Insect Conservation and Diversity

Insect Conservation and Diversity (2015) **8,** 562–572 doi: 10.1111/icad.12139

Land use change and pollinator extinction debt in exurban landscapes

SARAH CUSSER,[1] JOHN L. NEFF[2] and SHALENE JHA[1] [1]Department of Integrative Biology, The University of Texas at Austin, Austin, TX, USA and [2]Central Texas Melittological Institute, Austin, TX, USA

Abstract. 1. For the first time in more than a century, people across the planet are migrating en mass from cities to rural areas. In this process of 'exurbanisation' humans are rapidly converting natural and agricultural regions into low-density housing. Despite the scale of this exurban development and its potential negative impact on biodiversity, little is known about how this specific type of land conversion impacts wild pollinators.

2. In this study, we conduct an extensive survey of the wild pollinators of the peach agroecosystem and investigate the impact of current and historic land use at multiple spatial scales on pollinator community composition within agroecological landscapes that have recently undergone exurban development.

3. We reveal that the overall composition of the wild pollinator community is significantly associated with current local agricultural and natural land cover. Specifically, local agricultural land use was associated with ground-nesting bee community composition, whereas natural lands were associated with cavity-nesting bee composition, revealing that nesting materials drive community composition for these two groups in exurban habitats.

4. In contrast, community composition for butterflies and flies, which made up the smallest proportion of our communities, were not strongly associated with any particular land use type, likely due to their non-central place foraging strategy.

5. Most interestingly, our results indicate that historic land use remains a significant factor impacting the current abundance of all pollinators in the peach agroecosystem, offering the first evidence of extinction debt in this rapidly expanding exurban landscape.

Key words. Agroecology, land use change, regression trees, suburbanisation, Texas Hill Country.

Introduction

Rural areas of the Unites States are undergoing a dramatic transformation. For the first time in more than a century, people are migrating en mass from cities to rural areas (Johnson & Beale, 1998; Rudzitis, 1999) driving changes in land use across the nation (Brown *et al.*, 2005). Termed 'exurban development', the construction of low-density housing in historically natural and agricultural regions is now one of the fastest growing forms of land conversion in the United States (Brown *et al.*, 2005) and internationally (Scott *et al.*, 2011; Woods, 2011) and is likely having major impacts on biodiversity. While habitat loss (e.g. Fahrig, 2003) and increased impervious cover (e.g. Jha & Kremen, 2013a) resulting from human activity are well established as major threats to biodiversity, the specific impacts of exurban development have only recently become a topic of conservation priority.

Recent studies have revealed that exurban development can negatively impact biodiversity through changes in

Correspondence: Shalene Jha, Department of Integrative Biology, The University of Texas at Austin. 1 University Station C0930, Austin, TX 78712, USA. E-mail: sjha@austin.utexas.edu

habitat availability and the alteration of ecological processes and biotic interactions (reviewed by Hansen *et al.*, 2005). Studies examining a range of taxa, from bird and rodent community composition (Racey & Euler, 1982; Blair, 1996 respectively), to large carnivore population ecology (Mladenoff *et al.*, 1995), have indicated the negative impacts of exurban development on biodiversity (also see Temple & Cary, 1988; Hansen *et al.*, 2005). In fact, exurban development may have more devastating impacts on biodiversity than many other types of land use change because: (i) large areas of land are currently affected by exurbanisation (Brown *et al.*, 2005), (ii) pristine regions are often the target for conversion (Czech *et al.*, 2000; Marzluff & Ewing, 2001), and (iii) exurbanisation is occurring at a rapid rate (Johnson & Beale, 1998; Rudzitis, 1999). This last factor is especially important to recognise given that many taxa respond slowly to land use change, and the resulting slow extinction and emigration may delay the development of a new equilibrium (Krauss *et al.*, 2010). These delayed extinctions, or so called 'extinction debts' (Tilman *et al.*, 1994), 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. Tilman *et al.* (1994) suggests that even very abundant species are not immune to the effects of extinction debt. In the presence of extinction debt, land managers may overestimate species abundance and richness in habitats that cannot support species in the long-term (Hanski & Ovaskainen, 2002; Helm *et al.,* 2006).

Empirical studies on the topic have amassed evidence of extinction debt following land use change in a variety of taxa including lichens and fungi (Berglund & Jonsson, 2005), mammals (Cowlishaw, 1999), and vascular plants (Cousins *et al.*, 2007; Ellis & Coppins, 2007; Gustavsson *et al.*, 2007). Despite these efforts, the impacts of land use change remain to be assessed for a wide range of taxonomic groups. In particular, insects, which constitute more than half of the world's terrestrial species pool and are responsible for a wide range of ecosystem services (Losey & Vaughan, 2008), only constitute a small fraction of studies on extinction debt (but see Sang *et al.*, 2010; Bommarco *et al.*, 2014). Even less is understood about how insect communities experience extinction debt following the ever-expanding process of exurban development.

