lower species richness than seasons 2, 4, and 3. Therefore, season 8, which is the most recent season, generally had lower estimated species richness compared to estimates in 1920s–1950s based on extrapolation or trends lower, though non-significantly, based on the multi-season model.

3.2.2 | Question 2: Are there bee species that are no longer found in contemporary collections compared to historical collections?

Of the 328 species in our entire dataset (1900–2018), 195 species (59.5% of those in our dataset) were unique to the historical time frame (pre-1969) while only 19 species (5.8%) were unique to the contemporary time frame (2003–2018) (Figure 4a, Data S6 Table S2.5). In general, most of these unique historic and contemporary species had a few unique collection events, though there were some species collected only historically that had more than 10 unique collection records (Figure 4b). The 1920s had the highest number of species that were collected on less than 10 unique collection events (87) followed by the 1950s (58) and the 1940s (56) (Data S6 Table S2.6). The 1900s and 2000s had the fewest rare species collected at three and four species, respectively.

The trait composition of collected species changed with time; in general, those that were only collected historically comprised a more diverse group that had higher proportions of parasitic species, while those that were only collected recently comprised more generalist bees with a lower frequency of ground nesting species. Specifically, we found the following trends. The heatmap demonstrated that regardless of time frame, collected species tended to be native and solitary (Figure 5). Parasitic species were more likely to be collected during the historic period while social species were likely to be collected during both time periods. Species that nest below-ground were more likely to be collected during the historic period while in recent collections the proportion of above-ground to below-ground nesting species was more similar. Bee species building their own nests were common in both time frames, though historically there were more parasitic nesters. In recent collections the proportion of renters has increased. In general, many bee species nest in the soil, however recent collections indicate the number of species living in wood or stems has increased. Diet category indicated that generalist species have been collected both historically and recently at a higher frequency than either parasitic or specialist bees. Only two species (*Calliopsis coloradensis* Cresson 1878 and *Nomada parva* Robertson 1900) were excluded from the heatmap as these two species were only collected from 1970 to 1997. The number of species that we had information for each category in each time frame is summarized in Figure 5.

Top collectors contributed unique specimen records of 238 different bee species when singletons were removed. There was no
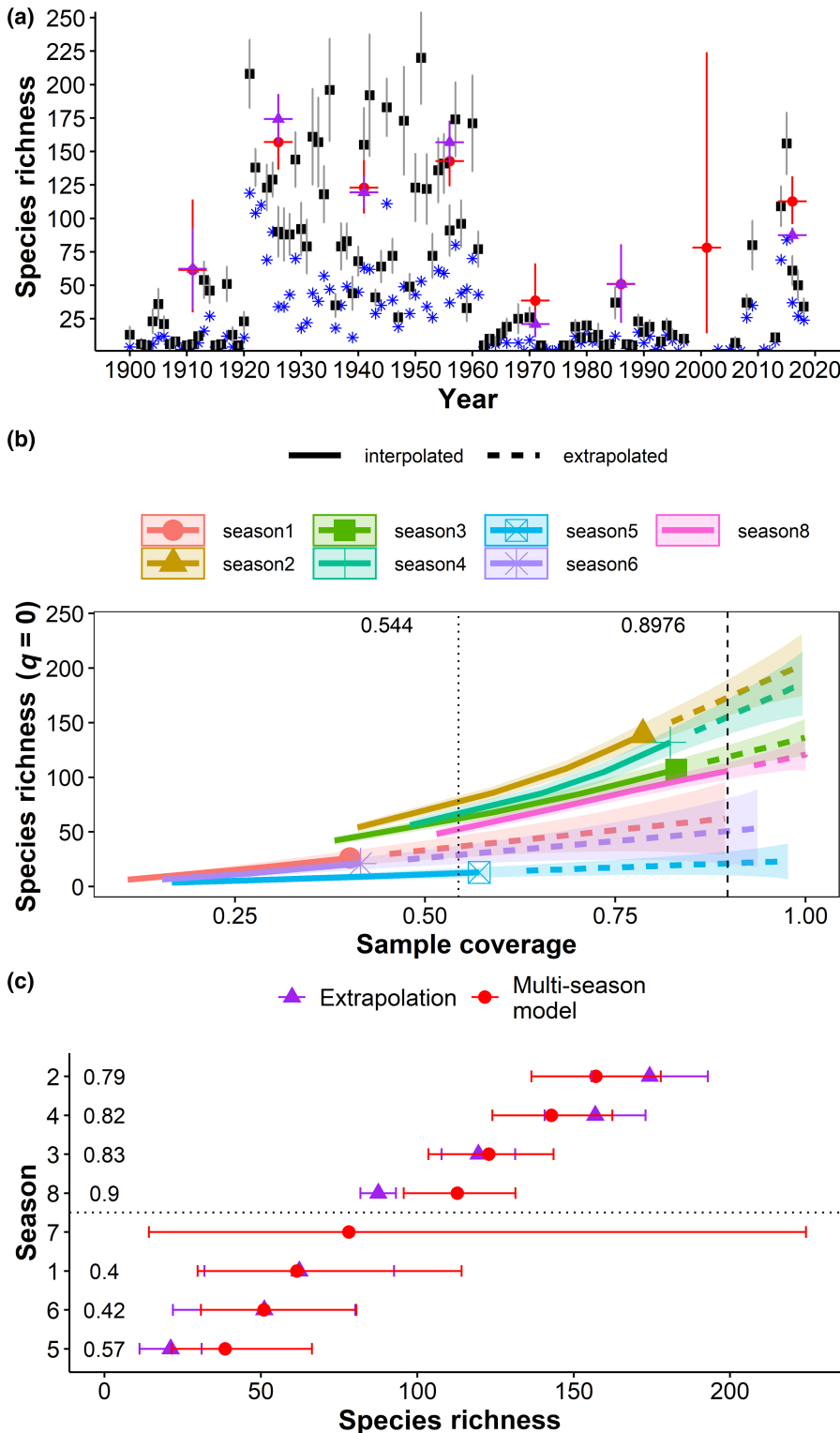
FIGURE 3 Patterns of estimated and observed bee species richness and sample coverage across time. (a) Estimates of species richness from 5-year seasons from the multi-season model (PRESENCE; red circles; ±99% confidence interval [CI]), 5-year seasons generated to a shared sample coverage from extrapolation (*iNEXT*; purple triangles; ±99% CI), annual SPECRICH2 outputs (black squares; ±SE), and observed species richness (blue stars). (b) Estimates for species richness (±99% CI) by sample coverage. Vertical lines represent the smallest sample coverage (0.544) at two times the smallest sample size (8), and the highest sample coverage (0.8976) using all the data. (c) Estimated species richness (±99% CI) generated either from the multi-season model or from extrapolation. The extrapolation output is obtained from the *estimateD* function to a shared sample coverage of approximately 0.90 in the *iNEXT* package. Numbers on the figure represent the sample coverage of the raw data for that season as determined using *iNEXT* and the dotted line separates out the seasons that had low sample coverage based on the raw data from seasons with greater sample coverage based on raw data. For season years, see Table 1.

