Landscape Ecol
https://doi.org/10.1007/s10980-019-00868-x

RESEARCH ARTICLE

Small but critical: semi-natural habitat fragments promote bee abundance in cotton agroecosystems across both Brazil and the United States

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Received: 22 February 2018 / Accepted: 2 July 2019

Abstract

Context Bees are the most important pollinators of crops worldwide. For most bees, patches of semi-natural habitat within or adjacent to crops can provide important nesting and food resources. Despite this, land cover change is rapidly reducing the abundance of semi-natural habitat within agroecological landscapes, with potentially negative consequences for bee communities and the services they provide.

Objectives Identify how the availability of semi-natural habitat impacts bee communities across biogeographic regions, which may reveal commonalities and key governing principles that transcend a single region or taxa.

Methods We analyze and compare the drivers of bee community composition in cotton fields within Brazil and the U.S. to reveal how land cover and land cover change impact bee community composition across these two regions.

Results We show that the most critical factors impacting bee communities in cotton agroecosystems are the same in Brazil and the U.S.: bee abundance increases with cotton bloom density and the

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Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10980-019-00868-x) contains supplementary material, which is available to authorized users.

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abundance of semi-natural habitat. Further, the loss of semi-natural habitat over a 5-year period negatively impacts bee abundance in both agroecosystems.

Conclusions Given the importance of bee abundance for the provision of pollination service in cotton plants, our findings highlight the significance of small semi-natural habitat fragments in supporting key ecosystem service providers for both tropical and temperate cotton agroecological systems. We underscore the important role that local land managers play in biodiversity conservation, and the potential contribution they can make to pollination provision by supporting agricultural landscapes that conserve fragments of semi-natural habitat.

Keywords *Gossypium hirsutum* · Agroecology · Mato Grosso, Brazil · Texas, U.S.

Introduction

Resource quality and availability can drive species diversity and abundance across a diverse suite of taxa within both natural and human-managed ecological systems (Tylianakis et al. 2008). By altering the distribution and density of key resources, human-induced land cover change poses a major threat to the persistence of native species in newly altered habitats (Thuiller et al. 2008). In particular, agricultural development in the last century has been one of the most important drivers of land cover change (Scialabba and Williamson 2004). Interestingly, this conversion of forest, grassland, and pasture, to agriculture also offers an ideal opportunity to study how large-scale land cover change and habitat loss alter population and community dynamics on a global scale. Because similar crops are grown across multiple biogeographic regions, researchers can use a comparative approach to investigate the fundamental dynamics of how environmental drivers, such as contemporary land cover or recent change in land cover, affect biological communities. By identifying common drivers of community response to land cover change across multiple biogeographic regions, there is potential to reveal key principles that govern community composition which transcend a single biogeographic region or population.

Pollination by animals is critical for more than 80% of all plant species (Ollerton et al. 2011), including more than 60% of global crop species (Klein et al. 2007) and bees are the most important pollinators of agricultural crops worldwide (McGregor 1976; Nabhan and Buchmann 1997). In many regions, the decline of bee abundance and diversity has been shown to correlate with similar declines in bee pollinated plant species (Kearns et al. 1998; Ashman et al. 2004; Biesmeijer et al. 2006). While the decline of wild bee populations has been attributed to a variety of causes (e.g. agrochemicals, pathogens, alien species, and climate change, Tylianakis et al. 2005; Potts et al. 2010; Goulson et al. 2015), land cover change, and the associated habitat loss, is well-documented as one of the most powerful threats to bee populations across the globe (Ghazoul 2005).

For wild bees to persist in a landscape, they require two major resources: (1) food in the form of pollen and nectar, provided by flowers, and (2) nesting habitat, provided by access to soil, woody vegetation/debri, and existing cavities. First, bee pollinators are thought to closely track floral resources within a landscape (Waser 1983; Ghazoul 2006). Assumed to act as optimal foragers, bees often exhibit increased visitation at forage patches with high floral density, a phenomenon known as the ‘concentration effect’ (Hegland and Boeke 2006; Pope and Jha 2018). Conversely, bee foragers are also documented to visit proportionally fewer flowers as patch size increases, a phenomenon known as the ‘dilution effect’ (Kunin 1993; Goulson 2000; Veddeler et al. 2006; Hegland et al. 2009; Jha and Vandermeer 2009). Second, beyond the availability of floral resources, the diversity and abundance of bee communities is often dependent on landscape characteristics that mediate the distribution of important nesting materials.

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Specifically, the amount of semi-natural habitat surrounding the agricultural sampling area is commonly used as a proxy for nesting habitat and has been found to be a significant predictor of bee abundance and diversity in many landscapes (Kruess and Tscharntke 2002; Xie et al. 2008; Kearns and Oliveras 2009).

