

1 **Land use change consistently reduces α but not β and γ diversity of bees**

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261 Running title: Land use change reduces bee diversity

Abstract

Land use change threatens global biodiversity and compromises ecosystem functions, including pollination and food production. Reduced taxonomic α diversity is often reported under land use change, yet the impacts could be different at larger spatial scales (i.e., γ diversity), either due to reduced β diversity amplifying diversity loss or increased β diversity dampening diversity loss. Additionally, studies often focus on taxonomic diversity, while other important biodiversity components, including phylogenetic diversity, can exhibit differential responses. Here, we evaluated how agricultural and urban land use alter the taxonomic and phylogenetic α , β , γ diversity of an important pollinator taxon – bees. Using a multi-continental dataset of 3,117 bee assemblages from 157 studies, we found that taxonomic α -diversity was reduced by 16-18% in both agricultural and urban habitats relative to natural habitats. Phylogenetic α diversity decreased by 11-12% in agricultural and urban habitats. Compared with natural habitats, taxonomic and phylogenetic β diversity increased by 11% and 6% in urban habitats respectively but exhibited no systematic change in agricultural habitats. We detected a 22% decline in taxonomic γ diversity and a 17% decline in phylogenetic γ diversity in agricultural habitats, but γ diversity of urban habitats was not significantly different from natural habitats. These findings highlight the threat of agricultural expansions to large-scale bee diversity due to systematic γ diversity decline. In addition, while both urbanization and agriculture lead to consistent declines in α diversity, their impacts on β or γ diversity vary, highlighting the need to study the effects of land use change at multiple scales.

Keywords: Land uses, bees, pollinators, biodiversity decline, agriculture, urban

Introduction

Human activities have transformed global terrestrial environments for anthropogenic land uses, mainly agriculture and urban developments (Ellis, Klein Goldewijk, Siebert, Lightman, & Ramankutty, 2010). These processes reduce biodiversity by creating environments with unsuitable biotic and abiotic conditions and enhancing competitive exclusion (Mayfield et al., 2010), ultimately threatening ecosystem functions (van der Plas, 2019). A common approach in evaluating the ecological impacts of land use change is to compare the number of taxa within assemblages (taxonomic α -diversity) between natural habitats and anthropogenic habitats (Purvis & Hector, 2000). Previous studies have found that taxonomic α -diversity in different taxa can be reduced by 19%-40% in agricultural habitats and 4%-50% in urban habitats on average (Newbold et al., 2015).

However, taxonomic α diversity analyses could fail to capture the potential effects of land use change on homogenizing assemblages, thus underestimating γ diversity loss (i.e., diversity at larger spatial scales) (Socolar, Gilroy, Kunin, & Edwards, 2016). Taxonomic β diversity, relatively understudied compared with taxonomic α diversity, captures compositional variations between assemblages and can determine how α diversity loss upscales to γ diversity (Mori, Isbell, & Seidl, 2018; Socolar et al., 2016). Specifically, reduced and increased β diversity can result in higher and lower γ diversity loss relative to what would be expected based on α diversity losses alone (Socolar et al., 2016). While land use change is expected to homogenize assemblages and reduce β diversity, empirical studies have shown mixed results (Newbold et al., 2016).

Regardless of the spatial scale at which it is measured, a limitation of taxonomic diversity is its inability to effectively reflect ecological differences between species, such as morphology,

physiology, and phenology (Purvis & Hector, 2000; Tucker et al., 2017). Recent studies have increasingly emphasized analyzing phylogenetic diversity alongside taxonomic diversity (Cadotte & Tucker, 2018; Tucker et al., 2017). As evolution shapes species traits, phylogenetic approaches can efficiently capture high-dimensional ecological differences, reducing the risks of omitting important traits (Tucker et al., 2017; Tucker, Davies, Cadotte, & Pearse, 2018). Additionally, phylogenetic diversity has exhibited similar or even better performance than taxonomic diversity in explaining ecosystem functions or services across sites (Tucker et al., 2019; van der Plas, 2019).

While not always the case, responses of phylogenetic diversity to land use change should largely follow taxonomic diversity change (Tucker & Cadotte, 2013). However, land use could also lead to more phylogenetic diversity loss than would be expected based on the taxonomic diversity loss. This is because land use change can strengthen phylogenetic habitat filtering (Grab et al., 2019; Nowakowski, Frishkoff, Thompson, Smith, & Todd, 2018), causing only a subset of phylogenetically similar species to persist under anthropogenic land uses due to conserved traits (Duarte, 2011). Interestingly, the filtering effects on α - and β -diversity can vary, again demonstrating the importance of analyzing both α and β diversity to better understand net impacts at larger spatial scales (i.e., γ diversity) (Nowakowski et al., 2018).

To understand how land use change affects taxonomic and phylogenetic diversity, we focused on a well-studied and ecologically important taxon, bees. Pollination services by bees can be greater in sites with high bee taxonomic and phylogenetic α diversity and landscapes with high taxonomic β diversity between sites (Grab et al., 2019; Weekers et al., 2022; Winfree et al., 2018), compared to lower-diversity sites and landscapes. Ongoing global land use change is known to reduce bee diversity generally (Cariveau & Winfree, 2015; De Palma et al., 2016;

Winfree, Bartomeus, & Cariveau, 2011). However, the exact effects can vary with land use types, with some studies reporting increased bee diversity under land use change (Cariveau & Winfree, 2015; Prendergast, Dixon, & Bateman, 2022; Winfree et al., 2011). Furthermore, the impacts of anthropogenic land uses are often evaluated using taxonomic α diversity, even though other biodiversity metrics could exhibit different patterns (De Palma et al., 2017; Harrison, Gibbs, & Winfree, 2018). Importantly, some bee lineages are especially sensitive to land use change, which could lead to a more substantial decline in phylogenetic diversity relative to taxonomic diversity (Grab et al., 2019; Harrison et al., 2018).

We examined the ecological impacts of land use change on global bee diversity using bee assemblage data from agricultural, urban, and natural habitats across all continents except Antarctica, where bees are absent. Our objectives were to 1) compare taxonomic and phylogenetic α , β and γ diversity between natural, agricultural and urban habitats, 2) investigate whether land use change leads to stronger phylogenetic habitat filtering, and 3) identify the genera particularly affected by the agricultural and urban habitats. For objective 1, we expected that natural habitats would contain greater taxonomic and phylogenetic α , β , and γ diversity. For objective 2, we predicted declines in phylogenetic diversity in urban and agricultural habitats, even after controlling for taxonomic diversity, due to increased phylogenetic habitat filtering.

