



Comparing diversity to flower-bee interaction networks reveals unsuccessful foraging of native bees in disturbed habitats



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ABSTRACT

As land is converted to agriculture (e.g., pastures), natural vegetation is repeatedly disturbed, creating various levels of habitat alteration in which flowering plants and pollinators (e.g., bees) interact. Community structure of flowering plants, bees, and flower-bee interactions may each respond to disturbance, but potentially in different ways or magnitudes. We studied flowering plants, bees, and their interactions across four mechanical disturbance levels in and near Archbold Biological Station, Florida (USA) for one year, using repeated sampling with standard techniques in replicated plots. Data were analyzed for community structure, flower-bee interactions and bipartite network structure. Over 7500 flowering plants (81 species) and almost 5000 bees (48 species) were sampled, representing >80% of estimated species richness. Disturbance altered available flower diversity and both shifted and simplified compositions of floral and bee communities. Importantly, the number of foraging bee species did not decrease with disturbance but fewer bee species interacted with flowers given greater disturbance, indicating that disturbance reduced successful foraging. Interaction networks became simpler with disturbance, and the non-native European honey bee (*Apis mellifera*) became more dominant as disturbance intensity increased. Flower-bee interactions were most sensitive to disturbance. For some native bees, anthropogenic disturbance may contribute to ecological trap conditions and drive long-term diversity patterns. Attention to interaction networks will help land managers identify plant species to conserve and restore flowering plants that are vital to native pollinator communities.

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1. Introduction

Among factors affecting terrestrial ecological communities, human land management is globally pervasive and dominates at local and regional scales (Foley et al., 2005). Land management disturbs natural vegetation to suit human purposes, and biotic diversity is typically reduced from natural to managed systems (Marrero et al., 2014; Murphy and Romanuk, 2014; Valiente-Banuet et al., 2015). Compared to natural lands, managed lands (e.g., managed forests, agricultural lands) have altered plant composition and diversity and contribute to fragmentation of habitat (Foster et al., 2003; Fischer and Lindenmayer, 2007).

Land management includes practices such as logging and conversion of natural vegetation to agriculture. Here we focus on mechanical disturbance as a type of disturbance, specifically roller chopping. Roller-chopping is a common practice, in which large machinery breaks and crushes vegetation (Menges and Gordon, 2010). Conservation lands may also require mechanical disturbance, such as when fire-suppressed scrub vegetation is roller chopped once to reduce fuel loads before

beginning a prescribed fire regime (Menges and Gordon, 2010). More intensive land management may include repeated roller chopping, clearing of woody debris, and seeding with grasses to convert natural vegetation to pasture (Boughton et al., 2010). Secondary succession may temporarily increase vegetation diversity and abundance in recently disturbed areas, but repeated and more intensive disturbance ultimately simplifies plant communities.

Pollinators also inhabit natural and managed lands and interact with flowering plants there. Pollinators (here we focus on bees) may be directly affected by land management (e.g., nest disruption) and/or indirectly by their interactions with flowering plants (Foley et al., 2005; Kremen et al., 2007; Winfree et al., 2009, 2011). Many people are most familiar with honey bees (*Apis mellifera* Linnaeus, 1758) because they are a widespread, generalist pollinator important to agriculture. While they contribute greatly to pollination, honey bees are not native to the US (Moritz et al., 2005). On the other hand, many native bee species are coevolved mutualists with native flowers, are often more specialized than honey bees, and can be diverse in natural lands and susceptible to land management (Wcislo and Cane, 1996; Schlaepfer et al., 2002; Fortuna and Bascompte, 2006; Greenleaf et al., 2007; Winfree et al., 2011). Also, honey bees are eusocial, whereas most native bees are solitary breeders, substantially smaller in body size, but often numerous and diverse (Batra, 1984). Smaller, solitary bees are more

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likely to nest near floral resources (Wcislo and Cane, 1996) and forage over shorter distances than larger bees (Greenleaf et al., 2007). As a result, native bee communities composed mostly of small, solitary species should be sensitive to land management that disturbs floral resources and habitat over large areas. Unfortunately, responses of flower-bee interactions and community compositional responses to land-use change are not sufficiently known (Winfree et al., 2011).

Bees may forage in managed lands (and thus contribute to observed pollinator diversity) but actually interact less with flowers when compared to undisturbed lands if flower composition has changed. If so, then bees should be expending substantial time and energy for this unsuccessful foraging without reward (e.g., pollen and nectar). This hypothesis - that vegetation disturbance by anthropogenic land management causes unsuccessful foraging by bees - is consistent with an ecological trap, which occurs when organisms choose to utilize altered habitat (that may have once been suitable) without success (Schlaepfer et al., 2002). To be clear, demonstrating fitness costs (i.e., survival and reproduction) would be a more complete demonstration of an ecological trap. Here we merely tested for general evidence of unsuccessful foraging among bee species given different levels of disturbance in managed lands, consistent with the need for more detailed research on native pollinators in anthropogenic habitats (Winfree et al., 2011).