Insect pollinators, including bees (Hymenoptera: Apoidea), flies (Diptera), and butterflies (Lepidoptera), are an important and taxonomically diverse group of animals united by the common behaviour of floral visitation and pollen transfer. As a whole, pollinators are thought to respond rapidly to habitat loss, reaching a new equilibrium in remnant habitat patches within a few years of disturbance due to their relatively short generation times, high mobility, and ability to track resources in the new environment (Kuussaari *et al.*, 2009; Krauss *et al.*, 2010). Nevertheless, within this larger group of wild pollinators, distinct pollinator communities are likely to respond differently to habitat loss and at different spatial scales depending on two factors unique to each community: (i) their degree of nest resource specialisation, and (ii) their foraging ability.

First, given that some pollinators exhibit very specific nesting preferences (e.g. Michener, 2007) it is possible that nest resource availability drives response to land use change for these communities. For example cavity-nesting bees require pre-excavated holes in which they provision their young, whereas ground-nesting bees depend on exposed soil in which they excavate tunnels. If both of these substrates are removed as the habitat is destroyed, both cavity and ground-nesting bees may exhibit declines or may go locally extinct (Potts *et al.*, 2005). In contrast, pollinators that do not require specific nesting material but rather depend on plants for oviposition and larval substrate, such as some butterflies and flies (e.g. Scott, 1992; Sadeghi & Gilbert, 2000), may remain in the habitat, even if it is severely altered, until those host plants have gone locally extinct (Bommarco *et al.*, 2014).

Second, different pollinator communities are also expected to vary in their susceptibility to habitat loss depending on their foraging ability. Wild bees are central place foragers and require suitable floral resources within their flight range, which may be limited, given that some of the smallest bees in our region forage only a few hundred metres from their nesting habitat (Greenleaf *et al.*, 2007). Unlike bees, most flies and butterflies are not central place foragers, but instead require that ovipositing and larval substrates be distributed throughout their habitat (Schweiger *et al.*, 2005). Thus, limited foraging abilities may prevent bees from quickly emigrating out of unsuitable habitat while insects that can move freely across landscapes during foraging bouts, including flies and butterflies (Jauker *et al.*, 2009; Stevens *et al.*, 2010), may not be as likely to remain in low-quality habitats during their lifetime. Previous research on a variety of pollinator taxa, including lepidopteran larvae (Roland & Taylor, 1997), hoverflies (Jauker *et al.*, 2009), and hymenoptera (Steffan Dewenter *et al.*, 2002), offer evidence that taxa with different life histories tend to respond to land use change at scales related to taxa-specific resource needs and physical constraints. Thus, while movement-limited pollinator taxa may respond to local resource densities, more vagile pollinators may be more limited by connectivity between patches and may respond to landscape changes at a larger spatial scale (Steffan Dewenter *et al.*, 2002).

In this study, we investigate the impact of current and historic land use on the wild pollinators of the peach agroecosystem to determine the factors and spatial scales that drive community composition and to identify the potential existence of extinction debt following recent exurban development. Specifically, we examine three main hypotheses: (i) given the constraints of pollinator flight range and the importance of the local landscape to pollinators in other agroecological systems (Steffan Dewenter *et al.*, 2002; Williams & Kremen, 2007; Concepcion *et al.*, 2012), we hypothesise that local land use is more predictive of pollinator community composition than regional land use, (ii) because pollinator food and nesting resources are often most available within remnant natural areas (Williams & Kremen, 2007), we hypothesise that natural land use will have the largest and most positive impact on pollinator communities, and (iii) given that exurban land use change is often rapid (Brown *et al*., 2005), we hypothesise that extinction debt exists across pollinator communities, with historic land use serving as a better predictor of pollinator abundance and richness than current land use. To address these hypotheses, we survey a number of wild pollinators that visit peach orchards in a rapidly urbanising Texas peach-growing region, and we measure the relative impact of local (200 m) versus regional (2 km) and current (2006) versus historic (1992) land use on pollinator community composition, richness, and abundance.

Materials and methods

Study system

Peach orchards are a common agroecological matrix found in humid subtropical climates and currently cover more than 45 680 ha in the United States (Perez & Pollack, 2003) and 1500 ha in Central Texas alone (USDA, National Agricultural Statistics Service, 2009). Many peach varieties benefit from pollination service, setting more fruits, that are larger, and ripen more quickly, than those not visited by pollinators (Langridge *et al*., 1977; Nyéki *et al*., 1997). In addition, peach blossoms are known to attract a wide range of visitors, which have the potential to act as pollinators (Langridge *et al*., 1977; Lizhong & Ning, 1997). In Texas, peaches bloom in very early spring (February), when very few other plants are in bloom. Because of the large, dense floral displays, and the relative lack of competition from other flowering plants, it may be safe to assume that during the brief period of bloom, peach orchards attract a majority of active pollinators in the immediate region.