Materials and Methods

Data collection, cleaning, and filtering

Bee data were collected from various sources, including the PREDICTS database (Hudson et al., 2014), a previous meta-analysis on bee diversity in agricultural systems (Kennedy et al., 2013), literature searches, and expert recommendations (see Section S1 for details and the

limitations of our dataset). We corrected species synonyms using a bee species guide and world checklist (Ascher & Pickering, 2022). Missing taxa were further reviewed by a taxonomist co-author (John S. Ascher). For 1% of 2,257 species-level identifications, no matches were found; these were treated as morphospecies instead of species. For morphospecies or genus-level data, we checked the validity of the genus in the checklist and corrected them when necessary.

Datasets were divided into different studies (see Table S1 for details of each study) according to their sampling strategies, which were broadly classified as: (1) “flower visitors”, if the study sampled flower-visiting bees within an area, (2) “targeted plants” if the study sampled flower-visiting bees of targeted plant species, and (3) “all bees” for any other method, such as pan traps, hand-netting, and vane traps. Thus, if a dataset provided bee data based on different sampling strategies, such as pan traps and hand netting bees from targeted plant species, the data would be separated into different studies. For each site within each study, we aggregated bee species abundance data across sampling dates (hereafter referred to as assemblage). We excluded *Apis mellifera* from all assemblages, as they were often from managed colonies.

We only included assemblages in our analyses if the following criteria had been met: 1) The sampling strategy had a broad taxonomic focus rather than only focusing on certain groups of bees (e.g., *Bombus* spp., solitary bees). 2) Spatial coordinates were recorded. 3) The number of individuals observed was recorded. 4) At least ten individuals were identified to at least the genus level to ensure reliable rarefaction results (see below). We did not use a threshold higher than ten individuals because this might bias the analyses against impoverished assemblages. The threshold is also consistent with or higher than that used in previous studies based on rarefaction (Blowes et al., 2022; van Klink et al., 2024). 5) The assemblages had sampling completeness of $\geq 50\%$ to ensure the reliability of diversity estimates. Sampling completeness was calculated

using the R package iNEXT.3D (Chao et al., 2021). 6) The assemblage had at least 95% of observed individuals identified to at least the genus level to ensure reliable estimations of phylogenetic diversity. We did not set a minimum number of assemblages to include in a study for subsequent analyses.

Definition of land uses

We classified the land use of each assemblage based on the predominant environment within the sampling area. Natural habitats were defined as areas primarily covered by vegetation resulting from natural succession or restoration (i.e., active attempts to bring the site to a more natural state). Agricultural habitats were defined as sites managed for growing resources, including food and animal products. Urban habitats included green spaces covered by planted vegetation (not natural succession) managed for amenity or recreation (e.g., lawns, gardens). See Section S2 for details of the land use classification.

Phylogeny

We used a global genus-level phylogeny to quantify the phylogenetic diversity of each assemblage (Hedtke, Patiny, & Danforth, 2013). Tip names on the phylogenetic tree were corrected using Ascher & Pickering (2022) and further reviewed by a taxonomist co-author (John S. Ascher). We converted the tree to ultrametric using a non-negative least square (Turley, Biddinger, Joshi, & López-Urbe, 2022). The strong cophenetic correlation (Pearson's $r = 0.93$) indicated that the tree's structure was largely conserved. Our data contained taxa from 355

genera, of which 32 were missing from the tree and were added to the closest sister genus available (Table S2). We randomly selected one species in the tree from each genus, then attached all species from each study as polytomies at the mid-point of its corresponding genus branch, as this approach has been demonstrated to capture phylogenetic diversity well when a species-level phylogeny is unavailable (Qian & Jin, 2021). While the use of a genus-level phylogeny might not fully capture phylogenetic patterns of assemblages, previous bee studies have used the same phylogeny and detected phylogenetic diversity changes and phylogenetic habitat filtering (De Palma et al., 2017; Harrison et al., 2018; Hendrix, Forbes, & MacDougall, 2018). We quantified the phylogenetic α -diversity of each assemblage by generating ten phylogenetic trees and found that the values of phylogenetic α -diversity were highly correlated (Pearson's $r > 0.99$). Thus, we only used the first phylogenetic tree for subsequent analyses.

α and γ diversity estimates

In our analyses, α and γ diversity always represent within- and across-sample diversity, respectively, within the same land use type. Thus, comparing α and γ diversity across habitats allows for assessing whether diversity loss is exacerbated at larger spatial scales by land use change (Chase et al., 2019; Socolar et al., 2016). To estimate taxonomic and phylogenetic α and γ diversity, we estimated both metrics with the Hill number equal to 1, as it considers the relative abundance of species within assemblages and is less prone to undersampling than lower Hill numbers (Roswell, Dushoff, & Winfree, 2021).

We estimated α diversity for all assemblages, while γ diversity was estimated only for studies with at least five assemblages from at least one land use. Additionally, γ diversity was only

estimated for studies that indicated sampling effort for each assemblage. We pooled species abundance data across assemblages of the same land uses within each study before conducting the γ diversity rarefaction analyses. To control for differences in sampling completeness between assemblages across studies, we extrapolated all α and γ diversities to their asymptotes (i.e., when sampling completeness equals 1). Each assemblage's taxonomic and phylogenetic diversity was estimated using iNEXT.3D (Chao et al., 2021).

β diversity estimates

For each land use in each study, we used multiplicative partitioning ($\beta = \gamma / \text{mean } \alpha$) to obtain their β diversity (Jost, 2007). This method is especially suitable to understand the spatial scaling of diversity loss, as it represents the scaling factor relating α and γ diversity (Baselga, 2013; Socolar et al., 2016). The metric also reflects the contribution of β diversity to γ diversity (Contribution of $\beta = (1 - \alpha/\gamma) * 100\% = (1 - 1/\beta) * 100\%$).

The corresponding γ and α diversities were taken from rarefaction analyses. As more abundant assemblages should more heavily influence γ diversity estimates, mean α diversity was weighted according to the total abundance of each assemblage (Crist, Veech, Gering, & Summerville, 2003). Consistent with the γ diversity analyses, our analyses included only studies with at least five assemblages in at least one land use.

Climatic and methodological variables

We collected a variety of climatic and methodological variables to control for their effects on bee diversity and to better quantify any effect of land use change (Table 1). For climatic variables, we collected mean annual temperature and annual precipitation, as well as the seasonality of each assemblage from the public database CHELSA v1.2 (Karger et al., 2017). Annual precipitation was square root transformed to reduce the effects of outliers. All data were at 30 arc-second (~1 km) resolution.

