1   **Title:**

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

4   **Authors:**

5   Sarah Cusser¹, John L. Neff², and Shalene Jha¹

6   **Affiliations:**

7   ¹Department of Integrative Biology, The University of Texas at Austin. 1

8   University Station C0930, Austin, TX 78712 USA

9   ²Central Texas Melittological Institute, 7307 Running Rope, Austin, TX 78731

10   USA

11   corresponding author, e-mail: sjha@austin.utexas.edu,

12   Telephone: 512.232.3521   Fax: 512-232-9529

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29   **Abstract:**

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

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55   **Keywords:** agroecology, ecosystem services, *Gossypium hirsutum* L., landscape
56   ecology, path analysis

57 **1. Introduction:**

58   Given the rapidly expanding human population, it is estimated that by
 59 the year 2050, humans will be challenged to provide fiber, food, and fuel for
 60 ~9.6 billion world inhabitants (United Nations News Centre, 2013). One
 61 proposed solution to this problem is to increase the intensity and
 62 homogenization of agricultural and forestry landscapes (Robinson and
 63 Sutherland, 2002, Benton et al., 2003). Although landscape homogenization has
 64 the potential to increase crop yield and efficiency (Green et al., 2005), increased
 65 agricultural intensity is also irrefutably one of the main causes of biodiversity
 66 loss (Adger et al., 2002, Roulston and Goodell, 2011, Kehoe et al. 2015). As a
 67 result, within intensely managed, homogeneous agricultural landscapes, yields
 68 often increase at the expense of biodiversity. Beneficial insects comprise an
 69 economically important group of biodiversity in agricultural systems as they
 70 provide ecosystem services critical to human survival; these organisms may act
 71 as natural enemies to crop pests or provide pollination services that benefit yield
 72 (Daily, 1997, Losey and Vaughn, 2006). The loss of such insect biodiversity in
 73 agricultural settings may lead to reduced ecosystem services, and decreased crop
 74 production in such environments. One particularly important group of beneficial
 75 insects are the pollinators, such as bees, butterflies and flies, which move pollen
 76 between plants, and increase yield and quality in many crops (Kevan et al.,
 77 1990). As land use intensification increases, however, and beneficial insect
 78 populations decline (Benton et al., 2003), services provided by these beneficial
 79 insects may be lost, negatively affecting yield (Elmqvist and Maltby, 2010), and
 80 potentially undermining the ecosystem processes on which these
 81 agroecosystems rely (Tscharntke et al., 2012).

82   Thus, although agriculture and biodiversity conservation may have
 83 traditionally been viewed as incompatible (Mittermeier et al., 2003), the two can
 84 be mutually considered in order to maximize long-term yields and promote the

85 preservation of ecosystem services. Past research investigating this subject has
 86 taken place largely in low intensity agriculture and polycultural systems such as
 87 shade coffee and cacao (Giller et al., 1997, Tscharntke et al., 2005, Schroth and
 88 Harvey, 2007, Firbank et al., 2008, but see Klein et al. 2012). These studies
 89 have shown that diversified agricultural practices can promote the establishment
 90 and long-term stability of biodiversity to enhance ecosystem services and aid in
 91 biodiversity conservation (Estrada and Coates, 2002, Daily et al., 2003,
 92 Mayfield and Daily, 2005, Kleijn et al. 2015, Winfree et al. 2015), while also
 93 contributing to increased crop production and rural income (Pretty et al., 2003).
 94 However, critics to this approach claim that it is largely relevant only in
 95 polycultural settings rather than in highly intensified agroecosystems (Green et
 96 al., 2005). Thus, at present it is not known if the dual optimization of
 97 biodiversity and crop yields is achievable in highly intensified agricultural
 98 landscapes.