In Texas, the peach agroecological landscape has changed rapidly in the last few decades, with land long-used for agriculture being converted into rural subdivisions, 'ranch-ettes', and other types of dispersed housing (Margo, 1992; Brown *et al*., 2005). We focused our sampling efforts on nine landscapes between Stonewall and Fredericksburg (30.235044, −98.663117 to 30.275376, −98.871315) in Gillespie County, Texas. This region is, both currently and historically, the largest peach-producing area in the state, with over 600 ha of peaches currently in commercial production, and accounts for over 40% of the Texas peach crop every year (TAMU Extension, 2013). While the region has a long history of agriculture and ranching (Wilkins *et al*., 2003), between 1992 and 2007, overall agricultural land use decreased by over 600 ha (Gillespie County, USDA, National Agricultural Statistics Service, 2009) and the number of residential properties increased by 26.7%, leading to increased land fragmentation and reduced average property size (Wilkins *et al*., 2003).

Current and historic land use at local and regional scales

Within each of the nine landscapes, we selected a central study site within a peach orchard for insect and floral resource surveying. Three 10 × 50 m long parallel transects were established at a distance of 25, 50, and 75 m from the central point of each study site. We calculated the proportion of land use surrounding a central point of each transect at the local scale (200 m diameter) and an averaged central point at the regional scale (2 km diameter) using land use data from the U.S. Geological Survey National Land Cover Database (NLCD) layers within the programme qGIS (Quantum G. I. S., 2012). Current land use information was obtained from 2006 NLCD layers, and historic land use information from 1992 NLCD layers. Land cover was grouped into four broad categories of interest: 'agricultural', 'developed', 'natural' and 'rangeland'. 'Agricultural' land included the NLCD categorisations of cultivated crops, row crops, small grains, orchards, and vineyards. 'Developed' included open-, low-, medium- and high-intensity residential, commercial, industrial, and transport land types. 'Natural' included deciduous forest, evergreen forest, mixed forest, scrubland, grassland, and herbaceous land types. 'Rangeland' included the pasture and hay land types. Other land use types accounted for <0.01% of our landscapes and were not included in our analysis.

Pollinator and floral sampling

Each transect included between five and eight blooming peach trees and was sampled three times over the course of the peach bloom in 2013 (08 March to 12 March, 16 March to 20 March and 20 March to 25 March). To record the number of open peach blossoms per transect, here after called 'bloom density', we counted the number of open peach blossoms on a single branch and multiplied it by the number of blooming branches per tree. To ensure that this was an accurate estimate of blossoms per tree, we counted the total number of blooms on five trees and compared it to our estimated counts. Given that estimates were within ~500 blooms of the actual counts, we felt comfortable using these estimates as a measure of floral blossom count per tree for the remainder of the study. To sample the pollinator community, we walked transects for 20 minutes collecting pollinators found actively foraging on peach blossoms. Only actively foraging insects, making contact with floral reproductive parts, were collected as they are the most likely to act as pollinators, transferring pollen between flowers. The European honey bee (*Apis mellifera*), while abundant, was not included in this study as they are managed by farmers in the region and fluctuations in their populations are not likely the result of changes in land use. Wild pollinators were collected into individual wax paper cones and placed into jars with ethyl acetate. Time was stopped while pollinator specimens were being processed to ensure that all transects were sampled for the same duration.

Statistics

To address our first and second hypotheses, concerning the importance of scale and land use in determining pollinator community composition, we tested for the influence of current and historic land use types at local and regional scales using Non-metric Multi-Dimensional Scaling (NMDS). We ordinated the entire pollinator community across sites to create a two-dimensional representation of pollinator community composition based on relative Bray–Curtis distances (R vegan package; Oksanen *et al*., 2010). We used 999 iterations with random starting positions, accepted stress <2 and instability <0.0003. NMDS uses rank distance for ordination and sites with similar composition fall out close together in the plot (Legendre & Legendre, 1998). Thus, the physical distance between sites in ordination space shows the relative similarity of their pollinator composition (McCune *et al*., 2002). As one site pair may have been close enough for pollinators to fly between (2.1 km apart), we checked for spatial autocorrelation between community composition and physical distance using a Mantel test (999 permutations) and found no significant autocorrelation (Mantel statistic $R = 0.01129$, $P = 0.439$).

