Land use change reduces the taxonomic and phylogenetic diversity of bees

Science and Engineering, Institute for Environmental Sciences
Escobedo-Kenefic, Natalia; Universidad de San Carlos de Guatemala
Fitch, Gordon; York University
Forrest, Jessica; University of Ottawa, Biology; Rocky Mountain Biological Laboratory,
Fournier, Valérie; Université Laval, Centre de recherche en innovation sur les végétaux
Fowler, Robert; University of Sussex
Freitas, Breno; Universidade Federal do Ceará, Departamento de Zootecnia
Gaines-Day, Hannah; University of Wisconsin Madison, Department of Entomology
Geslin, Benoît; 1, IMBE
Ghazoul, Jaboury; ETH Zurich, Department of Environmental Sciences
Glaum, Paul; University of California Davis; University of Michigan
González-Chaves, Adrian; Universidade de São Paulo
Gonzalez Andujar, Jose ; Institute for Sustainable Agriculture
Grab, Heather; Cornell University
Gratton, Claudio; University of Wisconsin, DOE Great Lakes Bioenergy Research Center
Ponisio, Lauren; University of Oregon
Bonebrake, Timothy; The University of Hong Kong, School of Biological Sciences

Keywords:	Land uses, Bees, Biodiversity decline, Agriculture, Urban, Pollinator

Abstract:	Land use change threatens global biodiversity and compromises ecosystem functions, including pollination and food production. However, we have a limited understanding of how land use affects diversity metrics other than taxonomic α-diversity. In particular, phylogenetic α-diversity considers the amount of evolutionary history within assemblages, while replacement reflects dissimilarities between assemblages contributed by distinct species in each assemblage. As diversity metrics can exhibit differential responses to environmental changes, here we analyzed how land use affects taxonomic and phylogenetic α-diversity and the replacement of an important pollinator taxon - bees. Using a multi-continental dataset of >3,100 bee assemblages from 154 studies, we found that taxonomic α-diversity was reduced by ~16% in both agricultural and urban habitats relative to natural habitats. Phylogenetic α-diversity decreased by ~12% in agricultural and ~10% in urban habitats. Furthermore, in agricultural habitats, taxonomic and phylogenetic replacement between communities was reduced by ~19% and ~29% relative to natural habitats. We also detected a strong correlation between all phylogenetic and taxonomic diversity metrics, and the effects of land use change on phylogenetic α-diversity and replacement were weak controlling for taxonomic α-diversity and replacement within assemblages. Our results demonstrate that declines in bee taxonomic diversity driven by land use change led to reduced phylogenetic diversity. Reduced taxonomic and phylogenetic diversity in agricultural habitats also suggests that loss in species diversity and evolutionary history at large spatial scales should be higher than α-diversity estimates otherwise indicate, highlighting the threat of agricultural expansion to bee global diversity through biotic homogenization.

4th October 2024

Dear Editor,

    We are resubmitting the manuscript "Land use change consistently reduces α but not β and γ diversity of bees" for your consideration. We thank the referees for their comments on the manuscript. Detailed responses to each comment are provided below. The major changes to the manuscript include: 1) revising the β diversity analyses using diversity partitioning, 2) adding γ diversity analyses, 3) pivoting the manuscript to how diversity loss varies across spatial scales, and 4) modifying the introduction and discussion accordingly.

    Thank you for considering our manuscript.

Best,
Authors

Editor's Comments to the Author:

Subject Editor: 1

Comments to Author :

Both reviewers (one of which was a reviewer for the initial submission) see major value in this manuscript. They both, however, raise a number of issues that must be addressed before we consider the article further. I am, atypically, going to provide such an opportunity but hasten to add that this will be the final opportunity to deal with the reviewer comments. Please respond to all reviewer comments.

Response: We have responded to all reviewer comments, as detailed below. Responses to major comments are 1) including α-β-γ diversity partitioning analyses and 2) discussing why land use effects may vary between alpha, beta, and gamma diversity.

Reviewer(s)' Comments to Author:

Reviewer: 3

Comments to the Author

This paper investigates the effects of land use change on bee diversity at the global scale. Beside taxonomic alpha diversity, the authors focus on beta diversity and phylogenetic diversity as understudied biodiversity facets. They found a decreased taxonomic and phylogenetic alpha diversity in both urban and agricultural habitats in comparison to natural habitats. However, a similar decrease in beta diversity was only observed in agricultural habitats and not in urban habitats. The study concludes with a discussion of the various effect of land use change on the studied diversity facets.

I overall enjoyed reading this manuscript. The manuscript is well-written although sometimes difficult to follow. The topic and extent of the study fits within the scope of the journal. Overall, the work and methods meet the expected scientific standards although several points need to be improved and/or clarified (see below). The compiled dataset is of good quality and satisfactory given the journal standards. Illustrations and tables are of good quality. The cited literature is appropriate.

Although the topic of the impact of land use on biodiversity has already been extensively studied, the authors were able to identify research gaps and present new and interesting results that are of global significance. For this reason, I think that the paper can be interesting for a broad audience in ecology and beyond. However, to gain visibility amid the many land use studies out there, the narrative of this study needs to be streamlined. I did not identify major issues or flaws in this study. However, I think that several aspects need to be clarified and/or improved before publication. I also make several suggestions for minor improvements. See my

comments below for further details.

General comments:
The text is rather complex and difficult to read which tends to dilute the main message. Several sections such as the Intro and Methods would greatly benefit from a more synthetic writing. Generally, I encourage the authors to shorten the text, simplify the main message, and move some of the intricacies to the SupMat. In addition, it is not easy to keep track of the different variables and models used in this study. To address that, I encourage the authors to add tables summarizing and briefly explaining the different variables used in the models and relating them to the main hypotheses.

Response: After incorporating other reviewer comments, the manuscript now focuses on assessing α, β, and γ diversity change across land uses, as well as testing how agricultural and urban land use enhance phylogenetic habitat filtering. These changes have shortened the introduction and simplified the manuscript. We added Table 1 to summarize different variables used in the models for different objectives.

We moved the formulas to Table S4. We also moved details on selecting genera for the abundance analyses to Text S4 to improve readability.

We removed the analyses on the scaling relationship between taxonomic diversity and phylogenetic diversity. We also removed the turnover and nestedness analyses as these are not as directly relevant to biodiversity loss across spatial scales, the key message of the manuscript.

Reviewer: Beta diversity is a central element of this study. However, we don´t know how much gamma diversity is accounted for by beta? Are we speaking of 5% or 95% of the total gamma diversity? How much beta is within- VS among-studies? The answer to these questions could change the interpretation and implications of the results. Furthermore, it would provide a more quantitative understanding of how and to what extent "loss of diversity at large geographic scales may be greater than estimates of α-diversity". Here, an ABG (alpha-beta-gamma) decomposition of diversity would be useful. The authors could also express the relative importance of turnover and nestedness as a function of total gamma diversity. The fact that the author focus on within-study beta diversity means that an additional study-specific ABG decomposition should be done. The question then becomes how does the relative contribution of beta to gamma vary among studies and does that influence the results of the models.

Response: We replaced our pairwise β diversity analyses with the multiplicative β diversity analyses. We also explained multiplicative β diversity analyses are more suitable to understand diversity loss across spatial scales relative to pairwise β diversity analyses (L467-469): "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)."

We added γ diversity analyses in the manuscript; thus, the manuscript now compares α, β, γ diversity across land uses. As γ diversity always pools data across samples, comparing α and γ diversity patterns can effectively assess diversity loss at increasing spatial scales. See sections "α and γ diversity estimates" and "β diversity estimates" for the quantification of these metrics. See sections "Objective 1a: α diversity", "Objective 1b: β diversity", and "Objective 1c: γ diversity" for the results.

The contribution of β diversity has been provided in the results: "The average taxonomic β-diversity was 1.75 (95% CI = 1.66, 1.83), making up 42.7% of the taxonomic γ diversity" (L678-679)… "Across datasets, phylogenetic β diversity averaged at 1.20 (95% CI = 1.17, 1.22), equivalent to 16.7% contribution of phylogenetic γ diversity." (L686-687).

We note that multiplicative β diversity can be directly converted into the contribution to γ diversity, (L469-470): "The metric also reflects the contribution of β diversity to γ diversity (Contribution of β = (1-α/γ) * 100% = (1-1/β) * 100%)."

We also extensively revised our intro and discussion to accommodate such changes by 1) highlighting the importance of studying β and γ diversity patterns (L294-303), 2) the potential mechanisms by which impacts on β and γ diversity vary across land uses (L745-759), and 3) the implications for modelling studies and conservation assessments (L806-821).

Reviewer: Several important factors are not considered in this study. The authors used a study-level random factors to account for them. The approach is valid and has the merit of keeping the conceptual frame of the study simple. However, it also put a black box on several important processes that can potentially impact beta diversity patterns. Examples of such processes include the influence of the landscape context, plot area – species richness relationship, within study environmental variability, and within-study land use-environment correlations. To me, this black box makes it difficult to understand what is going on with the model which decreases my confidence in the results. I strongly encourage the authors to include those aspects in the analyses (e.g. add an estimation of plot area to the model, add an objective quantification of landscape composition around each study sites), or, at least, to discuss more thoroughly how these aspects could impact the results and conclusion.

Response: We agree that investigating the individual processes contributing to the observed relationships would be interesting. We have added a paragraph discussing the potential processes that could be contributing to the observed changes (lines 518-527) and clarified throughout the manuscript that we are examining the general trend of how different diversity metrics are

affected by land use change. We put this in Methods as this is primarily explaining why we are using random effect models to account for these potentially important factors.

"Study-level variation can lead to varying estimates of land use effects. For example, the effects may be stronger in warmer landscapes with fewer natural habitats in the surrounding environments (Ganuza et al., 2022; Kennedy et al., 2013). Methodological factors such as sampling area (Azaele et al., 2015) and methods (Lee & Guénard, 2019) can also alter estimates of land use effects. Here, we focused on the general trend across studies rather than examining how within-site land use interacts with other environmental or methodological variables. Therefore, apart from a few climatic and methodological covariates, we used study identity as a random effect to control for such study-level variations."

While evaluating individual processes is valuable (e.g., how landscape context and plot size affect land use effects, etc.), we are concerned that this will be too much for a single study (particularly after adding the suggested diversity partitioning analyses) and at odds with the other comments indicating the main message was too complicated. We also don't expect that examining these individual processes will change the main conclusions of this study, as we have already used the random effect to account for these. As the reviewer correctly points out, using the random effect is intended to simplify the analyses and, therefore, the main message. Nevertheless, we have still added some methodological variables (e.g., number of assemblages, sampling effort variations) in the β diversity model to reinforce our results further.

Reviewer: Is the whole story about the scaling between TD and PD really useful and necessary? In any case, it is poorly integrated into the whole story line. How PD scale to TD is a fundamental question in ecology that is out of the scope of this study. However, if the authors can draw a clear and strong link between the shape of the scaling function and the effect of land use on PD, this approach might bring interesting results. I would look into the differences in the scaling function among land use type and relate these differences to clear hypotheses (e.g. higher phylogenetic habitat filtering in non-natural leads to less steep scaling functions). An alternative would be to simply drop the TD-PD scaling entirely (or move it to SupMat). To me, that wouldn't change the results and their interpretation but it would considerably simplify the story.

Response: We removed the story about scaling relationships between taxonomic and phylogenetic diversity.

Specific comments:

Abstract:
Reviewer: Nicely written until line 275. After that, the flow of ideas becomes more difficult to follow and the link between sentences weaker. I suggest removing the section about the scaling

of TD and PD between lines 275 and 279. That would simplify and streamline the story without losing any important message.

Response: We removed the section on the scaling of taxonomic and phylogenetic diversity.

The last sentence giving the main conclusion focuses on agricultural habitats which is not in line with the first objective of the study (compare diversity metrics among land use types). Please, consider reformulating.

Response: Our last sentence now highlights different land use drivers can affect biodiversity differently.

"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." (L278-280)

Introduction:

Reviewer: Overall, good but too long, and sometimes the logic of the arguments is hard to follow. This section would benefit from being shortened and written more synthetically.

Response: We reduced the word count from 1211 to 794 words. We removed the section about the relationship between taxonomic and phylogenetic diversity. We also simplified the explanation of the importance of phylogenetic diversity.

Material and methods:

Reviewer: The section provides all the required information but is sometime quite difficult to read and generally too long, especially the section about modelling. I encourage the authors to shorten and simplify the text, add tables to present the information in a synthetic way (list of variables used in the models, model formula…), and move some of the text to the SupMat.

Response: The formulas have been moved to SI. We created Table 1 to summarize each predictor and their relevance to different objectives. We also moved details of the abundance analyses into the SI, since it is not the primary aim of the study.

Reviewer: The general modelling strategy is fine to me (but see my comment about the black box above).

The methodological approach and underlying logic regarding spatial autocorrelation are sound to me. However, the whole story is a bit cryptic and I encourage the author to show more transparently how the addition of spatial covariate improved the model and got rid of spatial autocorrelation in the residuals (e.g. show a Mantel correlogram of the response variable compared to model residuals with and without spatial covariates).

Responses:

We added a comparison of conditional AIC changes between models with and without the spatial autocorrelation terms (L562-564): " 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 note that the spatial autocorrelation analyses do not remove signals from the residuals. The developer of the R package DHARMa, which is often used for model diagnostics, has pointed this out (https://github.com/florianhartig/DHARMa/issues/141). In fact, instead of "removing signals," the model directly considers the expected spatial autocorrelation effect when estimating the effects of different variables.

Reviewer: The spatial scale varies from study to study (from single traps to 10 ha plots). It is therefore unclear to me at what scale land use was determined and how this was considered in the analysis.

Responses: The land use classification is always relative to the sampling area unless the maximum length of the sampling area is smaller than 10 m (for which we used the surrounding 100 m² environment). We did not use a fixed scale because of the varying methodologies. Rather, the varying scale across studies would ensure the land use classification best reflects the environment of the assemblage data. This is also the approach used in many large-scale diversity analyses of land uses (e.g., Newbold et al. 2015, Nature). We have explained this in L401-403: "Because the sampling area varied strongly across studies (Table S1), we did not use a consistent spatial scale in classifying within-site land uses, similar to other global databases (Hudson et al., 2014). Rather, we determined land uses based on the predominant environment within the sampling area. However, for small sampling areas with a length < 10 m (e.g., single malaise trap, transect < 10 m), we classified the site based on the surrounding 100 m² environment (Hudson et al., 2014). For plots, the maximum length was determined by the diagonal of the whole plot (Hudson et al., 2014).".

We also provided a simple description of spatial scales in our dataset (L660-664): "Sampling methods in our datasets 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 <100m or within plots < 1ha (Table S1)."

We used the study-level random effect to address the potential effect of sampling areas (as well as other environmental variables):

"Methodological factors such as sampling area (Azaele et al., 2015) and methods (Lee & Guénard, 2019) can also alter estimates of land use effects….we used study identity as a random effect to control for such study-level variations." (lines 518-527)

Results:

Ok

Reviewer: I miss the basic information about general model performances. The authors directly start by discussing model output but, as a reader, I don´t know if those models are any good. While model performance (R2) are clearly presented in Table SX, I encourage the authors to add a short sentence in the main text stating that, overall, model performances were good (e.g. R2 between X and Y…).

The marginal R2 seems to vary more among diversity metrics than the conditional R2. Is that meaningful? Why?

Responses: We added a summary of the conditional R2 of all diversity models (Obj 1-2) (L665): "All diversity models had high conditional R^2 (0.63 – 0.91)."

It's difficult to pinpoint why marginal R2 (explained variance by fixed effects) varies more than conditional R2 (explained variance by fixed and random effects). It is possible that the fixed effect predictors (e.g., land use, climate) have varying explanatory power across diversity metrics. However, this can also be methodological, as the number of fixed effects included in models varied across diversity metrics. In the α diversity model, only land use, climate, and sampling methods have been included. In the β and γ diversity models, we also have other covariates, such as the number of assemblages (see Table 1). Sample size is also reduced in the model for β and γ diversity models.