Distinct species may respond differently to several factors including habitat loss depending on (1) their foraging range and (2) their degree of nest resource specialization. First, bees are central place foragers and require suitable floral resources within their flight range, which may be limited. For example, some of the smallest bees prefer to forage only a few hundred meters from their nesting habitat (Greenleaf et al. 2007), which in turn may mediate their response to land cover change. Second, given that some bees exhibit very specific nesting preferences (e.g. Michener 2007) it is possible that nest resource availability is a primary driver of their response to land cover and land cover change. Past studies have shown that as nesting substrates are removed in the conversion of semi-natural habitat to agriculture, bee populations decline or go locally extinct (Potts et al. 2005). Given their dependence on both floral and nesting resources, bees are likely to respond to habitat loss, reaching new population equilibriums in remnant habitat patches after disturbance. Due to their relatively short generation times, high mobility, and ability to track resources in a new environment, research has proposed that this delay may take only a few years before a new equilibrium is reached (Krauss et al. 2010). However, if some bee species respond more slowly to land cover conversion because of species specific traits such as foraging range or nest specialization, the gradual extinction may delay the development of a new equilibrium and increase the likelihood of a delayed reaction for that given species (Krauss et al. 2010). Specifically, among bees, extinction debt has been found for particular floral and nesting specialists (Cane et al. 2006). While a time lag can exist between land cover change and the loss of species from a community, very few studies of pollinators have explicitly considered time since land-use change took place when examining bee community composition.

In this study, we build off of past research (Cusser et al. 2016) to quantify and compare bee community composition in two major agroecosystems in northern and southern hemispheres: Mato Grosso, Brazil and Texas, U.S. Second, we investigate how floral density, land cover, and land cover change influence bee abundance and diversity across these two regions. Given the importance of landscape-level resources documented in past bee studies (Cane et al. 2006), we hypothesize that landscape factors, such as the abundance of semi-natural habitat, will be the primary feature differentially driving bee abundance and diversity in Brazil and the U.S. In addition, we expect to find evidence of a delayed reaction to land cover change for some species due to recent semi-natural habitat loss in both Brazil and the U.S.

Methods

Study system

We conducted our research in cotton fields across two distinct agroecosystems. Within west central Brazil, we sampled within the state of Mato Grosso and within the southern U.S., we sampled in the state of Texas. In Brazil, the state of Mato Grosso is the largest cotton producing area of the country, responsible for about 60% of Brazilian cotton (1.7 million hectares) (Mato Grosso Institute of Agricultural Economics 2014). Mato Grosso grows primarily the cotton species *Gossypium hirsutum* L. (Malvaceae). Aside from cotton, the state also stands out as a major producer of soybean and corn, and total agricultural land cover makes up the majority of the region (58%). The remainder of the region is covered by low density developed areas (4%), water (16%), and semi-natural habitat (22%), which includes forest, shrub, and grassland. 'Semi-natural habitat' is primarily a mixture of two dominant vegetation types: Cerrado and Amazon Forest. The Cerrado is a savanna-like biome with drylands that range from open grassland fields with a few shrubs to closed forests with canopy height of 12–15 m. These include periodically flooded wetlands called "Gallery Forests" (Ratter et al. 1997). The Amazon Forest is a biome in which drylands are composed primarily of closed canopy rainforests with canopy height more than 20 m, as well as wetlands (Myster 2016).

In the U.S., the state of Texas grows more than 25% of the country's cotton crop, and cotton covers roughly 1.9 million hectares of farmland in the state (Alvarez and Plocheck 2014). Similar to Mato Grosso, Texas also primarily grows the cotton species *Gossypium* *hirsutum* L. (Malvaceae). Total agriculture makes up the majority of land cover (55% in the region), and, similar to Mato Grosso, agriculture consists primarily of cotton, sorghum, corn, and soybean cropland. The remainder of the region is comprised of low density developed areas (6%), water (~ 1%) and semi-natural habitat (38%), including pasture, shrub, mixed woodland, and marsh areas along the Gulf Coast. Semi-natural habitat along the coast includes barrier islands, salt grass marshes surrounding bays and estuaries, remnant tallgrass prairies, oak parklands and oak mottes, and tall woodlands in the river bottomlands (Conner et al. 1989).

We conducted research in 17 sites in Mato Grosso located in three geographic regions between Primavera do Leste (− 12.35138, − 55.5235) and Campo Novo do Parecis, Mato Grosso (− 13.33132, − 57.50479) in 2016. The three geographic regions were separated by 228 km on average, and were near the towns of Primavera do Leste, Sorriso, and Campo Novo do Parecis. Sites were located within cotton fields that were at least 40 ha in size and at least 2 km apart. Similarly, in Texas, we conducted research in 12 sites located in three geographic regions between Telferner (28.847913, − 96.892975) and Woodsboro, Texas (28.303701, − 97.381612) in 2014 (Cusser et al. 2016). The three geographic regions of study were separated on average by 52 km and were located near the towns of Woodsboro, Austwell/Tivoli, and Telferner, Texas. Sites were located within cotton fields that were at least 35 ha in size and 2 km apart from each other (Fig. 1). To our knowledge, none of the farms in Mato Grosso or Texas managed or rented honey bees on their properties.

