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Agriculturally dominated landscapes reduce bee phylogenetic diversity and pollination services

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Land-use change threatens global biodiversity and may reshape the tree of life by favoring some lineages over others. Whether phylogenetic diversity loss compromises ecosystem service delivery remains unknown. We address this knowledge gap using extensive genomic, community, and crop datasets to examine relationships among land use, pollinator phylogenetic structure, and crop production. Pollinator communities in highly agricultural landscapes contain 230 million fewer years of evolutionary history; this loss was strongly associated with reduced crop yield and quality. Our study links landscape–mediated changes in the phylogenetic structure of natural communities to the disruption of ecosystem services. Measuring conservation success by species counts alone may fail to protect ecosystem functions and the full diversity of life from which they are derived.

A preponderance of evidence supports the positive relationship between biodiversity and ecosystem functioning (*1*–*3*), particularly the link between trait diversity and ecosystem function (*4*–*6*). In communities where species have high functional trait overlap, often owing to recent shared evolutionary history, each individual species contributes less to overall community function and potentially less to the many ecosystem services derived from the functioning of healthy ecosystems (*7*, *8*). Alternatively, closely related species may provide redundancy that ensures resilience of function under variable environmental conditions, or they may diverge in their traits through strong competition resulting in high function even among communities consisting of closely related species. Currently, it is unclear whether losses of more closely or distantly related species will have a greater affect on the magnitude of ecosystem functions. Phylogenetic diversity is a measure of the evolutionary history represented within a community. It not only captures similarities in traits that mediate responses to the environment (*9*) but also reflects similarities among taxa in the traits that contribute to ecosystem function (*10*). Understanding the role of nonrandom species loss with respect to phylogeny is essential for effectively prioritizing the conservation of either functionally important or evolutionarily diverse lineages and maintaining ecosystem function and associated ecosystem services.

Land-use change, associated with the transition from natural to agricultural lands, is a primary driver of biodiversity loss worldwide (*11*), threatening even those organisms that deliver essential ecosystem services to agriculture (*12*, *13*). Bees are responsible for pollinating the majority of our most valuable and nutritious crops (*14*, *15*). Diverse bee communities ensure high and stable delivery of pollination services (*16*), but habitat loss and agricultural intensification have been implicated in recent bee declines (*17*). The suite of traits exhibited by different bee species mediates their ability to persist in agricultural landscapes (*18*). These traits may be conserved among closely related taxa. Because lineages vary in their response to land-use change (*18*), loss of taxonomic diversity is not expected to be uniform across the phylogeny (*9*, *19*, *20*). However, the extent and pattern by which landscape simplification prunes the evolutionary history represented within pollinator communities remain poorly studied. Furthermore, we know little about the consequences of lost evolutionary history for ecosystem function, including pollination services.

To examine interactions among land-use change, phylogenetic diversity, and ecosystem function, we quantify changes in bee phylogenetic diversity across a landscape gradient. Specifically, we combine a time-calibrated genomic phylogeny (Fig. 1 and fig. S1) with extensive pollinator community and pollination datasets. The pollinator community data are derived from sampling in 27 apple orchards over 10 years (8700 records of 88 species). Landscape composition in a 750-m radius surrounding each orchard varied from a heterogeneous mix of forest, urban, old-field, and agricultural land to homogeneous landscapes dominated by agriculture (fig. S2). Our analyses focused on two unresolved questions: (i) How does land-use change influence the phylogenetic structure of pollinator communities in agroecosystems? (ii) What are the consequences of phylogenetic diversity loss on pollination services and crop yield?

We found that species loss due to agriculturally driven land-use change is not random across the bee phylogeny. Rather, some branches of the bee tree of life are "pruned" more heavily than others, resulting in communities that contain more closely related species in highly agricultural landscapes compared with those found in landscapes with less agricultural cover [$F_{(1,48)} = 10.25$, $P = 0.002$] (Fig. 2A). Although species richness was 55% lower in orchards with the highest proportion of agriculture in the landscape [$F_{(1,48)} = 8.19$, $P = 0.006$] (Fig. 2B), the loss of phylogenetic diversity was greater than would be expected as a result of changes in species richness alone [$F_{(1,48)} = 8.60$, $P = 0.005$] (fig. S3). We estimate that pollinator communities lose 35 million years of evolutionary history for every 10% increase in agricultural cover within the landscape [$F_{(1,48)} = 13.41$, $P = 0.001$] (Fig. 2C), which represents a 49% reduction in total evolutionary history compared with communities in landscapes with low agricultural cover.