99   Worldwide, cotton (*Gossypium spp.* (Malvaceae)) is one of the most
 100 intensely managed and economically important agroecosystems. The industry
 101 generates more than \$1 billion per annum and employs over 200,000 people in
 102 the US alone (USDA ERS, 2013). Cotton agroecosystems can host a wide range
 103 of beneficial insects, including lacewings, ladybird beetles, and spiders (Eyhorn
 104 et al., 2005). Furthermore, the large flowers of cotton, which produce copious
 105 amounts of pollen and nectar, can serve as a food resource for a diverse group of
 106 pollinating insects (Free, 1970, Moffett et al., 1976, Berger et al., 1988, Pires et
 107 al., 2014). Although cotton is known to be self-compatible, previous studies
 108 suggest that it benefits from pollination service given that cotton pollen is too
 109 heavy to move between flowers without an insect vector (Free, 1970, Rhodes,
 110 2002). Despite the likely importance of pollinators in cotton production, cotton
 111 growers do not currently utilize managed pollinators (e.g., honey bees or bumble

112 bees) nor do they use agricultural practices that promote the visitation of wild
113 pollinator communities in the southern US (Delaplane et al., 2010).

114   The composition of wild pollinator communities may be particularly
115 critical within agroecosystems because pollination service stability is often
116 associated with pollinator diversity and abundance (Garibaldi et al., 2013).
117 Pollinator diversity, in particular, appears to enhance the resilience and security
118 of pollination ecosystem services, especially in the face of regional land use
119 change (Peterson et al., 1998). Because of natural fluctuations in pollinator
120 populations, the diversity of wild pollinator communities is important in
121 providing stable crop pollination service between years (Williams et al., 2001,
122 Garibaldi et al. 2013). Specifically, pollinator diversity can buffer pollination
123 services against asynchronous fluctuations in single pollinator species over time
124 (Williams et al., 2001, Bartomeus et al. 2013). Mechanistically, greater fruit set
125 observed in more diverse pollinator communities is attributable to greater
126 pollination functional diversity across both space and time (e.g., Hoehn et al.,
127 2008, Garibaldi et al. 2013).

128   Finally, pollinator community composition and pollination service
129 assessment should be considered at multiple spatial scales given that many
130 insects are mobile, and often respond to land use change in areas that consist of
131 multiple habitat types (Turner, 1989, Dunning et al., 1992). Land use at the
132 regional landscape scale can be characterized by changes in the diversity of
133 habitats, as well as the size and arrangement, or complexity, of those habitats
134 (Gustafson, 1998). Recent studies have also demonstrated a relationship
135 between landscape complexity and the abundance and diversity of insect
136 pollinators (Steffan-Dewenter et al., 2002, but see Petersen et al. 2013, Gaines-
137 Day and Gratton 2015). This is probably due to the fact that many pollinator
138 species have diverse resource needs (e.g. floral and nesting), which are likely to
139 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

Study System

Texas grows more than 25% of the total US cotton crop, and cotton covers roughly 6 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,

168 and West Texas (TAMU, 2013). We conducted our research in the South Texas
 169 region, where cotton is a primary crop and one of the only crops that offers
 170 nectar and pollen resources to potential insect foragers in the area (National
 171 Cotton Council of America, 2014). The South Texas region is responsible for
 172 about 15% of the annual Texas cotton crop, and grows primarily Upland cotton
 173 varieties (*Gossypium hirsutum* L. (Malvaceae)). The region is characterized by
 174 shrink-and-swell clay soils and is predominantly rain fed. Agricultural land
 175 makes up the majority of the region (55%), and includes cotton, sorghum, corn,
 176 and soybean. The remainder of the region is comprised of cattle ranching (36%),
 177 low density developed areas (6%), and natural areas (2%), including shrub,
 178 mixed woodland, and marsh areas along the gulf coast.

179 We conducted research in 12 sites located in three regions between
 180 Telferner (28.847913, -96.892975) and Woodsboro, Texas (28.303701, -
 181 97.381612). We chose sites in an effort to include a wide range of landscape-
 182 level habitat heterogeneity, while controlling for geographic region.
 183 Specifically, the three geographic regions of study were near the towns of
 184 Woodsboro, Austwell/Tivoli, and Telferner, Texas. Within each landscape, sites
 185 were located within cotton fields that were at least 35ha in size and 2km apart
 186 from each other (Fig. 1). Sites were not sprayed with any chemical five days
 187 prior to, nor during, the 16-day sampling period.