We then used the results of the NMDS to test for the relation between current and historic land use at local and regional scales, bloom density, and pollinator community composition using a multivariate correlation analysis (R vegan function envfit, Oksanen *et al*., 2010). This approach provides a metric of the effect of the predictor variables on community composition in which longer vectors indicate stronger correlations between the explanatory variables (i.e. land use and bloom density) and the dependent variables (i.e. community composition). We ran 999 iterations of envfit to assess the significance of predictors. Significance was determined at the $P = 0.05$ level.

To address our third hypothesis we indirectly tested for extinction debt using historic and current land use data. Given that long-term data sets are rarely available, various indirect approaches have been suggested for detecting extinction debt (Kuussaari *et al*., 2009). One such approach is to compare historic and current land use to current community composition; if current species abundance or richness is better described by historic than by current landscape variables, then the presence of an extinction debt is likely (Paltto *et al*., 2006; Piha *et al*., 2007). To determine the importance of historic and current land use we used conditional inference trees, also called regression trees, which use a conditional inference framework to estimate the relative importance of explanatory variables through binary recursive partitioning. First, the regression trees test whether explanatory variables are independent of one another and independent of the response variable. If independent, then an algorithm is used to select the explanatory variable that has the strongest association with the response. This association is measured by a *P*-value corresponding to a test for the partial null hypothesis of a single explanatory variable and the response, and the response is split by that selected input variable. The algorithm repeats itself until there are no explanatory variables significantly associated with the response. In this way, regression trees estimate regression-type relationships in a non-parametric way and thus do not assume linearities in response variables. We used the R package ‘party’ to build our regression trees using historic and current land use at local and regional scales and bloom density as explanatory variables to explain the responses in pollinator richness and abundance (Hothorn *et al*., 2006).

Separate trees were made using local and regional data as explanatory variables, to explain responses in both total insect richness and total insect abundance across sites. At the local scale, insect samples were grouped over the three sample periods to produce a single measure of pollinator abundance and richness for each transect. At the regional scale, insect samples were grouped over the three transects to produce a single measure of pollinator abundance and richness for each site. Given that we examined abundance and richness at the transect level at the local scale, and to avoid biases related to potential non-independence of transects (De’ath & Fabricius, 2000), we also used the package ‘coin’ (Hothorn *et al*., 2008) to examine the relationship between the response variable and the explanatory variables given study site-level stratification. The null distribution of the test statistic was calculated using univariate *P*-values and these ‘site-stratified’ *P*-values were calculated for the first node of each tree and presented in the text below as ‘site-stratified *P*-values’.

Results

Current and historic land use at local and regional scales

Historically (1992), local scale (200 m) land use surrounding sites averaged 25.1% (SE: 3.2%) agriculture and 73.0% (SE: 3.3%) natural areas. Development and rangeland, on the other hand, historically covered 2.5% (SE: 0.5%) and 0.1% (SE: 0.001%) of the local landscape. On a regional scale (2 km), land use surrounding sites averaged 23.4% (SE: 1.8%) agriculture, 73.3% (SE: 1.7%) natural area, 2.5% (SE: 0.2%) development, and 0.6% (SE: 0.01%) rangeland (Fig. 1).

‘Current’ local land use, as of 2006, surrounding our sites was comprised of 19.3% agriculture (SE: 3.2%), 64.7% natural land (SE: 4.0%), 13.6% development (SE: 0.9%), and 3.2% rangeland (SE: 0.06%). Since 2006, it is possible that land use may have changed. Despite this, we refer to

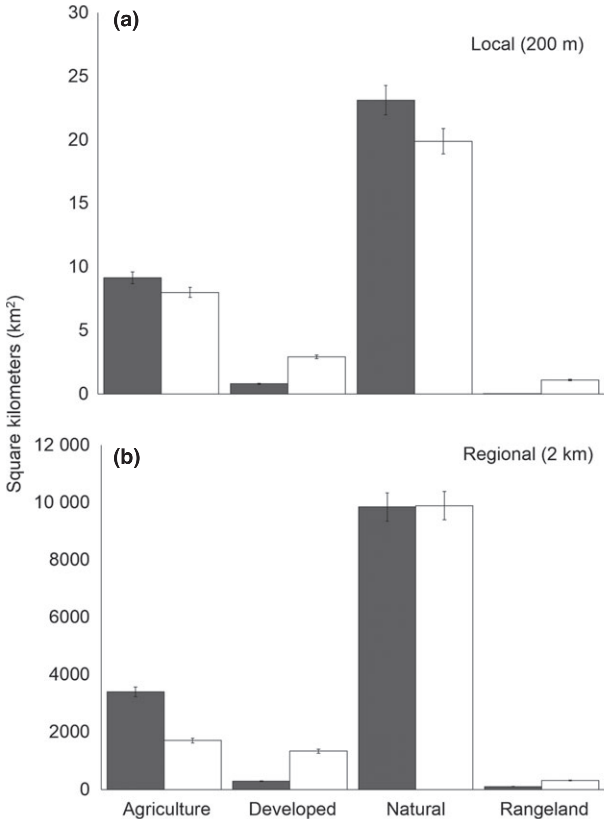

Fig. 1. Land use composition, describing the area of agriculture, development, natural, and rangeland surrounding study sites at (a) local (200 m) and (b) regional (2 km) scales in square kilometres. Historic land use (1992) is shown as dark grey bars, current land use (2006) is shown as light grey bars.