For the β and γ diversity analyses, we additionally included methodological variables in the models that might affect both diversity metrics, namely 1) study extent, 2) standard deviations in sampling efforts across assemblages, 3) the number of assemblages, 4) standard deviations in sampling completeness across assemblages, and 5) log-transformed mean sampling completeness across assemblages (Table 1; see Section S3 for details and rationales to include these variables).

Preliminary analyses found high collinearity (Pearson's $R > 0.7$) among climatic variables and among the mean and standard deviations in sampling completeness across assemblages. Thus, we conducted robust PCA separately for all climatic variables and the two methodological variables. We included climatic PC1 and PC2 for subsequent analyses, which captured >81% of the climatic variations within our dataset (Table S3). Increasing PC1 scores primarily reflect colder sites with high seasonality in temperature but low seasonality in precipitation, while increasing PC2 scores reflect warmer and wetter sites with lower temperature seasonality and lower precipitation seasonality.

For the two methodological variables, we extracted the PCA1 score to represent them, as it captured 93.1% variations across assemblages. A higher sampling effort PCA1 score indicates lower mean sampling completeness with higher variation across assemblages (Table S3). Robust PCA was conducted using R-package rrcov (Todorov & Filzmoser, 2009).

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463 **General modeling strategy**

464 We used mixed models to identify the effects of land use while controlling for methodological
465 and climatic covariates, as well as other unaccounted-for study differences using random effects.
466 Study-level variation can lead to varying estimates of land use effects. For example, the effects
467 may be stronger in warmer landscapes with fewer natural habitats in the surrounding
468 environments (Ganuza et al., 2022; Kennedy et al., 2013). Methodological factors such as
469 sampling area (Azaele et al., 2015) and methods (Lee & Guénard, 2019) can also alter estimates
470 of land use effects. Here, we focused on the general trend across studies rather than examining
471 how land use change interacts with other environmental or methodological variables. Therefore,
472 apart from a few climatic and methodological covariates, we used study identity as a random
473 effect to control for such study-level variations.

474 This statistical framework has been used in previous quantitative syntheses assessing land use
475 effects on diversity or abundance by comparing data from studies conducted in different regions
476 based on different methods. It also allows for studies with data on one land use only (De Palma
477 et al., 2016; Millard et al., 2021; Newbold et al., 2015). A summary of how mixed models work
478 is provided in Section S4. Additionally, we provide a simple simulation (Section S5) to justify
479 our approach of including study-level land use effects, despite some studies only providing bee
480 data for a single land use. We emphasize here that mixed models do not estimate study-level land
481 use effects (or in general any random slope) through modelling its relationship in each study
482 individually. Rather, the calculations involve calculating the fixed effects and the variance-
483 covariance matrix, which uses data from all studies (Raudenbush & Bryk, 2002). Below we

provided a brief description of the models. For mathematical expressions please refer to Table S4.

Objective 1a: α diversity

To examine how taxonomic and phylogenetic α -diversity varied across land uses, we built linear mixed models with Gaussian distributions using log-transformed α -diversity. We specified log-transformed α -diversity as the response to improve normality. For predictors, we included sampling method (three levels: All bees/ Flower visitors/ Targeted plants) and land use (three levels: Natural/Agricultural/Urban) of each site. Climatic PC1 and PC2 scores were also added as predictors to control for the effects of regional climate on bee α -diversity. Our analyses included nominal variables, so we set the intercepts as natural habitats sampled with methods targeting all bees. We further used sampling completeness as a weight in the regression, such that poorly sampled sites (and, therefore, those with higher uncertainty in diversity estimates) had lower weights in the analyses (Carvalho et al., 2013).

For random effects, study identity was added as a random intercept, with land use effects added as random slopes, so the estimates of land use effects could vary across studies. The random slopes were never correlated with random intercepts to facilitate model convergence (Matuschek, Kliegl, Vasishth, Baayen, & Bates, 2017).

Additionally, to control for spatial autocorrelation, we added an assemblage-level random intercept based on the spatial coordinates of each site. The Matérn correlation model was used to construct the correlation matrix and estimate the spatial random effect. All spatial random effects were study-specific, indicating that spatial autocorrelations were modelled within but not across

studies, as they had very different methodologies. Indeed, we detected substantial spatial autocorrelation between sites within the same study but not between sites across different studies (Section S6). We compared models with and without spatial random effects and found that the model including spatial autocorrelation had a significantly improved model fit, as indicated by a reduction of >490 in the conditional AIC.

We built the linear mixed model using R package spaMM, which allows including spatial random effects (Rousset & Ferdy, 2014). We then conducted an omnibus test for differences across land uses based on F tests using R package lmerTest (Kuznetsova, Brockhoff, & Christensen, 2017). If the effect of land use was significant, we further conducted pairwise comparisons across the three land uses, with the p-value adjusted by False Discovery Rate corrections.

Objective 1b & 1c: β and γ diversity

The β and γ diversity analyses were conducted at the study level (i.e., each land use from a study contributes one data point). In the models, log-transformed multiplicative β diversity (to improve normality) and untransformed γ diversity were the responses. Land uses, sampling methods, climatic PC1 and PC2 scores, number of sampling sites, standard deviations of sampling efforts, PC1 scores based on sampling completeness, and study extent were added as predictors. Climatic PC1 and PC2 scores were averaged across assemblages of the same land use in each study. Study extent and number of sampling sites were log-transformed, as their effects tend to be non-linear (Beck, Holloway, & Schwanghart, 2013; Marcon, Zhang, & Hérault, 2014; Marion, Fordyce, & Fitzpatrick, 2017; Soininen, McDonald, & Hillebrand, 2007). We added sampling completeness of γ diversity as weights in the models to account for some pooled

assemblages being more unreliable in diversity estimations due to low completeness. Study identity was added as a random intercept.

We started with a model that included the interaction between land use and study extent due to potential differences in distance-decay relationship across land uses. However, the interaction term was non-significant. Therefore, we included no interaction term in the final model. Again, an omnibus test was conducted for the effect of land use, and if significant, pairwise comparisons were conducted across land use. Linear mixed models were built with R package lme4 (Bates, Mächler, Bolker, & Walker, 2015) and p-values were obtained from lmerTest (Kuznetsova et al., 2017). Pairwise comparisons were conducted in emmeans (Lenth, 2024), with the p-values adjusted by False Discovery Rate corrections.