Bee community sampling

To quantify the bee community at each of our 29 sites, we netted bees found actively foraging within cotton flowers during 1-h sampling bouts. During each 1-h bout, collectors walked four parallel 50 m × 1 m transects, checking blooms for visitors and collecting them by net. Transects were located at the edge of cotton fields and were ~ 12 m apart, representing a total sampling area of 2500 m^2 at each site. Time spent moving specimens from the net into the killing jar was not included in the sampling time to ensure an even sampling effort between sites. In Mato Grosso, bee collections were performed during peak Brazilian bloom, from late March to early May in 2016. Due to weather, the number of sampling bouts per site ranged from one to four. In Texas, each site was sampled during peak U.S. bloom (June to July in 2014) and sampled three times during that period (Cusser et al. 2016). In Mato Grosso, bees were identified by D. C. de Luna and identities confirmed using the Entomological Collection of Professor J. M. F. Camargo, in Department of Biology at Faculty of Philosophy, Sciences, and Letters, University of São Paulo (Brazil). The species level identification of one of the most common species in Brazil (*Melissodes nigroanea*) was confirmed via DNA barcoding (Grando et al. 2018). In Texas, bees were identified by J. Neff at the Central Texas Melittological Institute.

Landscape composition

Floral resources

In both Mato Grosso and Texas, we collected data on the quantity of available floral resources that were attributable to the cotton crop during each of our bee sampling bouts. To calculate cotton bloom density, we counted the number of blooms on each of five randomly chosen cotton plants within each of the four transects, for a total of 20 cotton plants per sample per site. Bloom density was then calculated as the average number of blooms per plant across samples per site in both Mato Grosso and Texas.

Regional and historic land cover

In both Mato Grosso and Texas, we calculated the percentage of different land cover types surrounding each sampling site at a regional scale (1.5 km radius). This radius was chosen as it is small enough to ensure that the regional scale minimized overlap between sites, but also large enough to reflect the foraging distance of many bees (Greenleaf et al. 2007). In Mato Grosso we used information from the 2009 GlobCover Database (Arino et al. 2012). To quantify land cover, we summed the total amount of semi-natural habitat falling within the 1.5 km buffer in qGIS (Quantum Development Team 2017) and divided that number by the total amount of land cover surrounding each site within the buffer to determine percent cover. 'Semi-Natural' habitat includes the GlobCover categories: evergreen and deciduous forest, as well as all types of