188

189 2.1 Land Use Impacts on Pollinator Communities

190 2.1.1 Land Use:

191 We analyzed land use surrounding sites at local (250m radius) and
 192 regional (1km radius) scales using information from the 2011 National Land
 193 Cover Database (Jin et al., 2013) using qGIS (QGIS Development Team, 2013).
 194 It is important to note that because transects were located on the edge of the
 195 field, local land use includes non-cotton land use types. Land use was analyzed

196 in two ways. First, we calculated the percentage of land use types (26 types
 197 total) surrounding each site grouped into three broad categories: Agricultural,
 198 Natural, and Rangeland at local and regional scales (Agriculture: row crops
 199 including corn, sorghum, and soy as well as cotton itself; Rangeland: pasture,
 200 hay, and grassland; and Natural: riparian forest, deciduous and evergreen forest,
 201 and scrubland). Because human development (any man made surface) accounted
 202 for a relatively small amount of land use in the region (3% regionally), we did
 203 not specifically investigate this land use type. Next, we analyzed land use
 204 heterogeneity surrounding each of our sites. As per Turner (1989), heterogeneity
 205 was calculated as the total edge distance, or perimeter, between the different 26
 206 land use types. Other indices of heterogeneity, like habitat richness or diversity,
 207 do not capture the added edge distance and complexity created by small patch
 208 sizes. Thus, in this study, a landscape with a few land use types and minimal
 209 edge between types would have low heterogeneity, while a landscape with a
 210 large number of different land use types and a maximum edge between types
 211 would have high heterogeneity. Overall, the fixed variables used to describe
 212 land use in this study include the abundance of agriculture, rangeland, natural
 213 areas, as well as the heterogeneity of all land use types at local (250 m) and
 214 regional scales (1 km radius).

215 2.1.2 Pollinator Community Composition:

216 To quantify the pollinator community at each site we netted insects
 217 found actively foraging within cotton flowers during three one-hour sampling
 218 bouts at each site. During each one-hour bout, a single collector walked four
 219 parallel 50m x 1m transects checking blooms for visitors. Transects were located
 220 at the edge of fields and were ~12m apart, representing an area of 2500 m². The
 221 three sampling sessions were at least five days apart and covered the peak of
 222 cotton bloom in 2014 (June 16th- July 2nd). Because we only collected insects
 223 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.

2.1.3 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 multicollinearity. 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. 1994). 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

252 correlated, we investigated them in separate local and regional models. Land
 253 use variables were scaled around zero to account for differences in magnitude
 254 and Poisson distributions were used for abundance and richness. Top models
 255 were selected based on AICc using the “dredge” function in the R statistical
 256 package MuMIn (Bartoń, 2015). To characterize the top models, we used the
 257 function “model.avg” in the package MuMIn (Bartoń, 2015) to average models
 258 with an AICc of less than 2. GLMMs were preformed using the “glmer”
 259 function in the package lme4 (Bates et al., 2014).

260

261 2.2 Pollinator Community impacts on Pollen Limitation

262 2.2.1 Pollen Limitation Experiment:

263   We conducted a pollen limitation experiment at each of the 12 sites.
 264 Early in the flowering season (June 13th-15th, 2014), 10 virgin flowers were
 265 exposed to one of 5 treatments: closed (C), closed self-cross (CS), closed
 266 outcross (CO), open (O), and open outcross (OO), for a total of 50 experimental
 267 flowers at each site. Throughout the flowering period (24 hours), closed (C)
 268 flowers remained bagged with lightweight white organza bags that excluded
 269 pollinators. Closed self-cross flowers (CS) were bagged but supplemented with
 270 self-cross pollen from the same flower, and closed outcross (CO) flowers were
 271 bagged but received outcross pollen from three to five donors within a 10m
 272 radius of the focal plant. These three treatments evaluated the importance of
 273 outcross pollen to seed/fruit production, as conducted in other systems (Parker,
 274 1997, Yang et al., 2005, Benjamin et al., 2014). The fourth and fifth treatments
 275 were left unbagged throughout the flowering period to receive ambient
 276 pollination service: open flowers (O) measured the amount of ambient
 277 pollination service and open outcross flowers (OO), remained open but were
 278 also supplemented with an abundance of additional outcross pollen from 3 to 5
 279 donors within a 10m radius of the focal plant, saturating the stigma, and thus