2006 land use as 'current' to distinguish it from 'historic' (1992) land use. Regionally, sites were comprised of 10.3% agriculture (SE: 1.0%), 77.8% natural (SE: 1.4%), 10% developed (SE: 0.6%), and 2.1% rangeland (SE: 0.2%).

Pollinator sampling

We captured a total of 821 insect specimens of 61 species. The specimens were of three orders: Hymenoptera (37 species), Diptera (9 species), and Lepidoptera (14 species). Small *Lasioglossum* specimens of 12 species comprised 54% of the specimens. Another 15% of the sample was accounted for by the solitary bee species *Agapostemon texanus*, *Halictus ligatus*, and *Osmia subfasciata*. Of the remaining species, 32 were singletons and 5 were doubletons (see Appendix S1, for entire species list). Species accumulation curves (Fig. 2) suggest that sampling effectively captured most species present at some of our sites, those reaching an asymptote. Nevertheless, it seems that many of our sites were under sampled, not reaching an asymptote. Because of the short bloom, and temperamental weather of the early spring period, including high winds and frequent cold temperatures, it was not feasible to sample again during the peach bloom. To ensure that our sampling efforts were effective enough not to bias the results of our regression trees, we calculated the expected species richness from a random subsample of our communities (both 40 and 60 specimens) as per Hurlbert's (1971) formulation. Results for the 60-specimen subsample are supplied in the Data S1. We found no difference in our results based on either of the rarefied richness estimates as compared to our measured estimates. Consequently, we felt comfortable using our estimates of pollinator richness despite our species accumulation curves not reaching asymptote at all sites.

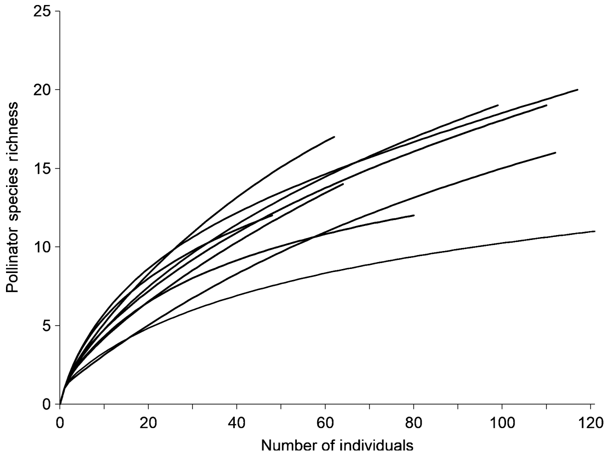

Fig. 2. Species accumulation curves for each study site.

Statistics

Of the explanatory variables, our NMDS plot illustrates that only current natural and agricultural variables at the local scale, shown as solid lines, were significant predictors of community composition at the $P = 0.05$ level ($P = 0.01$ and 0.04 respectively) (Fig. 3). While not statistically tested, there do exist some correlations between predictors of community composition and aspects of nesting habitat. Based on the ordination of the entire pollinator community, there is evidence to suggest that sites with a high proportion of current local agriculture tend to have more ground-nesting bees, including *Agapostemon*, *Dialictus*, and *Halictus* species, (shown as grey squares which tend to be aligned with the local agriculture area axis). Sites with more current local natural area tend to have more cavity-nesting bees (shown as black circles which align more with the local natural area axis), including *Osmia*, *Megachile*, and *Ashmeadiella* species. Non-central place foragers, Diptera and Lepidoptera (open circles), were not associated with any particular land use type. Bloom density was initially included in models but was found not to be significant ($P > 0.5$). As a result, bloom density was not included as an explanatory variable in our models.

