



Natural land cover drives pollinator abundance and richness, leading to reductions in pollen limitation in cotton agroecosystems



Sarah Cusser^a, John L. Neff^b, Shalene Jha^{a,*}

^a Department of Integrative Biology, The University of Texas at Austin, 1 University Station C0930, Austin, TX 78712, USA

^b Central Texas Melittological Institute, 7307 Running Rope, Austin, TX 78731, USA

ARTICLE INFO

Article history:

Received 24 May 2015

Received in revised form 21 April 2016

Accepted 22 April 2016

Available online xxx

Keywords:

Agroecology

Ecosystem services

Gossypium hirsutum L.

Landscape ecology

Path analysis

ABSTRACT

Cotton is the most economically and culturally important fiber crop worldwide. Though cotton may potentially benefit from animal mediated pollination, it is unknown if the species is indeed pollen limited across agroecological landscapes. Our study had three objectives: (1) identify the land use attributes that impact wild pollinator abundance and diversity, (2) investigate the relationship between pollinator community composition and cotton pollen limitation and (3) determine the extent of direct and indirect effects of land use on pollinator community composition and pollination service. To address these objectives, we used a combination of pollinator community surveys, GIS analysis, and pollen limitation experiments across 12 cotton landscapes in South Texas. Overall, we found that pollinator community composition was closely related to the abundance of natural areas (250 m radius). We also found evidence of substantial cotton pollen limitation, as significantly larger bolls were produced with the addition of outcross pollen. Further, we reveal that pollen limitation was negatively correlated with pollinator abundance and richness. Path analysis confirmed the two direct effects of land use composition on pollinator community and pollinator community composition on pollen limitation. Overall, our results reveal potential for increased crop yields via wild pollinator-mediated fruit set, equivalent to more than \$108/acre with a regional gain of over \$1.1 million USD. Further, our research provides insight into the specific land management practices that support pollinator communities within cotton agroecosystems. Cotton landscapes that maintain natural areas promote wild pollinator abundance and diversity, and subsequently experience reduced pollination limitation and increased crop yields.

© 2016 Elsevier B.V. All rights reserved.

1. Introduction

Given the rapidly expanding human population, it is estimated that by the year 2050, humans will be challenged to provide fiber, food, and fuel for ~9.6 billion world inhabitants (United Nations News Centre, 2013). One proposed solution to this problem is to increase the intensity and homogenization of agricultural and forestry landscapes (Robinson and Sutherland, 2002; Benton et al., 2003). Although landscape homogenization has the potential to increase crop yield and efficiency (Green et al., 2005), increased agricultural intensity is also irrefutably one of the main causes of

biodiversity loss (Adger et al., 2002; Roulston and Goodell, 2011; Kehoe et al., 2015). As a result, within intensely managed, homogeneous agricultural landscapes, yields often increase at the expense of biodiversity. Beneficial insects comprise an economically important group of biodiversity in agricultural systems as they provide ecosystem services critical to human survival; these organisms may act as natural enemies to crop pests or provide pollination services that benefit yield (Daily, 1997; Losey and Vaughan, 2006). The loss of such insect biodiversity in agricultural settings may lead to reduced ecosystem services, and decreased crop production in such environments. One particularly important group of beneficial insects are the pollinators, such as bees, butterflies, and flies, which move pollen between plants, and increase yield and quality in many crops (Kevan et al., 1990). As land use intensification increases, however, and beneficial insect

* Corresponding author.

E-mail address: sjha@austin.utexas.edu (S. Jha).

populations decline (Benton et al., 2003), services provided by these beneficial insects may be lost, negatively affecting yield (Elmqvist and Maltby, 2010), and potentially undermining the ecosystem processes on which these agroecosystems rely (Tscharrntke et al., 2012).

Thus, although agriculture and biodiversity conservation may have traditionally been viewed as incompatible (Mittermeier et al., 2003), the two can be mutually considered in order to maximize long-term yields and promote the preservation of ecosystem services. Past research investigating this subject has taken place largely in low intensity agriculture and polycultural systems such as shade coffee and cacao (Giller et al., 1997; Tscharrntke et al., 2005; Schroth and Harvey, 2007; Firbank et al., 2008, but see Klein et al., 2012). These studies have shown that diversified agricultural practices can promote the establishment and long-term stability of biodiversity to enhance ecosystem services and aid in biodiversity conservation (Estrada and Coates-Estrada, 2002; Daily et al., 2003; Mayfield and Daily, 2005; Kleijn et al., 2015; Winfree et al., 2015), while also contributing to increased crop production and rural income (Pretty et al., 2003). However, critics to this approach claim that it is largely relevant only in polycultural settings rather than in highly intensified agroecosystems (Green et al., 2005). Thus, at present it is not known if the dual optimization of biodiversity and crop yields is achievable in highly intensified agricultural landscapes.

Worldwide, cotton (*Gossypium* spp. (Malvaceae)) is one of the most intensely managed and economically important agroecosystems. The industry generates more than \$1 billion per annum and employs over 200,000 people in the US alone (USDA ERS, 2013). Cotton agroecosystems can host a wide range of beneficial insects, including lacewings, ladybird beetles, and spiders (Eyhorn et al., 2005). Furthermore, the large flowers of cotton, which produce copious amounts of pollen and nectar, can serve as a food resource for a diverse group of pollinating insects (Free, 1970; Moffett et al., 1976; Berger et al., 1988; Pires et al., 2014). Although cotton is known to be self-compatible, previous studies suggest that it benefits from pollination service given that cotton pollen is too heavy to move between flowers without an insect vector (Free, 1970; Rhodes, 2002). Despite the likely importance of pollinators in cotton production, cotton growers do not currently utilize managed pollinators (e.g., honey bees or bumble bees) nor do they use agricultural practices that promote the visitation of wild pollinator communities in the southern U.S. (Delaplane et al., 2010).

The composition of wild pollinator communities may be particularly critical within agroecosystems because pollination service stability is often associated with pollinator diversity and abundance (Garibaldi et al., 2013). Pollinator diversity, in particular, appears to enhance the resilience and security of pollination ecosystem services, especially in the face of regional land use change (Peterson et al., 1998). Because of natural fluctuations in pollinator populations, the diversity of wild pollinator communities is important in providing stable crop pollination service between years (Williams et al., 2001; Garibaldi et al., 2013). Specifically, pollinator diversity can buffer pollination services against asynchronous fluctuations in single pollinator species over time (Williams et al., 2001; Bartomeus et al., 2013). Mechanistically, greater fruit set observed in more diverse pollinator communities is attributable to greater pollination functional diversity across both space and time (e.g., Hoehn et al., 2008; Garibaldi et al., 2013).

Finally, pollinator community composition and pollination service assessment should be considered at multiple spatial scales given that many insects are mobile, and often respond to land use change in areas that consist of multiple habitat types (Turner, 1989; Dunning et al., 1992). Land use at the regional landscape scale can

be characterized by changes in the diversity of habitats, as well as the size and arrangement, or complexity, of those habitats (Gustafson, 1998). Recent studies have also demonstrated a relationship between landscape complexity and the abundance and diversity of insect pollinators (Steffan-Dewenter et al., 2002, but see Petersen et al., 2013; Gaines-Day and Gratton 2016). This is probably due to the fact that many pollinator species have diverse resource needs (e.g. floral and nesting), which are likely to occur in spatially separated habitats (Westrich, 1996). Therefore, in addition to the area of suitable local and regional habitat, the diversity and arrangement of habitat types is an important factor in determining pollinator abundance and diversity in human modified landscapes (Wiens et al., 1985; McCoy et al., 1986; Turner and Bratton, 1987; Steffan-Dewenter et al., 2002; Garibaldi et al., 2013). Further, past work has revealed that changes in the abundance of particular land use types can have important impacts on pollinator communities. For example, increasing isolation from natural habitats has been found to be associated with a decline in crop pollination (reviewed in Ricketts et al., 2008). This could be explained directly by a greater abundance and richness of pollinators near natural habitat, but also by an indirect effect of habitat on pollen-limitation via environmentally-driven changes in plant-pollinator interaction, such as pollinator foraging behavior (Kunin, 1993; Sih and Baltus, 1987).