Given the difficulty of pinpointing the exact reasons, we only added a sentence in the results reporting the range of conditional R2 across models without discussing the details.

Discussion

Reviewer: The discussion is generally well-written, but, to me, it is a bit underwhelming when it comes to the caveats and limitations of the study as well as the perspectives. I encourage the authors to add a full paragraph addressing these issues.

Response: We acknowledged many limitations in our methods, particularly limitations in data distribution. The relevant lines:

"As temporal approaches are rare in the literature (Davison, Rahbek, & Morueta-Holme, 2021), all collected datasets reflected spatial rather than temporal changes across land uses. While the focus on spatial approaches can underestimate impacts of land use changes (Christie et al., 2019), it minimizes spatial biases and maximizes generality. Despite our best efforts, regions known as bee diversity hotspots (Orr et al., 2021) or essential for global food security (Aizen et al., 2019), such as South and Central Asia (Fig. 1a), are still underrepresented." (L360-365)

"As our land use classification pooled different environments within the same land use category, the results should not be interpreted as estimates for a specific kind of urban, agricultural, or natural habitats. Our study broadly evaluates how bee diversity was affected by agriculturalization and urbanization, processes that can create different environments and degrade natural environments in various ways. Therefore, our classification system was designed to provide and compare average estimates across different environments within the same land uses." (L422-428).

We also acknowledge that the use of genus-level phylogeny can affect the results, although previous studies have used the same phylogeny and detected meaningful patterns (L440-443):

"While 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, Gibbs, & Winfree, 2018; Hendrix, Forbes, & MacDougall, 2018)."

For the abundance analyses, we discussed how to interpret our results despite the limitations in the discussion (L778-787): "Our analyses' low number of genera (≤51) can reduce the 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 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-Uribe, & Frank, 2017)."

Figures:
Reviewer: Figure 1. The map looks nice but it is difficult to assess if there are different biases in the latitudinal distribution of sampling locations among natural, urban, and agricultural habitats. Consider adding ridge lines on the side to show the density distribution of sampling locations along the latitudinal gradient. While some biases are (unfortunately) to be expected in such global studies, different latitudinal distribution of sampling locations among land use types could influence the results and the main conclusion of this study.
Response: We added a density plot to the map. We've designed the model to account for the uneven distribution across latitude (e.g., adding climatic covariates) with the methods available (but we also acknowledge the limitation).

Reviewer: Figure 4 provides all the necessary information but the tree structure makes it difficult to compare the trends between agricultural and urban land use. I suggest to use barplots showing the percentage change between natural and non-natural ecosystems where genera are sorted by

their abundance in natural ecosystems. That should provide a clearer and easier to read picture of the winners and losers of land use change.

Response: We have added the suggested figure to the supplement (Fig. S2). We sorted the genera alphabetically so that readers can easily identify the genera of interest.

Reviewer: Table S8: How were the p-values adjusted exactly?

Response: We specify that it is based on false discovery rate correction in the main text (L638-639): "We further adjusted pairwise comparison p-values using False Discovery Rate corrections".

Reviewer: Data and code availability:

I encourage the authors to provide the minimum data and code to replicated the analyses.

Responses: The code and >97% of the data will be released (see data accessibility statement). Three percent of the authors did not consent to publishing their data.

Reviewer: Overall, this is a very nice work and I hope that my comments will help to improve it further.

Response: Thank you, and we appreciate your thoughtful comments!

Reviewer: 2

Comments to the Author

Congratulations on a hugely improved manuscript! Thank you for the clarity you have added regarding the analysis methods, which has largely resolved my previous methodological concerns. My remaining concerns are listed below, again separated into larger and smaller issues.

Larger comments:

Reviewer: 1.) Lines 410-417. I have several concerns about the low stringency of the inclusion criteria: Can you please justify the threshold of only ten individuals? I recognize that these thresholds are ultimately arbitrary, but ten individuals seems very low, given that the bee fauna of many regions includes hundreds of possible species. I wouldn't expect estimates of sampling completeness to be reliable at such low sample sizes. Were any of the datasets actually that small? It would be good to include sample sizes in table S3. If only a few datasets are so small, I think you should omit them and state a higher threshold.

Responses: We used ten individuals because this is consistent with recent high-profile insect diversity analyses (Blowes et al., 2022, Ecology; van Klink et al., 2024, Nature). It is possible to include assemblages with many individuals only, but that also creates a bias due to the exclusion of highly impoverished assemblages. We clarify this in L374-377: "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 even higher than that used in previous studies based on rarefaction (Blowes et al., 2022; van Klink et al., 2024)."

The mean number of individuals across analyzed assemblages is reported in Table S1. Overall, the mean and median abundance across the 3,117 assemblages analyzed are 140 and 56 individuals, respectively. The number of assemblages would be reduced to 2,564 and 1,667 if we increase the threshold to 20 and 50 individuals, respectively.

We also note that our analysis focuses on Shannon index (i.e., when Hill number = 1), not species richness. Thus, while some regions can contain hundreds of species, Shannon diversity considers relative abundance of species. Therefore, missing rare species will have lower impacts on the analyses (L452-455): "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)"

Reviewer: Also, shouldn't each assemblage meet these thresholds in order to be included in the analysis? For example, why would an assemblage with 30% completeness be acceptable just because another assemblage in the same dataset had >50% completeness? I don't see a problem with including some assemblages from a dataset but excluding others because they don't meet necessary criteria for reliable diversity estimates. I appreciate the use of weighted regression based on sampling completeness, but it still seems important that each assemblage meets some threshold of sampling completeness in order to provide a reliable diversity estimate.
Responses: We clarified that we only included assemblages with ≥ 50% completeness in those studies. In other words, assemblages < 50% completeness were always excluded. But as long as the dataset has at least one assemblage > 50%, we will include the assemblages (but not those <50%).

We have clarified our explanation: "5) At least one assemblage had sampling completeness of ≥ 50% to ensure the reliability of diversity estimates. Sampling completeness was calculated using the R package iNEXT.3D (Chao et al., 2021). " (L377-379)… "We did not set a minimum number of assemblages to include in a dataset in our study. We included any assemblage in analyses if the sampling completeness and taxonomic resolution thresholds were met." (L379-383).

Reviewer: 2.) Lines 541-548. The supplemental explanation and simulation were very helpful for clarifying how this approach permits datasets with only one land use type. I think it would be good to incorporate one or two of the key points into the main text here. The following sentence was particularly helpful for alleviating my confusion: "We emphasize here that mixed models do not estimate study-level land use effects (or in general v_i) through modelling its relationship in each study individually. Rather, the calculations involve calculating the fixed effects and the

variance-covariance matrix, which uses data from all studies (Raudenbush & Bryk, 2002)."
Responses: Added (L536-537).

Reviewer: 3.) Lines 801-802. You could perhaps speculate briefly on the heterogeneity of the urban habitats where the datasets you used were collected and how you might expect that heterogeneity to contribute to turnover. You mention the variety of the urban habitats in lines 446-450. Do you think these might vary in the floral and nesting resources they provide to bees? A lot of your discussion points are very general, so some concrete examples would be nice.
Responses: The turnover analyses have been removed as we included the alpha-beta-gamma diversity analyses (as suggested by reviewer 3) and we streamlined the manuscript. However, we provide examples of why urban habitats have higher heterogeneity, such as different planting preferences and mowing frequency of individual owners. This can lead to different bee assemblages (L746-750): "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, Dixon, & Bateman, 2022), can increase environmental heterogeneity and, therefore, result in higher β diversity than natural habitats (Alberti, 2016). "

Reviewer: 4.) Lines 831-834. This statement is a bit vague, and I don't see how it follows from your results. Certainly, both richness and unique species should be considered in conservation strategies, but how do your results show that they are complementary? Again, concrete examples are helpful.

Responses: We shifted the focus of the manuscript to α, β, and γ diversity changes across land uses (see major comments by reviewer 3). To streamline the manuscript, we removed the nestedness and turnover analyses, and therefore this statement has been removed.

Smaller comments/typo corrections:

1.) Lines 279-281. I believe what you mean to say here is that the reduced taxonomic and phylogenetic β-diversity indicates greater diversity loss over large spatial scales that would be estimated from α-diversity alone. Just need to add the β to make this sentence make sense.

Response: Corrected

2.) Line 548. Missing the word "a" in "for a single land use".

Response: Corrected

3.) Line 657. Change "reduced" to "changed" or "increased or decreased" because some genera had higher abundance in agricultural or urban habitats.

Response: Corrected

4.) Lines 736-737. This is an incomplete sentence. Add "we detected" after "In contrast,".

Response: Corrected

5.) Line 740. "However" would be a better word that "alternatively" here.

Response: Corrected

6.) Line 762. Change subheading to match that on line 626.

Response: Corrected

7.) Lines 775, Fig. 4, Table S8. I'm not a taxonomist, but hasn't Peponapis been lumped into Eucera? Why are they treated separately here?

Response: We have updated the figure with the latest classification that *Peponapis* is a subgenus of Xenoglossa (Frietas et al. 2023).

Freitas, F. V., Branstetter, M. G., Franceschini-Santos, V. H., Dorchin, A., Wright, K. W., López-Uribe, M. M., ... & Almeida, E. A. (2023). UCE phylogenomics, biogeography, and classification of long-horned bees (Hymenoptera: Apidae: Eucerini), with insights on using specimens with extremely degraded DNA. *Insect Systematics and Diversity*, 7(4), 3.

8.) Line 780. Add the word "both" before "urban and agricultural".

Response: Corrected

9.) Line 818. Confusing sentence. Would read better as "…the contribution of turnover to both phylogenetic and taxonomic β-diversity was ~8% lower…"

Response: This has been deleted, as the nestedness and turnover analyses have been removed to streamline the manuscript.

10.) Lines 825, 828. I would replace "can" with "may" in these sentences.

Response: Corrected.

11.) Lines 872-873. I believe you mean to say "…the effectiveness of conservation measures for enhancing…"

Response: Fixed.

12.) Line 891. Change "to" to "for" ("…consequences of agricultural expansion for species diversity…")

Response: This has been deleted, as the last paragraph has been rewritten to accommodate the γ diversity results.

13.) SI lines 597, 637. Correct "insignificant" to "non-significant".

Response: Fixed.

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

2

3   Toby P. N. Tsang[1,2], A. A. Amado De Santis[3,4], Gabriela Armas-Quiñonez[5], John S. Ascher[6],

4   Eva Samanta Ávila-Gómez[7], András Báldi[8], Kimberly M. Ballare[9,10], Mario V. Balzan[11],

5   Weronika Banaszak-Cibicka[12], Svenja Bänsch[13], Yves Basset[14], Adam J. Bates[15], Jessica M.

6   Baumann[16], Mariana Beal-Neves[17], Ashley Bennett[18], Antonio Diego M. Bezerra[19], Betina

7   Blochtein[17], Riccardo Bommarco[20], Berry Brosi[21], Laura A. Burkle[22], Luísa G. Carvalheiro[23],

8   Ignacio Castellanos[24], Marcela Cely-Santos[25], Hamutahl Cohen[26], Drissa Coulibaly[27], Saul A.

9   Cunningham[28], Sarah Cusser[29], Isabelle Dajoz[30], Deborah A. Delaney[31], Ek Del-Val[32], Monika

10   Egerer[33], Markus P. Eichhorn[34,35], Eunice Enríquez[5], Martin H. Entling[36], Natalia Escobedo-

11   Kenefic[5], Pedro Maria Abreu Ferreira[17], Gordon Fitch[37], Jessica R. K. Forrest[38], Valérie

12   Fournier[39], Robert Fowler[40], Breno M. Freitas[41], Hannah R. Gaines-Day[42], Benoît Geslin[43,44],

13   Jaboury Ghazoul[45], Paul Glaum[46,47], Jose L. Gonzalez-Andujar[48], Adrian González-Chaves[49],

14   Heather Grab[50], Claudio Gratton[51], Solène Guenat[52], Catalina Gutiérrez-Chacón[53], Mark A.

15   Hall[54], Mick E. Hanley[55], Annika Hass[13], Ernest Ireneusz Hennig[56], Martin Hermy[57], Juliana

16   Hipólito[58,59], Andrea Holzschuh[60], Sebastian Hopfenmüller[61], Keng-Lou James Hung[62],

17   Kristoffer Hylander[63], Jordi Izquierdo[64], Mary A. Jamieson[65], Birgit Jauker[66], Steve Javorek[67],

18   Shalene Jha[68], Björn Klatt[69,70,71], David Kleijn[72], Alexandra-Maria Klein[73], Anikó Kovács-

19   Hostyánszki[8], Jochen Krauss[74], Michael Kuhlmann[75], Patricia Landaverde-González[5,76], Tanya

20   Latty[77], Misha Leong[78], Susannah B. Lerman[79], Yunhui Liu[80], Ana Carolina Pereira Machado[81],

21   Anson Main[82,83], Rachel Mallinger[84], Yael Mandelik[85], Bruno Ferreira Marques[86], Kevin

22   Matteson[87], Frédéric McCune[39], Ling-Zeng Meng[88], Jean Paul Metzger[89], Paula María Montoya-

23   Pfeiffer[90], Carolina Morales[91], Lora Morandin[92], Jane Morrison[64,93], Sonja Mudri-Stojnić[94],

24   Pakorn Nalinrachatakan[95], Olivia Norfolk[96], Mark Otieno[97], Mia G. Park[98], Stacy M. Philpott[99],

25   Gideon Pisanty[85,100], Montserrat Plascencia[101], Simon G. Potts[102], Eileen F. Power[103], Kit

26   Prendergast[104,105], Robyn D. Quistberg[99], Davi de Lacerda Ramos[106], André Rodrigo Rech[107],

27   Victoria Reynolds[108], Miriam H. Richards[109], Stuart P. M. Roberts[102,110], Malena Sabatino[111],

28   Ulrika Samnegård[112], Hillary Sardinas[113], Karina Sánchez-Echeverría[114], Fernanda Teixeira

29   Saturni[115], Jeroen Scheper[72], Amber R. Sciligo[116], C. Sheena Sidhu[117], Brian J. Spiesman[118],

30   Tuanjit Sritongchuay[119], Ingolf Steffan-Dewenter[120], Katharina Stein[121], Alyssa B. Stewart[122],

31   Jane C. Stout[103], Hisatomo Taki[123], Pornpimon Tangtorwongsakul[124], Caragh G. Threlfall[125],

32   Carla Tinoco[126], Teja Tscharntke[127], Katherine J. Turo[128,129], Chatura Vaidya[130], Rémy

33   Vandame[131], Carlos H. Vergara[132], Blandina F. Viana[58], Eric Vides-Borrell[131], Natapot Warrit[95],

34   Elisabeth Webb[133], Catrin Westphal[13], Jennifer B. Wickens[102], Neal M. Williams[134], Nicholas S.

35   G. Williams[16], Caleb J. Wilson[65,135], Panlong Wu[80,136], Elsa Youngsteadt[137], Yi Zou[138], Lauren C.

36   Ponisio[139], Timothy C. Bonebrake[1]

37

38   [1]School of Biological Sciences, The University of Hong Kong, Pokfulam Road, Hong Kong,

39   Hong Kong SAR, China

40   [2]Department of Biological Sciences, University of Toronto-Scarborough, Toronto, Ontario,

41   Canada

42   [3]Centro de Estudios Territoriales Ambientales y Sociales (CETAS-UNJu), Jujuy, Argentina

43   [4]Instituto de Ecorregiones Andinas (INECOA), Universidad Nacional de Jujuy - CONICET,

44   Facultad de Ciencias Agrarias, S. S. de Jujuy, Argentina

45   [5]Centro de Estudios Conservacionistas, Facultad de Ciencias Químicas y Farmacia, Universidad

46   de San Carlos de Guatemala

47   [6]Department of Biological Sciences, National University of Singapore, 16 Science Drive 4 S3