Loss of phylogenetic diversity from pollinator communities along the land-use gradient could occur in two different ways. First, clades may be pruned from the full set of species present in landscapes with low agricultural cover. Alternatively, agricultural landscapes may favor particular clades, whereas other, perhaps more diverse, branches of the tree are favored in more complex landscapes, as has recently been shown (*21*). The first scenario would generate a pattern in which communities along the land-use gradient exhibit a nested structure, and the second scenario would lead to a pattern of strong species turnover, as the clades present in highly agricultural landscapes are not those favored in more diverse landscapes and vice versa (fig. S4). Here, we find that bee communities ordered along the agricultural gradient exhibit greater nestedness ($t = -105.59$, df = 99, $P < 0.05$) (fig. S5) and lower turnover ($t = 96.63$, df = 99, $P < 0.05$) than would be expected by chance, which suggests that land-use changes are pruning lineages from the more complete communities present in landscapes with low agricultural cover.

Although individual taxa varied in their response to increasing agricultural land cover,

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closely related species responded more similarly than species pairs selected at random (Blomberg's K = 0.23, $P = 0.049$) (Fig. 1). The clades most resilient to land-use change included *Bombus* and *Lasioglossum* (*Dialictus*), which are among the most commonly collected wild bees in North America. Diversification rate analysis suggests that *L.* (*Dialictus*) has undergone a recent rapid radiation (fig. S6). This result indicates that agriculturally dominated landscapes favor more recent, less evolutionarily distinct species, a finding paralleled in neotropical birds (*22*). Our analyses reveal several clades sensitive to land-use change, including many *Andrena* species. The relative sensitivity of *Andrena* to land-use change compared with *Bombus* and *L.* (*Dialictus*) may be driven by their different life histories. *Andrena* are solitary and have a narrow flight phenology, whereas social species and those with longer flight phenology [e.g., *Bombus* and *L.* (*Dialictus*)] are favored in agricultural rather than more natural landscapes (*21*). Our results, therefore, underscore the utility of methods that account for shared evolutionary history for understanding how communities are altered in response to environmental stressors.

Clade loss may lead to a reduction in the suite of functional traits present in pollinator communities when these traits show phylogenetic signal. In this study, we found that closely