To determine how land management practices affect pollinator community composition and the pollination service provided in the cotton agroecosystem, we examine three predictive hypotheses: First, we expect to find that natural land cover and land use heterogeneity positively effect the richness and abundance of wild pollinators. Second, we predict that pollen limitation is a function of the abundance and diversity of the pollinator community, expecting to find a negative relationship between pollen limitation and the abundance and richness of local pollinators. And lastly, we predict that land use indirectly affects pollen limitation, expecting to find that greater natural area and heterogeneity indirectly reduce pollen limitation.

2. Materials and methods

2.1. Study system

Texas grows more than 25% of the total U.S. cotton crop, and cotton covers roughly six million acres of farmland in the state. In Texas, cotton is grown in four major regions: South Texas, the Blacklands and North Texas, El Paso, and West Texas (TAMU, 2013). We conducted our research in the South Texas region, where cotton is a primary crop and one of the only crops that offers nectar and pollen resources to potential insect foragers in the area (National Cotton Council of America, 2014). The South Texas region is responsible for about 15% of the annual Texas cotton crop, and grows primarily Upland cotton varieties (*Gossypium hirsutum* L. (Malvaceae)). The region is characterized by shrink-and-swell clay soils and is predominantly rain fed. Agricultural land makes up the majority of the region (55%), and includes cotton, sorghum, corn, and soybean. The remainder of the region is comprised of cattle ranching (36%), low density developed areas (6%), and natural areas (2%), including shrub, mixed woodland, and marsh areas along the gulf coast.

We conducted research in 12 sites located in three regions between Telferner (28.847913, -96.892975) and Woodsboro, Texas (28.303701, -97.381612). We chose sites in an effort to include a wide range of landscape-level habitat heterogeneity, while controlling for geographic region. Specifically, the three geographic regions of study were near the towns of Woodsboro, Austwell/Tivoli, and Telferner, Texas. Within each landscape, sites were located within cotton fields that were at least 35 ha in size and

2 km apart from each other (Fig. 1). Sites were not sprayed with any chemical five days prior to, nor during, the 16-day sampling period.

2.2. Land use impacts on pollinator communities

2.2.1. Land use

We analyzed land use surrounding sites at local (250 m radius) and regional (1 km radius) scales using information from the 2011

National Land Cover Database (Jin et al., 2013) using qGIS (QGIS Development Team, 2013). It is important to note that because transects were located on the edge of the field, local land use includes non-cotton land use types. Land use was analyzed in two ways. First, we calculated the percentage of land use types (26 types total) surrounding each site grouped into three broad categories: Agricultural, Natural, and Rangeland at local and regional scales (Agriculture: row crops including corn, sorghum,

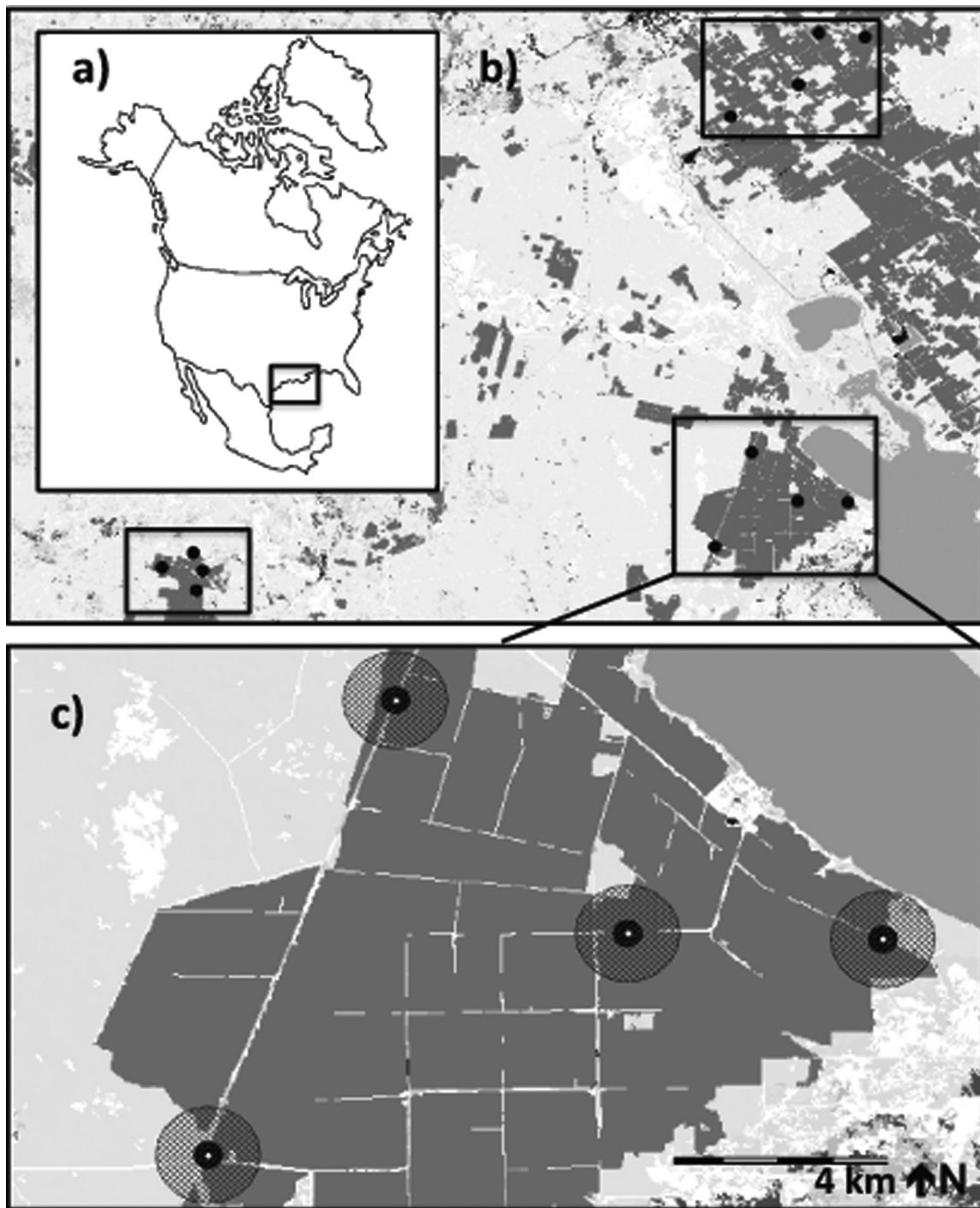


Fig. 1. Map of study sites. (a) North America and (b) map of 12 conventional cotton fields used as study sites along the South Texas Gulf Coast. Sites were located in three geographic areas near the towns of Woodsboro, Austwell/Tivoli, and Telferner, Texas, USA. (c) Within each region, four cotton field sites were chosen that were primarily surrounded by one of four habitat types: Developed (white), Natural Areas (light grey), Rangeland (medium grey), and Agriculture (dark grey). Sites were at least 35 ha in size and 2 km apart from each other. White dots represent sampling sites, dark buffers represent the 250 m radius local habitat, and hatched buffers represent 1 km radius regional habitat.

and soy as well as cotton itself; Rangeland: pasture, hay, and grassland; and Natural: riparian forest, deciduous and evergreen forest, and scrubland). Because human development (any man made surface) accounted for a relatively small amount of land use in the region (3% regionally), we did not specifically investigate this land use type. Next, we analyzed land use heterogeneity surrounding each of our sites. As per Turner (1989), heterogeneity was calculated as the total edge distance, or perimeter, between the different 26 land use types. Other indices of heterogeneity, like habitat richness or diversity, do not capture the added edge distance and complexity created by small patch sizes. Thus, in this study, a landscape with a few land use types and minimal edge between types would have low heterogeneity, while a landscape with a large number of different land use types and a maximum edge between types would have high heterogeneity. Overall, the fixed variables used to describe land use in this study include the abundance of agriculture, rangeland, natural areas, as well as the heterogeneity of all land use types at local (250 m) and regional scales (1 km radius).