48   Level 4, Singapore 117558

49   [7]Centro de Investigaciones Biológicas, Instituto de Ciencias Básicas e Ingeniería, Universidad

50   Autónoma del Estado de Hidalgo, Carretera Pachuca-Tulancingo km 4.5, C. P. 42184, Mineral

51   de la Reforma, Hidalgo, México

52   [8]Lendület Ecosystem Services Research Group, Institute of Ecology and Botany, HUN-REN

53   Centre for Ecological Research, Hungary

54   [9]Department of Integrative Biology, University of Texas at Austin, Austin, TX 78739, USA

55   [10]USDA Forest Service, Rocky Mountain Research Station, Bozeman, MT 59717, USA

56   [11]Institute of Applied Sciences, Malta College of Arts, Science and Technology, Paola,

57   PLA9032, Malta

58   [12]Department of Zoology, Poznań University of Life Sciences, Wojska Polskiego 71C, 60-625

59   Poznań, Poland

60   [13]Functional Agrobiodiversity, University of Göttingen, 37077, Göttingen, Germany

61   [14]Smithsonian Tropical Research Institute, Panama City, Republic of Panama

62   [15]School of Animal, Rural & Environmental Sciences, Nottingham Trent University,

63   Nottingham, UK

64   [16]School of Ecosystem and Forest Science, The University of Melbourne, Australia

65   [17]Programa de Pós-Graduação em Ecologia e Evolução da Biodiversidade, Pontifícia

66   Universidade Católica do Rio Grande do Sul, PUCRS, Av. Ipiranga 6681, prédio 12, bloco C,

67   sala 111, Porto Alegre, RS 90619-900, Brazil

68   [18]Department of Entomology, Michigan State University, 578 Wilson Road, East Lansing, MI

69   48824, United States

70   [19]Departamento de Zootecnia, Centro de Ciências Agrárias, Universidade Federal do Ceará,

71   Fortaleza, CE, Brazil

72   [20]Swedish University of Agricultural Sciences, Department of Ecology, 75007 Uppsala, Sweden

73   [21]Department of Biology, University of Washington, Seattle, Washington, USA

74   [22]Montana State University, Department of Ecology, Bozeman, MT USA 59717

75   [23]Departamento de Ecologia, Instituto de Ciências Biológicas, Universidade Federal de Goiás,

76   Goiânia, Brazil

77   [24]Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Hidalgo, Mineral

78   de la Reforma, Hidalgo, Mexico

79   [25]Department of Environmental Studies, University of California- Santa Cruz

80   [26]University of California, Division of Agriculture and Natural Resources, UC Cooperative

81   Extension Ventura County. Ventura, CA

82   [27]University Peleforo GON COULIBALY of Korhogo, Cote d'Ivoire

83   [28]Fenner School of Environment & Society, The Australian National University, Canberra,

84   Australia, 2601

85   [29]Santa Barbara Botanic Garden, 1212 Mission Canyon Rd, Santa Barbara, CA 93111, USA

86   [30]Université Paris-Cité, UMR CNRS 7618, Paris, France

87   [31]Department of Entomology & Wildlife Biology, University of Delaware, Newark, DE, United

88   States

89   [32]Insitituto de Investigaciones en Ecosistemas y Sustentabilidad, UNAM

90   [33]Department of Life Science Systems, TUM School of Life Sciences, Technical University of

91   Munich, Hans Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany

92   [34]School of Biological, Earth and Environmental Sciences, University College Cork, Cork,

93   Ireland

94   [35]Environmental Research Institute, University College Cork, Cork, Ireland

95   [36][37]iES Landau, Institute for Environmental Sciences, University of Kaiserslautern-Landau

96   (RPTU), Germany

97   [37]Department of Biology, York University, Toronto, ON, Canada

98   [38]Department of Biology, University of Ottawa, Ottawa, ON, Canada

99   [39]Centre de recherche et d'innovation sur les végétaux, Université Laval, Québec City, QC,

100   Canada

101   [40]University of Sussex, Falmer, Brighton, United Kingdom

102   [41]Departamento de Zootecnia, Centro de Ciências Agrárias, Universidade Federal do Ceará,

103   Fortaleza, CE, Brazil

104   [42]Department of Entomology, University of Wisconsin, Madison, Madison, WI, USA

105   [43]IMBE, Aix Marseille Univ., Avignon Univ., CNRS, IRD, Marseille, France

106   [44]Université de Rennes (UNIR), UMR 6553 ECOBIO, CNRS, Rennes, France

107   [45]Ecosystem Management, Department of Environmental Systems Science, ETH Zurich, Zurich,

108   Switzerland

109   [46]Department of Environmental Science and Policy, University of California-Davis, Davis, CA,

110   95616, USA

111   [47]Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI,

112   48109, USA

113   [48]Institute for Sustainable Agriculture (IAS), Spanish National Research Council (CSIC),

114   Cordoba, Spain

115   [49]Laboratório de Ecologia da Paisagem e Conservação, Instituto de Biociências, Universidade de

116   São Paulo, São Paulo, Brazil

117   [50]School of Integrative Plant Sciences, Cornell University, Ithaca NY 14853 USA

118   [51]Department of Entomology, University of Wisconsin-Madison, 1630 Linden Dr. Madison,

119   Madison, WI, 53706, USA

120   [52]Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Switzerland

121   [53]Wildlife Conservation Society –Colombia Program, Av 5N # 22N-11, Cali, Colombia

122   [54]Hawkesbury Institute for the Environment, Western Sydney University, Richmond, Australia

123   [55]School of Biological and Marine Sciences, University of Plymouth, Plymouth, PL4 8AA. UK.

124   [56]Federal Statistical Office, Division Territory and Environment, Section Geoinformation

125   [57]KU Leuven, University of Leuven (KU Leuven), dept Earth & Environmental Sciences,

126   Celestijnenlaan 200E, 3001 Heverlee

127   [58]Instituto de Biologia, Universidade Federal da Bahia, Salvador, BA, Brazil

128   [59]Instituto Nacional de Pesquisas da Amazônia, Manaus, AM, Brazil

129   [60]Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Am

130   Hubland, 97074 Würzburg, Germany

131   [61]Evolutionary Ecology and Conservation Genomics, Ulm University, Germany

132   [62]Oklahoma Biological Survey, University of Oklahoma, Norman, Oklahoma, USA

133   [63]Department of Ecology, Environment and Plant Sciences, Stockholm University, SE-106 91

134   Stockholm, Sweden

135   [64]Department of Agri-Food Engineering and Biotechnology, Universitat Politècnica de

136   Catalunya - Campus del Baix Llobregat, 08860 Castelldefels, Spain

137   [65]Department of Biological Sciences, Oakland University, Rochester, MI, United States

138   [66]Department of Animal Ecology, Justus Liebig University Giessen, Giessen, Germany

139 [67]Agriculture and Agri-Food Canada, Kentville Research and Development Centre, Kentville,

140 Nova Scotia, Canada

141 [68]Department of Integrative Biology & Lady Bird Johnson Wildflower Center, University of

142 Texas at Austin, Austin, TX 78739, USA

143 [69]Agroecology, Department of Crop Sciences, Göttingen University, Germany

144 [70]Biodiversity, Department of Biology, Lund University, Sweden

145 [71]Halmstad University, School of Business, Innovation and Sustainability, Biology &

146 Environmental Sciences, P.O. Box 823, 30118 Halmstad, Sweden

147 [72]Plant Ecology and Nature Conservation Group, Wageningen University & Research, 6700 AA

148 Wageningen, The Netherlands

149 [73]Nature Conservation and Landscape Ecology, University of Freiburg, Germany

150 [74]Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Am

151 Hubland, 97074 Würzburg, Germany

152 [75]Zoological Museum, University of Kiel, Germany, Hegewischstr. 3, D-24105 Kiel

153 [76]General Zoology, Institute for Biology, Martin-Luther University Halle-Wittenberg, Hoher

154 Weg 8, 06120 Halle (Saale), Germany

155 [77]School of Life and Environmental Sciences & Sydney Institute of Agriculture, University of

156 Sydney, Sydney, NSW, Australia

157 [78]California Academy of Sciences, San Francisco, CA, USA

158   [79]USDA Forest Service Northern Research Station, Amherst, MA, USA

159   [80]College of Resources and Environmental Sciences, China Agricultural University, Beijing

160   100193, China

161   [81]Programas de Pós-Graduação em Ciência Florestal e Biologia Animal, Universidade Federal

162   dos Vales do Jequitinhonha e Mucuri, Campus JK, Diamantina, MG, Brazil

163   [82]School of Natural Resources, University of Missouri, Columbia, MO, USA

164   [83]California Department of Pesticide Regulation, Sacramento, CA, 95812, USA

165   [84]Department of Entomology and Nematology, University of Florida, Gainesville, Florida, USA

166   [85]Department of Entomology, The Robert H. Smith Faculty of Agriculture, Food and

167   Environment, The Hebrew University of Jerusalem, Rehovot 7610001, Israel

168   [86]Programa de Pós Graduação em Ecologia e Evolução - Universidade Federal de Goiás,

169   Goiânia, Brasil

170   [87]Project Dragonfly/Department of Biology, Miami University, 111 Upham Hall, Oxford, OH

171   45056, USA

172   [88]College of Biological & Agricultural Sciences, Honghe University, Mengzi, Yunnan 661199,

173   China

174   [89]Department of Ecology, Institute of Biosciences, Institute of Advanced Studies, University of

175   São Paulo, SP, Brazil

176   [90]Laboratório de Abelhas, Departamento de Ecologia, Instituto de Biociências, Universidade de

177   São Paulo, São Paulo, Brazil

178   [91]Instituto de Investigaciones en Biodiversidad y Medio Ambiente (INIBIOMA), Universidad

179   Nacional del Comahue, Consejo Nacional de Investigaciones Científicas y Técnicas

180   (CONICET), Bariloche (8400), Argentina

181   [92]Pollinator Partnership, San Francisco, CA

182   [93]Department of Environment, Agriculture and Geography, Bishop's University, 2600 College

183   St., Sherbrooke, QC, J1M 1Z7, Canada

184   [94]University of Novi Sad, Faculty of Sciences, Department of Biology and Ecology, Trg Dositeja

185   Obradovića 2, 21000 Novi Sad, Serbia

186   [95]Center of Excellence in Entomology and Department of Biology, Faculty of Science,

187   Chulalongkorn University, Bangkok 10330, Thailand

188   [96]Deceased

189   [97]Water and Agricultural Resource Management, University of Embu, Embu, Kenya

190   [98]Department of Entomology, Cornell University, Ithaca, New York, USA

191   [99]Environmental Studies Department, University of California, Santa Cruz, CA 95064, USA

192   [100]The Steinhardt Museum of Natural History, Tel Aviv University, Tel Aviv, Israel

193   [101]Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, Santa

194   Cruz, CA 95064, USA

195   [102]Centre for Agri-Environmental Research, School of Agriculture, Policy and Development,

196   Reading University, RG6 6EU, UK

197   [103]Botany, School of Natural Sciences, Trinity College Dublin, Dublin, Ireland

198   [104]University of Sunshine Coast

199   [105]School of Molecular and Life Sciences, Curtin University, Kent Street, Bentley, WA, 6102,

200   Australia

201   [106]University of Brasília, Institute of Biological Sciences, Graduate Program in Ecology –

202   Campus Darcy Ribeiro, Asa Norte, Brasília-DF 70910-900, Brazil

203   [107]Centre of Advanced Studies on the Functioning of Ecological Systems and Interactions

204   (CAFESIN - MULTIFLOR), Federal University of Jequitinhonha and Mucuri Valleys. CEP

205   39100-000, Diamantina, Minas Gerais, Brazil

206   [108]University of Queensland, School of Biological Sciences, Brisbane, Australia

207   [109]Department of Biological Sciences, Brock University, 1812 Sir Isaac Brock Way, St.

208   Catharines, ON, L2T 1X6, Canada

209   [110]Université Libre de Bruxelles, Faculté des Sciences, Campus de la Plaine - CP 264/02,

210   Boulevard du Triomphe, ACC.2 ,1050 Bruxelles

211   [111]Centro de Investigaciones en Abejas Sociales (CIAS), IIPROSAM. CONICET – UNMDP

212   [112]Department of Biology, Lund University, 223 62 Lund, Sweden

213   [113]Department of Environmental Science, Policy and Management, University of California,

214   Berkeley

215   [114]Laboratorio de Ecología de Interacciones Bióticas. Facultad de Biología. Universidad

216   Michoacana de San Nicolás de Hidalgo. Morelia, Michoacán, México

217   [115]Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, Rua do

218   Matão, 321, Travessa 14, 05508-900 São Paulo, SP, Brazil

219   [116]The Organic Center, Washington D.C., USA

220   [117]Jasper Ridge Biological Preserve, Stanford University

221   [118]Department of Entomology, Kansas State University, Manhattan, KS 66506

222   [119]UFZ-Helmholtz Centre for Environmental Research, Department of Computational Landscape

223   Ecology, Permoserstr. 15, 04318 Leipzig, Germany

224   [120]Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Am

225   Hubland, 97074 Würzburg, Germany

226   [121]University of Potsdam, Working group Biodiversity/Systematic Botany, Maulbeerallee 1,

227   14469 Potsdam, Germany

228   [122]Department of Plant Science, Faculty of Science, Mahidol University, Bangkok, 10400

229   Thailand

230   [123]Forestry and Forest Products Research Institute, 1 Matsunosato, Tsukuba, Ibaraki, 305-8687,

231   Japan

232   [124]Conservation Ecology Program, King Mongkut's University of Technology Thonburi,

233   Bangkok 10150, Thailand

234   [125]School of Life and Environmental Sciences, Faculty of Science, The University of Sydney,

235   Camperdown, Australia

236   [126]Department of Ecology, Universidade Federal de Goiás, 74001-970 Goiânia, Brazil

237   [127]Department of Agroecology, University of Göttingen, Göttingen, Germany

238   [128]Department of Ecology, Evolution, and Natural Resources, Rutgers University, New

239   Brunswick, New Jersey, USA

240   [129]Department of Entomology, The Ohio State University, Columbus, Ohio, USA

241   [130]Department of Integrative Biology, University of Texas at Austin, Austin, TX 78712, USA

242   [131]El Colegio de la Frontera Sur, Departamento Agricultura Sociedad y Ambiente, San Cristóbal

243   de Las Casas, Chiapas, Mexico

244   [132]Departamento de Ciencias Químico-Biológicas, Universidad de las Américas Puebla, Cholula,

245   Puebla, México

246   [133]U.S. Geological Survey, Missouri Cooperative Fish and Wildlife Research Unit, University of

247   Missouri, Columbia, MO 65211, USA

248   [134]Department of Entomology and Nematology, University of California, One Shields Ave.,

249   Davis, CA 95616, USA

250   [135]Department of Entomology, University of Kentucky, Lexington, KY, USA

251 [136]School of Ecology and Environment, Inner Mongolia University, Hohhot 010021, China

252 [137]Department of Applied Ecology, North Carolina State University, Raleigh, NC, USA

253 [138]Department of Health and Environmental Sciences, Xi'an Jiaotong-Liverpool University,

254 Suzhou, China

255 [139]Institute for Ecology and Evolution, University of Oregon, Eugene, Oregon, USA

256

257 Corresponding: Toby, P. N. Tsang, Lauren C. Ponisio, Timothy C. Bonebrake

258 **Email:** paknok.tsang@utoronto.ca, lponisio@uoregon.edu, tbone@hku.hk

259

260 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 man-made 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,

306   physiology, and phenology (Purvis & Hector, 2000; Tucker et al., 2017). Recent studies have

307   increasingly emphasized analyzing phylogenetic diversity alongside taxonomic diversity

308   (Cadotte & Tucker, 2018; Tucker et al., 2017). As evolution shapes species traits, phylogenetic

309   approaches can efficiently capture high-dimensional ecological differences, reducing the risks of

310   omitting important traits (Tucker et al., 2017; Tucker, Davies, Cadotte, & Pearse, 2018).