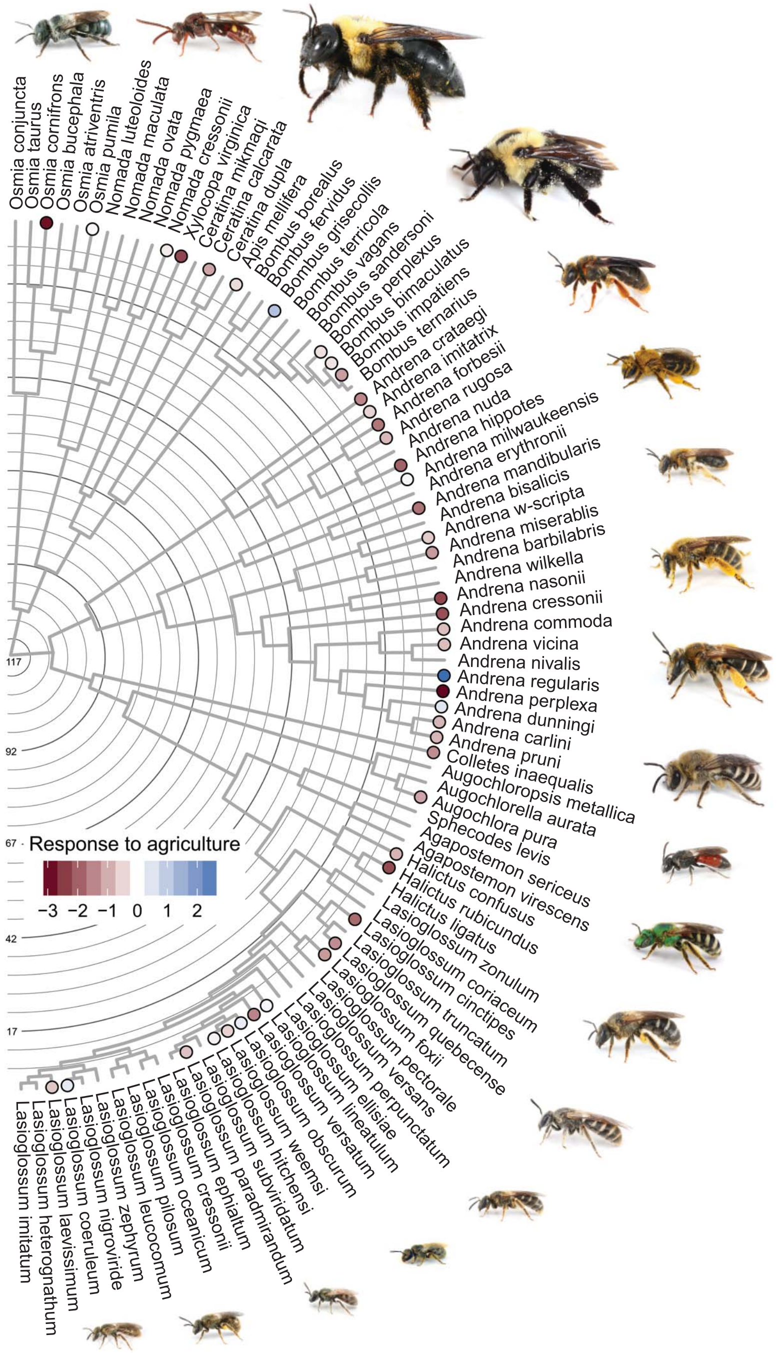

Fig. 1. Time-calibrated phylogeny of the apple bee community. Tip labels indicate species' response (*z*-score) to increasing agricultural land cover at the 750-m scale for the 44 taxa observed more than 10 times across all surveys. Color represents the magnitude of the response (dark red indicates strong negative, dark blue indicates strong positive). The root is at 117 million years (Ma) with 5 Ma increments to present. Posterior probabilities are 1.0 for all nodes. Communities in mixed-use landscapes are likely to contain species from across the entire tree, whereas those in agriculturally dominated landscapes will contain species with white or blue tip markers. [Bee images (copyright of Joseph Wilson) are used with permission.]

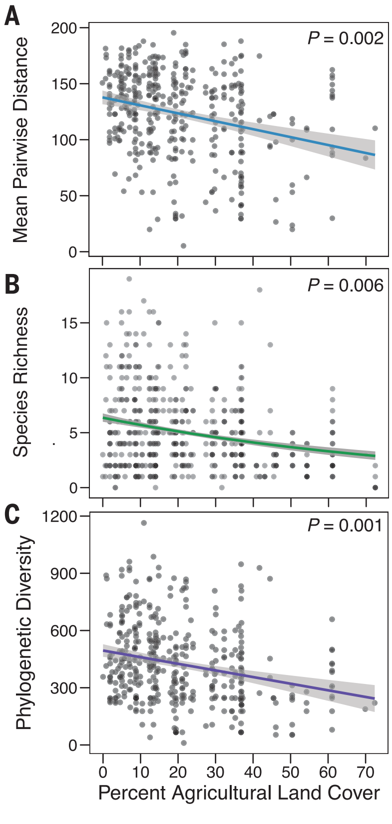

Fig. 2. Relationship between the percent agricultural cover in the surrounding landscape at a 750-m radius and per-transect community diversity metrics. In highly agricultural landscapes, (**A**) the mean pairwise phylogenetic distance separating individuals is lower, (**B**) fewer species are observed per transect, and (**C**) the evolutionary history represented by communities is lower. Points are semitransparent to aid in visualizing overlap. Solid lines indicate a significant relationship between variables at $P < 0.05$, shading represents 95% confidence interval.

