Agriculture, Ecosystems and Environment 226 (2016) 33–42

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

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

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ARTICLE INFO

Article history:
Received 24 May 2015
Received in revised form 21 April 2016
Accepted 22 April 2016
Available online 9 May 2016

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.

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

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http://dx.doi.org/10.1016/j.agee.2016.04.020

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 (Tscharntke 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; Tscharntke 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