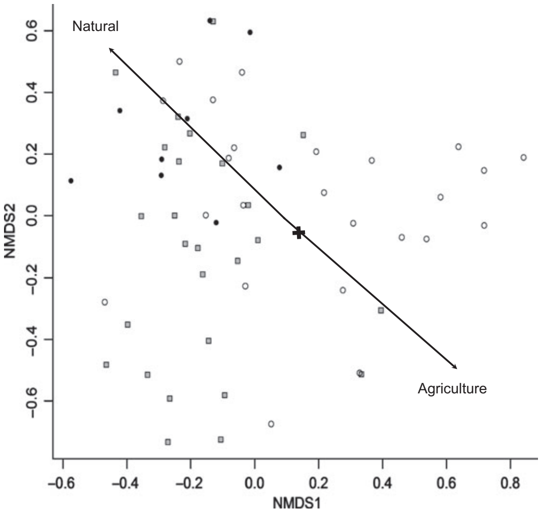

Fig. 3. Non-metric Multi-dimensional Scaling (NMDS) of the pollinating insect community. Explanatory factors are projected to maximally correlate with corresponding species variables, with longer vectors indicating stronger correlations. Current local natural and agricultural variables were significant at the $P = 0.05$ level. Sites with a high proportion of local agriculture have more ground-nesting bees (shown as grey squares) and sites with more local natural area have more cavity-nesting bees (shown as black circles). Non-central place foragers, Diptera and Lepidoptera (open circles), were not associated with any particular land use type.

On a local level, regression trees indicate that pollinator abundance was greater in transects with greater amounts of historic local agricultural area ($P = 0.012$). Specifically, transects historically surrounded by greater than 1.27 ha (40.5%) local agricultural land cover averaged significantly more insects per transect (Fig. 4a). Approximate general independence tests show that pollinator abundance stratified by site was also significantly greater in sites with greater than 1.27 ha historic agricultural land cover ($Z = -1.46$, $P = 0.03$). Pollinator richness was significantly greater in transects with greater current local natural area ($P = 0.004$). Specifically, those transects with more than 2.51 ha (80.0%) of local natural area had between 1 and 4 more species per transect. Approximate general independence tests show that pollinator richness stratified by site was greater in sites with greater than 2.51 ha of natural area ($Z = 1.5127$, $P = 0.038$). We found that no regional land use values, neither current nor historic, were significant in our models.

Discussion

In this study, we document the importance of spatial scale and the impact of current and historic land use on pollinator community ecology in exurban landscapes. First, we reveal that local land use is a better predictor of pollinator community composition in Central Texas peach orchards than regional land use. Second, we show that both current agricultural and natural land use types are important in shaping pollinator community composition. Finally, our analyses indicate that historic agriculture is an important factor affecting current pollinator abundance, offering indirect evidence of extinction debt in this rapidly expanding exurban landscape.

Spatial scale

We found that local (200 m) land use is more predictive than regional (2 km) land use in determining pollinator community composition. In agreement with other studies, this result is likely related to the constraints of the relatively short foraging distances that characterise many of the small-sized pollinators that we found in our study (Steffan Dewenter *et al.*, 2002). From a management perspective, these findings may have important ramifications for the conservation of diverse and robust pollinating assemblages. Management practices, such as the addition or maintenance of local floral and nesting resources have been documented to increase insect abundance and richness and alter community composition even in degraded regional landscapes (Batáry *et al.*, 2011; Munyuli, 2012; Williams & Winfree, 2013). Results from this study further support this claim, showing that local availability of habitat-related resources has a major impact on pollinator community composition.

Natural and agricultural land use

We also found evidence supporting our second hypothesis, that natural land use was highly predictive of pollinator community composition. To our surprise, local agricultural land was also an important factor in predicting pollinator community composition. This result is likely due to the direct relationship between the particular qualities of natural and agricultural lands in our region and pollinator nest-site availability. This finding is best evidenced by the divergent impacts on subsets of the pollinator community seen in pollinators with differing life history traits: ground-nesting bees, cavity-nesting bees, and non-central place foragers, including butterflies and flies.

We found evidence suggesting that ground-nesting bees were most diverse and abundant at sites with an abundance of local agricultural land, whereas cavity-nesting bees were most diverse and abundant at sites locally surrounded by an abundance of natural area. In our region, natural areas were predominantly comprised of deciduous, evergreen, and mixed forest, and thus provide the vegetative biomass and associated crevices for cavity-nesting bees. Other studies have confirmed this relationship, showing that the availability of nesting cavities directly impacts the richness and composition of local cavity-nesters (Potts *et al.*, 2005; Jha & Vandermeer, 2010).