311   Additionally, phylogenetic diversity has exhibited similar or even better performance than

312   taxonomic diversity in explaining ecosystem functions or services across sites (Tucker et al.,

313   2019; van der Plas, 2019).

314   While not always the case, responses of phylogenetic diversity to land use change should

315   largely follow taxonomic diversity change (Tucker & Cadotte, 2013). However, land use could

316   also lead to more phylogenetic diversity loss than would be expected based on the taxonomic

317   diversity loss. This is because land use change can strengthen phylogenetic habitat filtering

318   (Grab et al., 2019; Nowakowski, Frishkoff, Thompson, Smith, & Todd, 2018), causing only a

319   subset of phylogenetically similar species to persist under anthropogenic land uses due to

320   conserved traits (Duarte, 2011). Interestingly, the filtering effects on α- and β-diversity can vary,

321   again demonstrating the importance of analyzing both α and β diversity to better understand net

322   impacts at larger spatial scales (i.e., γ diversity) (Nowakowski et al., 2018).

323   To understand how land use change affects taxonomic and phylogenetic diversity, we focused

324   on a well-studied and ecologically important taxon, bees. Pollination services by bees can be

325   greater in sites with high bee taxonomic and phylogenetic α diversity and landscapes with high

326   taxonomic β diversity between sites (Grab et al., 2019; Weekers et al., 2022; Winfree et al.,

327   2018), compared to lower-diversity sites and landscapes. Ongoing global land use change is

328   known to reduce bee diversity generally (Cariveau & Winfree, 2015; De Palma et al., 2016;

329   Winfree, Bartomeus, & Cariveau, 2011). However, the exact effects can vary with land use

330   types, with some studies reporting increased bee diversity under land use change (Cariveau &

331   Winfree, 2015; Prendergast, Dixon, & Bateman, 2022; Winfree et al., 2011). Furthermore, the

332   impacts of anthropogenic land uses are often evaluated using taxonomic α diversity, even though

333   other biodiversity metrics could exhibit different patterns (De Palma et al., 2017; Harrison,

334   Gibbs, & Winfree, 2018). Importantly, some bee lineages are especially sensitive to land use

335   change, which could lead to a more substantial decline in phylogenetic diversity relative to

336   taxonomic diversity (Grab et al., 2019; Harrison et al., 2018).

337   We examined the ecological impacts of global land use on bee diversity using bee assemblage

338   data from agricultural, urban, and natural habitats across all continents except Antarctica, where

339   bees are absent. Our objectives were to 1) compare taxonomic and phylogenetic α, β and γ

340   diversity between natural, agricultural and urban habitats, 2) investigate whether land use change

341   leads to stronger phylogenetic habitat filtering, and 3) identify the genera particularly affected by

342   the agricultural and urban habitats. For objective 1, we expected that natural habitats would

343   contain greater taxonomic and phylogenetic α, β, and γ diversity. For objective 2, we predicted

344   declines in phylogenetic diversity in urban and agricultural habitats, even after controlling for

345   taxonomic diversity, due to increased phylogenetic habitat filtering.

346

347   **Materials and Methods**

348   **Data collection**

349   We first collected bee datasets from the PREDICTS database (Hudson et al., 2014) and from a

350   previous global study examining the effects of agricultural habitats on bee communities

351   (Kennedy et al., 2013). We then conducted a search on Google Scholar using different

352   combinations of keywords, including but not limited to "bee", "land use", "fragment",

353   "agriculture", "urban", "garden", "park", "green space", "cropland", "pasture", and "plantation".

354   After the broad search, we assessed the spatial distribution of datasets collected and identified

355   understudied regions in our data. We added these spatial descriptors as keywords (e.g.,

356   "tropical", "Asia", "Africa", and "South America") in subsequent searches to minimize spatial

357   biases. We also collected datasets from understudied regions by examining references of studies

358   and recommendations from bee experts to further minimize spatial biases in the dataset. We

359   contacted the authors for raw data if they were not published.

360   As temporal approaches are rare in the literature (Davison, Rahbek, & Morueta-Holme,

361   2021), all collected datasets reflected spatial rather than temporal changes across land uses.

362   While spatial approaches can underestimate the impacts of land use changes (Christie et al.,

363   2019), it minimizes spatial biases and maximizes generality. Despite our best efforts, regions

364   known as bee diversity hotspots (Orr et al., 2021) or essential for global food security (Aizen et

365   al., 2019), such as South and Central Asia (Figure 1a), are still underrepresented.

366   After data cleaning (see section *Data cleaning*) and before data analyses, we excluded *Apis*

367   *mellifera* (because they were often from managed colonies) from all sites, and aggregated data

368   from different sampling dates before checking whether the following criteria had been met: 1)

369   We only obtained datasets with a broad taxonomic focus. Therefore, datasets that included only

370   certain groups of bees (e.g., *Bombus* spp., solitary bees) were excluded. However, datasets that

371   did not capture *Apis mellifera* were included. 2) Spatial coordinates were recorded, which were

372   used to control for spatial autocorrelation in the analyses. 3) The number of individuals observed

373   was recorded. 4) At least ten individuals were identified to at least the genus level to ensure

374   reliable rarefaction results (see below). We did not use a threshold higher than ten individuals

375 because this might bias the analyses against impoverished assemblages. The threshold is also

376 consistent with or higher than that used in previous studies based on rarefaction (Blowes et al.,

377 2022; van Klink et al., 2024). 5) At least one assemblage had sampling completeness of $\geq 50\%$ to

378 ensure the reliability of diversity estimates. Sampling completeness was calculated using the R

379 package iNEXT.3D (Chao et al., 2021). 6) At least one assemblage had at least 95% of observed

380 individuals identified to at least the genus level to ensure reliable estimations of phylogenetic

381 diversity. We did not set a minimum number of assemblages to include in a dataset in our study.

382 We included any assemblage in analyses if the sampling completeness and taxonomic resolution

383 thresholds were met.

384   Datasets were divided into different studies according to their sampling strategies, which were

385 broadly classified as: (1) "flower visitors", if the study sampled flower-visiting bees within an

386 area, (2) "targeted plants" if the study sampled flower-visiting bees of targeted plant species, and

387 (3) "all bees" for any other method, such as pan traps, hand-netting, and vane traps. Thus, if a

388 dataset provided bee data based on different sampling strategies, such as pan traps and hand

389 netting bees from targeted plant species, the data would be separated into different studies.

390

391 **Data cleaning**

392   Before analyses, we corrected species synonyms using a bee species guide and world

393 checklist (Ascher & Pickering, 2022). Missing taxa were further reviewed by a taxonomist co-

394 author (John S. Ascher). For 1% of 2,247 species-level identifications, no matches were found;

395 these were treated as morphospecies instead of species. For morphospecies or genus-level data,

396 we checked the validity of the genus in the checklist and corrected them when necessary. Tip

397 names on the phylogenetic tree were also corrected using the same approaches.

398

399 **Definitions of land uses**

400 Our classification was primarily based on conditions within the sampling area rather than the

401 surrounding landscapes. Because the sampling area varied strongly across studies (Table S1), we

402 did not use a consistent spatial scale in classifying within-site land uses, similar to other global

403 databases (Hudson et al., 2014). Rather, we determined land uses based on the predominant

404 environment within the sampling area. However, for small sampling areas with a maximum

405 length < 10 m (e.g., single malaise trap, transect < 10 m), we classified the site based on the

406 surrounding 100 m^2 environment (Hudson et al., 2014). For plots, the maximum length was

407 determined by the diagonal of the whole plot (Hudson et al., 2014).

408   Natural habitats were defined as areas primarily covered by vegetation resulting from natural

409 succession or restoration (i.e., active attempts to bring the site to a more natural state). Natural

410 habitats also included sites within disturbed landscapes, such as forest or grassland fragments

411 within urban or agricultural landscapes. Agricultural habitats were defined as sites managed for

412 growing resources, including food, animal products, and other resources (e.g., cotton, rubber).

413 This included croplands, orchards, plantations, field margins (including those enhanced with

414 hedgerows or wildflower strips), and pastures. Urban habitats included green spaces covered by

415 planted vegetation (not natural succession) managed for amenity or recreation. Examples

416 included lawns, golf courses, green roofs, and gardens. Crop gardens were classified as urban

417 habitats since their local conditions and management are more similar to other urban green

418   spaces than the agricultural habitats defined above. Land uses of different sites were classified by

419   data contributors, or based on site descriptions provided in publications. We also used historical

420   images from Google Earth Pro to validate land uses when necessary. Sites that could not be

421   reliably classified were excluded from analyses.

422   As our land use classification pooled different environments within the same land use

423   category, the results should not be interpreted as estimates for specific kinds of urban,

424   agricultural, or natural habitats. Our study broadly evaluates how bee diversity is affected by

425   agriculturalization and urbanization, processes that can create different environments and

426   degrade natural environments in various ways. Therefore, our classification system was designed

427   to provide and compare average estimates across different environments within the same land

428   uses.

429

430   **Phylogeny**

431   We used a global genus-level phylogeny to quantify the phylogenetic diversity of each

432   assemblage (Hedtke, Patiny, & Danforth, 2013). We first converted the tree to ultrametric using

433   a non-negative least square (Turley, Biddinger, Joshi, & López-Uribe, 2022). The strong

434   cophenetic correlation (Pearson's r = 0.93) indicated that the tree's structure was largely

435   conserved. Our data contained taxa from 355 genera, of which 32 were missing from the tree and

436   were added to the closest sister genus available (Table S2). We randomly selected one species in

437   the tree from each genus, then attached all species from each study as polytomies at the mid-

438   point of its corresponding genus branch, as this approach has been demonstrated to capture

439   phylogenetic diversity well when a species-level phylogeny is unavailable (Qian & Jin, 2021).

440   While use of a genus level phylogeny might not fully capture phylogenetic patterns of

441   assemblages, previous bee studies have used the same phylogeny and detected phylogenetic

442   diversity changes and phylogenetic habitat filtering (De Palma et al., 2017; Harrison et al., 2018;

443   Hendrix, Forbes, & MacDougall, 2018). We quantified the phylogenetic α-diversity of each

444   assemblage by generating ten phylogenetic trees and found that the values of phylogenetic α-

445   diversity were highly correlated (Pearson's r > 0.99). Thus, we only used the first phylogenetic

446   tree for subsequent analyses.

447

448   **<u>α and γ diversity estimates</u>**

449   In our analyses, α and γ diversity always represent within- and across-sample diversity within

450   the same habitat and, therefore, an increase in spatial scale (Chase et al., 2019; Socolar et al.,

451   2016). Thus, comparing α and γ diversity across habitats allows for assessing whether diversity

452   loss is exacerbated at larger spatial scales by land use change. To estimate taxonomic and

453   phylogenetic α and γ diversity, we estimated both metrics with the Hill number equal to 1, as it

454   considers the relative abundance of species within assemblages and is less prone to

455   undersampling than lower Hill numbers (Roswell, Dushoff, & Winfree, 2021).

456   We estimated α diversity for all assemblages, while γ diversity was estimated only for studies

457   with at least five assemblages from at least one land use. Additionally, γ diversity was only

458   estimated for studies that indicated sampling effort for each assemblage. We pooled species

459   abundance data across assemblages of the same land uses within each study before conducting

460   rarefaction analyses. To control for differences in sampling completeness between assemblages

461   across studies, we extrapolated all α and γ diversities to their asymptotes (i.e., when sampling

462 completeness equals 1). Each assemblage's taxonomic and phylogenetic diversity was estimated

463 using iNEXT.3D (Chao et al., 2021).

464

465 **β diversity estimates**

466 For each land use in each study, we used multiplicative partitioning ($\beta = \gamma$ / mean α) to obtain

467 their β diversity (Jost, 2007). This method is especially suitable to understand the spatial scaling

468 of diversity loss, as it represents the scaling factor relating α and γ diversity (Baselga, 2013;

469 Socolar et al., 2016). The metric also reflects the contribution of β diversity to γ diversity

470 (Contribution of $\beta = (1-\alpha/\gamma) * 100\% = (1-1/\beta) * 100\%$).

471 The corresponding γ and α diversities were taken from rarefaction analyses. As more

472 abundant assemblages should more heavily influence γ diversity estimates, mean α diversity was

473 weighted according to the total abundance of each assemblage (Crist, Veech, Gering, &

474 Summerville, 2003). Consistent with the γ diversity analyses, our analyses included only studies

475 with at least five assemblages in at least one land use.

476

477 **Climatic and methodological variables**

478 We collected a variety of climatic and methodological variables to control for their effects on

479 bee diversity and to better quantify any effect of land use change (Table 1). Mean annual

480 temperature and annual precipitation, as well as the seasonality of each assemblage from 1979-

481 2013, were obtained from the public database CHELSA v1.2 (Karger et al., 2017). Annual

482 precipitation was square root transformed to reduce the effects of outliers. All data were at 30

483   arc-second (~1 km) resolution. Since these values are correlated, we used robust PCA to reduce

484   the dimensionality of the variables. We included PC1 and PC2 for subsequent analyses, which

485   captured >76% of the climatic variation within the dataset (Table S3). Increasing PC1 scores

486   primarily reflect colder and drier sites with high seasonality in both temperature and

487   precipitation, while increasing PC2 scores reflect colder and wetter sites with higher temperature

488   seasonality and lower precipitation seasonality. Robust PCA was conducted using R-package

489   rrcov (Todorov & Filzmoser, 2009).

490   For the β and γ diversity models, we additionally included methodological variables in the

491   models that might affect both diversity metrics, namely 1) study extent, 2) variations in sampling

492   efforts, 3) number of sites, 4) variations in sampling completeness, and 5) mean sampling

493   completeness.

494   We quantified the study extent as the maximum linear distance between assemblages of the

495   same land uses. Pooling assemblages with unstandardized sampling effort can distort abundance

496   distribution, and the effect cannot be removed by rarefaction alone (see Chao & Jost (2012) for

497   the theory of rarefaction based on sampling coverage). Thus, we included variation in sampling

498   effort across habitats in the analyses. We quantified the sampling effort of each assemblage

499   based on the most countable units (e.g. traps, transects, plots, sampling hours) in each study.

500   Assemblages with the highest sampling effort would be one, while other assemblages would

501   have a sampling effort lower than one. Therefore, the metric quantifies within-study sampling

502   effort variations. Standard deviations of sampling effort were calculated across assemblages to

503   represent its variation within each study.

504   We also calculated the number of assemblages for each land use, which tends to increase β

505   and γ diversity (Crist & Veech, 2006; Jost, 2007; Marion, Fordyce, & Fitzpatrick, 2017).

506   Sampling completeness can also vary across assemblages and affect β and γ diversity (Beck,

507   Holloway, & Schwanghart, 2013). Thus, before pooling assemblage data to estimate β and γ

508   diversity, we calculated the mean and standard deviation of sampling completeness for all

509   assemblages of the same land use within a study. Mean sampling completeness was log-

510   transformed because of its non-linear effect on diversity metrics (Beck et al., 2013; Chao & Jost,

511   2012). The mean and standard deviations of sampling completeness across assemblages were

512   highly correlated, so we further used a robust PCA and extracted the PCA1 score to represent

513   them, as it captured 93.1% variations within the dataset. A higher sampling effort PCA1 score

514   indicates lower mean sampling completeness with higher variation across assemblages (Table

515   S3).

516

517   **General modeling strategy**

518   We used mixed models to identify the effects of land use while controlling for methodological

519   and climatic covariates, as well as other unaccounted-for study differences using random effects.

520   Study-level variation can lead to varying estimates of land use effects. For example, the effects

521   may be stronger in warmer landscapes with fewer natural habitats in the surrounding

522   environments (Ganuza et al., 2022; Kennedy et al., 2013). Methodological factors such as

523   sampling area (Azaele et al., 2015) and methods (Lee & Guénard, 2019) can also alter estimates

524   of land use effects. Here, we focused on the general trend across studies rather than examining

525   how land use change interacts with other environmental or methodological variables. Therefore,

526   apart from a few climatic and methodological covariates, we used study identity as a random

527   effect to control for such study-level variations.