significant effect of time period (historical vs. contemporary) on the assemblage of bee specimen records contributed to the dataset per collector (NMDS: stress = 0.00; perMANOVA: strata = fixed by collector, $F_1 = 3.10$, $p = .07$; Figure 4c). Twenty-five bee species separated the top collectors (Table 3). The remaining 213 bee species were not significant and thus were weak predictors of the different collector assemblages.

There was a significant but weak positive correlation between decimal latitude and year (Spearman's rho = 0.18, $S = 3,148,673,117$, $p < .001$) and a significant but moderate negative correlation between decimal longitude and year (Spearman's rho = −0.38, $S = 5,311,489,577$, $p < .001$), indicating that collecting effort shifted slightly north and west within the county over time. In general, there was a greater breadth of sampling locations in contemporary time

TABLE 2 Summary of how bee species richness estimates correlate with time.

Method	Time correlate	Test statistic (*S*)	Rho	*p*	Notes
Multi-season occupancy model (PRESENCE)	Seasons	108	−0.29	.50	
SPECRICH2	Annual	157,508	−0.10	.32	Cannot compute exact *p*-value with ties
Extrapolation (*iNEXT*)	Seasons[a]	78	−0.39	.40	
Extrapolation (*iNEXT*)	Annual	173,808	−0.22	.04	Cannot compute exact *p*-value with ties

Note: Spearman correlations between bee species richness (estimated by different methods) and time (expressed as seasons or as years with at least three collection events). Extrapolation estimates were obtained using the *estimateD* function to a shared sample coverage.

[a]Extrapolation using *iNEXT* with data set up similar to that used in PRESENCE had one season dropped due to low sample size.

periods, though this may be due to having more specific sampling localities than in historical time periods (Data S6 Figure S2.2). For example, in the early 1900s it was common for labels to report a generic location (e.g., "Raleigh", "Apex", etc.) without coordinates, which we then filled in using Google Earth (see Data S5 for more information).