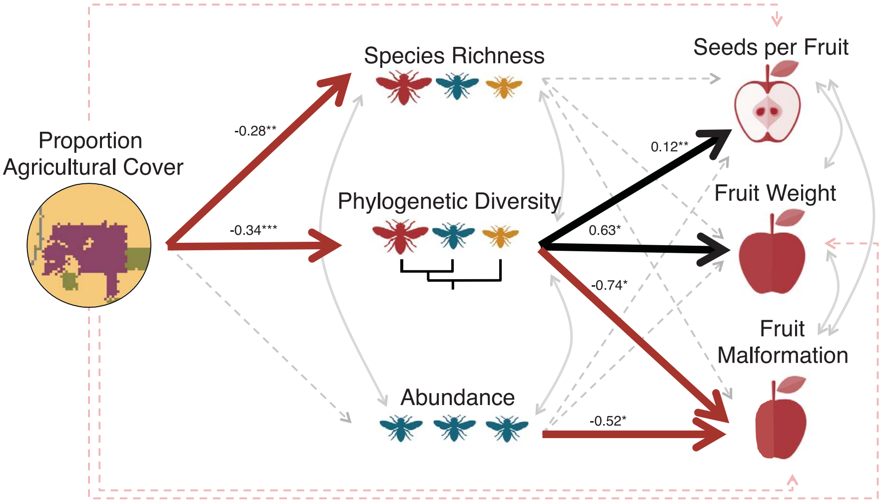

Fig. 3. Land-use change has an indirect impact on pollination services and crop production mediated by a reduction in observed mean pairwise phylogenetic distances separating individuals in a community. Community data include wild and managed bees and the following apple variables: the number of seeds per fruit, fruit weight, and fruit shape in the varieties Golden Delicious and McIntosh. Curved lines indicate correlated errors among variables. For straight lines, solid lines indicate a significant relationship between variables and their color indicates direction (black indicates positive, red indicates negative). Numbers above lines are the standardized coefficients, with asterisks indicating level of significance (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).

related bee species share many behavioral and morphological traits including body size, plant fidelity, and visitation rate but not flower-handling behavior (fig. S7), which may influence their effectiveness as crop pollinators. To assess the impact of phylogenetic diversity loss on pollination services, we quantified seed set, fruit weight, and shape (a measure of fruit quality) in two apple varieties, Golden Delicious and McIntosh, at 12 orchards. We employed a structural equation modeling approach to evaluate the importance of phylogenetic diversity, species richness, and abundance, which allowed us to explicitly model the covariation between these predictor variables and to evaluate the direct and indirect effects of landscape structure on pollination services. Land-use change had an indirect impact on pollination services and crop production mediated by a reduction in mean pairwise phylogenetic distances separating individuals in a community (Fig. 3 and fig. S8). In both varieties, fruit weight and seed set were best predicted by the observed pairwise phylogenetic distances separating individuals in a community as compared to either abundance or species richness, whereas fruit shape was best predicted by both phylogenetic diversity and abundance (tables S1 to S3).

Our findings reveal that landscape-mediated loss of evolutionary history from bee communities has consequences for current ecosystem functioning and the delivery of ecosystem services to agriculture (Fig. 3). Specifically, we show that loss of phylogenetic diversity from pollinator communities has a negative effect on pollination services. In light of ongoing land-use change worldwide (*23*), our results have clear implications for the functional and evolutionary potential of bee communities to respond to future challenges. Conservation practices that measure their success only by the number of species conserved may fail to protect the full diversity of life impacted by these stressors (*24*). Greater understanding of how shared evolutionary history shapes responses to environmental stressors is essential for assessing the potential mechanisms driving biodiversity declines in agricultural landscapes and their effects on ecosystem functions and services.

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SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/363/6424/282/suppl/DC1
Materials and Methods
Figs. S1 to S8
Tables S1 to S6
References (*26*–*70*)

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