2.2.2. Pollinator community composition

To quantify the pollinator community at each site we netted insects found actively foraging within cotton flowers during three one-hour sampling bouts at each site. During each one-hour bout, a single collector walked four parallel 50 m × 1 m transects checking blooms for visitors. Transects were located at the edge of fields and were ~12 m apart, representing an area of 2500 m². The three sampling sessions were at least five days apart and covered the peak of cotton bloom in 2014 (June 16th–July 2nd). Because we only collected insects actively foraging on the reproductive parts of the flower, we consider all specimens as potential pollinators. 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. Pollinators were placed into jars with ethyl acetate until the end of the sampling period and then transferred into individual vials of ethanol. To determine pollinator abundance and richness at each site we pooled the three samples taken at each site. Thus, pollinator abundance was determined as the total number of specimens pooled for the three sampling bouts, and pollinator richness was determined as the total richness of specimens pooled for the three sampling bouts at each site.

2.2.3. Land use impacts on pollinator community analysis

To determine the relationship between land use and pollinator abundance and richness, we first screened land use variables for multi-collinearity. To do this we calculated variance inflation factors (hereafter referred to as VIFs) using the “vifstep” function in the R statistical package usdm (Naimi, 2013). Because land use variables are inherently related to one another, we chose a conservative theta value of VIF < 2 to eliminate collinearity from our models (Myers, 1990; Cariveau et al., 2004). At the local scale, of the four variables checked for collinearity (Rangeland, Natural, Agriculture, and Heterogeneity), only Natural land use and Heterogeneity were found to be non-collinear (Local Natural, VIF = 1.17, Local Heterogeneity, VIF = 1.17). Similar to the local scale, at the regional scale, of the four variables checked for collinearity (Rangeland, Natural, Agriculture and Heterogeneity), only Natural and Heterogeneity were found to be non-collinear (Regional Natural, VIF = 1.49, Regional Heterogeneity, VIF = 1.49).

Once collinear variables were removed, we used geographic region (Woodsboro, Austwell/Tivoli, and Telferner) as a random effect, and land use variables at local and regional scales (percent Natural and Heterogeneity) as fixed effects. Because local and regional land use variables were highly correlated, we investigated them in separate local and regional models. Land use variables were scaled around zero to account for differences in magnitude

and Poisson distributions were used for abundance and richness. Top models were selected based on AICc using the “dredge” function in the R statistical package MuMIn (Bartoń, 2015). To characterize the top models, we used the function “model.avg” in the package MuMIn (Bartoń, 2015) to average models with an AICc of less than 2. GLMMs were performed using the “glmer” function in the package lme4 (Bates et al., 2014).

2.3. Pollinator community impacts on pollen limitation

2.3.1. Pollen limitation experiment

We conducted a pollen limitation experiment at each of the 12 sites. Early in the flowering season (June 13th–15th, 2014), 10 virgin flowers were exposed to one of 5 treatments: closed (C), closed self-cross (CS), closed outcross (CO), open (O), and open outcross (OO), for a total of 50 experimental flowers at each site. Throughout the flowering period (24 h), closed (C) flowers remained bagged with lightweight white organza bags that excluded pollinators. Closed self-cross flowers (CS) were bagged but supplemented with self-cross pollen from the same flower, and closed outcross (CO) flowers were bagged but received outcross pollen from three to five donors within a 10 m radius of the focal plant. These three treatments evaluated the importance of outcross pollen to seed/fruit production, as conducted in other systems (Parker, 1997; Yang et al., 2005; Benjamin et al., 2014). The fourth and fifth treatments were left unbagged throughout the flowering period to receive ambient pollination service: open flowers (O) measured the amount of ambient pollination service and open outcross flowers (OO), remained open but were also supplemented with an abundance of additional outcross pollen from three to five donors within a 10 m radius of the focal plant, saturating the stigma, and thus representing maximum pollination service. From the fourth and fifth treatments, we evaluated potential limitation in boll set resulting from inadequate pollination service. All pollination treatments happened between the hours 0800 and 1300, when cotton flowers are most receptive (Free, 1970). Bags were removed after floral senescence, 24 h after treatment, and bolls were left to mature for 6 weeks in the field before they were hand-collected. Because there was no significant difference in boll weight between flowers that received the closed outcross pollen treatment and those that received the open outcross pollen, we assume there was no significant effect of the exclusion bag on boll development (see results below). Collected bolls were then assessed for seed-cotton weight. Seed-cotton weight is the total weight of both the lint and seeds of a single cotton boll and was used as a metric of yield. While lint is the primary product of cotton production, cottonseed is also an economically important outcome of production. Seeds are processed for oil, as well as protein-rich animal meal, and roughage (National Cotton Council of America, 2014). Consequently, changes in both lint and seed production are economically important to cotton growers. Pollen limitation was measured as the difference in seed-cotton weight, between open outcross (OO) treatment flowers and open (O) flowers that received ambient pollination service (as per Klein et al., 2003; Groeneveld et al., 2010; Holzschuh et al., 2012; Benjamin et al., 2014). To test for differences between treatments, we used a Shapiro-Wilk test to check for a normal distribution of seed-cotton weight, then ANOVA and Tukey HSD tests to determine the significance of differences in seed-cotton weight between treatments.

2.3.2. Pollinator community impacts on pollen limitation analysis

To determine the relationship between pollinator abundance and richness and the extent of pollen limitation, we followed a similar series of statistical tests as described above (Section 2.1.3). First, we screened fixed variables (pollinator abundance and

richness) for collinearity, eliminating variables leading to $VIF > 2$ (Myers, 1990; Cariveau et al., 2004). Testing for collinearity between pollinator abundance and richness, we found the two variables were not collinear. Using those two variables, model selection found that both variables were important in predicting pollen limitation. The dependent variable (pollen limitation) was checked for normality using the Shapiro-Wilk test (R Development Core Team, 2014), and a Gaussian distribution was used for the model. Top models ($\Delta AICc < 2$) were averaged and GLMMs were performed using the “glmer” function in the package lme4 (Bates et al., 2014).

2.4. Path analysis to assess indirect & direct effects on pollen limitation

To analyze the combined importance of land use and pollinator community composition on pollen limitation, we used path analysis and structural equation modeling. To fit the structural equations we used the “sem” function in the R package Lavaan (Rosseel, 2012).

2.4.1. Parameterizing the model

To parameterize the model we used the explanatory variables described in the previous sections: Land use was parameterized as the percent of local natural area surrounding sites, pollinator community composition as both pollinator abundance and richness, and pollen limitation by the difference in seed-cotton weight between Open (O) and Open Outcross (OO) pollination treatments (See Section 3).

2.4.2. Analyzing the model

We examined the SEM model according to the criteria of Kline 2011: accepted models had a chi square value greater than 0.05, comparative fit index (CFI) and Tucker-Lewis Index (TLI) greater than 0.9, and standardized root mean square residuals (SRMR) less than 0.1. We calculated direct effects (standardized partial regression coefficients), indirect effects, and significance.

3. Results

3.1. Land use impacts on pollinator communities

3.1.1. Land use

On the local scale, land use surrounding sites averaged 72.8% (SE: 2.4%) agriculture, 12.4% (SE: 1.8%) natural, and 7.5% (SE: 0.7%) rangeland. On the regional scale, land use surrounding sites averaged 67.7% (SE: 1.8%) agriculture, 1.5% (SE: 0.2%) natural, and 27.5% (SE: 1.6%) rangeland. Heterogeneity averaged 9046 m at the local scale (SE: 206.3 m) and 99,034 m regionally (SE: 2094.9 m).