4 | DISCUSSION

We investigated whether there was a trend in bee species richness over time with increasing urbanization within Wake County, North Carolina, United States using museum specimens, online occurrence repositories, and researcher collections. Using multiple methods, we determined that although bee species richness varied among seasons, there was no clear trend of bee species richness with time in this increasingly urbanized landscape. However, there has been a decrease in bee richness in the most recent season (2014–2018), at least compared to the mid- to late-1920–1950s based on rarefaction and extrapolation methods. Over 59% (195 species) of the species in our dataset have not been collected since 1969 and less than 6% (19) have only been collected starting in 2003. Additionally, the trait composition of collected species has changed. Those that were only collected historically comprised a more diverse group that had higher proportions of parasitic species, while those that were only collected recently comprised more generalist bees with a lower frequency of ground nesting species.

Multiple studies have used museum specimens to fill in temporal data gaps to answer questions about bee diversity patterns (e.g., Bartomeus, Ascher, et al., 2013; Jacobson et al., 2018; Mathiasson & Rehan, 2019), response to environmental stress (Arce et al., 2023), and pollination networks (Mathiasson & Rehan, 2020). Studies that looked at diversity patterns using museum specimens either investigated across multiple time periods, finding weak declines in richness that were non-significant except for some wild bee species (e.g., some *Bombus* species, Bartomeus, Ascher, et al., 2013), or split the data into two time periods (historic vs. contemporary; e.g., Jacobson et al., 2018; Mathiasson & Rehan, 2019). When comparing across two time periods, some wild bee species demonstrated declines in abundance while some increased in abundance (Jacobson et al., 2018; Mathiasson & Rehan, 2019). However, none

of these studies included contemporary research collections, used occupancy models, or modeled how local colonization or extinction could have occurred across the time periods they selected. Recently, occupancy models have been used to assess bee species richness trends with long-term datasets (e.g., Duchenne et al., 2020; Van Dooren, 2019), and studies are beginning to assess whether occupancy models can be used successfully with museum specimen data (Shirey et al., 2022). For example, Shirey et al. (2022) found that depending on the dataset, museum specimens can be used with occupancy models to accurately estimate trends in occupancy over time. Specifically, occupancy estimates tend to be more accurate when datasets have a large number of sampling events that focus on communities or groups of organisms rather than individual species, and have many intervals from which to estimate probability of occupancy (Shirey et al., 2022). Occupancy models were often just as accurate at estimating gamma diversity as other methods when using the same data (Tingley et al., 2020). Additionally, using occupancy models has been demonstrated to produce less biased estimates of occupancy and change in occupancy when restricting analyses to species ranges (e.g., Guzman et al., 2021). Many of these studies that used museum collections to investigate richness or population trends recognized that limitations stem from the use of presence-only records with unknown sampling effort (Bartomeus, Ascher, et al., 2013; Shirey et al., 2022).

Studies of bee species richness find varied results on the relationship between richness and time or increasing urbanization. Some longitudinal studies have found a non-significant negative trend with time (e.g., non-significant negative trends for all bees in the Northeastern United States except *Bombus* which exhibited a significant negative trend, Bartomeus, Ascher, et al., 2013) which is similar to our study. Other longitudinal studies have found a significant decrease in species richness with time. For example, studies focusing on the city of Curitiba, Brazil have found a decline in bee species richness with time (35% decline in ground-nesting bees between surveys in 1955–1956 and 2018–2019, Pereira et al., 2021; 45% decline of bee species between 1981–1982 and 2015–2016, Cardoso & Gonçalves, 2018). The percent of urban cover in Curitiba was 0.4% in 1955–1956 and rose to 56% in 2018–2019 (Pereira et al., 2021). Additionally, Zattara and Aizen (2021) used online bee occurrence records deposited in GBIF to suggest that there has been a global decline in bee species richness with time. Cross-sectional studies that investigate the effect of

(a)

(b)