Specifically, we hypothesized that vegetation changes may cause bees to respond in three ways, only one of which is consistent with an ecological trap (Fig. 1). First, bees closely co-evolved with flowering plants may track vegetation in both diversity and interactions (Fig. 1a) because they actively depend on specific floral resources (Kearns et al., 1998; Deyrup et al., 2002; Lennartsson, 2002; Van der Putten et al., 2004; Fontaine et al., 2005). If this is the case, we would expect to see declines in foraging and interacting bees with reduced flowering plant diversity (Fig. 1a). Alternatively, most foraging bees may act as generalists and forage at spatial scales beyond local vegetation disturbance, so that bee diversity and interactions are robust to local disturbance (Memmott et al., 2004; Fortuna and Bascompte, 2006; Nielsen and Totland, 2014). In that case (Fig. 1b), diversity of both foraging and interacting bees should change little with vegetation disturbance and bees should continue to interact with various flowering plants across disturbance regimes. Finally we hypothesized that most bees may forage unsuccessfully in disturbed lands because available flowers do not match coevolved adaptations (Fig. 1c), consistent with an ecological trap (Schlaepfer et al., 2002; Winfree et al., 2009). In that case, bees should be observed in the disturbed habitats but should not interact with flowers as often as in less-disturbed habitats.

To evaluate the above hypotheses (Fig. 1), we estimated diversity of available flowers and foraging bees as well as plant-bee interactions. We used bipartite networks to analyze interactions, where network complexity should contribute to ecosystem stability (Bascompte and Jordano, 2007). In principle, interaction networks in conservation lands should be more complex, whereas those in disturbed habitats should be simpler and more dominated by generalists, reflecting reduced diversity of each community (Moreira et al., 2015). We evaluated the hypotheses (Fig. 1) for a year in four habitats managed differently but located <8.5 km of each other. Disturbance levels studied here ranged from reference conditions to pastures; more extreme disturbance levels (e.g., row crops, suburban and urban areas, industrial lands) that may also contribute to expectations (Fig. 1) were not included here. In effect, this study evaluated relatively low-level disturbance effects on floral and bee diversity and their interactions.

We expected that regional bees may access all habitats throughout the year, though distance between habitats may exceed forage distances of individual bees (Zurbuchen et al., 2010). We predicted flowering plant communities would be affected by disturbance. We also expected a diverse bee community with various seasonal foraging and interaction behaviors, and thus a mixture of species' responses. We also anticipated annual, cumulative effects would be important to bees that forage

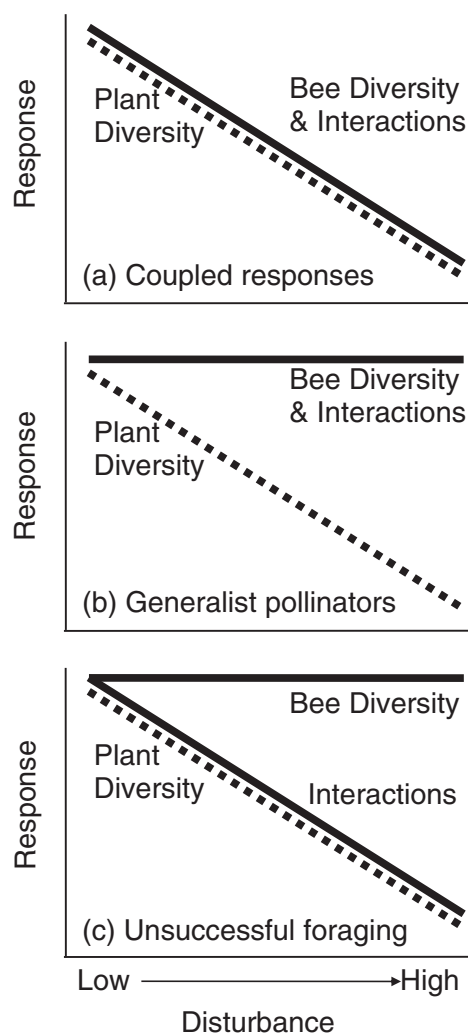


Fig. 1. Alternative hypotheses for the responses of plant and bee diversity (e.g., species richness) and plant-bee interactions to increasing levels of disturbance. Actual trends may differ from simple straight lines; relative positions among trends are most important. (a) Bees track vegetation responses in both diversity and interactions due to specialized, co-evolved foraging and feeding behaviors. (b) Bees are robust to local change in available flowers because they are mobile generalists. (c) Bee diversity does not track local disturbance of available flowers because bees continue to forage over disturbed habitats while flower-bee interactions are reduced with disturbance, indicating unsuccessful foraging.

through seasonal flowering events (Kremen et al., 2007). We therefore examined and compared both detailed (i.e., repeated measures analyses) and cumulative (e.g., annual richness) responses of flowers and bees to disturbance. We also expected native bees co-evolved with native flowers to more often demonstrate effects of land-use management than the non-native, generalist *A. mellifera*, which we predicted to be relatively insensitive to vegetation disturbance. The comparative approach used here (detailed and cumulative diversity and flower-bee networks) attempts to provide a more complete view of plant-pollinator responses to disturbance in our study system. This approach should be applicable in other study systems and help to inform conservation and restoration of community diversity and network structure.

2. Materials and methods

2.1. Study sites and sampling

This study was conducted in current and former scrub habitats on the Lake Wales Ridge of Florida (USA), which is a series of Pleistocene

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