3.1.2. Pollinator community composition

We captured a total of 841 pollinator specimens comprised of 52 species. The specimens were of four orders: Hymenoptera (37 species), Diptera (5 species), Lepidoptera (7 species), and Coleoptera (3 species). The solitary bee, *Melissodes tepaneca*, and the European honey bee, *Apis mellifera*, made up 21% and 19% of total specimens collected, respectively. The syrphid fly, *Allograpta exotica*, comprised another 16% of the specimens. Lastly, *LasioGLOSSUM* specimens of at least nine species made up 15% of the specimens. Of the remaining pollinators, 24 were singleton species, and 10 were doubletons (See section 8, Appendix, for entire species list).

3.1.3. Land use impacts on pollinator community

At the local scale, model selection revealed that natural area was the best predictor of pollinator abundance as well as pollinator richness (Table 1a and b). The averaged top models ($\Delta AICc < 2$) showed a strong positive relationship between pollinator

Table 1

Model averaged coefficients for top models ($\Delta AICc < 2$) examining the impact of local land use (250m) on (a) pollinator abundance and (b) richness, and the impact of regional land use (1 km radius) on (c) pollinator abundance and (d) richness.

	Estimate	Std. Error	z value	P value
Local Land Use				
(a) Abundance				
Intercept	4.09368	0.31321	11.230	<0.001
Local Natural	0.15692	0.04498	3.024	0.002
Local Hetero.	0.04801	0.04019	1.015	0.31
(b) Richness				
Intercept	2.66000	0.07742	29.588	<0.001
Local Natural	0.25571	0.06740	3.273	0.001
Local Hetero.	0.06079	0.09030	0.572	0.57
Regional Land Use				
(c) Abundance				
Intercept	4.09866	0.33486	10.566	<0.001
Regional Natural	0.07166	0.04375	1.412	0.16
Regional Hetero.	0.05662	0.05231	0.952	0.34
(d) Richness				
Intercept	1.97431	1.17381	1.680	0.093
Regional Forest	0.11842	0.10643	1.022	0.31
Regional Hetero.	-0.01767	0.06443	0.242	0.81

abundance and the abundance of natural land use at the local level (250 m radii)(estimate = 0.157, z value = 3.024, p value = 0.002, Table 1a). The top model for richness also showed a strong positive relationship between richness and the abundance of natural land use at the local level (250 m radii)(estimate = 0.255, z value = 3.273, p value = 0.001, Table 1b).

At the regional scale, model selection also revealed that regional forest was the best predictor of pollinator abundance as well as pollinator richness. Regional models followed very similar trends as local models, though were generally weaker, and not significant at the $p = 0.01$ level (Table 1c and d). Details of all four models, including model selection, averaging, and model summary are provided in the supplementary materials section.

3.2. Pollinator community composition and pollen limitation

3.2.1. Pollen limitation

We found that flowers receiving outcross pollen had heavier bolls than either flowers receiving no pollen or self-cross pollen (Fig. 2C, CO, CS). Also, our results revealed that flowers supplemented with additional outcross pollen produced bolls that were significantly heavier than those flowers receiving ambient pollination service (Fig. 2O, OO) (Seed-cotton weight: f value = 47.86, $p < 0.001$). Outcross pollen increased seed-cotton weight by 18%. The closed outcross (CO) treatment was statistically indistinguishable from the open outcross (OO) treatment, revealing that hand-pollination resulted in adequately and effectively pollinated flowers with no negative affect of the closed bagged treatments on fruit set (Fig. 2). We also found a great deal of variation in the degree of limitation between sites. Although most sites were pollen limited, producing bolls between 0.3 g and 3.4 g heavier in seed-cotton weight on average with the addition of outcross pollen, two sites produced slightly smaller bolls on average and revealed no pollen limitation. Those sites with no pollen limitation were among those with the greatest abundance and diversity of pollinators (Fig. 3).

3.2.2. Pollinator community impacts on pollen limitation analysis

Only one model had $\Delta AICc < 2$ Myers (1990), Cariveau et al. (2004), and it revealed a negative relationship between pollen limitation and the explanatory variables pollinator abundance

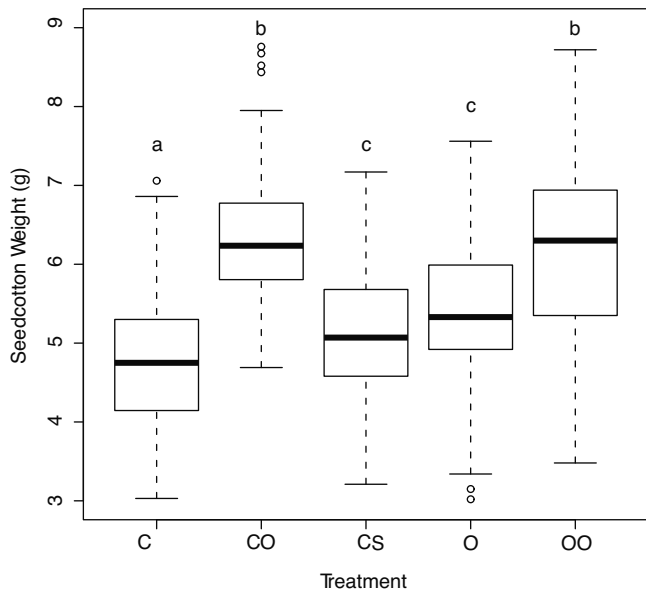


Fig. 2. Boxplot comparing seed-cotton weight between the five pollen limitation treatments: closed (C), closed outcross (CO), closed self-cross (CS), open (O), and open outcross (OO). Closed (C) flowers remained bagged with lightweight white organza bags throughout the flowering period, closed out (CO) flowers were bagged but received outcross pollen from three to five donor flowers in the vicinity, closed self-cross flowers (CS) were bagged but supplemented with self-cross pollen, open flowers (O) remained unbagged to measure the amount of ambient pollination service, and open outcross flowers (OO) remained open but were also supplemented with an abundance of additional outcross pollen. The central bar gives treatment mean, boxes give the 1st and 3rd quartiles, and closed circles show outliers. ANOVA and Tukey HSD statistics were used to compare seed-cotton weight between treatments. Significance is shown with letters.

(estimate = -3.855 , t value = -4.212 , p value = 0.002 , Table 2) and pollinator richness (estimate = -1.985 , z value = -2.169 , p value = 0.058 , Table 2).

3.3. Path analysis to assess indirect & direct effects on pollen limitation

3.3.1. Parameterizing the model

Based on results of the previous sections, we parameterized the SEM using percent local natural area as an indicator of land use, pollinator abundance and richness as indicators of pollinator community composition, and the difference in seed-cotton weight between the Open (O) and Open Outcross (OO) treatments as an indicator of pollen limitation at each site.

3.3.2. Analyzing the model

We found that local land use had a positive direct effect on pollinator community composition (estimate = 0.495 , $SE = 0.290$, z value = 1.910 , p value = 0.047). Pollinator community composition (pollinator abundance and richness) had a strong negative direct effect on pollen limitation (difference in seed-cotton weight between Open (O) and Open Outcross (OO) pollination treatments) (estimate = -0.909 , $SE = 0.433$, z value = -2.051 , p value = 0.040). The indirect effect of land use on pollen limitation was weak and positive (estimate = 0.148 , $SE = 0.344$, z value = 0.430 , p value = 0.67) (Fig. 4).