(c)
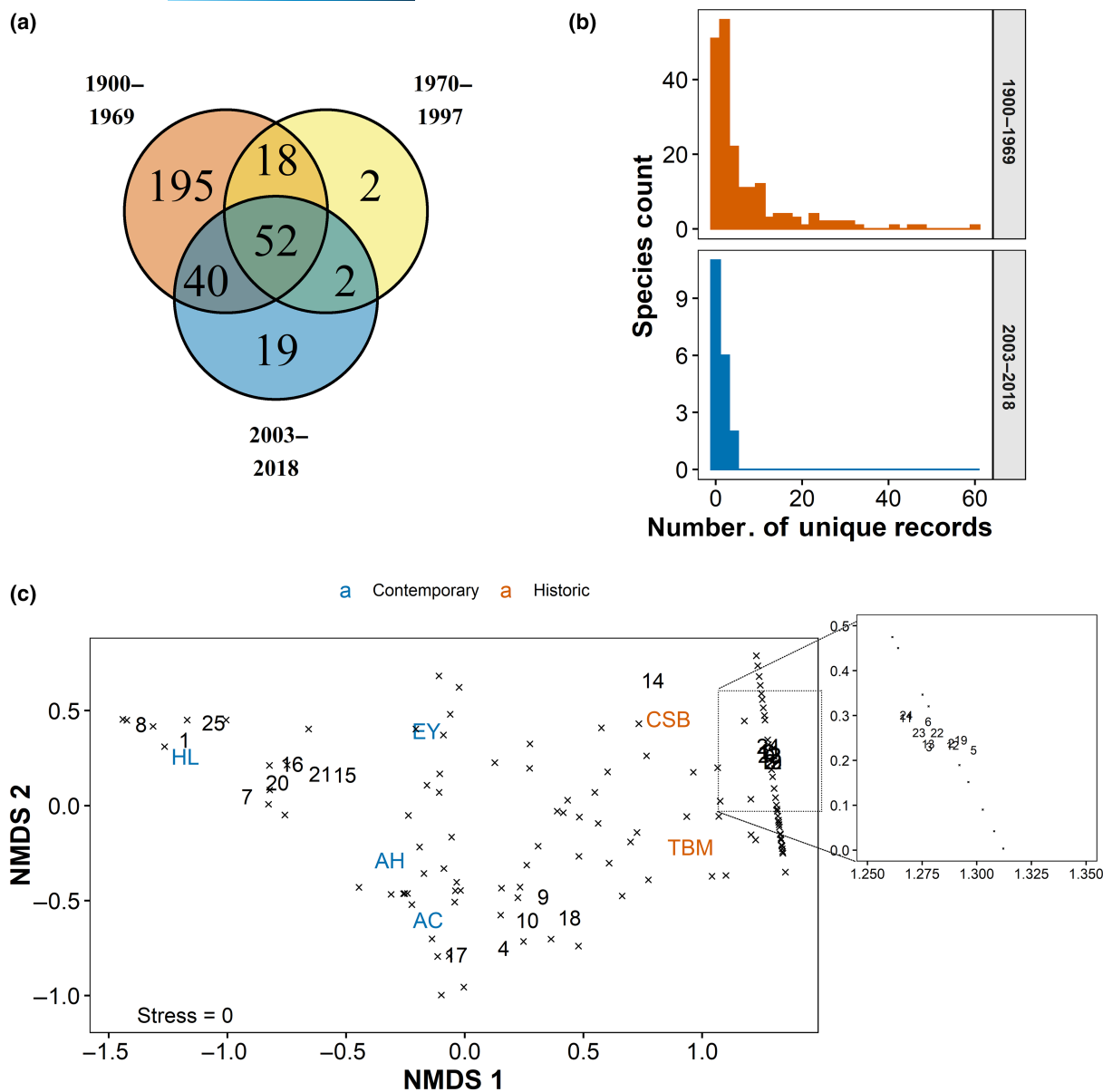
FIGURE 4 Changes in when bee species were captured. (a) Venn diagram of years when species were captured. More species were only captured by hand netting before the 1970s with fewer species uniquely captured in recent time periods (2003–2018). (b) Histogram of the number of species by number of unique collection records. Species were either only collected historically (1900–1969) or only collected contemporarily (2003–2018). (c) Non-metric multidimensional scaling (NMDS) depicting the relationship between bee specimens collected by top collectors in different time frames. Letters denote the collector: AC = A. Carper; AH = A. Hamblin; CSB = C.S. Brimley; EY = E. Youngsteadt; TBM = T.B. Mitchell. Numbers refer to significant bee species (see Table 3) while x's denote bee species that do not significantly separate out collections over time. Species that load at the far right on NMDS1 were only collected historically. Zoom insert shows right portion of figure where significant bee species cluster. For easier viewing, these species positions were jittered by 0.015 horizontally and vertically.

urbanization or suburbanization on bee species richness are more common than longitudinal studies but still have mixed findings. For example, Prendergast et al. (2022) conducted a review of 215 studies, 51 of which compared bee communities between urban and either agricultural or natural landscapes. Out of these studies, 48% found lower species richness in urban sites compared to natural sites, and 44% found greater species richness in urban sites compared to agricultural sites. Fewer studies found no differences between landscapes,

