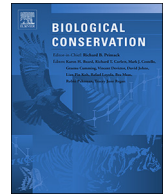




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Taxon-specific associations of tallgrass prairie flower visitors with site-scale forb communities and landscape composition and configuration



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ABSTRACT

Pollinators are integral to global plant biodiversity and agroecosystems, yet our understanding of the multi-scale drivers of pollinator community structure remains underdeveloped. In this study, we used a dataset comprising almost 7000 highly taxonomically resolved records of tallgrass prairie forbs and flower visiting insects to evaluate potential roles of site-scale forb communities as well as the composition and configuration of the surrounding landscapes, in structuring flower visitor communities. We examined the whole flower visitor community and three focal subgroups—bees (the principal pollinators worldwide), butterflies (often less efficient pollinators, but potentially useful as indicator taxa) and syrphid/bombyliid flies (which, as non-bee taxa, are often overlooked). At the site-scale, the composition of the entire flower visitor community was significantly associated with forb composition, but only bees were significantly, positively associated with forb α -diversity. Bee, butterfly, and fly diversity exhibited taxon-specific relationships with landscape composition and configuration. Butterfly richness was positively correlated with the combined extent of warm-season grasslands and woodlands, whereas bees were associated with the extent of warm-season grasslands, only. Bee and fly diversity was higher in landscapes with greater grassland edge density, indicating that habitat heterogeneity may be beneficial for these taxa. Our work adds to the growing body of research indicating that pollinators' responses to floral resources and land use in highly modified landscapes are often complex, taxon-specific and scale dependent, and our results highlight the importance of distinguishing among different types of natural and semi-natural lands when formulating pollinator conservation and restoration plans.

1. Introduction

Pollinators are critical to the maintenance of plant biodiversity and agroecosystems worldwide. Almost 90% of flowering plants are animal-pollinated (Ollerton et al., 2011), and over one-third of global crop production is pollinator-dependent (Klein et al., 2007). Despite their importance, it is becoming increasingly apparent that multiple human-mediated pressures are threatening pollinator populations. Foremost among these threats is habitat loss (Brown and Paxton, 2009) which often accompanies agricultural intensification (Bukovinszky et al., 2017).

Although bees are the world's primary pollinators (Cane, 2008), a recent review by Ollerton (2017) has emphasized the incredible taxonomic diversity of insect pollinators. Unfortunately, monitoring and conserving insects, which comprise the majority of pollinators (Grimaldi and Engle, 2005), remains challenging for several reasons. Insect communities are often species-diverse and exhibit a wide variety

of life history traits, making it difficult to formulate comprehensive conservation plans that encompass their wide-ranging resource requirements (Shuey, 2013). Furthermore, many insects (e.g. bees; Cane, 2001) are difficult to identify without specialized training or the assistance of taxonomists. This underscores the need to evaluate the utility of more easily-identified insect groups (e.g. butterflies) as indicators for the responses of these taxa.

Conservation of insect pollinators is further complicated by their mobility, as pollinators often utilize resources across spatial scales that encompass both focal sites (e.g. crop fields, habitat restorations) and the surrounding landscapes (Kremen et al., 2007). Pollinators often respond positively to increasing site-scale floral resources (Steffan-Dewenter and Tscharntke, 2001; Potts et al., 2003; Marini et al., 2009; Kennedy et al., 2013), but researchers in many systems have also found that relationships between forb- and pollinator α -diversity are weak or absent (e.g. Davis et al., 2008; Grass et al., 2016). Plant species composition at a focal site may also play an important role in structuring

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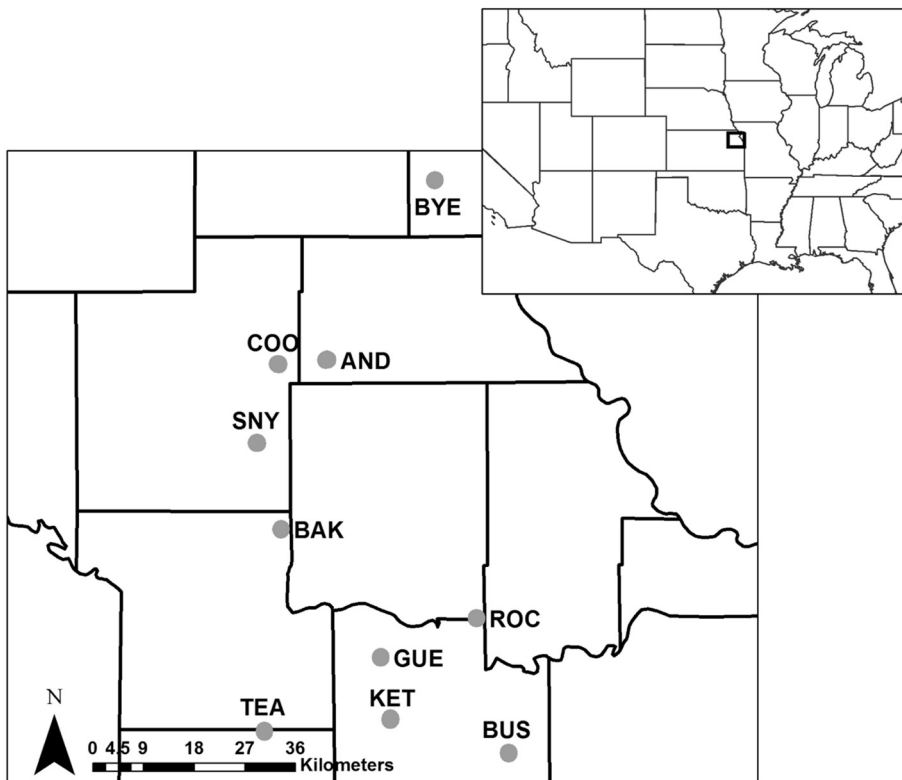