280 representing maximum pollination service. From the fourth and fifth treatments,
 281 we evaluated potential limitation in boll set resulting from inadequate
 282 pollination service. All pollination treatments happened between the hours 0800
 283 and 1300, when cotton flowers are most receptive (Free, 1970). Bags were
 284 removed after floral senescence, 24 hours after treatment, and bolls were left to
 285 mature for 6 weeks in the field before they were hand-collected. Because there
 286 was no significant difference in boll weight between flowers that received the
 287 closed outcross pollen treatment and those that received the open outcross
 288 pollen, we assume there was no significant effect of the exclusion bag on boll
 289 development (see results below). Collected bolls were then assessed for seed-
 290 cotton weight. Seed-cotton weight is the total weight of both the lint and seeds
 291 of a single cotton boll and was used as a metric of yield. While lint is the
 292 primary product of cotton production, cottonseed is also an economically
 293 important outcome of production. Seeds are processed for oil, as well as protein-
 294 rich animal meal, and roughage (National Cotton Council of America, 2014).
 295 Consequently, changes in both lint and seed production are economically
 296 important to cotton growers. Pollen limitation was measured as the difference in
 297 seed-cotton weight, between open outcross (OO) treatment flowers and open (O)
 298 flowers that received ambient pollination service (as per Klein et al., 2003,
 299 Groeneveld et al., 2010, Holzschuh et al., 2012, Benjamin et al., 2014). To test
 300 for differences between treatments, we used a Shapiro-Wilk test to check for a
 301 normal distribution of seed-cotton weight, then ANOVA and Tukey HSD tests
 302 to determine the significance of differences in seed-cotton weight between
 303 treatments.

304 2.2.2 Pollinator Community impacts on Pollen Limitation Analysis:

305 To determine the relationship between pollinator abundance and
 306 richness and the extent of pollen limitation, we followed a similar series of
 307 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. 1994). 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 Core Team, 2014), and a Gaussian distribution was used for the model. Top models ($\Delta AIC_c < 2$) were averaged and GLMMs were preformed using the “glmer” function in the package lme4 (Bates et al., 2014).

2.3 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).

2.3.1 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 results below).

2.3.2 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.

336

337 3. Results

338 3.1 Land Use Impacts on Pollinator Communities

339 3.1.1 Land use:

340 On the local scale, land use surrounding sites averaged 72.8% (SE: 2.4
341 %) agriculture, 12.4% (SE: 1.8%) natural, and 7.5% (SE: 0.7%) rangeland. On
342 the regional scale, land use surrounding sites averaged 67.7 % (SE: 1.8%)
343 agriculture, 1.5% (SE: 0.2%) natural, and 27.5% (SE: 1.6%) rangeland.
344 Heterogeneity averaged 9,046 m at the local scale (SE: 206.3 m) and 99,034 m
345 regionally (SE: 2094.9 m).

346 3.1.2 Pollinator Community Composition:

347 We captured a total of 841 pollinator specimens comprised of 52
348 species. The specimens were of four orders: Hymenoptera (37 species), Diptera
349 (5 species), Lepidoptera (7 species), and Coleoptera (3 species). The solitary bee
350 species, *Melissodes tepaneca*, and the European honey bee, *Apis mellifera*, made
351 up 21% and 19% of total specimens collected, respectively. The syrphid fly,
352 *Allograpta exotica*, comprised another 16% of the specimens. Lastly,
353 *Lasioglossum* specimens of at least nine species made up 15% of the specimens.
354 Of the remaining pollinators, 24 were singleton species, and 10 were doubletons
355 (See section 8, Appendix, for entire species list).

356 3.1.3 Land Use Impacts on Pollinator Community:

357 At the local scale, model selection revealed that natural area was the
358 best predictor of pollinator abundance as well as pollinator richness (Table 1a
359 and b). The averaged top models (AICc <2) showed a strong positive
360 relationship between pollinator abundance and the abundance of natural land use
361 at the local level (250 meter radii)(estimate = 0.157, z value = 3.024, p value =
362 0.002, table 1a). The top model for richness also showed a strong positive
363 relationship between richness and the abundance of natural land use at the local

level (250 meter 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.