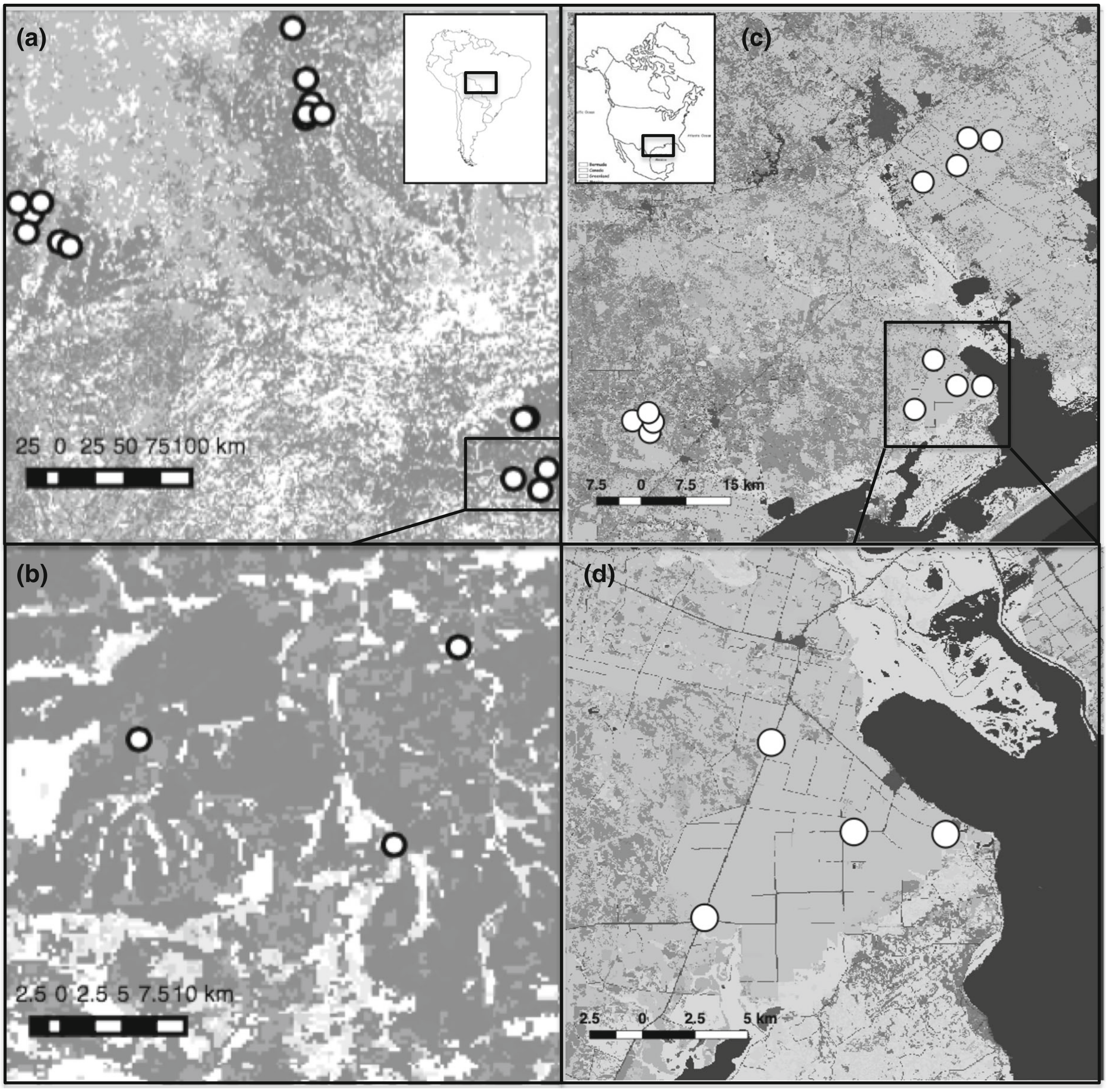

Fig. 1 Map of study sites. Top Left Inset) South America. **a** Map of 17 cotton fields used as study sites in Mato Grosso, Brazil. Sites were located in three geographic areas near the towns of Sorriso, Primavera do Leste, and Campo Novo, Mato Grosso, Brazil. Sites are shown as white dots. **b** An enlargement of the Primavera do Leste region showing three cotton field sites. Top Right Inset: North America. **c** Map of 12 cotton fields used as study sites. Sites were located in three geographic areas near the towns of Woodsboro, Austwell/Tivoli, and Telferner, Texas, U.S. **d** An enlargement of the Austwell/Tivoli region showing four cotton field sites

shrub and grassland. Semi-natural habitat cover was negatively correlated with the abundance of agricultural land surrounding each site (Pearson's correlation = − 0.55, p value = 0.021). Thus, the percent of semi-natural habitat cover surrounding sites within the buffer in Mato Grosso serves as a description of land composition surrounding sites in general. Similarly, in Texas, we measured the quantity of different types of land cover surrounding each site at a regional scale (1.5 km radius), using information from the 2011 National Land Cover Database (Han et al. 2014). As described above, we quantified percent land cover as the total amount of semi-natural habitat falling within the 1.5 km buffer around each site divided by the total amount of land cover surrounding each site. 'Semi-Natural' habitat cover in Texas includes the National Land Cover Database categories: Evergreen and Deciduous forest, Shrubland, Grassland, Pasture/Hay, and Wetlands. As in Mato Grosso, Texas semi-natural habitat was negatively correlated with the cover of agriculture surrounding each site, but the magnitude of correlation was much stronger (Pearson's correlation $= -0.9976$, p value < 0.001). Thus, semi-natural habitat cover in Texas also serves as a description of the land cover surrounding sites in general.

In Mato Grosso, we used the difference in the abundance of semi-natural habitat from the years 2004 and 2009 to determine how semi-natural habitat cover has changed over a recent, 5-year period. The difference in the semi-natural habitat cover between these years was calculated for each site within a 1.5 km buffer, using the GlobCover Database maps from those years (Arino et al. 2012). Similarly, to quantify land cover change in Texas over a recent 5-year period, we measured the change in semi-natural habitat cover surrounding sites within a 1.5 km buffer using National Land Cover Database maps from the years 2006 and 2011 (Han et al. 2014). These data sets were the most similar in years, and time between years, that were publicly available for both biogeographic regions.

Bee response to land-use change

First, to summarize the differences in bee community composition between Mato Grosso and Texas, we used the extant entomological literature to group bees by their taxonomic tribe (which generally share important life-history characteristics), their sociality (Solitary, Social, or Kleptoparasitic), and nesting preference. Nesting preference is divided into three groups: "Ground" refers to ground-nesting bees, "Wood/Stem" refers to wood-nesting bees, and "Large Cavity" refers to the nesting habit of bees that occupy large (> 5 cm) tree hollows or rodent burrows, including honey, stingless, and bumble bees. To examine statistical differences in groupings between Mato Grosso and Texas, we used non-metric multidimensional scaling (NMDS, Anderson 2001). Using the 'vegan' package in the R statistical computing language (Oksanen et al. 2007), we calculated Bray–Curtis dissimilarity using the abundance of pollinators of each tribe, sociality, and then nesting group. Permutational MANOVA (function 'adonis' in the 'vegan' package) was used to determine if differences between the states were statistically significant (Anderson 2001), after verifying the assumption of homogeneity of group dispersion.