Fig. 1. Map of northeast Kansas tallgrass prairies surveyed for forbs and flower visitors from 2013 to 2015: Anderson Family (AND), Baker Farm Restoration (BAK), Busby (BUS), Byers Family (BYE), Coombs (COO), Guess (GUE), Kettle-Look (KET), Rockefeller (ROC), Snyder Prairie (SNY), and Teal Lake (TEA). AND, GUE, ROC, SNY and TEA are remnant prairies, and the remaining sites are prairies reconstructed on former croplands.

pollinator communities, as many pollinators exhibit strong trophic specialization as larvae and/or adults (Robertson, 1929; Ehrlich and Raven, 1964; Kopper et al., 2000) and will be unable to successfully colonize a site unless specific plants are present.

In addition to responding to site-scale floral resources, pollinators often exhibit strong associations with the composition of the surrounding landscape, responding negatively to the extent of agricultural land and positively to natural and semi-natural lands (Kennedy et al., 2013; Senapathi et al., 2017). The effects of landscape configuration, the spatial arrangement of habitat patches within a landscape, on pollinators remain less clear (Hass et al., 2018). In heavily modified, fragmented landscapes, pollinators are more likely to encounter habitat edges (Fahrig, 2003). Habitat edges may facilitate or impede pollinator movement throughout a landscape and can have varying effects on pollinator distributions and abundance (Hadley and Betts, 2012). On one hand, edges are frequently ecologically distinct compared to patch interiors (Ries et al., 2004), and in agricultural landscapes, edges can provide important foraging resources and nesting sites for pollinators (e.g. bumble bees; Svensson et al., 2000; Kells and Goulson, 2003; Pywell et al., 2005). On the other hand, flower visitors (e.g. butterflies; Ries and Debinski, 2001; Schtickzelle et al., 2006; Mair et al., 2015) have been demonstrated to be less likely to cross habitat boundaries, potentially affecting colonization and persistence within highly modified landscapes. Even within the same landscape, the responses of flower visiting insects to habitat edges can be taxon-specific (Ries and Debinski, 2001; Holzschuh et al., 2010).

Because of pollinators' complex and multi-scale responses, studies that address the drivers of pollinator community structure at focal sites must consider both the site-scale provisioning of resources and the landscapes within which focal sites are situated (Kremen et al., 2007). However, our understanding of the varied, multi-scale drivers of pollinator community structure remains underdeveloped, especially with respect to many non-bee pollinators (Grass et al., 2016; Senapathi et al., 2017).

We assessed potential drivers of insect flower visitor structure on remnant and reconstructed (“restored” on former crop fields) tallgrass

prairies in the agricultural landscapes of northeast Kansas, USA. Our previous work in this system revealed that flower visitor diversity and abundance were comparable across remnant and reconstructed prairies (Denning and Foster, 2018) but did not assess potential multi-scale drivers of flower visitor communities. Herein, we evaluated relationships between flower visitor community structure (richness, diversity, and composition) and both site-scale forb communities (richness, abundance and composition) and landscape-scale composition and configuration in the tallgrass prairie ecosystem. Grasslands comprise 37% of global terrestrial land cover and play an integral role in global food security yet have been subject to extensive degradation and agricultural conversion (O'Mara, 2012). The tallgrass prairie is North America's most threatened ecosystem, having lost extensive land cover to agricultural conversion (Sampson and Knopf, 1994). Remnant and reconstructed prairies are often small and embedded within highly modified landscapes. Taken together, this lends particular urgency to improving our understanding of tallgrass prairie pollinator communities.

We used a highly taxonomically resolved dataset to evaluate local and landscape-scale correlations involving the entire flower visitor community, as well three subgroups—bees, butterflies, and syrphid/bombyliid flies. Our focus on bees was driven by their global importance as pollinators. Butterflies are less efficient pollinators in temperate ecosystems (Cane, 2001) but are a diverse group of pollinators globally (Ollerton, 2017), and their relative ease of identification could make them useful indicators of suitable pollinator habitats (Thomas et al., 1992). Syrphid and bombyliid flies (Diptera:Syrphidae, Bombyliidae) can be important pollinators (Larson et al., 2001) but, like many non-bee pollinators, they are often overlooked by researchers (Rader et al., 2016). We hypothesized that (1) flower visitor α -diversity would be significantly associated with site-scale forb α -diversity and abundance; (2) sites more similar in forb composition would also be more similar in flower visitor composition; (3) flower visitor α -diversity would be positively associated with the extent of native grasslands in the surrounding landscapes, as well as the combined extent of native grasslands and woodlands (together, considered “natural/semi-natural”

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