528   This statistical framework has been used in previous quantitative syntheses assessing land use

529   effects on diversity or abundance by comparing data from studies conducted in different regions

530   based on different methods. It also allows for studies with data on one land use only (De Palma

531   et al., 2016; Millard et al., 2021; Newbold et al., 2015). A summary of how mixed models work

532   is provided in Text S1. Additionally, we provide a simple simulation (Text S2) to justify our

533   approach of including study-level land use effects, despite some studies only providing bee data

534   for a single land use. We emphasize here that mixed models do not estimate study-level land use

535   effects (or in general any random slope) through modelling its relationship in each study

536   individually. Rather, the calculations involve calculating the fixed effects and the variance-

537   covariance matrix, which uses data from all studies (Raudenbush & Bryk, 2002). Below we

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

539   S4.

540

541   **Objective 1a: α diversity**

542   To examine how taxonomic and phylogenetic α-diversity varied across land uses, we built linear

543   mixed models with Gaussian distributions using log-transformed α-diversity. We specified log-

544   transformed α-diversity as the response to improve normality. For predictors, we included

545   sampling method (three levels: All bees/ Flower visitors/ Targeted plants) and land use (three

546   levels: Natural/Agricultural/Urban) of each site. Climatic PC1 and PC2 scores were also added

547   as predictors to control for the effects of regional climate on bee α-diversity. Our analyses

548   include nominal variables, so we set the intercepts as natural habitats sampled with methods

549   targeting all bees. We further used sampling completeness as a weight in the regression, such

550   that poorly sampled sites (and, therefore, those with higher uncertainty in diversity estimates)

551   had lower weights in the analyses (Carvalheiro et al., 2013).

552   For random effects, study identity was added as a random intercept, with land use effects

553   added as random slopes, so the estimates of land use effects could vary across studies. The

554   random slopes were never correlated with random intercepts to facilitate model convergence

555   (Matuschek, Kliegl, Vasishth, Baayen, & Bates, 2017).

556   Additionally, to control for spatial autocorrelation, we added an assemblage-level random

557   intercept based on the spatial coordinates of each site. The Matérn correlation model was used to

558   construct the correlation matrix and estimate the spatial random effect. All spatial random effects

559   were study-specific, indicating that spatial autocorrelations were modelled within but not across

560   studies, as they had very different methodologies. Indeed, we detected substantial spatial

561   autocorrelation between sites within the same study but not between sites across different studies

562   (Text S3). We compared models with and without spatial random effects and found that the

563   model including spatial autocorrelation had a significantly improved model fit, as indicated by a

564   reduction of >490 in the conditional AIC.

565   We built the linear mixed model using R package spaMM, which allows including spatial

566   random effects (Rousset & Ferdy, 2014). We then conducted an omnibus test for differences

567   across land uses based on F tests using R package lmerTest (Kuznetsova, Brockhoff, &

568   Christensen, 2017). If the effect of land use was significant, we further conducted pairwise

569   comparisons across the three land uses, with the p-value adjusted by False Discovery Rate

570   corrections.

571

572   **<u>Objective 1b & 1c: β and γ diversity</u>**

573   The β and γ diversity analyses were conducted at the study level (i.e., each land use from a

574   study contributes one data point). In the models, log-transformed multiplicative β diversity (to

575   improve normality) and untransformed γ diversity were the responses. Land uses, sampling

576   methods, climatic PC1 and PC2 scores, number of sampling sites, standard deviations of

577   sampling efforts, PC1 scores based on sampling completeness, and study extent were added as

578   predictors. Climatic PC1 and PC2 scores were averaged across assemblages of the same land use

579   in each study. Study extent and number of sampling sites were log-transformed, as their effects

580   tend to be non-linear (Beck et al., 2013; Marcon, Zhang, & Hérault, 2014; Marion et al., 2017;

581   Soininen, McDonald, & Hillebrand, 2007). We added sampling completeness of γ diversity as

582   weights in the models to account for some pooled assemblages being more unreliable in diversity

583   estimations due to low completeness. Study identity was added as a random intercept.

584   We started with a model that included the interaction between land use and study extent due

585   to potential differences in distance-decay relationship across land uses. However, the interaction

586   term was non-significant. Therefore, we included no interaction term in the final model. Again,

587   an omnibus test was conducted for the effect of land use, and if significant, pairwise comparisons

588   were conducted across land use. Linear mixed models were built with R package lme4 (Bates,

589   Mächler, Bolker, & Walker, 2015) and p-values were obtained from lmerTest (Kuznetsova et al.,

590   2017). Pairwise comparisons were conducted in emmeans (Lenth, 2024), with the p-values

591   adjusted by False Discovery Rate corrections.

592

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

594   If agricultural and urban land uses increase phylogenetic habitat filtering, their negative effect

595   on phylogenetic diversity should still be significant after adding taxonomic diversity as a

596   covariate. Previous studies have used this approach to assess whether environments have less

597   phylogenetic diversity than expected based on taxonomic diversity (Barreto, Graham, & Rangel,

598   2019; Sol, Bartomeus, González-Lagos, & Pavoine, 2017). We did not use null model analyses

599   because some of the studies in our meta-data set included studies with a single land use, which

600   did not capture species that fail to persist in different land uses (Lessard, Belmaker, Myers,

601   Chase, & Rahbek, 2012).

602   We added taxonomic diversity as an additional predictor to the phylogenetic diversity models

603   described in Objective 1a-c. For α and γ diversity, the relationship between phylogenetic and

604   taxonomic diversity is a decelerating relationship, but for β diversity, it is largely linear (Figure

605   S1). Thus, we added log-transformed taxonomic diversity into each model. Note that for α and β

606   diversity models, the responses were also log-transformed. This effectively models a power law

607   relationship, which can range from linear to non-linear. We only conducted pairwise

608   comparisons between land uses if the omnibus test revealed a significant effect.

609

610   **<u>Objective 3: Genus abundance across land uses</u>**

611   To facilitate interpretations of diversity patterns, we further identified genera that have reduced

612   abundance in agricultural and urban habitats relative to natural habitats. We conducted the

613   analyses at the genus- rather than species-level, as the latter would lead to strong temperate

614   region biases, given that more tropical studies relied on morphospecies or genus-level

615   identifications. We selected 51 genera for this objective, as they are frequently detected across

616   studies, and thus, the effects of land use can be reliably quantified (see Text S4 for details).

617   Our analyses included genera with different geographical distributions, such as the

618   cosmopolitan genus *Megachile* and the Neotropical genus *Partamona* (Michener, 2007). Thus,

619   different trends across genera could be driven by their varying sensitivity to land use changes

620   and regional differences in the extent of environmental changes and management intensity.

621   Quantifying the contributions of each mechanism would require additional life-history and

622   environmental data. Nevertheless, our results can identify the genera more systematically

623   affected by different land use drivers regardless of the underlying mechanisms

624   We built a model for each genus with their abundance in each assemblage as the response and

625   land use, sampling method, and climatic PC1 and PC2 scores as predictors. Random effects were

626   identical with the α-diversity models (Objective 1a), with study identity as a random intercept

627   and land use as a random slope to control for between-study differences. Again, a spatial term

628   based on Matérn correlation nested within studies was added to control for spatial

629   autocorrelation. We used negative binomial mixed models to analyze abundance changes across

630   land uses (Warton, 2005). An offset capturing log-transformed sampling effort of each

631   assemblage was also added.

632   For one genus (*Dasypoda*), abundance data based on sampling flower visitors of all or

633   targeted plant species were not available. Thus, we dropped sampling method from the model.

634   For 31 genera, the effects of land use were only compared between agricultural and natural

635   habitats, as there was a lack of urban studies containing abundance data of these genera. When

636   three land uses were analyzed, we conducted pairwise comparisons if a significant result was

637   obtained from the omnibus test. As we analyzed multiple genera, results might be affected by

638   multiple comparisons. We further adjusted pairwise comparison p-values using False Discovery

639   Rate corrections.

640   We extracted the predicted abundance for each model at each land use while holding climatic

641   PC1 and PC2 at their mean values. We predicted abundance based on sampling that targets all

642   bees. We then calculated the ratio of predicted abundance between agricultural (or urban) and

643   natural habitats (Agricultural or Urban/Natural). We further log-transformed these ratios to

644   convert them into arithmetic scales (Agresti, 2007). We then used the package *phytools* (Revell,

645   2012) to assess if there were phylogenetic signals in the log-transformed ratio based on Pagel's

646   λ.

647   Briefly, Pagel's λ assesses whether any biological characteristics follow Brownian motion, a

648   standard evolutionary model that assumes the differences in the characteristics accumulate

649   through a random walk over evolutionary time scales (Pagel, 1999). λ equals one when the

650   characteristics are consistent with Brownian motion expectations. Alternatively, λ can be as low

651   as zero when the characteristics deviate from the evolutionary model. While other metrics to

652   measure evolutionary signals exist, Pagel's λ is known to be the most robust metric according to

653   simulation studies (Münkemüller et al., 2012).

654

655   **<u>Results</u>**

656   Our analyses included bee assemblage data from 3,117 assemblages and 437,091 individuals of

657   4,002 taxonomic units from 157 studies. The majority of the data (2,574 assemblages from 120

658   studies) were in temperate regions (i.e., absolute latitude > 23.4°), mainly North America and

659   Europe, while 543 assemblages from 37 studies were in the tropics (Figure 1a). All studies

660   identified specimens to species-level or morphospecies-level whenever possible, except two

661   studies, which identified specimens to genus-level. Sampling methods in our datasets range from

662   point-based sampling (e.g., single vane trap) to aggregating samples within an area as large as 10

663   ha. In general, most studies were conducted along transects <100m or within plots < 1ha (Table

664   S1). Forty-two studies (27%) provided data on bee assemblages in more than one land use. All

665   diversity models had high conditional R^2 (0.63 – 0.91, Table S5-S8).

666

667   **Objective 1a: α diversity**

668   Taxonomic α-diversity declined by an average of 15.8% in agricultural ($P = 0.006$; 95% CI:

669   1.9%, 27.6%) and 19.6% in urban habitats ($P = 0.006$; 95% CI: 3.1%, 33.2%) compared with

670   natural habitats after controlling for climatic and sampling differences (linear mixed models;

671   Figure 1b, Table S5). Using the genus-level phylogeny of bees (Hedtke *et al.*, 2013), we found

672   that phylogenetic α-diversity declined by an average of 11.0% in agricultural habitats ($P = 0.005$;

673   95% CI: 2.7%, 18.7%) and 11.6% ($P = 0.017$; 95% CI: 1.0%, 21.1%) in urban habitats relative to

674   natural habitats (Figure 1c, Table S5). Pairwise comparisons between agricultural and urban

675   habitats were non-significant for both diversity metrics.

676

677   **Objective 1b: β diversity**

678   The average taxonomic β-diversity was 1.75 (95% CI = 1.66, 1.83), making up 42.7% of the

679   taxonomic γ diversity. Using linear mixed models, we observed a 6.4% decline in taxonomic β-

680   diversity in agricultural habitats relative to natural habitats, although the results were marginally

681   non-significant (p = 0.06; 95% CI = 1.1%, 11.4%; Figure 1c, Table S6). Pairwise comparisons

682   also revealed marginally non-significant differences between urban and natural habitats, with

683   8.8% higher taxonomic β-diversity in urban habitats (p = 0.06; 95% CI = -0.4%, 18.7%; Figure

684   1c, Table S6). However, we detected 16.2% higher taxonomic β-diversity in urban compared to

685   agricultural habitats (p = 0.004; 95% CI = 6.5%, 26.8%).

686   Across datasets, phylogenetic β diversity averaged at 1.20 (95% CI = 1.17, 1.22), equivalent

687   to 16.7% contribution of phylogenetic γ diversity. Phylogenetic β-diversity was highest in urban

688   habitats—6.4% higher than natural habitats (p = 0.004; 95% CI = 2.2%, 10.7%; Figure 1c, Table

689   S5) and 8.8% higher than agricultural habitats (p < 0.001; 95% CI: 4.5%, 13.3%). However, we

690   found minimal evidence of differences between agricultural and natural habitats.

691

692   **Objective 1c: γ diversity**

693   Taxonomic γ diversity was, on average, 25.2% lower in agricultural than in natural habitats (p

694   = 0.008; 95% CI: 10.5%, 39.9%; Figure 1d, Table S7). A 15.6% decline was also observed in

695   urban habitats relative to natural habitats, but the difference was not statistically significant.

696   Differences between urban and agricultural habitats were also non-significant.

697   Similarly, we found that phylogenetic γ diversity declined by 17.8% (p = 0.006; 95% CI:

698   8.7%, 26.7%) in agricultural habitats relative to natural habitats (Figure 1d, Table S7). The

699   pairwise comparison between natural and urban habitats, as well as between agricultural and

700   urban habitats, was non-significant.

701

702   **Objective 2: Increasing phylogenetic filters in agricultural and urban habitats**

703   After controlling for their taxonomic counterparts using linear mixed models, phylogenetic α

704   and γ diversity metrics exhibited minimal differences across land uses (Figure 2a, 2c, Table S8).

705   However, we found that phylogenetic β diversity was highest in urban habitats, while

706   agricultural and natural habitats exhibited similar values (Figure 2b, Table S8). Specifically,

707   phylogenetic β diversity in urban habitats was 3.9% higher than in natural habitats (p = 0.03;

708   95% CI: 0.44%, 7.5%) and 4.5% higher than in agricultural habitats (p = 0.03; 95% CI: 0.84%,

709   7.97%).

710

711   **Objective 3: Genus abundance across land uses**

712   Compared with their average abundance in natural habitats, 73% and 61% of common genera

713   exhibited reduced average abundance in agricultural and urban habitats, respectively, echoing the

714   results of diversity analyses (Table S9, Figure S2). Nine genera showed significantly lower

715   abundance in agricultural habitats, four belonging to the family Megachilidae (*Osmia*, *Hoplitis*,

716   *Megachile*, *Anthidium*). Only *Protandrena* (mining bees, ground nesters) had increased

717   abundance in agricultural habitats relative to natural habitats. For urban habitats, only *Osmia*

718   (mason bees, primarily cavity nesters) exhibited a significant response to land use, with reduced

719   abundance in urban relative to natural habitats. We detected some phylogenetic signal in the

720   responses to agricultural (Pagel's $\lambda = 0.40$, $P = 0.06$) and minimal signals in the responses to

721   urban habitats (Pagel's $\lambda < 0.001$, $P = 1$) (Figure 3). After controlling phylogeny, responses of

722   bee genera to urban and agricultural habitats were weakly correlated (Pearson's r = 0.02) (Figure

723   S2).

724

725   **Discussion**

726   Biodiversity loss observed at local scales (α diversity) can be dampened or amplified at

727   larger spatial scales (γ diversity), depending on changes in the scaling factor (β diversity)

728 (Socolar et al., 2016). We synthesized the trends in how two major land use drivers, namely

729 agriculturalization and urbanization, affect bee taxonomic and phylogenetic α, β, and γ diversity.

730 We found that the trends in α, β, and γ diversity are largely consistent between taxonomic and

731 phylogenetic metrics when responding to the same land use driver. The α diversity declines

732 under the different anthropogenic land uses are consistent with our expectations and previous

733 studies based on other taxa (Millard et al., 2021; Newbold et al., 2015). The responses of β

734 diversity to land uses are more variable, as urban habitats exhibited higher β diversity than

735 natural habitats. At the same time, we found some support for agricultural habitats having

736 reduced taxonomic β but not phylogenetic β diversity. These ultimately lead to reduced

737 taxonomic and phylogenetic γ diversity in agricultural habitats, but not urban habitats, where we

738 failed to detect significant γ diversity loss compared to natural habitats. For bees, these results

739 provide additional evidence of the threats of agricultural and urban expansion (Dicks et al., 2021)

740 by demonstrating their negative impacts on phylogenetic α diversity in addition to taxonomic α

741 diversity. The findings also highlight the threat of agricultural expansions to large-scale bee

742 diversity due to systematic γ diversity decline. Broadly, our results provide empirical evidence

743 showing that, although α diversity responses may be similar across land use drivers, β diversity

744 responses vary, resulting in different γ diversity consequences.