4. Discussion

In this study we document substantial pollen limitation across cotton agroecological landscapes. Additionally, we reveal a direct negative relationship between the extent of pollen limitation and the abundance and richness of the local pollinator community. We also found a direct positive relationship between natural area

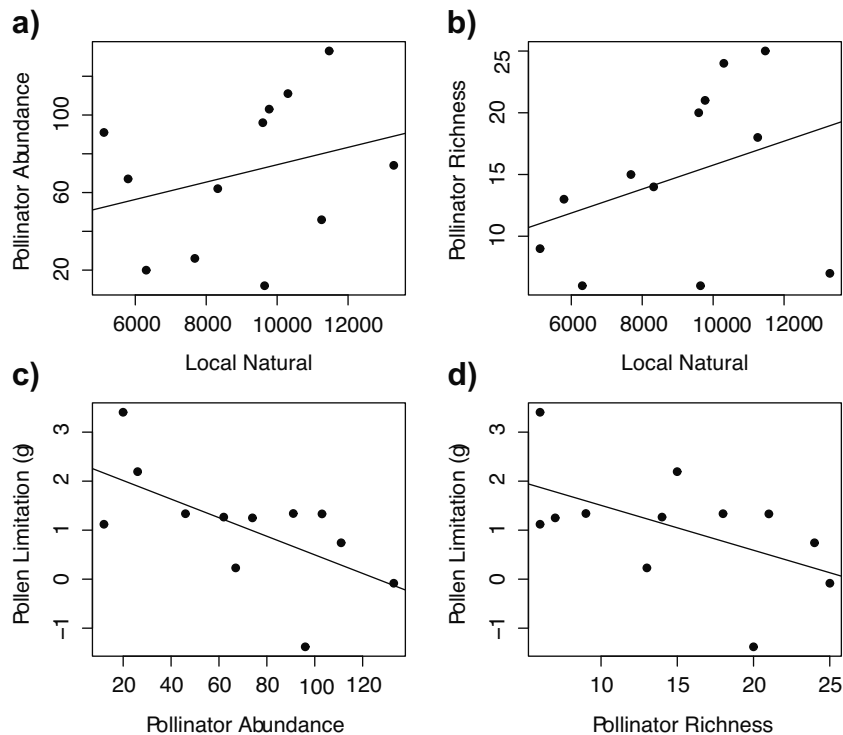


Fig. 3. Scatterplots showing the relationship between (a) local natural area and pollinator abundance, (b) local natural area and pollinator richness, (c) pollinator abundance and pollen limitation, and (d) pollinator richness and pollen limitation. Pollen limitation is determined as the difference in seed-cotton weight between the open outcross (OO) pollen treatment and the open (O) pollen treatment.

Table 2
Model coefficients for the top model for pollen limitation.

	Estimate	Std. Error	t value	P value
Intercept	4.2507	0.6112	6.954	<0.001
Abundance	-3.8555	0.9154	-4.212	0.002
Richness	-1.9854	0.9154	-2.169	0.058

cover and pollinator abundance and richness, and a weak indirect relationship between natural area cover and pollen limitation.

First, we show that the abundance of local natural areas is an important driver of pollinator community composition. Modern agricultural intensification efforts, manifested in fields that are amalgamated and enlarged to enhance farming efficiency, often result in homogeneous landscapes with little non-crop area (Tilman et al., 2002). The loss of natural areas in agricultural habitats may negatively affect pollinators in two major ways. First, pollinators may exhibit a decline due to a reduction in overall resource diversity. Landscape diversity has been shown to create a wider array of foraging niches for different functional groups of pollinators (Fenster et al., 2004) and environmental changes that alter the spatial and temporal distribution of important nesting and food resources can influence pollinator community composition (reviewed by Kremen et al., 2002; Williams et al., 2010). Second, the loss of local natural areas may alter the ability of pollinators to move across landscapes. Because many invertebrate pollinators must forage across multiple land use types to exploit resources important for their livelihood (e.g. food or nesting resources), simplified landscapes may actually prohibit the persistence of pollinators unable to travel between resources in landscapes lacking one of many key resources (e.g. partial landscapes) (Westrich, 1996). In addition to foraging movement, simple landscapes may negatively affect pollinator populations by reducing the likelihood of dispersal and recolonization events. Because pollinator populations naturally fluctuate over time, pollinator assemblages are characterized by rare local extinction events. Thus, a patchwork of high quality habitats, even as small remnants or restored hedgerows, could provide refuge and sources of recolonization for pollinators into newly disturbed sites, thus reducing the negative influence of local extinction events over time

(Perfecto and Vandermeer, 2010; Tschamtko and Brandl, 2004; Steffan-Dewenter et al., 2007).

Second, we show that pollen limitation is closely linked to local pollinator abundance and richness, a pattern also detected in native plant communities (reviewed in Ashman et al., 2004) as well as crop systems (reviewed in Garibaldi et al., 2013). Indeed, diverse and abundant pollinator assemblages have been shown to maximize crop yields, compared to the abundance of a single pollinator species, specifically the European honey bee, *A. mellifera* (e.g., Klein et al., 2003; Hoehn et al., 2008; Winfree and Kremen, 2009; reviewed in Garibaldi et al., 2013), and help to ensure consistent pollination service over multiple years, even in the face of natural fluctuations in the abundances of some species (Kaiser-Bunbury et al., 2010). While recent studies suggest that a few dominant species conduct the majority of the pollination services (Kleijn et al., 2015; Winfree et al., 2015), we posit that diversity may be particularly important in systems where flowering can vary substantially across years and where one of the most stable and abundant pollinators is not particularly effective. Depending on weather and planting, cotton bloom time can range substantially in the southern, often between April and July (National Cotton Council of America, 2014); given that many bee species only forage for a few weeks at a time (Michener, 2007), pollinator diversity may be particularly important for handling plants with substantial inter-annual flowering variation (as seen in Hoehn et al., 2008; Blüthgen and Klein, 2011). Pollinator diversity may also be especially critical for cotton given that one of the most abundant pollinators, the European honey bee, has been shown to be a relatively ineffective pollinator of the crop (Vaissière et al., 1984). While we cannot assume that each pollinator in our community is critical for cotton pollination service, our future research aims specifically towards investigating the effectiveness of different pollinator species and determining the role of pollinator diversity beyond the most abundant species.

For now, a closer look at the composition of our pollinator community indicates that the majority of our pollinators were of three species: *M. tepaneca* (Hymenoptera), *A. mellifera* (Hymenoptera), and *A. exotica* (Diptera). Interestingly, these three species vary widely in their life history, which has important implications for how they respond to agricultural land use change. The most

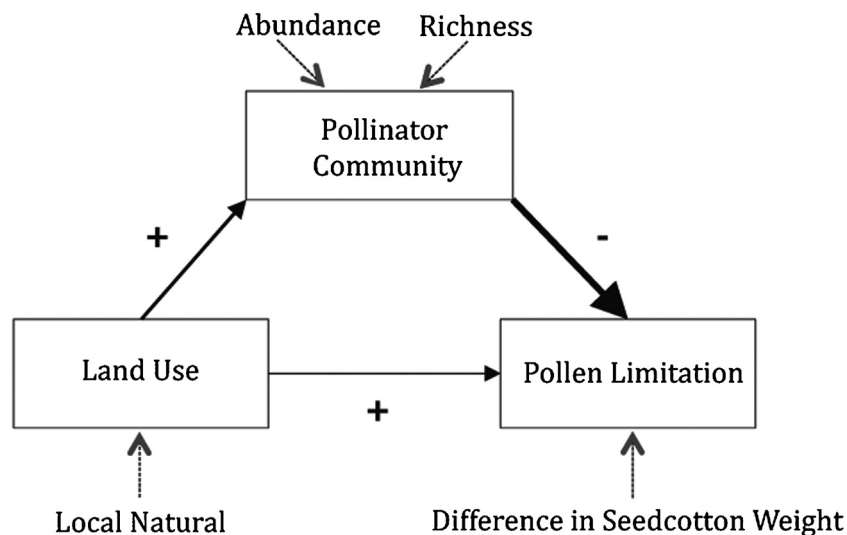


Fig. 4. Path diagram for the effects of land use and pollinator community composition on pollen limitation in cotton identified using SEM. Positive effects are indicated by (+), and negative effects by (-). The widths of the arrows indicate the magnitude of the standardized path coefficients.