To determine the relationship between landscape variables and bee abundance (pooled across species), we used Poisson generalized linear mixed models (GLMMs). We fit separate models for data from Mato Grosso and Texas. We first screened land cover variables for multi-collinearity by calculating variance inflation factors (VIFs) using the 'vifstep' function in the R package 'usdm' (Naimi 2013). Because land cover variables are inherently related to one another, we chose a conservative threshold of VIF > 4 as an indicator of substantial collinearity (O'Brien 2007). Of the three variables checked for collinearity in Mato Grosso and Texas (bloom density, semi-natural habitat cover, and change in semi-natural habitat cover over a 5-year period), none were found to be collinear. To determine the specific aspects of land cover that drive bee diversity, we pooled specimens from the multiple sampling bouts within each site, and calculated species diversity using the Chao diversity metric (Chao et al. 2005). Chao diversity accounts for the potential role of unsampled species in the estimate of diversity. We used Gaussian GLMMs and fit separate models for data from Mato Grosso and Texas.

For both bee abundance and diversity, we included a geographic region as a random intercept, and included bloom density, semi-natural habitat cover, and change in semi-natural habitat cover as fixed effects. To account for differences in sampling effort among sites in Mato Grosso, we included the number of sampling rounds as an offset in that model. We tested for overdispersion for the Poisson GLMMs, and found no evidence of overdispersion. We fit the GLMMs with the 'glmer' function in the R package 'lme4' (Bates et al. 2014); and we used the second-order Akaike Information Criterion (AICc, Burnham and Anderson 2003) to select among all possible combinations of the fixed effects using the 'dredge' function in the R package 'MuMIn' (Barton 2016).

Results

Bee community sampling

In Mato Grosso, we captured a total of 1476 bee specimens of 29 species, representing 12 tribes. The European honey bee, *Apis mellifera*, and the solitary bee, *M. nigroaenea* made up 59% and 27% of total specimens, respectively. Of the remaining bee species, 7 were singletons (only found once), and 4 were doubletons. 69% of specimens from Mato Grosso were social, including honey and stingless bees, 31% were solitary, and none of the collected bees were kleptoparasitic. In terms of nesting, 69% of specimens in Mato Grosso prefer large cavities in the ground or trees (> 5 cm), 30% nest in the ground, and less than 1% nest in pithy stems or small wood cavities (< 5 cm).

In Texas, we captured a total of 601 bee specimens comprised of 45 species, represented by nine tribes (Cusser et al. 2016). The European honey bee, *A. mellifera* and the solitary bee, *Melissodes tepaneca*, made up 27% and 30% of total specimens collected, respectively. *Lasioglossum* specimens of at least 18 morpho-species made up 21% of the Texas specimens. Of the remaining bee species, 20 were singletons, and 7 were doubletons. Thirty-two percent of specimens from Texas were social, including honey and bumble bees, 67% were solitary, and the remaining bees were kleptoparasitic (0.04%). In terms of nesting, 27% of specimens in Texas prefer to nest in large cavities (> 5 cm), 68% nest in the ground, and 4% nest in pithy stems or small wood cavities (< 5 cm) (Supplementary Material, Table S2).

Landscape composition

Mato Grosso sites averaged 1.07 cotton blooms/plant (SE: 0.02). Regional land cover surrounding sites averaged 24.7% (SE: 1.2%) semi-natural habitat in the 1.5 km buffer. Mato Grosso sites lost on average ~ 4% of semi-natural habitat (SE: 0.5%) between the years 2004 and 2009. While most of the sites in Mato Grosso lost semi-natural habitat cover, five sites gained a marginal amount of semi-natural habitat over the 5-year period. Texas sites averaged 2.69 cotton blooms/plant (SE: 0.03). Regional land cover surrounding sites averaged 32.8% (SE: 1.6%) semi-natural habitat in the 1.5 km buffer. On average, Texas lost ~ 2% of semi-natural habitat (SE: 0.04%) between the years 2006 and 2011. While many of the sites in Texas lost semi-natural habitat cover, six sites gained a marginal amount of semi-natural habitat over the 5-year period.

Bee response to land-use change

Results from the PERMANOVA confirm that the composition of tribes was statistically different between Mato Grosso and Texas (df = 1, r sq = 0.15, p value = 0.001) (Fig. 2). Results from the PERMANOVA confirm that the composition of sociality was statistically different between Mato Grosso and Texas (df = 1, r sq = 0.12, p value = 0.005). Results from the PERMANOVA also confirm that the composition of nesting preference was statistically different between Mato Grosso and Texas (df = 1, r sq = 0.09, p value = 0.016) (Fig. 2).

Exploring our primary question, we found that Mato Grosso bee abundance was positively correlated with cotton bloom density and the percent abundance of semi-natural habitat cover within a 1.5 km radius of the site and was negatively correlated with the loss of semi-natural habitat cover between 2004 and 2009. Texas bee abundance followed a similar pattern, responding positively to bloom density and negatively to the loss of semi-natural habitat cover between the years 2006 and 2011 (Table 1, Fig. 3). Separating the dominant social European Honey bee, *Apis mellifera,* from the data, and analyzing the bees separately, we found the same patterns hold for both *A. mellifera* and native bee abundance (Supplementary Material, Table S1 a). Neither Mato Grosso nor Texas bee species diversity (Chao) responded significantly to any of the explanatory variables in our models (Supplementary Material, Table S1 b).