745   In our study, most datasets compared assemblages within a single city or landscape, with the

746 mean and 95% percentile of the study extent being 38 km and 478 km, respectively. At these

747 scales, different management practices within cities, such as varying ornamental plants or

748 mowing frequencies due to owner preferences (Aronson et al., 2017; Lerman, Contosta, Milam,

749 & Bang, 2018; Prendergast et al., 2022), can increase environmental heterogeneity and,

750 therefore, result in higher β diversity than natural habitats (Alberti, 2016). Conversely, β

751   diversity exhibited varying trends or marginal declines in agricultural habitats across studies.

752   While agricultural activities reduce environmental heterogeneity, particularly in monocultural

753   croplands (Leong, Ponisio, Kremen, Thorp, & Roderick, 2016), the effects can be more variable

754   in subsistence agriculture systems (Landaverde-González et al., 2017), potentially explaining the

755   marginal results. This ultimately led to detectable declines of γ diversity in agricultural habitats

756   but not urban habitats. Thus, our results indicate that while land use impacts are usually reported

757   to affect α diversity negatively across terrestrial taxa, these conclusions do not necessarily extend

758   to γ diversity, particularly with urbanization (Fenoglio, Rossetti, & Videla, 2020; Liang, He,

759   Theodorou, & Yang, 2023; Newbold et al., 2015; Sol et al., 2017).

760   We found no evidence that land use change systematically strengthens phylogenetic habitat

761   filtering, and in fact, we found relaxed filtering in urban habitats for β diversity of bees. Previous

762   bee studies have found variable phylogenetic habitat filtering effects across different types of

763   agricultural and urban environments (Bartomeus, Cariveau, Harrison, & Winfree, 2018; Odanaka

764   & Rehan, 2019; Ramírez, Hernández, Link, & López-Uribe, 2015; Villalta, Bouget, Lopez-

765   Vaamonde, & Baude, 2022), potentially leading to no generalizable patterns when coarse land

766   use classification is used. Studies of phylogenetic habitat filtering for β diversity are rare. The

767   weakly relaxed phylogenetic habitat filtering in urban habitats detected can again be explained

768   by increased environmental heterogeneity in cities compared with natural and agricultural

769   habitats (Alberti, 2016; Aronson et al., 2017). For example, given the strong co-evolutionary

770   history between bees and plants (Brown & Cunningham, 2022), different planting preferences

771   across urban green spaces can attract varying bee lineages, leading to higher phylogenetic β

772   diversity than expected based on taxonomic β diversity. Nevertheless, the weakly relaxed

773   phylogenetic filtering for phylogenetic β diversity did not propagate to γ diversity of bees in

774 urban habitats, as phylogenetic β diversity only contributed to 16.7% of γ diversity across

775 studies.

776   Apart from their varying impacts on bee diversity, another difference between the two land

777 uses is that the genus-level abundance changes exhibited an intermediate phylogenetic signal in

778 agricultural habitats but minimal signal in urban habitats. Our analyses' low number of genera

779 (≤51) limited our statistical power (Münkemüller et al., 2012), while genus-level analyses can

780 underestimate phylogenetic signals (Rabosky, 2015). Species-level analyses, including rare

781 species, are needed to determine the true extent of phylogeny in governing bees' responses to the

782 two land uses. Nevertheless, the stronger phylogenetic signals in agricultural habitats suggest a

783 higher importance of evolutionarily conserved traits, such as nesting biology and lecty (Odanaka

784 & Rehan, 2019), in determining species abundance in these environments (Grab et al., 2019).

785 Alternatively, species responses to urban habitats may be more driven by stochasticity (Sattler et

786 al., 2010) or evolutionarily labile traits, such as thermal tolerances (Hamblin, Youngsteadt,

787 López-Uribe, & Frank, 2017).

788   As phylogenetic and taxonomic diversity respond similarly to agricultural and urban land

789 uses, conservation measures that increase taxonomic diversity in agricultural and urban habitats

790 are expected to increase their phylogenetic counterparts. These findings can facilitate decision-

791 making in management targeting multiple diversity metrics, as the responses of phylogenetic

792 diversity to different environmental drivers are less understood than those of taxonomic diversity

793 (Cadotte & Tucker, 2018). For α diversity, measures such as organic farming, crop

794 diversification, establishing flower strips, and planting gardens have been found to increase

795 pollinator taxonomic α-diversity in meta-analyses or quantitative syntheses (Kennedy et al.,

796 2013; Lichtenberg et al., 2017; Majewska & Altizer, 2020; Scheper et al., 2013). Studies have

797 also evaluated the effectiveness of conservation measures in enhancing taxonomic β diversity

798 (Ponisio, M'Gonigle, & Kremen, 2016), although they are relatively rare compared with studies

799 focusing on taxonomic α diversity. The same environmental drivers could increase taxonomic α

800 diversity but reduce taxonomic β diversity in bees (Steinert, Sydenham, Eldegard, & Moe, 2020),

801 meaning that associated conservation measures can simultaneously mitigate and exacerbate the

802 impacts of land use change, leading to unclear net effects on γ diversity. Thus, we emphasize the

803 importance of conducting additional taxonomic β and γ diversity assessments on the

804 effectiveness of conservation measures to better understand their contributions to mitigating land

805 use impacts.

806   Many large-scale conservation assessments focusing on the impacts of land uses are based on

807 projecting α diversity models to different land use scenarios (Chaudhary, Verones, de Baan, &

808 Hellweg, 2015; De Palma et al., 2017; Newbold et al., 2015). While α diversity patterns are

809 helpful for conservation planning, they might not apply to biodiversity at larger spatial scales

810 (e.g., national, regional, or landscape-level biodiversity), which might have

811 exacerbated/weakened diversity loss depending on β diversity changes (Socolar et al., 2016). Our

812 findings demonstrate that qualitative conclusions about land use impacts can differ between α

813 and γ diversity analyses. Based on our results, while taxonomic and phylogenetic α diversity of

814 bees might exhibit similar changes in agriculturalization and urbanization hotspots, the

815 consequences for γ diversity can be very different, with more substantial impacts at larger scales

816 expected in agriculturalization hotspots such as West Africa and Southeast Asia (Williams et al.,

817 2021). Given the need to conserve biodiversity and its associated ecosystem functions at multiple

818 scales (Socolar et al., 2016; Winfree et al., 2018), our study confirms the threat of agricultural

819 expansions to global bee diversity. It also highlights the need to understand processes

820 determining β and γ diversity changes and integrate the two-diversity metrics into conservation

821 assessments.

822

823 **Author Contributions:** T.P.N.T, L.C.P and T.C.B. conceived the idea. All authors except

824 T.P.N.T. and T.C.B. provided bee community data. T.P.N.T., L.C.P., and J.S.A. collated and

825 cleaned the bee data from all authors. T.P.N.T. designed the methods and analyses, while T.C.B.

826 and L.C.P. provided significant input. T.P.N.T analyzed the data. T.P.N.T. led the manuscript

827 writing. All authors contributed to revision and editing.

828

829 **Conflict of Interest Statement:** We declare there is no conflict of interest.

830

831 **Data availability:** R-scripts and 97% (152 of 157 analyzed studies) diversity and genus

832 abundance data will be uploaded to Zenodo (DOI: 10.5281/zenodo.10659631) and GitHub

833 (https://github.com/tpaknok/Bee_and_land_use). For the remaining 3% of studies with restricted

834 access, please contact the co-authors listed in Table S1 directly.

835

941

942   References

943   Agresti, A. (2007). An introduction to categorical data analysis. Hoboken, NJ: Wiley-

944   Interscience.

945   Aizen, M., Aguiar, S., Biesmeijer, J., Garibaldi, L., Inouye, D., Jung, C., . . . Seymour, C. (2019).

946   Global agricultural productivity is threatened by increasing pollinator dependence

947   without a parallel increase in crop diversification. Global Change Biology, 25(10), 3516-

948   3527. doi:https://doi.org/10.1111/gcb.14736

949   Alberti, M. (2016). Cities that think like planets: complexity, resilience, and innovation in hybrid

950   ecosystems: University of Washington Press.

951   Aronson, M., Lepczyk, C., Evans, K., Goddard, M., Lerman, S., MacIvor, J., . . . Vargo, T.

952   (2017). Biodiversity in the city: key challenges for urban green space management.

953   Frontiers in Ecology and the Environment, 15(4), 189-196.

954   doi:https://doi.org/10.1002/fee.1480

955 Ascher, J. S., & Pickering, J. (2022). Discover Life bee species guide and world checklist

956   (Hymenoptera: Apoidea: Anthophila) - Draft 56.

957 Azaele, S., Maritan, A., Cornell, S. J., Suweis, S., Banavar, J. R., Gabriel, D., & Kunin, W. E.

958   (2015). Towards a unified descriptive theory for spatial ecology: predicting biodiversity

959   patterns across spatial scales. Methods in Ecology and Evolution, 6(3), 324-332.

960   doi:https://doi.org/10.1111/2041-210X.12319

961 Barreto, E., Graham, C. H., & Rangel, T. F. (2019). Environmental factors explain the spatial

962   mismatches between species richness and phylogenetic diversity of terrestrial mammals.

963   Global Ecology and Biogeography, 28(12), 1855-1865.

964   doi:https://doi.org/10.1111/geb.12999

965 Bartomeus, I., Cariveau, D. P., Harrison, T., & Winfree, R. (2018). On the inconsistency of

966   pollinator species traits for predicting either response to land-use change or functional

967   contribution. Oikos, 127(2), 306-315. doi:https://doi.org/10.1111/oik.04507

968 Baselga, A. (2013). Multiple site dissimilarity quantifies compositional heterogeneity among

969   several sites, while average pairwise dissimilarity may be misleading. Ecography, 36(2),

970   124-128. doi:https://doi.org/10.1111/j.1600-0587.2012.00124.x

971 Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models

972   Using lme4. Journal of Statistical Software, 67(1), 1 - 48.

973   doi:https://doi.org/10.18637/jss.v067.i01

974 Beck, J., Holloway, J. D., & Schwanghart, W. (2013). Undersampling and the measurement of

975   beta diversity. Methods in Ecology and Evolution, 4(4), 370-382.

976   doi:https://doi.org/10.1111/2041-210x.12023

977   Blowes, S. A., Daskalova, G. N., Dornelas, M., Engel, T., Gotelli, N. J., Magurran, A. E., . . .

978   Chase, J. M. (2022). Local biodiversity change reflects interactions among changing

979   abundance, evenness, and richness. Ecology, 103(12), e3820.

980   doi:https://doi.org/10.1002/ecy.3820

981   Brown, J., & Cunningham, S. A. (2022). Biogeographic history predicts bee community

982   structure across floral resource gradients in south-east Australia. Diversity and

983   Distributions, 28(7), 1475-1486. doi:https://doi.org/10.1111/ddi.13583

984   Cadotte, M. W., & Tucker, C. M. (2018). Difficult decisions: Strategies for conservation

985   prioritization when taxonomic, phylogenetic and functional diversity are not spatially

986   congruent. Biological conservation, 225, 128-133.

987   doi:https://doi.org/10.1016/j.biocon.2018.06.014

988   Cariveau, D. P., & Winfree, R. (2015). Causes of variation in wild bee responses to

989   anthropogenic drivers. Current Opinion in Insect Science, 10, 104-109.

990   doi:https://doi.org/10.1016/j.cois.2015.05.004

991   Carvalheiro, L. G., Kunin, W. E., Keil, P., Aguirre-Gutiérrez, J., Ellis, W. N., Fox, R., . . .

992   Biesmeijer, J. C. (2013). Species richness declines and biotic homogenisation have

993   slowed down for NW-European pollinators and plants. Ecology Letters, 16(7), 870-878.

994   doi:https://doi.org/10.1111/ele.12121

995   Chao, A., Henderson, P. A., Chiu, C.-H., Moyes, F., Hu, K.-H., Dornelas, M., & Magurran, A. E.

996   (2021). Measuring temporal change in alpha diversity: A framework integrating

997   taxonomic, phylogenetic and functional diversity and the iNEXT.3D standardization.

998   Methods in Ecology and Evolution, 12(10), 1926-1940. doi:https://doi.org/10.1111/2041-

999   210X.13682

1000   Chao, A., & Jost, L. (2012). Coverage-based rarefaction and extrapolation: standardizing

1001   samples by completeness rather than size. Ecology, 93(12), 2533-2547.

1002   doi:https://doi.org/10.1890/11-1952.1

1003   Chase, J. M., McGill, B. J., Thompson, P. L., Antão, L. H., Bates, A. E., Blowes, S. A., . . .

1004   Supp, S. R. (2019). Species richness change across spatial scales. Oikos, 128(8), 1079-

1005   1091. doi:https://doi.org/10.1111/oik.05968

1006   Chaudhary, A., Verones, F., de Baan, L., & Hellweg, S. (2015). Quantifying Land Use Impacts

1007   on Biodiversity: Combining Species–Area Models and Vulnerability Indicators.

1008   Environmental Science & Technology, 49(16), 9987-9995.

1009   doi:https://doi.org/10.1021/acs.est.5b02507

1010   Christie, A. P., Amano, T., Martin, P. A., Shackelford, G. E., Simmons, B. I., & Sutherland, W.

1011   J. (2019). Simple study designs in ecology produce inaccurate estimates of biodiversity

1012   responses. Journal of Applied Ecology, 56(12), 2742-2754.

1013   doi:https://doi.org/10.1111/1365-2664.13499

1014   Crist, T. O., & Veech, J. A. (2006). Additive partitioning of rarefaction curves and species–area

1015   relationships: unifying α-, β- and γ-diversity with sample size and habitat area. Ecology

1016   Letters, 9(8), 923-932. doi:https://doi.org/10.1111/j.1461-0248.2006.00941.x

1017   Crist, T. O., Veech, J. A., Gering, J. C., & Summerville, K. S. (2003). Partitioning species

1018   diversity across landscapes and regions: a hierarchical analysis of α, β, and γ diversity.

1019   The American Naturalist, 162(6), 734-743. doi:https://doi.org/10.1086/378901

1020   Davison, C. W., Rahbek, C., & Morueta-Holme, N. (2021). Land-use change and biodiversity:

1021   Challenges for assembling evidence on the greatest threat to nature. Global Change

1022   Biology, 27(21), 5414-5429. doi:https://doi.org/10.1111/gcb.15846

1023   De Palma, A., Abrahamczyk, S., Aizen, M. A., Albrecht, M., Basset, Y., Bates, A., . . . Purvis, A.

1024   (2016). Predicting bee community responses to land-use changes: Effects of geographic

1025   and taxonomic biases. Scientific Reports, 6(1), 31153.

1026   doi:https://doi.org/10.1038/srep31153

1027   De Palma, A., Kuhlmann, M., Bugter, R., Ferrier, S., Hoskins, A. J., Potts, S. G., . . . Purvis, A.

1028   (2017). Dimensions of biodiversity loss: Spatial mismatch in land-use impacts on species,

1029   functional and phylogenetic diversity of European bees. Diversity and Distributions,

1030   23(12), 1435-1446. doi:https://doi.org/10.1111/ddi.12638

1031   Dicks, L. V., Breeze, T. D., Ngo, H. T., Senapathi, D., An, J., Aizen, M. A., . . . Potts, S. G.

1032   (2021). A global-scale expert assessment of drivers and risks associated with pollinator

1033   decline. Nature Ecology & Evolution, 5(10), 1453-1461. doi:10.1038/s41559-021-01534-

1034   9

1035   Duarte, L. d. S. (2011). Phylogenetic habitat filtering influences forest nucleation in grasslands.

1036   Oikos, 120(2), 208-215. doi:https://doi.org/10.1111/j.1600-0706.2010.18898.x

1037   Ellis, E. C., Klein Goldewijk, K., Siebert, S., Lightman, D., & Ramankutty, N. (2010).

1038   Anthropogenic transformation of the biomes, 1700 to 2000. Global ecology and

1039   biogeography, 19(5), 589-606.