Objective 2: Phylogenetic habitat filtering in natural, agricultural, and urban habitats

If agricultural and urban land uses increase phylogenetic habitat filtering, their negative effect on phylogenetic diversity should still be significant after adding taxonomic diversity as a covariate. Previous studies have used this approach to assess whether environments have lower phylogenetic diversity than expected based on taxonomic diversity (Barreto, Graham, & Rangel, 2019; Sol, Bartomeus, González-Lagos, & Pavoine, 2017). We did not use null model analyses because some of the studies in our meta-data set included studies with a single land use, which did not capture species that fail to persist in different land uses (Lessard, Belmaker, Myers, Chase, & Rahbek, 2012).

We added taxonomic diversity as an additional predictor to the phylogenetic diversity models described in Objective 1a-c. For α and γ diversity, the relationship between phylogenetic and

taxonomic diversity is a decelerating relationship, but for β diversity, it is largely linear (Figure S1). Thus, we added log-transformed taxonomic diversity into each model. Note that for α and β diversity models, the responses were also log-transformed. This effectively models a power law relationship, which can range from linear to non-linear. We only conducted pairwise comparisons between land uses if the omnibus test revealed a significant effect.

Objective 3: Genus abundance across land uses

To facilitate interpretations of diversity patterns, we further identified genera that have reduced abundance in agricultural and urban habitats relative to natural habitats. We conducted the analyses at the genus- rather than species-level, as the latter would lead to strong temperate region biases, given that more tropical studies relied on morphospecies or genus-level identifications. For this objective, we selected 51 genera that were frequently detected across studies, and thus, the effects of land use can be reliably quantified (see Section S7 for details).

Our analyses included genera with different geographical distributions, such as the cosmopolitan genus *Megachile* and the Neotropical genus *Partamona* (Michener, 2007). Thus, different trends across genera could be driven by their varying sensitivity to land use changes and regional differences in the extent of environmental changes and management intensity. Quantifying the contributions of each mechanism would require additional life-history and environmental data. Nevertheless, our results can identify the genera more systematically affected by different land use drivers regardless of the underlying mechanisms

We built a model for each genus with their abundance in each assemblage as the response and land use, sampling method, and climatic PC1 and PC2 scores as predictors. Random effects were

identical with the α -diversity models (Objective 1a), with study identity as a random intercept and land use as a random slope to control for between-study differences. Again, a spatial term based on Matérn correlation nested within studies was added to control for spatial autocorrelation. We used negative binomial mixed models to analyze abundance changes across land uses (Warton, 2005). An offset capturing log-transformed sampling effort of each assemblage was also added.

For one genus (*Dasypoda*), abundance data based on sampling flower visitors of all or targeted plant species were not available. Thus, we dropped sampling method from the model. For 31 genera, the effects of land use were only compared between agricultural and natural habitats, as there was a lack of urban studies containing abundance data of these genera. When three land uses were analyzed, we conducted pairwise comparisons if a significant result was obtained from the omnibus test. As we analyzed multiple genera, results might be affected by multiple comparisons. We further adjusted pairwise comparison p-values using False Discovery Rate corrections.

We extracted the predicted abundance for each model for each land use while holding climatic PC1 and PC2 at their mean values, as well as holding the sampling strategy at “All bees”. We then calculated the ratio of predicted abundance between agricultural (or urban) and natural habitats (Agricultural or Urban/Natural). We further log-transformed these ratios to convert them into arithmetic scales (Agresti, 2007). We then used the package phytools (Revell, 2012) to assess if there were phylogenetic signals in the log-transformed ratio based on Pagel’s λ .

Briefly, Pagel’s λ assesses whether any biological characteristics follow Brownian motion, a standard evolutionary model that assumes the differences in the characteristics accumulate through a random walk over evolutionary time scales (Pagel, 1999). λ equals one when the

characteristics are consistent with Brownian motion expectations. Alternatively, λ can be as low as zero when the characteristics deviate from the evolutionary model. While other metrics to measure evolutionary signals exist, Pagel's λ is known to be the most robust metric according to simulation studies (Münkemüller et al., 2012).

Results

Our analyses included bee assemblage data from 3,117 assemblages and 437,091 individuals of 4,002 taxonomic units from 157 studies. The majority of the data (2,574 assemblages from 120 studies) were in temperate regions (i.e., absolute latitude $> 23.4^\circ$), mainly North America and Europe, while 543 assemblages from 37 studies were in the tropics (Figure 1a). All studies identified specimens to species-level or morphospecies-level whenever possible, except two studies, which identified specimens to genus-level. Sampling methods of individual studies range from point-based sampling (e.g., single vane trap) to aggregating samples within an area as large as 10 ha. In general, most studies were conducted along transects $< 100\text{m}$ or within plots $< 1\text{ha}$ (Table S1). Forty-two studies (27%) provided data on bee assemblages in more than one land use. All diversity models had high conditional R^2 (0.63 – 0.91, Table S5-S8).

Objective 1a: α diversity

Taxonomic α -diversity declined by an average of 15.8% in agricultural ($P = 0.006$; 95% CI: 1.9%, 27.6%) and 19.6% in urban habitats ($P = 0.006$; 95% CI: 3.1%, 33.2%) compared with natural habitats after controlling for climatic and sampling differences (linear mixed models; Figure 1b, Table S5). Using the genus-level phylogeny of bees (Hedtke *et al.*, 2013), we found that phylogenetic α -diversity declined by an average of 11.0% in agricultural habitats ($P = 0.005$;

95% CI: 2.7%, 18.7%) and 11.6% ($P = 0.017$; 95% CI: 1.0%, 21.1%) in urban habitats relative to natural habitats (Figure 1c, Table S5). Pairwise comparisons between agricultural and urban habitats were non-significant for both diversity metrics.

Objective 1b: β diversity

The average taxonomic β -diversity was 1.75 (95% CI = 1.66, 1.83), making up 42.7% of the taxonomic γ diversity. Using linear mixed models, we observed a 6.4% decline in taxonomic β -diversity in agricultural habitats relative to natural habitats, although the results were marginally non-significant ($P = 0.06$; 95% CI = 1.1%, 11.4%; Figure 1c, Table S6). Pairwise comparisons also revealed marginally non-significant differences between urban and natural habitats, with 8.8% higher taxonomic β -diversity in urban habitats ($P = 0.06$; 95% CI = -0.4%, 18.7%; Figure 1c, Table S6). However, we detected 16.2% higher taxonomic β -diversity in urban compared to agricultural habitats ($P = 0.004$; 95% CI = 6.5%, 26.8%).