abundant pollinator, *M. tepaneca*, is a native ground-nesting solitary bee (Michener, 2007). In contrast, the social European honey bee, *A. mellifera*, which is likely feral and unmanaged in the region, lives exclusively in large and complex social nests. Like all bees, both are central place foragers, and forage within some specific distance from their nest site. The native hover fly species, *A. exotica*, however, is not a central place forager. Rather, *Allograpta* adults move through landscapes, visiting flowers to drink nectar, and lay eggs on larval host plants where the larvae develop and feed on aphids and other crop pests (Bugg, 2008). Given that these three pollinators have vastly different life history strategies, land management practices are likely to differentially affect their population dynamics. For instance, deep tillage, a practice popular in cotton, would have no effect on either *Apis* or *Allograpta* species, but could have devastating effects on ground nesting bee populations (Shuler et al., 2005), such as those of *Melissodes*. On the other hand, pesticides sprayed onto crop plants during the larval development of *Allograpta*, may negatively affect fly populations (Moens et al., 2011). Given that pollinator diversity is important to crop yield, we argue that the development of land management practices, like low till and low pesticide application, should be kept in mind to preserve ecosystem service provision.

In this study we also provide clear evidence that outcross pollen improves boll set and we show that cotton yield in our study system is indeed limited by the pollination service it receives. In other words, our pollen limitation findings offer evidence that crop yields in South Texas cotton agroecosystems can be increased through the improved management of pollinators. One other study by Pires et al. (2014) has provided similar evidence that cotton is benefitted from insect pollination and may be impacted by human management. Unlike the Pires study, ours did not investigate the influence of farming practices; instead we provide an explicit test of the benefits of outcross pollen on seed-cotton weight and a landscape-level analysis of land use and pollinator community impacts on pollen limitation. Despite these differences, both studies document similar beneficial effects of pollinators on cotton yield. Although only a few of the world's crops are completely dependent on animal pollination (Richards, 2001), most have been found to exhibit yield benefits from pollination service (reviewed in Klein et al., 2007). Specifically, this well-cited meta-analysis shows that 39 of the leading 57 world crops exhibit increased yield with services provided by pollinating animals (Klein et al., 2007); though cotton is the most valued non-food crop on the planet, this crop was not on this list. Our results reveal cotton growers could gain as much as an 18% increase in seed-cotton weight with increased pollination service. In the South Texas cotton growing region, which covers ~10,000 acres, cotton is worth approximately \$600 per acre, or \$6 million (National Agriculture Statistics Service, 2013). If all farmers engaged in management practices to increase their pollination service and boll weight by 18%, the increased production could be worth as much as \$108/acre with a regional gain of over \$1.1 million USD.

Lastly, addressing our third hypothesis, our path analysis shows a weak relationship between natural area cover and pollen limitation. This finding demonstrates that the influence of land use on pollen limitation was weaker than we had predicted, instead only affecting pollen limitation through changes in the pollinator community. These findings are similar to those of Klein et al., 2003 who found a strong relationship between the pollinator community and pollination service and a separate relationship between distance to natural habitat use and pollinator community composition. While the positive relationship between natural land cover and pollen limitation was not significant in this study, it is possible that land use could affect the level of con-specific pollen deposited by pollinators, though future studies are required.

Understanding the ecological and economic importance of natural areas in supporting biodiverse communities is especially relevant given the current trajectory of global farming towards simplified landscapes (Robinson and Sutherland, 2002). As the demands on agricultural lands to produce fiber, food, and fuel continue to expand, effective strategies are needed to balance biodiversity conservation and agricultural production. Two approaches, with opposing strategies but similar goals, have been proposed to address this problem: land sharing and land-sparing. The land sparing approach promotes smaller, more intensely farmed, homogeneous areas to maximize yields, while separate reserves target biodiversity conservation. The argument for land-sparing is rooted in the increased efficiency and productiveness it supposedly affords in intensely farmed landscapes, while preserving remaining wild areas exclusively for biodiversity (Balmford et al., 2005; Green et al., 2005). Land sharing, in contrast, integrates conservation and agriculture within more heterogeneous landscapes, relying on farming practices that benefit wildlife and, presumably, biodiversity in general. Typical characteristics of land-sharing landscapes include patches of native remnant or restored vegetation scattered throughout the productive landscapes, agricultural areas that are structurally similar to native vegetation, and overall spatial heterogeneity (Luck et al., 2003; Fischer et al., 2006; Perfecto and Vandermeer, 2008). In this way, small patches of local natural area are maintained by planting a diversity of crops in a range of small fields, retaining habitat features within fields (e.g. scattered trees), or conserving habitat features along the margins of fields (e.g. hedgerows: Benton et al., 2003; Harvey et al., 2006; Manning et al., 2006).

In this study, we offer evidence in support of the positive effects of land sharing techniques, showing that landscapes with higher levels of local natural areas positively affect total yield via the pollination services they receive from beneficial insects. We argue that management objectives that promote the preservation and restoration of natural lands can be developed and widely applied across a variety of agricultural systems (Benton et al., 2003). Interestingly, we found that local (250 m radius) natural areas were more important than regional (1 km radius) natural areas in driving pollinator richness and abundance. This result has been documented in other agroecosystems (e.g., Jha and Vandermeer, 2010) and underscores the importance of local, small-scale restoration efforts for the conservation of diverse pollinator populations. These findings are encouraging, given that even small changes to local land use may have far reaching benefits for the pollinator community, even within highly degraded regional landscapes.

5. Conclusions

This research is one of the first to document the entire set of interactions between pollination service provision, pollinator community composition, and landscape drivers of biodiversity within a single study, and the first to do so within the cotton agroecological landscape. Further, these results provide compelling evidence that the cotton agroecosystem can serve as a novel habitat in which to dually improve biodiversity while also enhancing pollination services and yield. Our work has on-the-ground implications for crop management and, more generally, offers insights into conservation policy. Given the immense scale of the cotton agroecosystem, the benefits it receives from animal-mediated pollination services, and its potential to provide important forage for a wide range of insects, we propose that cotton is an important system in which to promote the conservation of pollinator diversity and simultaneously increase crop yields. Through these combined efforts, it may be possible to

provide cotton for our growing global population, while increasing the ecological sustainability of the fiber that touches all our lives.

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. In addition, the help of Texas A&M 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 lab for helpful feedback and support, as well as help in the field from Nicole Vojnovich, Alan Ritchie Jr., Sarah Cunningham, and Rebecca Ruppel. S.C. and S.J. were funded by the Texas Parks and Wildlife Department, the Army Research Office, and the National Science Foundation.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2016.04.020>.