higher species richness in urban sites compared to natural sites, or lower species richness in urban sites compared to agricultural sites. However, Carper et al. (2014), who sampled in the Raleigh-Durham, North Carolina area, found no significant differences in bee species richness between suburban forests and natural forests. It is important to note though that a subset of the data in Carper et al. (2014) was included in this study. It is possible that different regions exhibit different species richness trends.
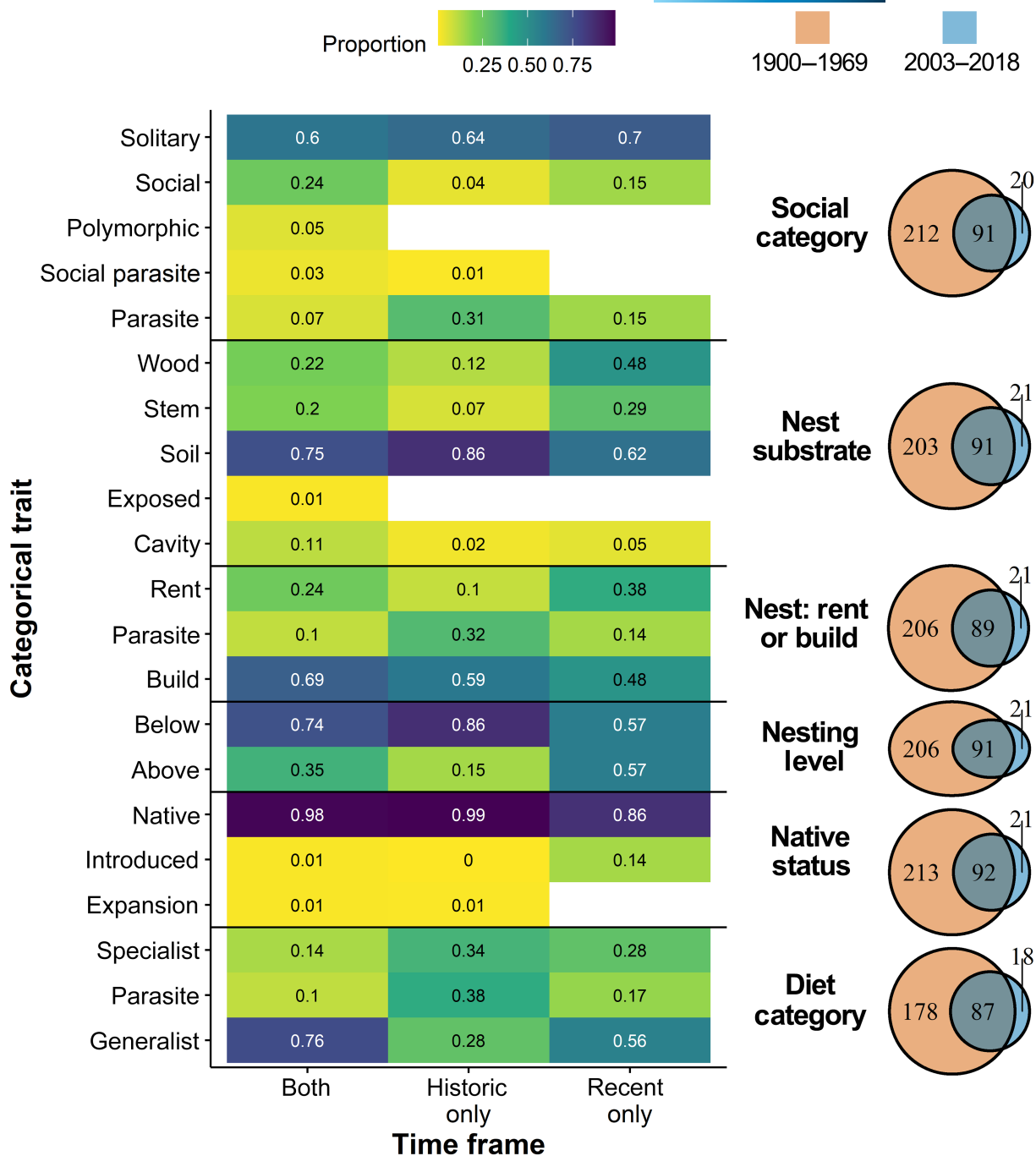
FIGURE 5 Relative frequency of bee functional traits by trait category and time frame. Darker, more purple colors on the heatmap are more frequent (higher percentage of species from that time frame), while lighter, more yellow colors are less frequent. Venn diagrams represent the number of species with trait information by trait category and by time frame. The historical time frame was 1900–1969 and the recent time frame was 2003–2018.

4.1 | Using collections data to assess biodiversity changes over time

There are many challenges to understanding long-term biodiversity trends (Didham et al., 2020) when using museum specimens (Davis et al., 2023), online repositories such as GBIF (Rocha-Ortega et al., 2021), and opportunistic observations such as those from participatory or citizen science initiatives (e.g., from iNaturalist, Di Cecco

et al., 2021). Here we discuss the main issues regarding spatial and temporal biases, unknown sampling effort, and collector preference, what we have done to address them, and how they may still impact our findings. Spatially, not all areas are sampled equally, even within well sampled locations such as the southeastern United States. This can be because observations can be biased towards areas that are easier to access, are more likely to have the species of interest, or are where people generally already are or go for recreation (e.g.,

TABLE 3 Bee species that significantly separate top collectors using nonmetric multidimensional scaling (NMDS).