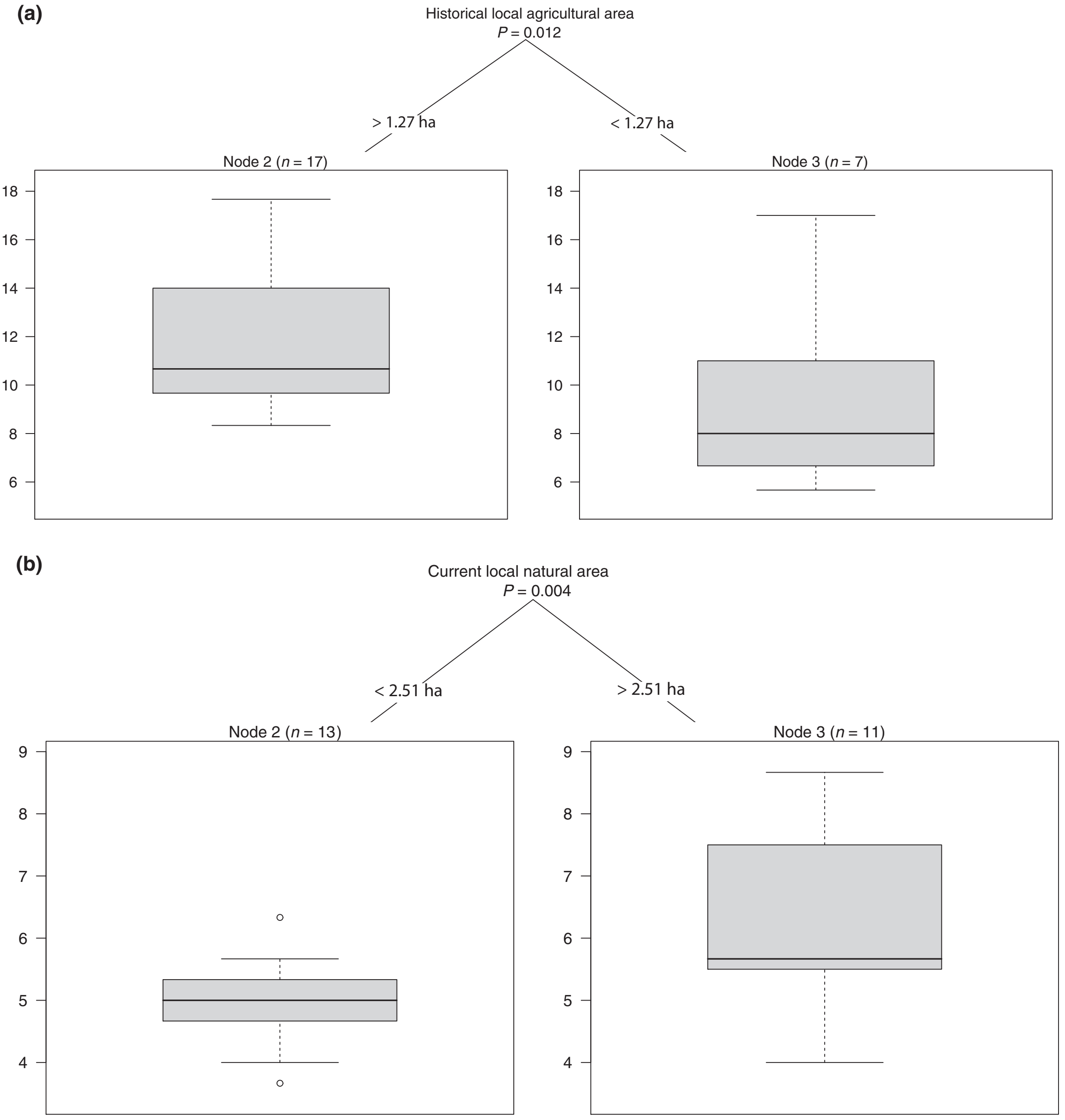

Fig. 4. Regression trees for (a) pollinator abundance and (b) pollinator richness and local land use explanatory variables. The *P*-values listed at each node represent the test of independence between the listed variable and the response variable. Box plots show the distribution of the abundance data within that branch. Boxes represent the inner-quartile range of the data, dark horizontal lines within the boxes represent the median, whereas whiskers represent the extent of data within the 1.5 × inner-quartile range. Circles above and below the whiskers represent data points outside of this range. The number of transects that fall within each branch (*n*) are listed above the box plots.

Furthermore, other studies have shown that forested natural areas are strongly associated with cavity-nesting bees (Tylianakis *et al.*, 2006), and that conversion of natural habitat to other land use types can cause reductions in this group (Williams *et al.*, 2010). Agricultural land use, on the other hand, offers a very different suite of nesting resources. In our study region, agricultural land is comprised of orchards, vineyards, and a few row crops. Thus, one of the most obvious impacts of agricultural development in the region is the clearance of forests and consequent exposure of bare ground, which remains largely untilled due to utilisation for orchards and vineyards. Ground-nesting bees require this type of exposed and undisturbed soil in which they excavate tunnels to provision their young. Potts *et al.* (2005) found similar results, showing that nearly half of the variation in bee community composition and species richness was explained by the availability of nesting resources, which was closely related to land use and disturbance regimes at a given site. Likewise, Williams *et al.* (2010) found that ground-nesting bee species richness did not suffer from human activities such as agricultural intensification, because disturbance improves access to bare soil. Furthermore, this result is confirmed by other studies which have shown that some wild bees may actually benefit from agricultural development, such as those ground-nesting bees that use disturbed areas for nesting, pollinators that benefit from pollen-rich crop fields (Westphal *et al.*, 2003), or bees that benefit from ecosystems in which agricultural areas provide a greater diversity, continuity or abundance of floral resources than original habitat types (Winfree *et al.*, 2007, 2011). The distinction of our study from others that have investigated ground-nesting bees in agricultural habitats is that our system lacks the intense and destructive tillage practices that have the potential to disrupt ground-nesting bees (Williams & Kremen, 2007).