1040   Fenoglio, M. S., Rossetti, M. R., & Videla, M. (2020). Negative effects of urbanization on

1041   terrestrial arthropod communities: A meta-analysis. Global Ecology and Biogeography,

1042   29(8), 1412-1429. doi:https://doi.org/10.1111/geb.13107

1043   Ganuza, C., Redlich, S., Uhler, J., Tobisch, C., Rojas-Botero, S., Peters, M. K., . . . Steffan-

1044   Dewenter, I. (2022). Interactive effects of climate and land use on pollinator diversity

1045   differ among taxa and scales. Science Advances, 8(18), eabm9359.

1046   doi:http://doi.org/10.1126/sciadv.abm9359

1047   Grab, H., Branstetter, M. G., Amon, N., Urban-Mead, K. R., Park, M. G., Gibbs, J., . . .

1048   Danforth, B. N. (2019). Agriculturally dominated landscapes reduce bee phylogenetic

1049   diversity and pollination services. Science, 363(6424), 282-284.

1050   doi:https://doi.org/10.1126/science.aat6016

1051   Hamblin, A. L., Youngsteadt, E., López-Uribe, M. M., & Frank, S. D. (2017). Physiological

1052   thermal limits predict differential responses of bees to urban heat-island effects. Biology

1053   letters, 13(6), 20170125. doi:https://doi.org/10.1098/rsbl.2017.0125

1054   Harrison, T., Gibbs, J., & Winfree, R. (2018). Phylogenetic homogenization of bee communities

1055   across ecoregions. Global Ecology and Biogeography, 27(12), 1457-1466.

1056   doi:https://doi.org/10.1111/geb.12822

1057   Hedtke, S. M., Patiny, S., & Danforth, B. N. (2013). The bee tree of life: a supermatrix approach

1058   to apoid phylogeny and biogeography. BMC Evolutionary Biology, 13(1), 138.

1059   doi:https://doi.org/10.1186/1471-2148-13-138

1060   Hendrix, S. D., Forbes, A. A., & MacDougall, C. E. D. (2018). Variation in the phylogenetic

1061   diversity of wild bees at produce farms and prairies. Agriculture, ecosystems &

1062   environment, 259, 168-173. doi:https://doi.org/10.1016/j.agee.2018.03.005

1063   Hudson, L. N., Newbold, T., Contu, S., Hill, S. L. L., Lysenko, I., De Palma, A., . . . Purvis, A.

1064   (2014). The PREDICTS database: a global database of how local terrestrial biodiversity

1065   responds to human impacts. Ecology and Evolution, 4(24), 4701-4735.

1066   doi:https://doi.org/10.1002/ece3.1303

1067   Jost, L. (2007). Partitioning diversity into independent alpha and beta components. Ecology,

1068   88(10), 2427-2439. doi:https://doi.org/10.1890/06-1736.1

1069   Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., . . . Kessler, M.

1070   (2017). Climatologies at high resolution for the earth's land surface areas. Scientific

1071   Data, 4(1), 170122. doi:https://doi.org/10.1038/sdata.2017.122

1072   Kennedy, C. M., Lonsdorf, E., Neel, M. C., Williams, N. M., Ricketts, T. H., Winfree, R., . . .

1073   Kremen, C. (2013). A global quantitative synthesis of local and landscape effects on wild

1074   bee pollinators in agroecosystems. Ecology Letters, 16(5), 584-599.

1075   doi:https://doi.org/10.1111/ele.12082

1076   Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest Package: Tests in

1077   Linear Mixed Effects Models. Journal of Statistical Software, 82(13), 1 - 26.

1078   doi:https://doi.org/10.18637/jss.v082.i13

1079   Landaverde-González, P., Quezada-Euán, J. J. G., Theodorou, P., Murray, T. E., Husemann, M.,

1080   Ayala, R., . . . Paxton, R. J. (2017). Sweat bees on hot chillies: provision of pollination

1081   services by native bees in traditional slash-and-burn agriculture in the Yucatán Peninsula

1082   of tropical Mexico. Journal of Applied Ecology, 54(6), 1814-1824.

1083   doi:https://doi.org/10.1111/1365-2664.12860

1084   Lee, R. H., & Guénard, B. (2019). Choices of sampling method bias functional components

1085   estimation and ability to discriminate assembly mechanisms. Methods in Ecology and

1086   Evolution, 10(6), 867-878. doi:https://doi.org/10.1111/2041-210X.13175

1087   Lenth, R. (2024). emmeans: Estimated Marginal Means, aka Least-Squares Means. Retrieved

1088   from https://rvlenth.github.io/emmeans/

1089   Leong, M., Ponisio, L. C., Kremen, C., Thorp, R. W., & Roderick, G. K. (2016). Temporal

1090   dynamics influenced by global change: bee community phenology in urban, agricultural,

1091   and natural landscapes. Global Change Biology, 22(3), 1046-1053.

1092   doi:https://doi.org/10.1111/gcb.13141

1093   Lerman, S. B., Contosta, A. R., Milam, J., & Bang, C. (2018). To mow or to mow less: Lawn

1094   mowing frequency affects bee abundance and diversity in suburban yards. Biological

1095   Conservation, 221, 160-174. doi:https://doi.org/10.1016/j.biocon.2018.01.025

1096   Lessard, J.-P., Belmaker, J., Myers, J. A., Chase, J. M., & Rahbek, C. (2012). Inferring local

1097   ecological processes amid species pool influences. Trends in Ecology & Evolution,

1098   27(11), 600-607. doi:https://doi.org/10.1016/j.tree.2012.07.006

1099   Liang, H., He, Y.-D., Theodorou, P., & Yang, C.-F. (2023). The effects of urbanization on

1100   pollinators and pollination: A meta-analysis. Ecology Letters, 26(9), 1629-1642.

1101   doi:https://doi.org/10.1111/ele.14277

1102   Lichtenberg, E. M., Kennedy, C. M., Kremen, C., Batáry, P., Berendse, F., Bommarco, R., . . .

1103   Crowder, D. W. (2017). A global synthesis of the effects of diversified farming systems

1104   on arthropod diversity within fields and across agricultural landscapes. Global Change

1105   Biology, 23(11), 4946-4957. doi:https://doi.org/10.1111/gcb.13714

1106   Majewska, A. A., & Altizer, S. (2020). Planting gardens to support insect pollinators.

1107   Conservation Biology, 34(1), 15-25. doi:https://doi.org/10.1111/cobi.13271

1108   Marcon, E., Zhang, Z., & Hérault, B. (2014). The Decomposition of Similarity-Based Diversity

1109   and its Bias Correction. Retrieved from https://agroparistech.hal.science/hal-00989454

1110   Marion, Z. H., Fordyce, J. A., & Fitzpatrick, B. M. (2017). Pairwise beta diversity resolves an

1111   underappreciated source of confusion in calculating species turnover. Ecology, 98(4),

1112   933-939. doi:https://doi.org/10.1002/ecy.1753

1113   Matuschek, H., Kliegl, R., Vasishth, S., Baayen, H., & Bates, D. (2017). Balancing Type I error

1114   and power in linear mixed models. Journal of Memory and Language, 94, 305-315.

1115   doi:https://doi.org/10.1016/j.jml.2017.01.001

1116   Mayfield, M. M., Bonser, S. P., Morgan, J. W., Aubin, I., McNamara, S., & Vesk, P. A. (2010).

1117   What does species richness tell us about functional trait diversity? Predictions and

1118   evidence for responses of species and functional trait diversity to land-use change. Global

1119   Ecology and Biogeography, 19(4), 423-431. doi:https://doi.org/10.1111/j.1466-

1120   8238.2010.00532.x

1121   Michener, C. D. (2007). The bees of the world (2nd ed.). Baltimore: Johns Hopkins University

1122   Press.

1123   Millard, J., Outhwaite, C. L., Kinnersley, R., Freeman, R., Gregory, R. D., Adedoja, O., . . .

1124   Newbold, T. (2021). Global effects of land-use intensity on local pollinator biodiversity.

1125   Nature Communications, 12(1), 2902. doi:https://doi.org/10.1038/s41467-021-23228-3

1126   Mori, A. S., Isbell, F., & Seidl, R. (2018). β-Diversity, Community Assembly, and Ecosystem

1127   Functioning. Trends in Ecology & Evolution, 33(7), 549-564.

1128   doi:https://doi.org/10.1016/j.tree.2018.04.012

1129   Münkemüller, T., Lavergne, S., Bzeznik, B., Dray, S., Jombart, T., Schiffers, K., & Thuiller, W.

1130   (2012). How to measure and test phylogenetic signal. Methods in Ecology and Evolution,

1131   3(4), 743-756. doi:https://doi.org/10.1111/j.2041-210X.2012.00196.x

1132   Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Gray, C. L., Scharlemann, J. P. W., . . .

1133   Purvis, A. (2016). Global patterns of terrestrial assemblage turnover within and among

1134   land uses. Ecography, 39(12), 1151-1163. doi:https://doi.org/10.1111/ecog.01932

1135   Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., . . . Purvis, A.

1136   (2015). Global effects of land use on local terrestrial biodiversity. Nature, 520(7545), 45-

1137   50. doi:https://doi.org/10.1038/nature14324

1138   Nowakowski, A. J., Frishkoff, L. O., Thompson, M. E., Smith, T. M., & Todd, B. D. (2018).

1139   Phylogenetic homogenization of amphibian assemblages in human-altered habitats across

1140   the globe. Proceedings of the National Academy of Sciences, 115(15), E3454-E3462.

1141   doi:http://doi.org/10.1073/pnas.1714891115

1142   Odanaka, K. A., & Rehan, S. M. (2019). Impact indicators: Effects of land use management on

1143   functional trait and phylogenetic diversity of wild bees. Agriculture, Ecosystems &

1144   Environment, 286, 106663. doi:https://doi.org/10.1016/j.agee.2019.106663

1145   Pagel, M. (1999). Inferring the historical patterns of biological evolution. Nature, 401(6756),

1146   877-884. doi:https://doi.org/10.1038/44766

1147   Ponisio, L. C., M'Gonigle, L. K., & Kremen, C. (2016). On-farm habitat restoration counters

1148   biotic homogenization in intensively managed agriculture. Global Change Biology, 22(2),

1149   704-715. doi:https://doi.org/10.1111/gcb.13117

1150   Prendergast, K. S., Dixon, K. W., & Bateman, P. W. (2022). A global review of determinants of

1151   native bee assemblages in urbanised landscapes. Insect Conservation and Diversity,

1152   15(4), 385-405.

1153   Purvis, A., & Hector, A. (2000). Getting the measure of biodiversity. Nature, 405(6783), 212-

1154   219. doi:10.1038/35012221

1155   Qian, H., & Jin, Y. (2021). Are phylogenies resolved at the genus level appropriate for studies on

1156   phylogenetic structure of species assemblages? Plant Diversity, 43(4), 255-263.

1157   doi:https://doi.org/10.1016/j.pld.2020.11.005

1158   Rabosky, D. L. (2015). No substitute for real data: a cautionary note on the use of phylogenies

1159   from birth–death polytomy resolvers for downstream comparative analyses. Evolution,

1160   69(12), 3207-3216. doi:https://doi.org/10.1111/evo.12817

1161   Ramírez, S. R., Hernández, C., Link, A., & López-Uribe, M. M. (2015). Seasonal cycles,

1162   phylogenetic assembly, and functional diversity of orchid bee communities. Ecology and

1163   Evolution, 5(9), 1896-1907. doi:https://doi.org/10.1002/ece3.1466

1164   Raudenbush, S. W., & Bryk, A. S. (2002). Hierarchical linear models : applications and data

1165   analysis methods (2nd ed.). Thousand Oaks, CA: Sage Publications.

1166   Revell, L. J. (2012). phytools: an R package for phylogenetic comparative biology (and other

1167   things). Methods in Ecology and Evolution, 3(2), 217-223.

1168   doi:https://doi.org/10.1111/j.2041-210X.2011.00169.x

1169   Roswell, M., Dushoff, J., & Winfree, R. (2021). A conceptual guide to measuring species

1170   diversity. Oikos, 130(3), 321-338. doi:https://doi.org/10.1111/oik.07202

1171   Rousset, F., & Ferdy, J.-B. (2014). Testing environmental and genetic effects in the presence of

1172   spatial autocorrelation. Ecography, 37(8), 781-790.

1173   doi:https://doi.org/10.1111/ecog.00566

1174   Sattler, T., Borcard, D., Arlettaz, R., Bontadina, F., Legendre, P., Obrist, M. K., & Moretti, M.

1175   (2010). Spider, bee, and bird communities in cities are shaped by environmental control

1176   and high stochasticity. Ecology, 91(11), 3343-3353. doi:https://doi.org/10.1890/09-

1177   1810.1

1178   Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S. G., Rundlöf, M., Smith, H. G., & Kleijn, D.

1179   (2013). Environmental factors driving the effectiveness of European agri-environmental

1180   measures in mitigating pollinator loss – a meta-analysis. Ecology Letters, 16(7), 912-920.

1181   doi:https://doi.org/10.1111/ele.12128

1182   Socolar, J. B., Gilroy, J. J., Kunin, W. E., & Edwards, D. P. (2016). How Should Beta-Diversity

1183   Inform Biodiversity Conservation? Trends in Ecology & Evolution, 31(1), 67-80.

1184   doi:https://doi.org/10.1016/j.tree.2015.11.005

1185   Soininen, J., McDonald, R., & Hillebrand, H. (2007). The distance decay of similarity in

1186   ecological communities. Ecography, 30(1), 3-12. doi:https://doi.org/10.1111/j.0906-

1187   7590.2007.04817.x

1188   Sol, D., Bartomeus, I., González-Lagos, C., & Pavoine, S. (2017). Urbanisation and the loss of

1189   phylogenetic diversity in birds. Ecology Letters, 20(6), 721-729.

1190   doi:https://doi.org/10.1111/ele.12769

1191   Steinert, M., Sydenham, M. A. K., Eldegard, K., & Moe, S. R. (2020). Conservation of solitary

1192   bees in power-line clearings: Sustained increase in habitat quality through woody debris

1193   removal. Global Ecology and Conservation, 21, e00823.

1194   doi:https://doi.org/10.1016/j.gecco.2019.e00823

1195   Todorov, V., & Filzmoser, P. (2009). An Object-Oriented Framework for Robust Multivariate

1196   Analysis. Journal of Statistical Software, 32(3), 1 - 47.

1197   doi:https://doi.org/10.18637/jss.v032.i03

1198   Tucker, C. M., Aze, T., Cadotte, M. W., Cantalapiedra, J. L., Chisholm, C., Díaz, S., . . . Mooers,

1199   A. O. (2019). Assessing the utility of conserving evolutionary history. Biological

1200   Reviews, 94(5), 1740-1760. doi:https://doi.org/10.1111/brv.12526

1201   Tucker, C. M., & Cadotte, M. W. (2013). Unifying measures of biodiversity: understanding

1202   when richness and phylogenetic diversity should be congruent. Diversity and

1203   Distributions, 19(7), 845-854. doi:https://doi.org/10.1111/ddi.12087

1204   Tucker, C. M., Cadotte, M. W., Carvalho, S. B., Davies, T. J., Ferrier, S., Fritz, S. A., . . . Mazel,

1205   F. (2017). A guide to phylogenetic metrics for conservation, community ecology and

1206   macroecology. Biological Reviews, 92(2), 698-715.