Species	NMDS1	NMDS2	*r*	*p*-value	Number
Agapostemon virescens	−0.83	0.56	.71	.021	1
Andrena andrenoides	0.90	0.44	.82	.033	2
Andrena erigeniae	0.90	0.44	.83	.033	3
Andrena macra	0.030	−1.0	.87	.042	4
Andrena nida	0.90	0.44	.83	.033	5
Anthidium maculifrons	0.86	0.52	.83	.033	6
Apis mellifera	−1.0	0.077	.80	.047	7
Bombus pensylvanicus	−0.80	0.60	.63	.019	8
Calliopsis andreniformis	0.17	−0.99	.91	.047	9
Ceratina strenua	0.096	−1.0	.98	.014	10
Colletes brevicornis	0.86	0.52	.83	.033	11
Dianthidium curvatum	0.90	0.44	.83	.033	12
Epeolus pusillus	0.90	0.44	.82	.033	13
Eucera pruinosa	0.37	0.93	.83	.033	14
Halictus confusus	−0.85	0.53	.98	.001	15
Halictus ligatus/poeyi	−0.84	0.54	.73	.010	16
Heriades carinata	−0.065	−1.0	.80	.050	17
Lasioglossum coreopsis	0.20	−0.98	.96	.014	18
Macropis steironematis	0.90	0.44	.82	.033	19
Megachile mendica	−0.96	0.29	.83	.014	20
Megachile petulans	−0.87	0.49	.92	.013	21
Nomada articulata	0.87	0.49	.83	.033	22
Nomada ovata	0.87	0.49	.83	.033	23
Paranthidium jugatorium	0.83	0.56	.83	.033	24
Svastra obliqua	−0.72	0.69	.71	.019	25

Note: The arrow endpoints for the species on the first (NMDS1) and second (NMDS2) as well as the goodness-of-fit statistic (*r* = squared correlation coefficient), and *p*-value. The arrow endpoints indicate both the length of the arrow, which corresponds to the strength of the correlation (longer arrows have stronger predictions), and the direction of the arrow which corresponds to the direction in which the abundance of that species captured in assemblages changes most rapidly (Oksanen et al., 2019). Species included were significant based on using the *envfit* function in the *vegan* package at the *p* < .05 level. Number refers to the label on Figure 4c which depicts where the species loads on the NMDS.

iNaturalist users, Di Cecco et al., 2021). While we limited our analyses to Wake County, we did find that most of the records within our dataset came from within the current definition of Raleigh city limits (Data S5). However, the trends we found when limiting the analyses to the specimens collected within Raleigh were highly correlated to those for all of Wake County (Data S5). Additionally, sampling can be temporally biased. Within our dataset, we found more unique records from 1920 to 1969 and 2003 to 2018 than from other time periods. To address how this may have impacted our results, we chose our seasons using a sliding framework and using two different methods that estimated species richness either for 5-year time blocks or annually. This difference in temporal sampling also ties into unknown sampling effort, which we addressed by complementing our occupancy analyses with sample-based rarefaction and extrapolation to determine which of our chosen seasons suffered from a lack of coverage based on the raw data. We also extrapolated richness estimates to shared sample coverage, but focused on the seasons

that initially had ≥79% coverage so that artefacts of an initial low coverage would not impact our final estimates.

4.2 | Time as a proxy for increased human population and urbanization

As expected, we found a positive correlation between time and measures of increased human development (Brown et al., 2005; Li et al., 2021; Terando et al., 2014). Both the population of Wake County and the urban extent of Raleigh were positively correlated with time. However, we did not find evidence to support that urban extent influenced bee species richness trends; the latter remained fairly constant over time and did not decrease or increase with urban trend. Our best-supported model indicated that local extinction probability varied over time, that is, some species present in any given season were not observed in the next. This finding does not exclude

that other factors, aside from urban growth, influenced species detected in samples over time. For example, since 1985 the average annual temperature in North Carolina has risen about 0.56°C (Kunkel et al., 2020) and with urban heat island effects (Bornstein, 1968), some areas of Wake County could have experienced this shift faster. But temperature increase was not always linear, as some years in the Piedmont region of North Carolina were warmer than average (generally 1930s–50s, consistently increasing since 1990), others cooler (1950s–70s), and the warmest years were in 2015–2018 (Kunkel et al., 2020). Additionally, around the time when we saw the greatest probability of local extinction based on the best supported multi-season model (the transition between 1954–1958 and 1969–1973), there were fewer hot days and fewer warm nights in the Piedmont region than in other time periods (Kunkel et al., 2020). The change from warm to cool around the 1950s happened about a decade before we saw the largest probability of local extinction in the best supported multi-season model. It is not feasible with the current dataset to disentangle the effects of temperature or urbanization on bee communities, but neither stressor appears to be strongly linked to bee species richness in our dataset.