Discussion

We found significant differences in the composition of tribes, sociality, and nesting preferences of bees visiting cotton flowers in Mato Grosso, Brazil and Texas, U.S. Interestingly, despite these differences, bee community abundance in both states responded to the same landscape variables. Specifically, we show that bee abundance increased with increasing cotton bloom density in both states. In Mato Grosso and

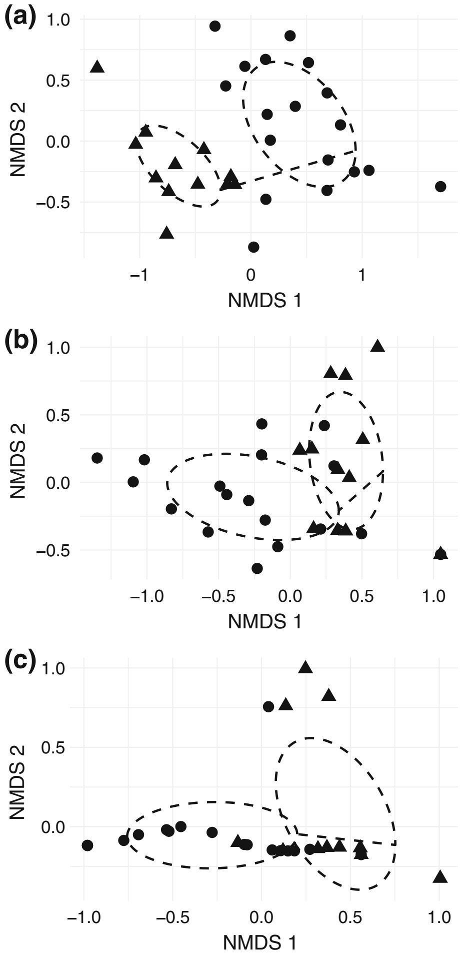

Fig. 2 Non-metric multidimensional scaling (NMDS) comparing the composition of **a** tribes **b** sociality **c** nesting preferences between Mato Grosso, Brazil and Texas, U.S. We calculated Bray–Curtis dissimilarity using the abundance of pollinators of each group. Permutational MANOVA was used to determine that differences between states were statistically significant, after verifying the assumption of homogeneity of group dispersion. Mato Grosso is shown as circles, and Texas as triangles

Texas, bee abundance also increased with the abundance of semi-natural habitat cover within 1.5 km of the sampling point, though this pattern was only statistically significant in Mato Grosso. Further, we show that land cover changes also influenced the abundance of bees in both systems. Specifically, in both states, we found the abundance of bees was lower in sites with greater losses of semi-natural habitat cover over a recent 5-year period. Lastly, we did not identify any landscape variable that significantly influenced bee diversity in either state. Overall, our results provide evidence that both current and historic aspects of land cover impact the abundance of bee pollinators in cotton agroecosystems across two distinct biogeographic regions.

Our exploratory analyses of bee communities in each state highlight some of the key differences of the bee community between Mato Grosso and Texas. Mato Grosso had more Augochlorini and Meliponini, than Texas, which had more Emphorini and Halictini. Meliponines, which were abundant in Mato Grosso, are eusocial, stingless bees that can be found in most tropical and subtropical regions of the world. Brazil is home to dozens of species of stingless bees, with more than 300 species described and probably more yet to be discovered (Pedro 2014). Small *Lasioglossum* of the subgenus *Dialictus*, drove much of the Halictini abundance we observed in Texas. *Dialictus* are well known for their abundance and diversity, especially in temperate regions (Michener 2007).

In comparing nesting preferences, we found that Mato Grosso had more large cavity nesting bee species, while Texas had more wood/stem nesters. This again, is likely related to the high abundance of social meliponine bees in Mato Grosso which prefer to nest in large tree cavities common to parts of the Cerrado and Amazon Forest. In Texas, most small cavity-nesting bees require above-ground, pre-excavated holes in which they provision their young. Above ground nesting resources are likely to be ample in semi-natural grassland habitats which were more abundant in Texas. Both states had similar abundances of ground-nesting bees, which require exposed soil in which they excavate tunnels (Potts et al. 2005).