Table 1: Model averaged coefficients for top models ($\Delta AIC_c < 2$) 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

3.3 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. 2: C, 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. 2: O, 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 grams to 3.4 grams 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 AICc <2, and it revealed a negative relationship between pollen limitation and the explanatory variables pollinator abundance (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).

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

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 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

464 farming efficiency, often result in homogeneous landscapes with little non-crop
 465 area (Tilman et al. 2002). The loss of natural areas in agricultural habitats may
 466 negatively affect pollinators in two major ways. First, pollinators may exhibit a
 467 decline due to a reduction in overall resource diversity. Landscape diversity has
 468 been shown to create a wider array of foraging niches for different functional
 469 groups of pollinators (Fenster et al., 2004) and environmental changes that alter
 470 the spatial and temporal distribution of important nesting and food resources can
 471 influence pollinator community composition (reviewed by Kremen et al., 2002,
 472 Williams et al., 2010). Second, the loss of local natural areas may alter the
 473 ability of pollinators to move across landscapes. Because many invertebrate
 474 pollinators must forage across multiple land use types to exploit resources
 475 important for their livelihood (e.g. food or nesting resources), simplified
 476 landscapes may actually prohibit the persistence of pollinators unable to travel
 477 between resources in landscapes lacking one of many key resources (e.g. partial
 478 landscapes)(Westrich, 1996). In addition to foraging movement, simple
 479 landscapes may negatively affect pollinator populations by reducing the
 480 likelihood of dispersal and recolonization events. Because pollinator populations
 481 naturally fluctuate over time, pollinator assemblages are characterized by rare
 482 local extinction events. Thus, a patchwork of high quality habitats, even as small
 483 remnants or restored hedgerows, could provide refuge and sources of
 484 recolonization for pollinators into newly disturbed sites, thus reducing the
 485 negative influence of local extinction events over time (Perfecto and
 486 Vandermeer, 2010, Tscharntke and Brandl, 2004, Steffan-Dewenter et al.,
 487 2007).

488   Second, we show that pollen limitation is closely linked to local
 489 pollinator abundance and richness, a pattern also detected in native plant
 490 communities (reviewed in Ashman et al., 2004) as well as crop systems
 491 (reviewed in Garibaldi et al., 2013). Indeed, diverse and abundant pollinator

492 assemblages have been shown to maximize crop yields, compared to the
 493 abundance of a single pollinator species, specifically the European honey bee,
 494 *Apis mellifera* (e.g., Klein et al., 2003, Hoehn et al., 2008, Winfree and Kremen,
 495 2009, reviewed in Garibaldi et al., 2013), and help to ensure consistent
 496 pollination service over multiple years, even in the face of natural fluctuations in
 497 the abundances of some species (Kaiser-Bunbury et al., 2010). While recent
 498 studies suggest that that a few dominant species conduct the majority of the
 499 pollination services (Kleijn et al. 2015, Winfree et al. 2015), we posit that
 500 diversity may be particularly important in systems where flowering can vary
 501 substantially across years and where one of the most stable and abundant
 502 pollinators is not particularly effective. Depending on weather and planting,
 503 cotton bloom time can range substantially in the southern US, often between
 504 April and July (National Cotton Council of America, 2014); given that many bee
 505 species only forage for a few weeks at a time (Michener 2007), pollinator
 506 diversity may be particularly important for handling plants with substantial
 507 inter-annual flowering variation (as seen in Hoehn et al, 2008, Blüthgen and
 508 Klein 2011). Pollinator diversity may also be especially critical for cotton
 509 given that one of the most abundant pollinators, the European honey bee, has
 510 been shown to be a relatively ineffective pollinator of the crop (Vaissière et al.,
 511 1983). While we cannot assume that each pollinator in our community is critical
 512 for cotton pollination service, our future research aims specifically towards
 513 investigating the effectiveness of different pollinator species and determining
 514 the role of pollinator diversity beyond the most abundant species.