4.3 | The influence of rare species and collector behavior

The 1920s had the greatest number of rare species (i.e., fewer than 10 unique collection records) while the 1950s and 1940s had the next most, and 1900–1919 and 2000–2018 had the fewest (Data S6 Table S2.6). This could have been because rare species are more vulnerable to land use change (Harrison et al., 2019) or because of changes in collector behavior over the years.

A shift in collector purpose is supported by looking at the top collectors in the dataset, though detailed records of how historic collectors sampled are unavailable. The top two historic collectors, C.S. Brimley and T.B. Mitchell, both contributed most of their unique collection records in the 1920s (Data S6 Table S2.7). Both C.S. Brimley and T.B. Mitchell worked to inventory bees in North Carolina. C.S. Brimley was a naturalist and worked for the Division of Entomology (Metcalf, 1947; Mitchell, 1960). Though also interested in other taxa (e.g., birds, reptiles, amphibians; Metcalf, 1947; Mitchell, 1960), he was involved in creating species inventories of the insects of North Carolina which included bees (Brimley, 1938). T.B. Mitchell was a taxonomist who moved to North Carolina in 1920 (Youngsteadt et al., 2016). He was primarily known for his work in revising *Megachile* and *Coelioxys* (e.g., Mitchell, 1935a, 1935b, 1936, 1937a, 1937b) and publishing *The Bees of the Eastern United States* (Mitchell, 1960, 1962), and joined C.S. Brimley and Franklin Sherman in documenting all of the insects in North Carolina. At the beginning of this survey work, only about 60 bee species were known from North Carolina (Mitchell, 1960), and Mitchell described numerous new species (Mitchell, 1951) and added new state records. In contrast, most of the top contemporary collectors were seeking to answer ecological questions, such as how the urban landscape or

heat island affects bee species richness and abundance (see Data S5 for more information on recent collections data sources). Thus, earlier time periods may have detected more unique species because taxonomists specifically sought to maximize the diversity of their collections, whereas later ecologists—whose work became possible after the fauna was well characterized—sought not to detect all species but to characterize specific focal habitats with repeatable methods.

Top collectors differed in how often they collected different bee species, though this was not consistent by time period. For example, within the NMDS, both Hamblin's (Hamblin et al., 2018) and Carper's (Carper et al., 2014) bee records cluster more closely together than the others, and they also addressed similar ecological questions. Both collectors focused on urban habitats, collecting in urban yards (Hamblin et al., 2018) or having a subset of their specimens collected from urban forests (Carper et al., 2014). These two assemblages also tended to include more specimens of *Andrena macra* Mitchell 1951, *Calliopsis andreniformis* Smith 1853, *Ceratina strenua* Smith 1879, *Heriades carinata* Cresson 1964, and *Lasioglossum coreopsis* (Robertson 1902) than the other contemporary collections. Additionally, Levenson's (Levenson & Tarpy, 2023) recent collection from agricultural habitats included more specimens of *Agapostemon virescens* (Fabricius 1775), *Bombus pensylvanicus* (De Geer 1773), and *Svastra obliqua* (Say 1837), and C.S. Brimley's collections included more *Eucera pruinosa* (Say 1873). Though collectors themselves collected species in different frequencies, there was no strong change in behavior between historical collectors and contemporary collectors. However, this analysis excluded any species that had only been collected once by any collector, which removed more specimens from the historic collectors than from any of the contemporary collectors (Data S6 Table S2.1).

4.4 | Bee traits, urbanization and time

Numerous studies have investigated whether bee life history traits mediate responses to urbanization, with the most commonly investigated traits being sociality, diet specialization, and nesting habits (e.g., see Wenzel et al., 2020 and citations within). Social species have been thought to have greater ecological and behavioral flexibility in novel environments (Banaszak-Cibicka & Żmihorski, 2012; Wenzel et al., 2020), while parasitic species may be more vulnerable if their host species is also lost. For example, both the parasitic *Nomada cuneata* (Robertson 1903) and its host *Andrena vicina* Smith 1853 (Miliczky & Osgood, 1995) have only been collected two times each in Wake County. Both were collected in 1923, but after 1924 *N. cuneata* was no longer collected while its host was last collected in 1957. Bees with narrower diet breadths may be more sensitive to environmental change due to their inability to switch hosts (Bartomeus, Ascher, et al., 2013; Mattila et al., 2008). The availability of nesting substrate can also limit bee abundances (Potts et al., 2005; Stubbs et al., 1997) and this availability can be altered by land use change and urbanization (Cane et al., 2006;

Wenzel et al., 2020). For example, we found a slight decrease in the number of below-ground nesting species and an increasing number of above-ground, wood and stem-nesting species. These patterns may be due to a decrease in available bare-ground nesting habitat as impervious surface increases with urbanization (e.g., Fortel et al., 2014; Pereira et al., 2021) and an increasing amount of construction or buildings could potentially provide more wood and stem habitats for bees.