Across studies, phylogenetic β diversity averaged at 1.20 (95% CI = 1.17, 1.22), equivalent to 16.7% contribution of phylogenetic γ diversity. Phylogenetic β -diversity was highest in urban habitats—6.4% higher than natural habitats ($P = 0.004$; 95% CI = 2.2%, 10.7%; Figure 1c, Table S5) and 8.8% higher than agricultural habitats ($P < 0.001$; 95% CI: 4.5%, 13.3%). However, we found minimal evidence of differences between agricultural and natural habitats.

Objective 1c: γ diversity

Taxonomic γ diversity was, on average, 25.2% lower in agricultural than in natural habitats ($P = 0.008$; 95% CI: 10.5%, 39.9%; Figure 1d, Table S7). A 15.6% decline was also observed in

urban habitats relative to natural habitats, but the difference was not statistically significant. Differences between urban and agricultural habitats were also non-significant.

Similarly, we found that phylogenetic γ diversity declined by 17.8% ($P = 0.006$; 95% CI: 8.7%, 26.7%) in agricultural habitats relative to natural habitats (Figure 1d, Table S7). The pairwise comparison between natural and urban habitats, as well as between agricultural and urban habitats, was non-significant.

Objective 2: Phylogenetic habitat filtering in natural, agricultural, and urban habitats

After controlling for their taxonomic counterparts using linear mixed models, phylogenetic α and γ diversity metrics exhibited minimal differences across land uses (Figure 2a, 2c, Table S8). However, we found that phylogenetic β diversity was highest in urban habitats, while agricultural and natural habitats exhibited similar values (Figure 2b, Table S8). Specifically, phylogenetic β diversity in urban habitats was 3.9% higher than in natural habitats ($P = 0.03$; 95% CI: 0.44%, 7.5%) and 4.5% higher than in agricultural habitats ($P = 0.03$; 95% CI: 0.84%, 7.97%).

Objective 3: Genus abundance across land uses

Compared with their average abundance in natural habitats, 73% and 61% of common genera exhibited reduced average abundance in agricultural and urban habitats, respectively, echoing the results of diversity analyses (Table S9, Figure S2). Eight genera showed significantly lower abundance in agricultural habitats, four belonging to the family Megachilidae (*Osmia*, *Hoplitis*, *Megachile*, *Anthidium*). Only *Protandrena* (mining bees, ground nesters) had increased

abundance in agricultural habitats relative to natural habitats. For urban habitats, only *Osmia* (mason bees, primarily cavity nesters) exhibited a significant response to land use, with reduced abundance in urban relative to natural habitats. We detected some phylogenetic signals in the responses to agricultural (Pagel's $\lambda = 0.38$, $P = 0.08$) and minimal signals in the responses to urban habitats (Pagel's $\lambda < 0.001$, $P = 1$) (Figure 3). After controlling phylogeny, responses of bee genera to urban and agricultural habitats were weakly correlated (Pearson's $r = 0.09$) (Figure S2).

Discussion

Biodiversity loss observed at local scales (α diversity) can be dampened or amplified at larger spatial scales (γ diversity), depending on changes in the scaling factor (β diversity) (Socolar et al., 2016). We synthesized the trends in how two major land use drivers, namely agriculturalization and urbanization, affect bee taxonomic and phylogenetic α , β , and γ diversity. We found that the trends in α , β , and γ diversity are largely consistent between taxonomic and phylogenetic metrics when responding to the same land use driver. The α diversity declines under the different anthropogenic land uses are consistent with our expectations and previous studies based on other taxa (Millard et al., 2021; Newbold et al., 2015). These results provide additional evidence of the threats of agricultural and urban expansion (Dicks et al., 2021) by demonstrating their negative impacts on phylogenetic α diversity in addition to taxonomic α diversity. The responses of β diversity to land uses are more variable, as urban habitats exhibited higher β diversity than natural habitats, which is in contrast with the general expectation that urbanization drives biotic homogenization (Socolar et al., 2016). At the same time, we found some support for agricultural habitats having reduced taxonomic β but not phylogenetic β

diversity. These ultimately lead to reduced taxonomic and phylogenetic γ diversity in agricultural habitats, but not urban habitats, where we failed to detect significant γ diversity loss compared to natural habitats. The β and γ diversity results highlight the threat of agricultural expansions to large-scale bee diversity due to systematic γ diversity decline. Broadly, our results provide empirical evidence showing that, although α diversity responses may be similar across land use drivers, β diversity responses vary, resulting in different γ diversity consequences.

The differing responses of β diversity to urban and agricultural land use may be a result of differing environmental heterogeneity within these land use categories. In our dataset, most studies compared assemblages within a single city or landscape, with the mean and 95% percentile of the study extent being 38 km and 478 km, respectively. At these scales, different management practices within cities, such as varying ornamental plants or mowing frequencies due to owner preferences (Aronson et al., 2017; Lerman, Contosta, Milam, & Bang, 2018; Prendergast et al., 2022), can increase environmental heterogeneity and, therefore, result in higher β diversity than natural habitats (Alberti, 2016). Conversely, β diversity exhibited varying trends or marginal declines in agricultural habitats across studies. While agricultural activities reduce environmental heterogeneity, particularly in monocultural croplands (Leong, Ponisio, Kremen, Thorp, & Roderick, 2016), the effects can be more variable in subsistence agriculture systems (Landaverde-González et al., 2017), potentially explaining the marginal results. This ultimately led to detectable declines of γ diversity in agricultural habitats but not urban habitats. Thus, our results indicate that while land use impacts are usually reported to affect α diversity negatively across terrestrial taxa, these conclusions do not necessarily extend to γ diversity, particularly with urbanization (Fenoglio, Rossetti, & Videla, 2020; Liang, He, Theodorou, & Yang, 2023; Newbold et al., 2015; Sol et al., 2017).