References

- Adger, W.N., Kelly, P.M., Winkels, A., Huy, L.Q., Locke, C., 2002. Migration, remittances, livelihood trajectories, and social resilience. *AMBIO* 31, 358–366.
- Ashman, T.L., Knight, T.M., Steets, J.A., Amarasekare, P., Burd, M., Campbell, D.R., et al., 2004. Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. *Ecology* 85, 2408–2421.
- Balmford, A., Bennun, L., Ten Brink, B., Cooper, D., Côté, I.M., Crane, P., et al., 2005. The convention on biological diversity's 2010 target. *Science* 307.
- Bartoń, K., 2015. MuMIn: Multi-Model Inference. R Package Version 1.13.4. <http://CRAN.R-project.org/package=MumIn>.
- Bartomeus, I., Park, M.G., Gibbs, J., Danforth, B.N., Lakso, A.N., Winfree, R., 2013. Biodiversity ensures plant–pollinator phenological synchrony against climate change. *Ecol. Lett.* 16, 1331–1338.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2014. lme4: Linear Mixed-effects Models Using Eigen and S4. R Package Version 1.1–7, URL: <http://CRAN.R-project.org/package=lme4>.
- Benjamin, F., Reilly, R.J., Winfree, R., 2014. Pollinator body size mediates the scale at which land use drives crop pollination services. *J. Appl. Ecol.* 51, 440–449.
- Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.* 18, 182–188.
- Berger, L.A., Vaissière, B.E., Moffett, J.O., Merritt, S.J., 1988. *Bombus* spp. (Hymenoptera: Apidae) as pollinators of male-sterile upland cotton on the Texas High Plains. *Environ. Entomol.* 17, 789–794.
- Blüthgen, N., Klein, A.M., 2011. Functional complementarity and specialization: the role of biodiversity in plant–pollinator interactions. *Basic Appl. Ecol.* 12, 282–291.
- Bugg, R.L., 2008. Flower Flies *Syrphidae* and Other Biological Control Agents for Aphids in Vegetable Crops. University of California, Division of Agriculture and Natural Resources.
- Cariveau, D., Irwin, R.E., Brody, A.K., Garcia-Mayeya, L.S., Von Der Ohe, A., 2004. Direct and indirect effects of pollinators and seed predators to selection on plant and floral traits. *Oikos* 104, 15–26.
- Daily, G., 1997. Nature's Services: Societal Dependence on Natural Ecosystems. Island Press.
- Daily, G.C., Ceballos, G., Pacheco, J., Suzán, G., Sanchez-Azofeifa, 2003. Countryside biogeography of neotropical mammals: conservation opportunities in agricultural landscapes of Costa Rica. *Conserv. Biol.* 17, 1814–1826.
- Delaplane, K.S., Thomas, P.A., McLaurin, W.J., 2010. Bee Pollination of Georgia Crop Plants. University of Georgia, Athens.
- Dunning, J.B., Danielson, B.J., Pulliam, H.R., 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 169–175.
- Elmqvist, T., Maltby, E., 2010. The Economics of Ecosystems and Biodiversity. Earthscan, Oxford.
- Estrada, A., Coates-Estrada, R., 2002. Dung beetles in continuous forest, forest fragments and in an agricultural mosaic habitat island at Los Tuxtlas, Mexico. *Biodivers. Conserv.* 11, 1903–1918.
- Eyhorn, F., Ramakrishnan, M., Mäder, P., 2005. The Impact of Organic Cotton Farming on the Livelihoods of Smallholders. Evidence from the Maikaal Biore Project in Central India. Research Institute of Organic Agriculture FiBL, Frick, Switzerland.
- Fenster, C.B., Armbruster, W.S., Wilson, P., Dudash, M.R., Thomson, J.D., 2004. Pollination syndromes and floral specialization. *Annu. Rev. Ecol. Syst.* 37, 403–403.
- Firbank, L.G., Petit, S., Smart, S., Blain, A., Fuller, R.J., 2008. Assessing the impacts of agricultural intensification on biodiversity: a British perspective. *Phil. Trans. R. Soc. B* 363, 777–787.
- Fischer, J., Lindenmayer, D.B., Manning, A.D., 2006. Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. *Front. Ecol. Environ.* 4, 80–86.
- Free, J.B., 1970. Insect Pollination of Crops. Academic Press, London.
- Gaines-Day, H.R., Gratton, C., 2016. Crop yield is correlated with honey bee hive density but not in high-woodland landscapes. *Agric. Ecosys. Environ.* 218, 53–57.
- Giller, K.E., Beare, M.H., Lavelle, P., Izac, A., Swift, M.J., 1997. Agricultural intensification, soil biodiversity and agroecosystem function. *Appl. Soil Ecol.* 6, 3–16.
- Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A., et al., 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* 339, 1608–1611.
- Green, R.E., Cornell, S.J., Scharlemann, J.P., Balmford, A., 2005. Farming and the fate of wild nature. *Science* 307, 550–555.
- Groeneveld, L.F., Lenstra, J.A., Eding, H., Toro, M.A., Scherf, B., Pilling, D., et al., 2010. Genetic diversity in farm animals—a review. *Anim. Genet.* 41, 6–31.
- Gustafson, E.J., 1998. Quantifying landscape spatial pattern: what is the state of the art? *Ecosystems* 1, 143–156.
- Harvey, C.A., Medina, A., Sánchez, D.M., Vilchez, S., Hernández, B., Saenz, J.C., et al., 2006. Patterns of animal diversity in different forms of tree cover in agricultural landscapes. *Ecol. Appl.* 16, 1986–1999.
- Holzschuh, A., Dudenhöffer, J.H., Tschardtke, T., 2012. Landscapes with wild bee habitats enhance pollination, fruit set and yield of sweet cherry. *Biol. Conserv.* 153, 101–107.
- Hoehn, P., Tschardtke, T., Tylianakis, J.M., Steffan-Dewenter, I., 2008. Functional group diversity of bee pollinators increases crop yield. *Proc. R. Soc. B* 275, 2283–2291.
- Jha, S., Vandermeer, J.H., 2010. Impacts of coffee agroforestry management on tropical bee communities. *Biol. Conserv.* 143, 1423–1431.
- Jin, S., Yang, L., Danielson, P., Homer, C., Fry, J., Xian, G., 2013. A comprehensive change detection method for updating the National Land Cover Database to circa 2011. *Remote Sens. Environ.* 132, 159–175.
- Kaiser-Bunbury, C.N., Muff, S., Memmott, J., Müller, C.B., Cafisch, A., 2010. The robustness of pollination networks to the loss of species and interactions: a quantitative approach incorporating pollinator behaviour. *Ecol. Lett.* 13, 442–452.
- Kevan, P.G., Clark, E., Thomas, V.G., 1990. Insect pollinators and sustainable agriculture. *Am. J. Altern. Agric.* 5, 13–22.
- Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L.G., Henry, M., Isaacs, R., et al., 2015. Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nat. Commun.* 6.
- Klein, A.M., Steffan-Dewenter, I., Tschardtke, T., 2003. Bee pollination and fruit set of *Coffea arabica* and *C. canephora* (Rubiaceae). *Am. J. Bot.* 90, 153–157.
- Klein, A.M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tschardtke, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B* 274, 303–313.
- Klein, A.M., Brittain, C., Hendrix, S.D., Thorp, R., Williams, N., Kremen, C., 2012. Wild pollination services to California almond rely on semi-natural habitat. *J. Appl. Ecol.* 49, 723–732.
- Kehoe, L., Kuemmerle, T., Meyer, C., Levers, C., Václavík, T., Kreft, H., 2015. Global patterns of agricultural land-use intensity and vertebrate diversity. *Divers. Distrib.* 21, 1308–1318.
- Kremen, C., Williams, N.M., Thorp, R.W., 2002. Crop pollination from native bees at risk from agricultural intensification. *Proc. Natl. Acad. Sci. U. S. A.* 99, 16812–16816.
- Kunin, W.E., 1993. Sex and the single mustard: population density and pollinator behavior effects on seed-set. *Ecology* 2145–2160.
- Losey, J.E., Vaughan, M., 2006. The economic value of ecological services provided by insects. *Bioscience* 56, 311–323.
- Luck, G.W., Daily, G.C., Ehrlich, P.R., 2003. Population diversity and ecosystem services. *Trends Ecol. Evol.* 18, 331–336.
- Manning, A.D., Fischer, J., Lindenmayer, D.B., 2006. Scattered trees are keystone structures—implications for conservation. *Biol. Conserv.* 132, 311–321.
- Mayfield, M.M., Daily, G.C., 2005. Countryside biogeography of neotropical herbaceous and shrubby plants. *Ecol. Appl.* 15, 423–439.
- McCoy, E.D., Bell, S.S., Walters, K., 1986. Identifying biotic boundaries along environmental gradients. *Ecology* 67, 749–759.
- Michener, C.D., 2007. The Bees of the World. John Hopkins University Press, Baltimore.
- Mittermeier, R.A., Mittermeier, C.G., Brooks, T.M., Pilgrim, J.D., Konstant, W.R., Da Fonseca, G.A., Kormos, C., 2003. Wilderness and biodiversity conservation. *Proc. Natl. Acad. Sci. U. S. A.* 100, 10309–10313.
- Moens, J., De Clercq, P., Tirry, L., 2011. Side effects of pesticides on the larvae of the hoverfly *Episyrphus balteatus* in the laboratory. *Phytoparasitica* 39, 1–9.
- Moffett, J.O., Stith, L.S., Shipman, C.W., 1976. Influence of distance from pollen plant on seed produced by male-sterile cotton. *Crop Sci.* 16, 765–766.
- Myers, R.H., 1990. Classical and Modern Regression with Applications. PWS Kent, Boston.
- Naimi, B., 2013. USDM: Uncertainty Analysis for Species Distribution Models. R Package Version 1.1–12. <http://CRAN.R-project.org/package=usdm>.
- National Cotton Council of America, 2014. January 1. <http://www.cotton.org/> (accessed 16.04.15.).
- National Agriculture Statistics Service, 2013. <http://www.nass.usda.gov/> (accessed 16.04.15.).