Mato Grosso had more social bees than Texas. While both states had a large proportion of social honey bees, the meliponines of Mato Grosso are eusocial bees, whereas most non-*Apis* bees in Texas were solitary. Studies of other recently fragmented agricultural landscapes have found that large expanses of tropical cropland tend to be dominated by social bees. These studies suggest that the success of social bees in these novel tropical environments might lie in their recruitment-based foraging strategy and versatile nesting preferences (Roubik 1980; Brosi et al. 2008). Solitary bees on the other hand, may lack this ability to exploit pulses and mass flowering events as they are constrained by their lack of communication. Thus, it may be that the abundance of agricultural cover in the

Table 1 Parameter estimates for the best-performing models of bee abundance in Mato Grosso and Texas

Mato grosso bee abundance	Estimate	Std. error	Z value	Pr(> |z|)
Intercept	− 2.52127	1.50727	− 1.67	− 0.0944
Bloom density	1.54709	0.08941	17.30	< 0.001*
Semi natural Habitat	1.05701	0.03281	132.22	< 0.001*
Change in semi natural habitat	− 1.84545	0.03719	− 49.62	< 0.001*
Texas bee abundance	**Estimate**	**Std. error**	**Z value**	**Pr(> |z|)**
Intercept	3.60043	0.46394	7.761	< 0.001*
Bloom density	0.28344	0.04836	5.861	< 0.001*
Semi natural habitat	0.05601	0.05124	1.093	0.274
Change in semi natural habitat	− 0.25743	0.06499	− 3.961	< 0.001*

Asterisks indicate statistical significance (p value < 0.05)

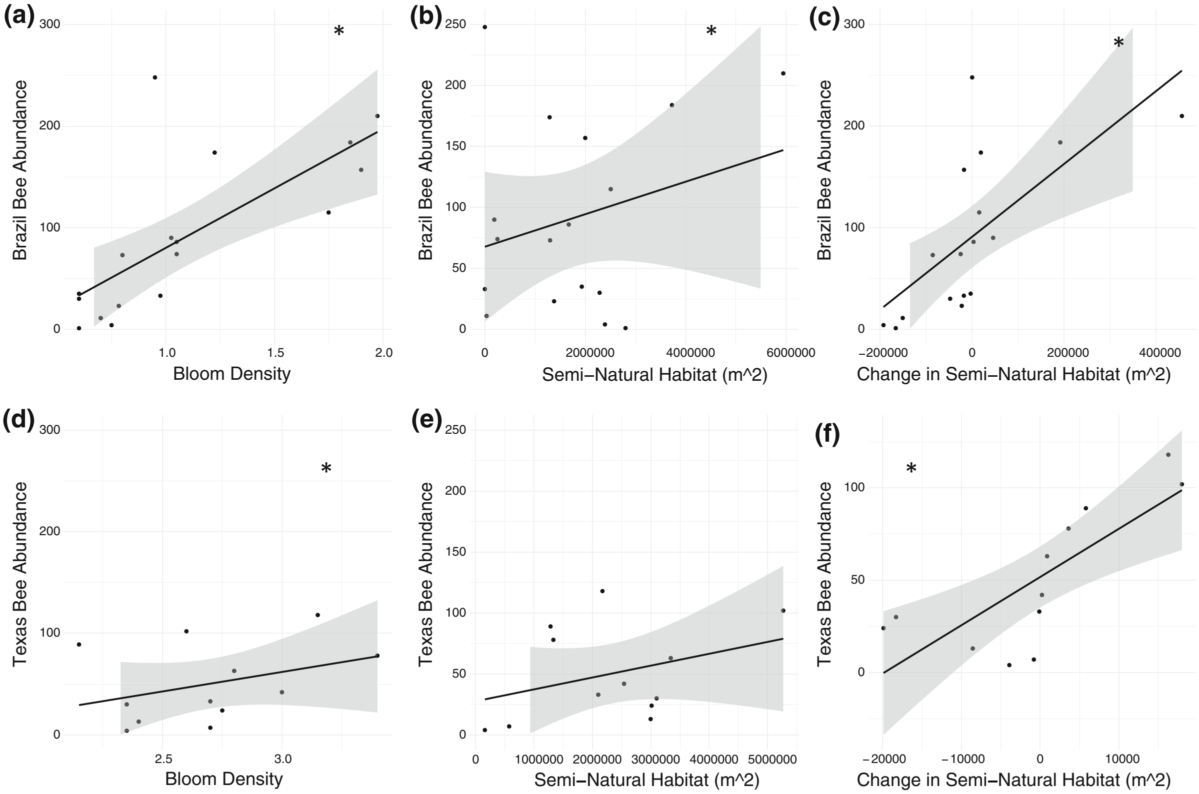

Fig. 3 Bee abundance in Mato Grosso and Texas as a function of **a**, **d** Bloom density, **b**, **e** semi-natural habitat cover, **c**, **f** change in semi-natural habitat cover. Linear regression fits and confidence regions were made using geom_smooth in ggplot2, shaded areas are 95% confidence intervals, asterisks indicate statistical significance (p value < 0.05)

Mato Grosso region predisposes the landscape towards tropical social bees, like meliponines.