We found no evidence that land use change systematically strengthens phylogenetic habitat filtering, and in fact, we found relaxed filtering in urban habitats for β diversity of bees. Previous bee studies have found variable phylogenetic habitat filtering effects across different types of agricultural and urban environments (Bartomeus, Cariveau, Harrison, & Winfree, 2018; Odanaka & Rehan, 2019; Ramírez, Hernández, Link, & López-Urbe, 2015; Villalta, Bouget, Lopez-Vaamonde, & Baude, 2022), potentially leading to no generalizable patterns when coarse land use classification is used. Studies of phylogenetic habitat filtering for β diversity are rare. The weakly relaxed phylogenetic habitat filtering in urban habitats detected can again be explained by increased environmental heterogeneity in cities compared with natural and agricultural habitats (Alberti, 2016; Aronson et al., 2017). For example, given the strong co-evolutionary history between bees and plants (Brown & Cunningham, 2022), different planting preferences across urban green spaces can attract varying bee lineages, leading to higher phylogenetic β diversity than expected based on taxonomic β diversity. Nevertheless, the weakly relaxed phylogenetic filtering for phylogenetic β diversity did not propagate to γ diversity of bees in urban habitats, as phylogenetic β diversity only contributed to 16.7% of γ diversity across studies.

Apart from their varying impacts on bee diversity, another difference between the two land uses is that the genus-level abundance changes exhibited an intermediate phylogenetic signal in agricultural habitats but minimal signal in urban habitats. The small number of genera in our analyses (≤ 51) limited our statistical power (Münkemüller et al., 2012), while genus-level analyses can underestimate phylogenetic signals (Rabosky, 2015). Species-level analyses, including rare species, are needed to determine the true extent of phylogeny in governing bees' responses to the two land uses. Nevertheless, the stronger phylogenetic signals in agricultural

habitats suggest a higher importance of evolutionarily conserved traits, such as nesting biology and lecty (Odanaka & Rehan, 2019), in determining species abundance in these environments (Grab et al., 2019). Alternatively, species responses to urban habitats may be more driven by stochasticity (Sattler et al., 2010) or evolutionarily labile traits, such as thermal tolerances (Hamblin, Youngsteadt, López-Urbe, & Frank, 2017).

As phylogenetic and taxonomic diversity respond similarly to agricultural and urban land uses, conservation measures that increase taxonomic diversity in agricultural and urban habitats are expected to increase their phylogenetic counterparts. These findings can facilitate decision-making in management targeting multiple diversity metrics, as the responses of phylogenetic diversity to different environmental drivers are less understood than those of taxonomic diversity (Cadotte & Tucker, 2018). For α diversity, measures such as organic farming, crop diversification, establishing flower strips, and planting gardens have been found to increase pollinator taxonomic α -diversity in meta-analyses or quantitative syntheses (Kennedy et al., 2013; Lichtenberg et al., 2017; Majewska & Altizer, 2020; Scheper et al., 2013). Studies have also evaluated the effectiveness of conservation measures in enhancing taxonomic β diversity (Ponisio, M'Gonigle, & Kremen, 2016), although they are relatively rare compared with studies focusing on taxonomic α diversity. The same environmental drivers could increase taxonomic α diversity but reduce taxonomic β diversity in bees (Steinert, Sydenham, Eldegard, & Moe, 2020), meaning that associated conservation measures can simultaneously mitigate and exacerbate the impacts of land use change, leading to unclear net effects on γ diversity. Thus, we emphasize the importance of conducting additional taxonomic β and γ diversity assessments on the effectiveness of conservation measures to better understand their contributions to mitigating land use impacts.

Many large-scale conservation assessments focusing on the impacts of land uses are based on projecting α diversity models to different land use scenarios (Chaudhary, Verones, de Baan, & Hellweg, 2015; De Palma et al., 2017; Newbold et al., 2015). While α diversity patterns are helpful for conservation planning, they might not apply to biodiversity at larger spatial scales (e.g., national, regional, or landscape-level biodiversity), which might have exacerbated/weakened diversity loss depending on β diversity changes (Socolar et al., 2016). Our findings demonstrate that qualitative conclusions about land use impacts can differ between α and γ diversity analyses. Based on our results, while taxonomic and phylogenetic α diversity of bees might exhibit similar changes in agriculturalization and urbanization hotspots, the consequences for γ diversity can be very different, with more substantial impacts at larger scales expected in agriculturalization hotspots such as West Africa and Southeast Asia (Williams et al., 2021). Given the need to conserve biodiversity and its associated ecosystem functions at multiple scales (Socolar et al., 2016; Winfree et al., 2018), our study confirms the threat of agricultural expansions to global bee diversity. It also highlights the need to understand processes determining β and γ diversity changes and integrate these diversity metrics into conservation assessments.

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Data availability: R-scripts and 97% (152 of 157 analyzed studies) diversity and genus abundance data have been uploaded to Zenodo (DOI: 10.5281/zenodo.14201156) and GitHub (<https://github.com/tpaknok/BeeLandUse>). For the remaining 3% of studies with restricted access, please contact the co-authors listed in Table S1 directly.