Interestingly, the non-central place foragers, butterflies and flies, were not significantly associated with any particular land use type. Unlike bees, butterflies and flies are not tethered to particular nest sites and may forage for longer distances than many bees (Jauker *et al.*, 2009). Nevertheless, butterflies and flies require substrates for ovipositioning and larval development to be distributed throughout the habitat (Schweiger *et al.*, 2005). While we did not measure host-plant availability, our results are congruent with past studies that suggest that butterfly and fly assemblages respond to different aspects of land use (Bergman *et al.*, 2004; Jauker *et al.*, 2009) and larger spatial scales (Schweiger *et al.*, 2005) than bees.

Historic land use and exurban development

Lastly, we found evidence to support our third hypothesis, the existence of extinction debt in landscapes experiencing rapid exurbanisation. We found that historic agricultural area was the most important variable in explaining pollinator abundance across groups and was more predictive than the presence or absence of current habitats. Given that agricultural lands offer important resources to wild pollinators, it follows that its conversion into residential/commercial human development and resulting increase in impervious cover has far-reaching detrimental effects on local pollinator fauna. Our findings resonate with studies that document negative impacts of impervious surfaces on bee dispersal in rapidly urbanising areas (Davis *et al.*, 2010; Jha & Kremen, 2013a,b). Nevertheless, it is important to emphasise that urbanisation is not likely to have an uniform effect on pollinator communities across the globe. Instead, urbanisation is likely to affect the pollinator community in a manner that is specific to the type of land being converted, the intensity of urbanisation, and the pollinator community itself. In fact, a growing body of research has found urbanisation to have the opposite effect of what we find here, showing instead that urbanisation significantly increases the diversity of pollinators as compared to less urbanised environments (Cane *et al.*, 2006; Baldock *et al.*, 2015; Sirohi *et al.*, 2015). Furthermore, our data reveal that current pollinator communities reflect not only current but historic land use composition, providing evidence of possible extinction debt.

While one might not expect that pollinator abundance, rather than richness or diversity, would be the measure to best reflect extinction debt resulting from land use changes, past studies have shown that pollinator abundance is often dependent, in part, on past floral resources. Crone (2013) found that solitary bees experienced demographical responses to pulsed resources in the following year. The study, in agreement with others (Minckley *et al.*, 1994; Williams & Kremen, 2007), showed that in environments where resources change over time, increased floral resources in 1 year affect bee fecundity in that year and consequently the abundance of bees in the following year. While, other studies have also hypothesised this type of delayed impact of floral resources on bee abundance (e.g. Tepedino and Stanton 1981; Potts *et al.*, 2003), only two studies thus far have documented the relationship (Inari *et al.*, 2012; Crone, 2013). Our study is the first to suggest that this type of relationship may persist over multiple years.

Future directions and conclusions

While more time intensive, we suggest that future studies investigating extinction debt following exurban development should examine pollinator species composition before, immediately after, and more than 5 years after the disturbance. Given that we documented differences in pollinator community response to land use periods separated by 5 years, we suggest this as a starting point for assessing extinction debt, and posit that some pollinator communities may stabilise only after many more years. In addition, we posit that pollinator surveys conducted across a time series would allow for the assessment of biodiversity changes as a result of the initial land conversion as well as the delayed impact of exurbanisation over time. In conclusion, it is clear that exurbanising areas have threatened a wide variety of organisms in the recent past (Beatley, 2000). Our study offers one of the first assessments of exurbanisation impacts on wild pollinators, reveals the importance of local natural and agricultural lands to community composition, and provides evidence for potential pollinator extinction debt following exurban land development.

Acknowledgements

We are grateful to the Hill Country Fruit Council for their support and permission to conduct research on their land. In addition, the manuscript was greatly improved by feedback from an anonymous reviewer and associate editor, as well as members of the Jha lab including Kim Ballare, Nathaniel Pope, Rebecca Ruppel, Antonio Castillo, and Laurel Trevino. The authors declare no conflict of interest. This project was funded by the Texas Parks and Wildlife Department, the National Science Foundation, and the University of Texas, Austin.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/icad.12139:

Data S1. Regression trees for expected species richness from a random subsample of our communities (60 specimens) and local land use explanatory variables.

Appendix S1. Complete species list.

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Accepted 29 July 2015

Editor: Simon R. Leather
Associate editor: Matt Heard