515   For now, a closer look at the composition of our pollinator community
 516 indicates that the majority of our pollinators were of three species: *Melissodes*
 517 *tepaneca* (Hymenoptera), *Apis mellifera* (Hymenoptera), and *Allograpta exotica*
 518 (Diptera). Interestingly, these three species vary widely in their life history,
 519 which has important implications for how they respond to agricultural land use

520 change. The most abundant pollinator, *Melissodes tepaneca*, is a native ground-
 521 nesting solitary bee (Michener, 2007). In contrast, the social European honey
 522 bee, *Apis mellifera*, which is likely feral and unmanaged in the region, lives
 523 exclusively in large and complex social nests. Like all bees, both are central
 524 place foragers, and forage within some specific distance from their nest site.
 525 The native hover fly species, *Allograpta exotica*, however, is not a central place
 526 forager. Rather, *Allograpta* adults move through landscapes, visiting flowers to
 527 drink nectar, and lay eggs on larval host plants where the larvae develop and
 528 feed on aphids and other crop pests (Bugg, 2008). Given that these three
 529 pollinators have vastly different life history strategies, land management
 530 practices are likely to differentially affect their population dynamics. For
 531 instance, deep tillage, a practice popular in cotton, would have no effect on
 532 either *Apis* or *Allograpta* species, but could have devastating effects on ground
 533 nesting bee populations (Shuler et al., 2005), such as those of *Melissodes*. On
 534 the other hand, pesticides sprayed onto crop plants during the larval
 535 development of *Allograpta*, may negatively affect fly populations (Moens et al.,
 536 2011). Given that pollinator diversity is important to crop yield, we argue that
 537 the development of land management practices, like low till and low pesticide
 538 application, should be kept in mind to preserve ecosystem service provision.
 539   In this study we also provide clear evidence that outcross pollen
 540 improves boll set and we show that cotton yield in our study system is indeed
 541 limited by the pollination service it receives. In other words, our pollen
 542 limitation findings offer evidence that crop yields in South Texas cotton
 543 agroecosystems can be increased through the improved management of
 544 pollinators. One other study by Pires and colleagues (2014) has provided similar
 545 evidence that cotton is benefitted from insect pollination and may be impacted
 546 by human management. Unlike the Pires study, ours did not investigate the
 547 influence of farming practices; instead we provide an explicit test of the benefits

548 of outcross pollen on seed-cotton weight and a landscape-level analysis of land
549 use and pollinator community impacts on pollen limitation. Despite these
550 differences, both studies document similar beneficial effects of pollinators on
551 cotton yield. Although only a few of the world's crops are completely dependent
552 on animal pollination (Richards, 2001), most have been found to exhibit yield
553 benefits from pollination service (reviewed in Klein et al., 2007). Specifically,
554 this well-cited meta-analysis shows that 39 of the leading 57 world crops exhibit
555 increased yield with services provided by pollinating animals (Klein et al.,
556 2007); though cotton is the most valued non-food crop on the planet, this crop
557 was not on this list. Our results reveal cotton growers could gain as much as an
558 18% increase in seed-cotton weight with increased pollination service. In the
559 South Texas cotton growing region, which covers ~10,000 acres, cotton is worth
560 approximately \$600 per acre, or \$6 million (National Agriculture Statistics
561 Service, 2013). If all farmers engaged in management practices to increase their
562 pollination service and boll weight by 18%, the increased production could be
563 worth as much as \$108/acre with a regional gain of over \$1.1 million USD.

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

575   Understanding the ecological and economic importance of natural areas
576 in supporting biodiverse communities is especially relevant given the current
577 trajectory of global farming towards simplified landscapes (Robinson and
578 Sutherland, 2002). As the demands on agricultural lands to produce fiber, food,
579 and fuel continue to expand, effective strategies are needed to balance
580 biodiversity conservation and agricultural production. Two approaches, with
581 opposing strategies but similar goals, have been proposed to address this
582 problem: land sharing and land-sparing. The land sparing approach promotes
583 smaller, more intensely farmed, homogeneous areas to maximize yields, while
584 separate reserves target biodiversity conservation. The argument for land-
585 sparing is rooted in the increased efficiency and productiveness it supposedly
586 affords in intensely farmed landscapes, while preserving remaining wild areas
587 exclusively for biodiversity (Balmford et al., 2005, Green et al., 2005). Land
588 sharing, in contrast, integrates conservation and agriculture within more
589 heterogeneous landscapes, relying on farming practices that benefit wildlife and,
590 presumably, biodiversity in general. Typical characteristics of land-sharing
591 landscapes include patches of native remnant or restored vegetation scattered
592 throughout the productive landscapes, agricultural areas that are structurally
593 similar to native vegetation, and overall spatial heterogeneity (Luck and Daily,
594 2003, Fischer et al., 2006, Perfecto and Vandermeer, 2008). In this way, small
595 patches of local natural area are maintained by planting a diversity of crops in a
596 range of small fields, retaining habitat features within fields (e.g. scattered
597 trees), or conserving habitat features along the margins of fields (e.g.
598 hedgerows: Benton et al., 2003, Harvey et al., 2006, Manning et al., 2006).