1207   doi:https://doi.org/10.1111/brv.12252

1208   Tucker, C. M., Davies, T. J., Cadotte, M. W., & Pearse, W. D. (2018). On the relationship

1209   between phylogenetic diversity and trait diversity. Ecology, 99(6), 1473-1479.

1210   doi:https://doi.org/10.1002/ecy.2349

1211   Turley, N. E., Biddinger, D. J., Joshi, N. K., & López-Uribe, M. M. (2022). Six years of wild bee

1212   monitoring shows changes in biodiversity within and across years and declines in

1213   abundance. Ecology and Evolution, 12(8), e9190. doi:https://doi.org/10.1002/ece3.9190

1214   van der Plas, F. (2019). Biodiversity and ecosystem functioning in naturally assembled

1215   communities. Biological Reviews, 94(4), 1220-1245.

1216   doi:https://doi.org/10.1111/brv.12499

1217   van Klink, R., Bowler, D. E., Gongalsky, K. B., Shen, M., Swengel, S. R., & Chase, J. M.

1218   (2024). Disproportionate declines of formerly abundant species underlie insect loss.

1219   Nature, 628(8007), 359-364. doi:https://doi.org/10.1038/s41586-023-06861-4

1220   Villalta, I., Bouget, C., Lopez-Vaamonde, C., & Baude, M. (2022). Phylogenetic, functional and

1221   taxonomic responses of wild bee communities along urbanisation gradients. Science of

1222   The Total Environment, 832, 154926.

1223   doi:https://doi.org/10.1016/j.scitotenv.2022.154926

1224   Warton, D. I. (2005). Many zeros does not mean zero inflation: comparing the goodness-of-fit of

1225   parametric models to multivariate abundance data. Environmetrics, 16(3), 275-289.

1226   doi:https://doi.org/10.1002/env.702

1227   Weekers, T., Marshall, L., Leclercq, N., Wood, T. J., Cejas, D., Drepper, B., . . . Vereecken, N. J.

1228   (2022). Ecological, environmental, and management data indicate apple production is

1229   driven by wild bee diversity and management practices. Ecological Indicators, 139,

1230   108880. doi:https://doi.org/10.1016/j.ecolind.2022.108880

1231   Williams, D. R., Clark, M., Buchanan, G. M., Ficetola, G. F., Rondinini, C., & Tilman, D.

1232   (2021). Proactive conservation to prevent habitat losses to agricultural expansion. Nature

1233   Sustainability, 4(4), 314-322. doi:https://doi.org/10.1038/s41893-020-00656-5

1234   Winfree, R., Bartomeus, I., & Cariveau, D. P. (2011). Native Pollinators in Anthropogenic

1235   Habitats. Annual Review of Ecology, Evolution, and Systematics, 42(Volume 42, 2011),

1236   1-22. doi:https://doi.org/10.1146/annurev-ecolsys-102710-145042

1237   Winfree, R., Reilly, J. R., Bartomeus, I., Cariveau, D. P., Williams, N. M., & Gibbs, J. (2018).

1238   Species turnover promotes the importance of bee diversity for crop pollination at regional

1239   scales. Science, 359(6377), 791-793. doi:https://doi.org/10.1126/science.aao2117

1240

1241

1242   Table 1. Predictors for the models related to each objective. Objectives 1a, 1b, and 1c are to
1243   compare α, β, γ, diversity across three land uses, respectively. Objectives 2a, 2b, and 2c are to
1244   assess whether agricultural and urban habitats exhibited stronger phylogenetic habitat filtering in
1245   α, β, γ diversity, respectively. Objective 3 is to identify genera with altered abundance in
1246   agricultural and urban habitats relative to natural habitats. The rationales including different
1247   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.	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 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 latitude and longitude of each assemblage.	1a, 2a, 3a

1248

1249

1250   **Figure**

(a)
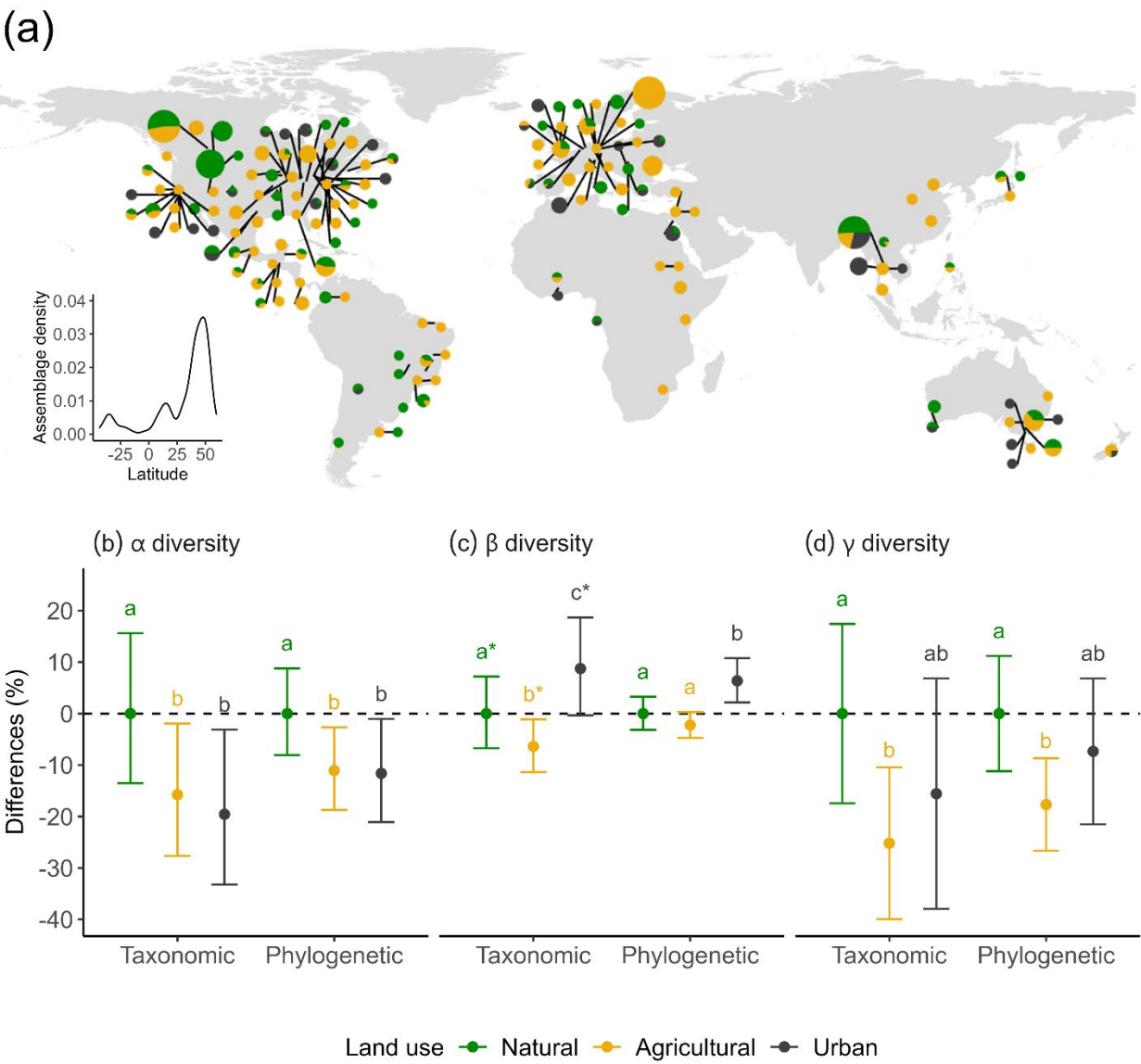
1251

1252   **Figure 1.** (a) Map showing locations of 157 studies included, and the proportion of natural,

1253   agricultural, and urban habitats sampled within the study. Pie size is proportional to the number

1254   of sampled sites in each study, ranging from 1 to 368. The density plot indicates the distribution

1255   of the studied assemblages (n = 3,117) along the latitudinal gradient. (b-d) Diversity changes

1256   relative to values of natural habitats, with each panel showing responses of one diversity metric:

1257   (b) α, (c) β, and (d) γ diversity. Point estimates represent model predictions of each land use

1258   based on fixed effects only, while error bars are 95% confidence intervals. The estimations of α

1259   diversity were obtained by holding other covariates at the mean or mode values. For β and γ

1260   diversity, the estimation reflects a standardized sampling study with all assemblages having

1261   100% sampling completeness, and other covariates at the mean or mode values. Small letters

1262   above error bars indicate results from pairwise comparisons, with different letters representing

1263   different groups. *indicates that the pairwise comparisons included marginally non-significant
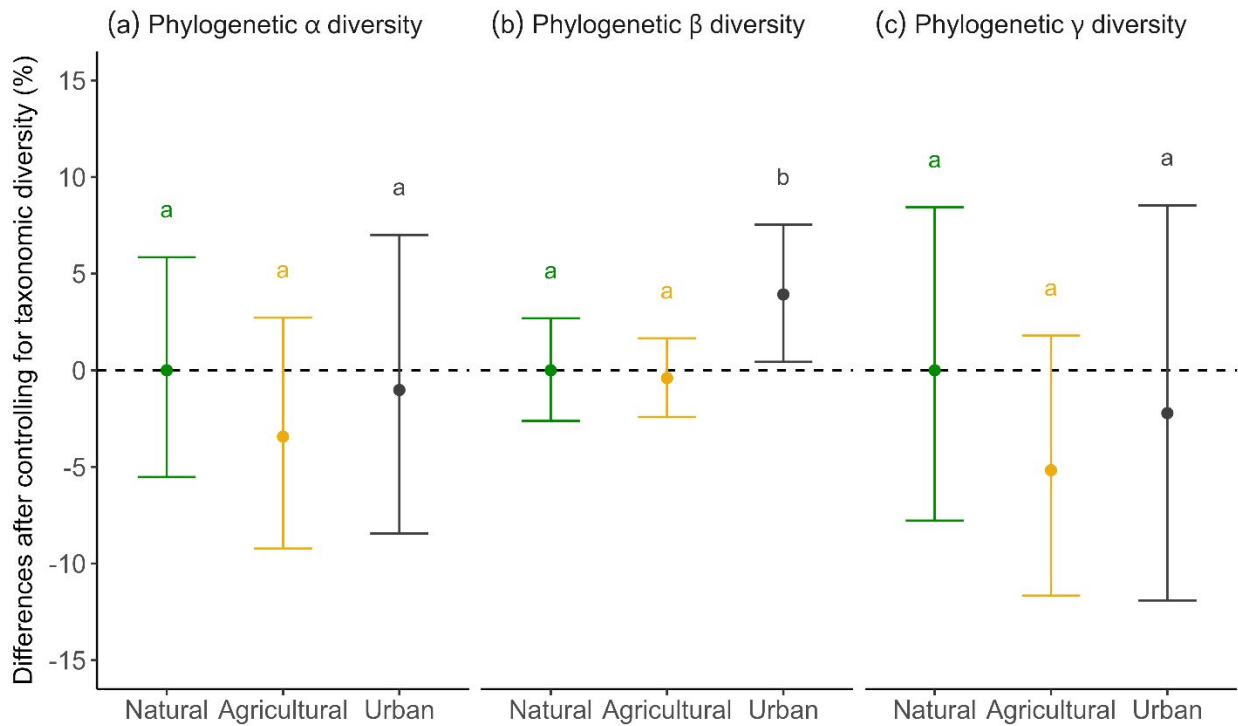
1264   results (p = 0.06).

1265

1266

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

Ratio (Agricultural or Urban / Natural)

0.1 0.3 1.0 3.0
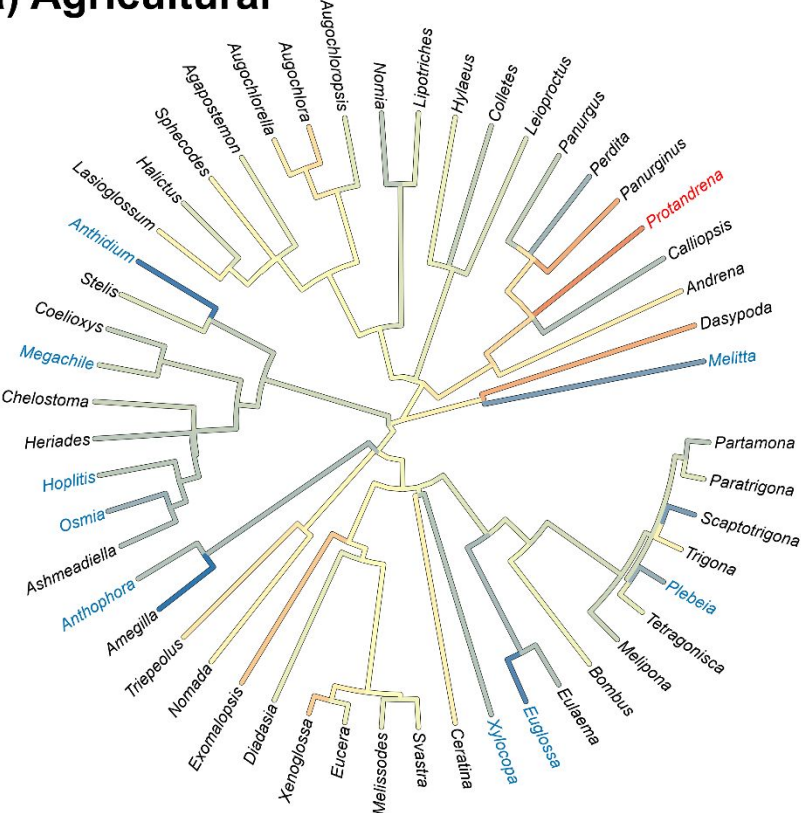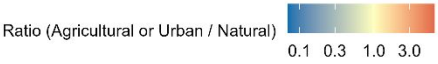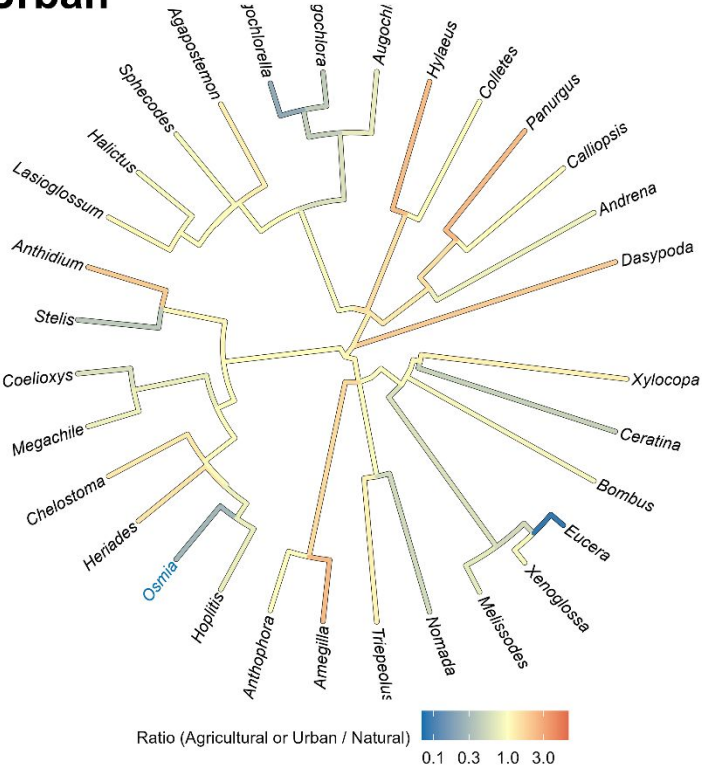
1278   **Figure 3.** Phylogenetic relationships of all genera examined and their responses to agricultural

1279   (a) and urban land uses (b) in terms of abundance. When the ratio equals 1, genus abundance in

1280   agricultural or urban habitats is the same as in natural habitats. Genera in red and blue are

1281   significantly more and less abundant in anthropogenic land uses, respectively.