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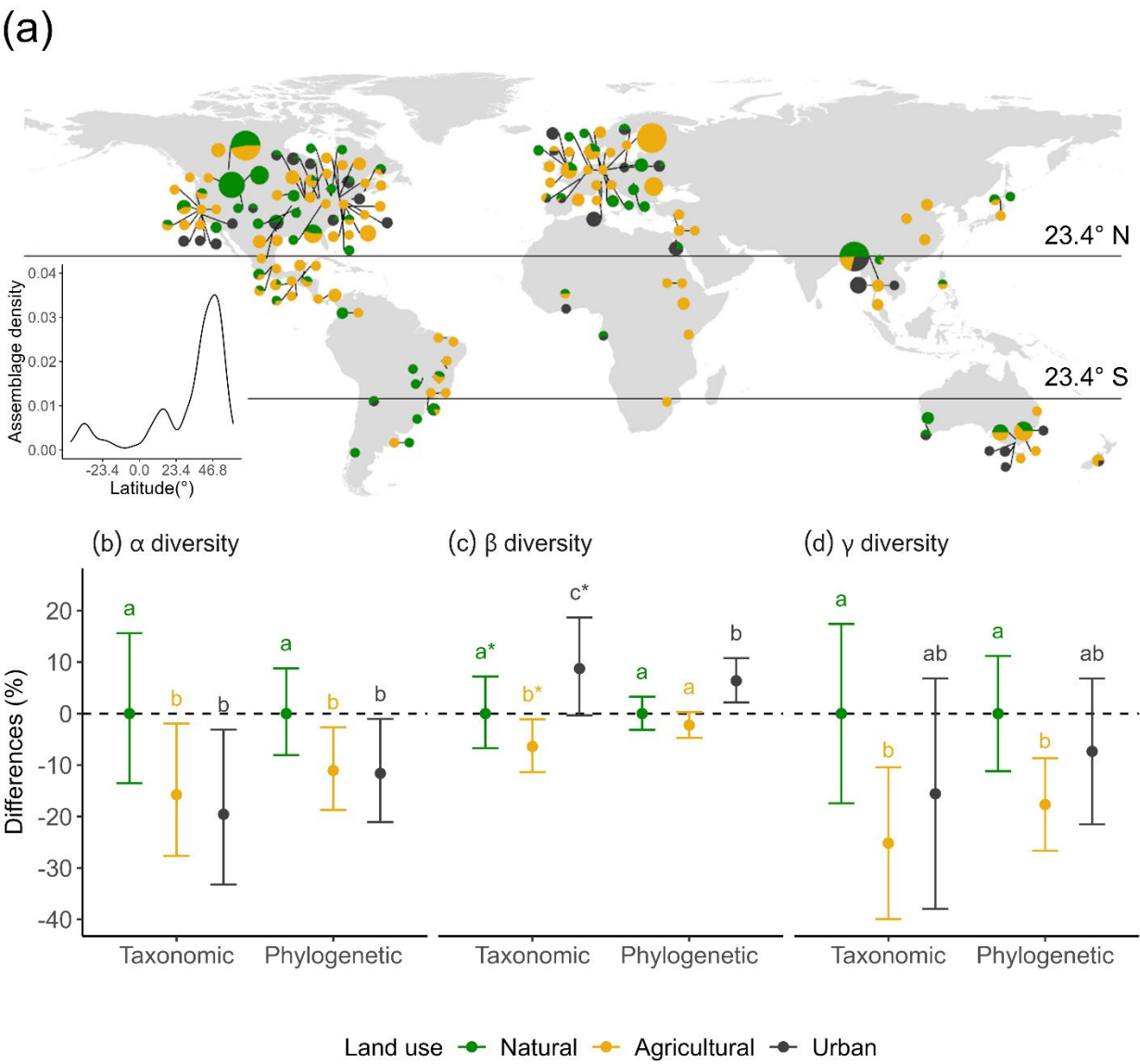
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1169

1170 Table 1. Predictors for the models related to each objective. Objectives 1a, 1b, and 1c are to
 1171 compare α , β , γ , diversity across three land uses, respectively. Objectives 2a, 2b, and 2c are to
 1172 assess whether agricultural and urban habitats exhibited stronger phylogenetic habitat filtering in
 1173 α , β , γ diversity, respectively. Objective 3 is to identify genera with altered abundance in
 1174 agricultural and urban habitats relative to natural habitats. The rationales including different
 1175 variables and their transformations have been described in the main text.

Variable name	Description	Objectives
Land use	A factor with three levels: Natural / Agricultural / Urban	1-3
Sampling method	A factor with three levels: All bees / Floral visitor only / Floral visitor of targeted plants	1-3
Climate PCA1	PCA1 score based on mean annual temperature, annual precipitation, as well as temperature and precipitation seasonality of each assemblage.	1-3
Climate PCA2	PCA2 score based on the aforementioned climatic variables.	1-3
log(Number of assemblages)	Number of assemblages of each land use within a study.	1b-1c, 2b-2c
Sampling effort S.D.	The standard deviation of sampling efforts between assemblages of the same land use within a study.	1b-1c, 2b-2c
Sampling completeness PCA1	PCA1 score based on the mean and standard deviation of sampling completeness between assemblages of the same land use within a study.	1b-1c, 2b-2c
log(Sampling extent)	Maximum distance between assemblages of the same land use within a study.	1b-1c, 2b-2c
log(Taxonomic diversity)	The taxonomic counterpart of phylogenetic α , β , and γ diversity.	2
Study identity	Added as random effects to account for other differences between studies.	1-3
Spatial autocorrelation term	Controlling for spatial autocorrelation within each study based on the latitude and longitude of each assemblage.	1a, 2a, 3a



1179

1180 **Figure 1.** (a) Map showing locations of 157 studies included, and the proportion of natural,

1181 agricultural, and urban habitats sampled within the study. Pie size is proportional to the number

1182 of sampled sites in each study, ranging from 1 to 368. The density plot indicates the distribution

1183 of the studied assemblages (n = 3,117) along the latitudinal gradient. (b-d) Diversity changes

1184 relative to values of natural habitats, with each panel showing responses of one diversity metric:

(b) α , (c) β , and (d) γ diversity. Point estimates represent model predictions of each land use based on fixed effects only, while error bars are 95% confidence intervals. The estimations of α diversity were obtained by holding other covariates at the mean or mode values. For β and γ diversity, the estimation reflects a standardized sampling study with all assemblages having 100% sampling completeness, and other covariates at the mean or mode values. Small letters above error bars indicate results from pairwise comparisons, with different letters representing different groups. *indicates that the pairwise comparisons included marginally non-significant results ($p = 0.06$).