599   In this study, we offer evidence in support of the positive effects of
600 land sharing techniques, showing that landscapes with higher levels of local
601 natural areas positively affect total yield via the pollination services they receive
602 from beneficial insects. We argue that management objectives that promote the

603 preservation and restoration of natural lands can be developed and widely
604 applied across a variety of agricultural systems (Benton et al., 2003).
605 Interestingly, we found that local (250m radius) natural areas were more
606 important than regional (1km radius) natural areas in driving pollinator richness
607 and abundance. This result has been documented in other agroecosystems (e.g.,
608 Jha and Vandermeer, 2010) and underscores the importance of local, small-scale
609 restoration efforts for the conservation of diverse pollinator populations. These
610 findings are encouraging, given that even small changes to local land use may
611 have far reaching benefits for the pollinator community, even within highly
612 degraded regional landscapes.

613

614 **5. Conclusions**

615 This research is one of the first to document the entire set of
616 interactions between pollination service provision, pollinator community
617 composition, and landscape drivers of biodiversity within a single study, and the
618 first to do so within the cotton agroecological landscape. Further, these results
619 provide compelling evidence that the cotton agroecosystem can serve as a novel
620 habitat in which to dually improve biodiversity while also enhancing pollination
621 services and yield. Our work has on-the-ground implications for crop
622 management and, more generally, offers insights into conservation policy. Given
623 the immense scale of the cotton agroecosystem, the benefits it receives from
624 animal-mediated pollination services, and its potential to provide important
625 forage for a wide range of insects, we propose that cotton is an important system
626 in which to promote the conservation of pollinator diversity and simultaneously
627 increase crop yields. Through these combined efforts, it may be possible to
628 provide cotton for our growing global population, while increasing the
629 ecological sustainability of the fiber that touches all our lives.

630

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974 **Figure captions:**

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

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985 Figure 2: Boxplot comparing seed-cotton weight between the five pollen
 986 limitation treatments: closed (C), closed outcross (CO), closed self-cross (CS),
 987 open (O), and open outcross (OO). Closed (C) flowers remained bagged with
 988 lightweight white organza bags throughout the flowering period, closed out
 989 (CO) flowers were bagged but received outcross pollen from 3-5 donor flowers
 990 in the vicinity, closed self-cross flowers (CS) were bagged but supplemented
 991 with self-cross pollen, open flowers (O) remained unbagged to measure the
 992 amount of ambient pollination service, and open outcross flowers (OO)
 993 remained open but were also supplemented with an abundance of additional
 994 outcross pollen. The central bar gives treatment mean, boxes give the 1st and 3rd
 995 quartiles, and closed circles show outliers. ANOVA and Tukey HSD statistics
 996 were used to compare seed-cotton weight between treatments. Significance is
 997 shown with letters.

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999 Figure 3: Scatterplots showing the relationship between (a) local natural area
1000 and pollinator abundance, (b) local natural area and pollinator richness, (c)
1001 pollinator abundance and pollen limitation, and (d) pollinator richness and
1002 pollen limitation. Pollen limitation is determined as the difference in seed-cotton
1003 weight between the open outcross (OO) pollen treatment and the open (O)
1004 pollen treatment.

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1006 Figure 4: Path diagram for the effects of land use and pollinator community
1007 composition on pollen limitation in *Gossypium hirsutum* L. identified using
1008 SEM. Positive effects are indicated by (+), and negative effects by (-). The
1009 widths of the arrows indicate the magnitude of the standardized path
1010 coefficients.

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Figure 1

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