- Parker, I.M., 1997. Pollinator limitation of *Cytisus scoparius* Scotch broom, an invasive exotic shrub. *Ecology* 78, 1457–1470.
- Perfecto, I., Vandermeer, J., 2008. Biodiversity conservation in tropical agroecosystems. *Ann. N. Y. Acad. Sci.* 1134, 173–200.
- Perfecto, I., Vandermeer, J., 2010. The agroecological matrix as alternative to the land-sparing/agriculture intensification model. *Proc. Natl. Acad. Sci. U. S. A.* 107, 5786–5791.
- Peterson, G., Allen, C.R., Holling, C.S., 1998. Ecological resilience, biodiversity, and scale. *Ecosystems* 11, 6–18.
- Petersen, J.D., Reiners, S., Nault, B.A., 2013. Pollination services provided by bees in pumpkin fields supplemented with either *Apis mellifera* or *Bombus impatiens* or not supplemented. *PLoS One* 8, e69819.
- Pretty, J.N., Morison, J.I., Hine, R.E., 2003. Reducing food poverty by increasing agricultural sustainability in developing countries. *Agric. Ecosyst. Environ.* 95, 217–234.
- Pires, V.C., Silveira, F.A., Sujii, E.R., Torezani, K.R.S., Rodrigues, W.A., Albuquerque, F. A., et al., 2014. Importance of bee pollination for cotton production in conventional and organic farms in Brazil. *J. Pollinat. Ecol.* 13, 151–160.
- QGIS Development Team, 2013. QGIS Geographic Information System. Open Source Geospatial Foundation Project. Development Team. <http://qgis.osgeo.org>.
- R Development Core Team, 2014. R: A Language and Environment for Statistical Computing. The R Foundation for Statistical Computing. <http://www.R-project.org/>.
- Richards, A.J., 2001. Does low biodiversity resulting from modern agricultural practice affect crop pollination and yield? *Ann. Bot.* 88, 165–172.
- Ricketts, T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Bogdanski, A., et al., 2008. Landscape effects on crop pollination services: are there general patterns? *Ecol. Lett.* 11, 499–515.
- Rhodes, J., 2002. Cotton pollination by honeybees. *Anim. Prod. Sci.* 42, 513–518.
- Robinson, R.A., Sutherland, W.J., 2002. Post-war changes in arable farming and biodiversity in Great Britain. *J. Appl. Ecol.* 39, 157–176.
- Rosseel, Y., 2012. Lavaan: an R package for structural equation modeling. *J. Stat. Softw.* 48, 1–36. <http://www.jstatsoft.org/v48/i02/>.
- Roulston, T.A.H., Goodell, K., 2011. The role of resources and risks in regulating wild bee populations. *Annu. Rev. Entomol.* 56, 293–312.
- Schroth, G., Harvey, C.A., 2007. Biodiversity conservation in cocoa production landscapes: an overview. *Biodivers. Conserv.* 16, 2237–2244.
- Shuler, R.E., Tai, H.R., Farris, G.E., 2005. Farming practices influence wild pollinator populations on squash and pumpkin. *J. Econ. Entomol.* 98, 790–795.
- Sih, A., Baltus, M.S., 1987. Patch size, pollinator behavior, and pollinator limitation in catnip. *Ecology* 1679–1690.
- Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C., Tschardtke, T., 2002. Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* 83, 1421–1432.
- Steffan-Dewenter, I., Kessler, M., Barkmann, J., Bos, M.M., Buchori, D., Erasmí, S., et al., 2007. Tradeoffs between income, biodiversity, and ecosystem functioning during tropical rainforest conversion and agroforestry intensification. *Proc. Natl. Acad. Sci. U. S. A.* 104, 4973–4978.
- TAMU, Texas A&M AgriLife Extension, 2013. <http://cotton.tamu.edu/index.html> (accessed 16.04.15.).
- Tilman, D., Cassman, K.G., Matson, P.A., Naylor, R., Polasky, S., 2002. Agricultural sustainability and intensive production practices. *Nature* 418, 671–677.
- Tschardtke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity—ecosystem service management. *Ecol. Lett.* 8, 857–874.
- Tschardtke, T., Clough, Y., Wanger, T.C., Jackson, L., Motzke, I., Perfecto, I., et al., 2012. Global food security, biodiversity conservation and the future of agricultural intensification. *Biol. Conserv.* 151, 53–59.
- Tschardtke, T., Brandl, R., 2004. Plant-insect interactions in fragmented landscapes. *Annu. Rev. Entomol.* 49, 405–430.
- Turner, M.G., 1989. Landscape ecology: the effect of pattern on process. *Annu. Rev. Evol. Syst.* 171–197.
- Turner, M.G., Bratton, S.P., 1987. *Landscape Heterogeneity and Disturbance*. Springer, New York.
- United Nations News Centre, 2013. <http://www.un.org/news/> (accessed 16.04.15.).
- USDA ERS, 2013. <http://www.ers.usda.gov/> (accessed 16.04.15.).
- Vaissière, B.E., Moffett, J.O., Loper, G.M., 1984. Honey bees as pollinators for hybrid cotton seed production on the Texas high plains. *Argon. J.* 76, 1005–1010.
- Westrich, P., 1996. *The Conservation of Bees*. Academic Press for the Linnean Society of London and IBRA, London.
- Wiens, J.A., Crawford, C.S., Gosz, J.R., 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. *Oikos* 45, 421–427.
- Williams, N.M., Minckley, R.L., Silveira, F.A., 2001. Variation in native bee faunas and its implications for detecting community changes. *Conserv. Ecol.* 5, 7.
- Williams, N.M., Crone, E.E., Tai, H.R., Minckley, R.L., Packer, L., Potts, S.G., 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. *Biol. Conserv.* 143, 2280–2291.
- Winfree, R., Kremen, C., 2009. Are ecosystem services stabilized by differences among species? A test using crop pollination. *Proc. R. Soc. B* 276, 229–237.
- Winfree, R., Fox, J., Williams, N.M., Reilly, J.R., Cariveau, D.P., 2015. Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecol. Lett.* 18, 626–635.
- Yang, C.F., Sun, S.G., Guo, Y.H., 2005. Resource limitation and pollen source (self and outcross) affecting seed production in two louseworts, *Pedicularis siphonantha* and *P. longiflora* (Orobanchaceae). *J. Linn. Soc.* 147, 83–89.