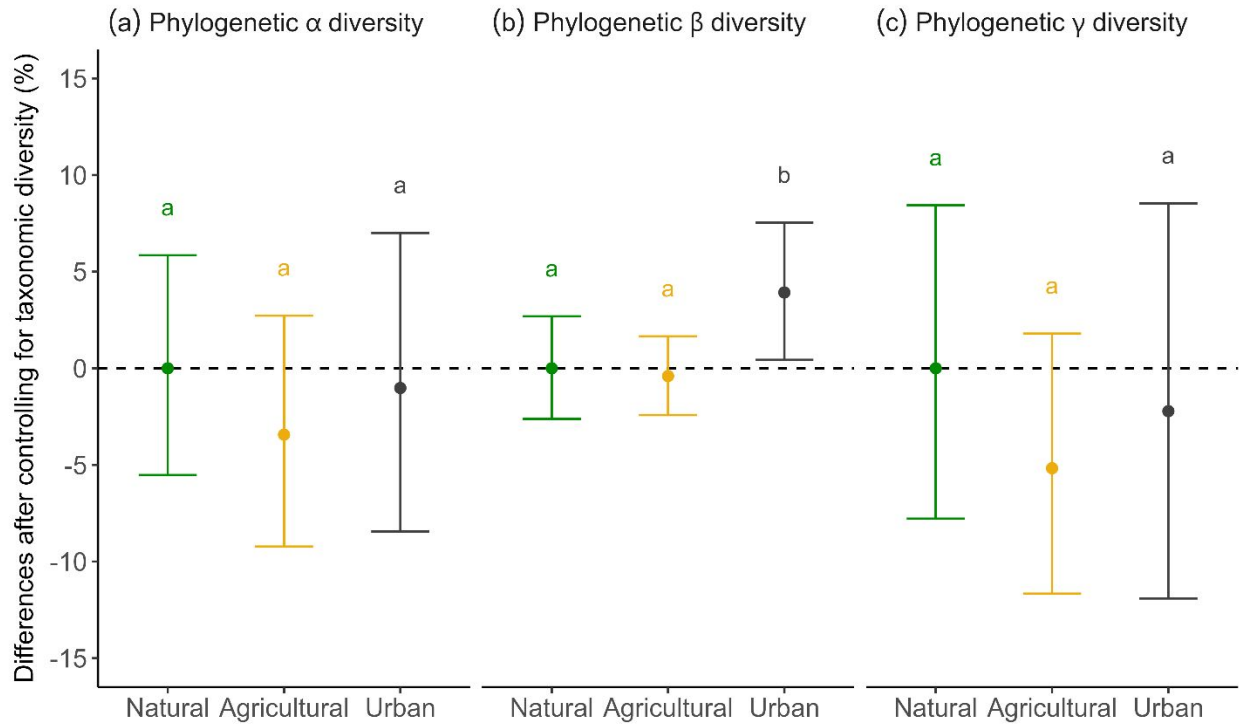
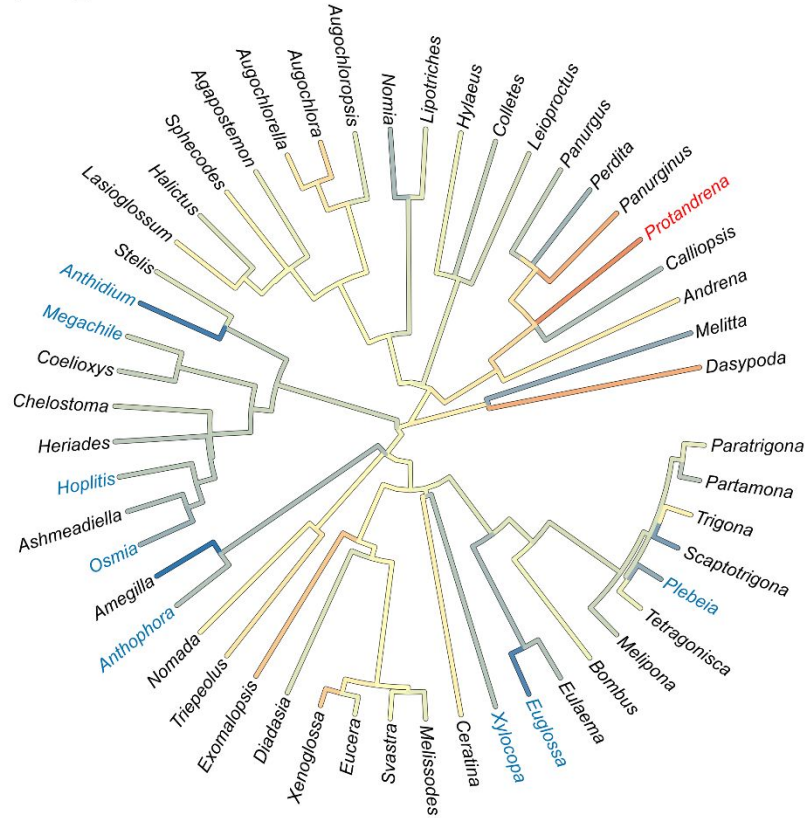
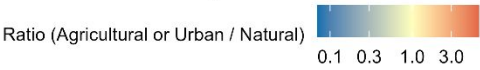
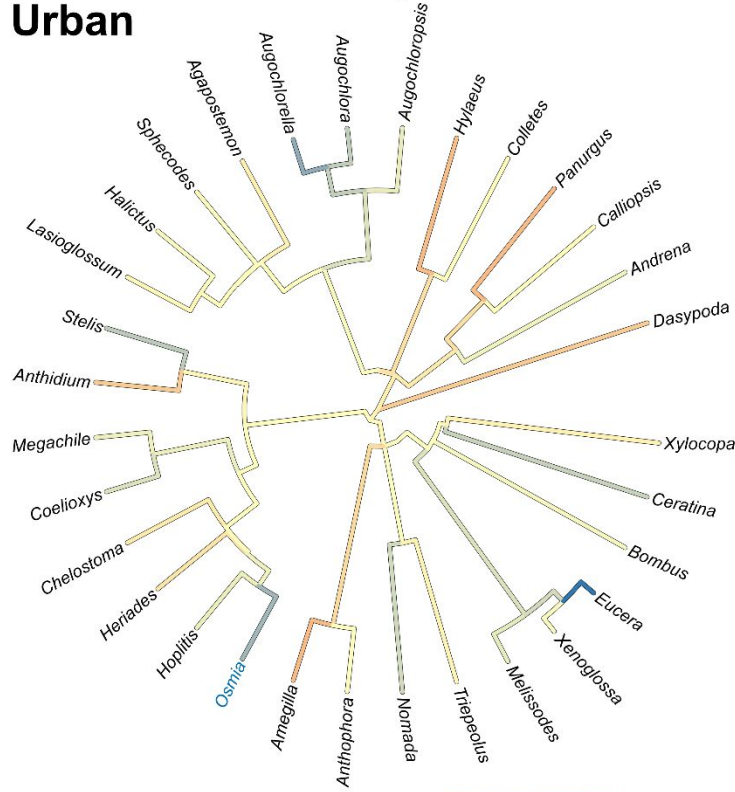


Figure 2. Percent differences in phylogenetic (a) α , (b) β , and (c) γ diversity metrics after controlling for their taxonomic counterparts, using natural habitats as the baseline. Error bars represent 95% confidence intervals, while point estimates present model predictions based on fixed effects only. The estimated α diversity was based on holding all other covariates at the mean or mode values. The estimated β and γ diversity were based on assuming studies with standardized sampling and all assemblages with 100% sampling completeness, while other covariates were at the mean or mode values. Small letters above error groups indicate different grouping based on pairwise comparisons.

(a) Agricultural



(b) Urban



1206 **Figure 3.** Phylogenetic relationships of all genera examined and their responses to agricultural
1207 (a) and urban land uses (b) in terms of abundance. When the ratio equals 1, genus abundance in
1208 agricultural or urban habitats is the same as in natural habitats. Genera in red and blue are
1209 significantly more and less abundant in anthropogenic land uses, respectively. See Fig. S2 for bar
1210 plots representing how individual genera respond to agricultural and urban land uses differently.