Despite substantial differences in community composition and natural history, we found that bee community abundance responded to cotton bloom cover, land cover, and land cover change in similar ways in Mato Grosso and Texas. Bee abundance in both states responded positively to the density of cotton bloom, becoming more abundant at higher densities of bloom. This finding is an example of the ‘concentration effect’ as found in other pollination studies (Hegland and Boeke 2006). Bee abundance in both states also responded positively to the abundance of semi-natural habitats surrounding sites, the trend being significant in Mato Grosso. Semi-natural habitat, beyond the floral resources it provides, has been shown to provide an abundance of nesting resources important to bees, including trees, large and small cavities, and pithy stems (Potts et al. 2005). Several reviews have highlighted that bee abundance responds positively to increased abundance and proximity to semi-natural habitat (Ricketts et al. 2008; Garibaldi et al. 2011). Because bees are central place foragers, the proximity of nesting habitat within flight range of target crops is essential if land managers hope to take advantage of wild bee pollination services. Lastly, we saw that in both states, bee abundance responded negatively to the loss of semi-natural habitat cover over a 5-year period. Historically, bee pollinators have been thought to respond quickly to habitat loss, reaching a new equilibrium in remnant habitat patches within a couple of years after disturbance. Despite this, along with the results we present here, several studies have shown that bee species are not immune to the effects of extinction debt (Sang et al. 2010; Bommarco et al. 2014; Cusser et al. 2015). As such, these delayed extinctions are critical to consider from a conservation perspective given that delayed extinction following land use change may lead to overly optimistic assessments of the status of biodiversity. In the presence of delayed extinction, land managers may overestimate species abundance and richness in habitats that cannot support species in the long-term (Hanski and Ovaskainen 2002; Helm et al. 2006).

Interestingly, we found that none of our explanatory variables predicted differences in bee diversity in either state, possibly due to the short cotton bloom season and survey period (7 weeks), as pollinators emerging at different time periods may respond to different land cover cues (Hegland et al. 2009). While our study may not have detected changes in bee diversity with land cover, changes in bee abundance have been shown to have important and far reaching effects on service provision in both natural and agricultural systems. When species contribute to community function in proportion to their abundance, as proposed by the mass ratio hypothesis (Grime 1998), then a small number of dominant species can make a disproportionate contribution to ecosystem function. Indeed, previous research of pollination service provision has shown that the abundance of a few, common, bee species in a community can contribute disproportionally to overall community function (Vázquez et al. 2005; Kleijn et al. 2015). Thus, while numerous rare species often drive changes in regional bee diversity, these changes in diversity may have little effect on overall pollination service provision. As such, our finding that bee abundance responds to semi-natural habitat cover across biogeographic regions has important implications for managing landscapes to promote the provision of important ecosystem services, like pollination.

Declines in semi-natural habitat cover have long been shown to be critically linked to biodiversity loss within agricultural landscapes (Benton et al. 2003; Tscharntke et al. 2005). Here, we find evidence in support of that claim, and additionally document habitat loss-mediated extinction debt across two distinct biogeographic regions. However, our results indicate that cotton growers do not need to rely solely on distant large-scale semi-natural habitat reserves to provide pollinator resources. Instead, farmers can contribute to biodiversity conservation by preserving small patches of semi-natural habitat on their own farms and by creating heterogeneous and resource-rich agricultural matrices (Perfecto and Vandermeer 2008). Specifically, more than a third of bees were found in less than 7% of our sites; across both geographic regions these sites averaged 3.0 blooms per plant (as compared to the overall average of 1.7 per plant) and more than 3.7 km^2 of semi-natural habitat in a 1.5 km radius (as compared to the overall average of 2.7 km^2), suggesting that critical minimum bloom and natural habitat thresholds may exist for optimizing bee abundance in cotton agroecosystems. Cotton growers can promote bee abundance within their own farms by diversifying their landscapes, creating a mosaic of flowering patches and nesting resources that attract and support foraging bees. Given the benefit of bee pollination to cotton yields (Pires et al. 2014; Cusser et al. 2016), there is powerful incentive for growers to improve agroecosystems management to dually support biodiversity conservation and enhance ecosystem service provision.

Acknowledgements Special thanks to the growers and landowners that allowed us to sample on their lands; without them none of this work would have been possible. For sampling and research permits in Brazil, we thank Chico Mendes Institute for Biodiversity Conservation (ICMBio). This research was supported by the São Paulo Research Foundation (FAPESP—2014/50738-9), The National Council for Scientific and Technological Development (CNPq—310446/2015-5), and the

Coordination for the Improvement of Higher Education Personnel CAPES- Programa Biologia Computacional (CAPES-1572813). In the U.S., the help of Texas Agricultural & Mining extension agents, crop consultants, and The Welder Wildlife Foundation, including Roy Parker, Stephen Biles, Lee Hutchins Jr., Kenneth Hanslik, and Terry Blankenship, was invaluable. Thanks to the Jha lab for helpful feedback and support, as well as help in the field from Nicole Vojnovich, Alan Ritchie Jr., Sarah Cunningham, and Rebecca Ruppel. Funding in Texas was provided by the Texas Parks and Wildlife Department, the Army Research Office, and the National Science Foundation.

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