Cross-sectional studies have found differences in the frequency of bee functional traits across different land uses and urbanization intensities (e.g., Harrison et al., 2018; Villalta et al., 2022; Wilson & Jamieson, 2019), although patterns were not always in the same direction or strength between studies. For example, both Harrison et al. (2018) and Villalta et al. (2022) found that urban areas favored social species, though the trend in Harrison et al. (2018) was non-significant after phylogenetic correction. In contrast, Wilson and Jamieson (2019) found that solitary bees were more common in areas of greater urban intensity. Over time, we found that there remained a high proportion of solitary bee species in Wake County. Using historical specimens, Bartomeus, Ascher, et al. (2013) determined that species with a narrow diet breadth were more likely to be in decline. We found that both the bee species gained in contemporary periods and ones that were collected in both time periods were more likely to be generalists than bee species that were lost. However, bee species that exhibit traits that are now represented in low frequencies may have declined for several reasons. Traits that are now present in low frequencies could be indicative of traits that make bee species vulnerable to being lost in the future, or these traits may only be present in species that are less easily detected in current ecological sampling plans. For example, *Macropis steironematis* Robertson 1891 was collected on only four occasions in 1921 and 1922 and is a diet specialist on *Lysimachia* (*Steironema*) flowers (Fowler, 2016) which are uncommon in Wake County. It is possible that *M. steironematis* is no longer present in Wake County, or that it has been missed because no recent sampling effort targeted its uncommon host. Further investigation would help distinguish between these possibilities.

5 | CONCLUSIONS

Using a combination of complimentary data analyses, we explored and accounted for a variety of potential biases in bee specimens collected from 1900 to 2018. The complimentary methods we employed help cultivate a better understanding of bee species richness trends than any method alone would offer. Rarefaction helped us determine which time periods we should include in our comparisons, while occupancy models provided estimates of detection, local colonization, and local extinction probabilities and allowed us to test additional models of how these parameters may vary over time. These approaches could help avoid some of the biases described by Didham et al. (2020) that come from choices of which historic and contemporary baselines are used for

comparisons. Using these methodologies, we found that although bee species richness varied in different seasons, there was no trend in bee species richness over time in this urbanizing region in the southeastern United States. Nonetheless, we found that contemporary collections were missing 195 bee species relative to historic collections. This change in species composition was associated with bee traits, with above-ground nesters and dietary generalists most likely to persist through time. Overall, museum specimens can help fill historic gaps in occurrence records to facilitate investigation of long-term species richness trends in areas that lack long-term monitoring data (e.g., Boakes et al., 2010). However, potential sources of bias need to be explored and accounted for through data filtering and use of complimentary analyses (e.g., Davis et al., 2023). Although a historical collection accumulated with unknown methods and sampling effort will never substitute for a true monitoring dataset, these collections nevertheless harbor a wealth of information that can point to potential species losses and vulnerabilities that can motivate and focus modern detection efforts.

AUTHOR CONTRIBUTIONS

Selina A. Ruzi: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; validation; visualization; writing – original draft; writing – review and editing. **Elsa Youngsteadt:** Conceptualization; data curation; investigation; resources; supervision; writing – original draft; writing – review and editing. **April Hamblin Cherveny:** Data curation; investigation; resources; writing – review and editing. **Jessica Kettenbach:** Data curation; investigation; resources; writing – review and editing. **Hannah K. Levenson:** Data curation; investigation; resources; writing – review and editing. **Danesha Seth Carley:** Data curation; investigation; resources; writing – review and editing. **Jaime A. Collazo:** Conceptualization; formal analysis; investigation; methodology; resources; software; supervision; validation; writing – original draft; writing – review and editing. **Rebecca E. Irwin:** Conceptualization; funding acquisition; investigation; resources; supervision; writing – original draft; writing – review and editing.

CONFLICT OF INTEREST STATEMENT

The corresponding author confirms on behalf of all authors that there are no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in a public GitHub repository available at https://github.com/sruzi 24/Ruzi_etal_temporal_bee_richness and http://doi.org/10.5281/ zenodo.10105284.

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SUPPORTING INFORMATION

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