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Exotic plants promote pollination niche overlap in an agroecosystem

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ABSTRACT

Agricultural land management modifies ecosystem structure and functioning in natural landscapes. Pollinators are a key functional group that may suffer from such intensification. Here we evaluate how agricultural land management influences the diversity of pollen transported by pollinators and the pollination niche overlap among plants. We described pollen transport networks (which allow assessing the contribution of pollinators to the flow of pollen among plants) in agricultural and restored fragments in three sites representative of the pampas region of Argentina. We analyzed diversity of pollen transported by pollinators and the pollination niche overlap among plants in both types of fragments with general and generalized linear mixed models. The agricultural fragments were associated to increased diversity of transported pollen and pollination niche overlap among plants. Greater pollination niche overlap in agricultural fragments was associated with increased abundance of exotic plants. Our results indicate that agricultural intensification has significantly increased the diversity of pollen and the pollination niche overlap in natural communities by promoting exotic plants and generalized plant-pollinator interactions. Strategies to encourage improvements in the quality of pollination in agroecosystems could range from controlling the levels of exotic species to mechanisms that promote increased diversity of native plants.

1. Introduction

Over the last three centuries the intensification in agricultural land management produced a profound transformation of earth's surface (Ellis et al., 2010). Agricultural land management may greatly influence the structure of ecological communities and the functioning of ecosystems in natural landscapes (Kremen et al., 2007; Marrero et al., 2014; Kremen and M'Gonigle, 2015). Animal pollinators, which play a key ecological role in many ecosystems, are being greatly influenced by such intensification. Their pollination service may be affected by changes in pollen flow and pollination quantity and quality (i.e., the amount and type of pollen reaching floral stigmas, Larson et al., 2006; Garibaldi et al., 2011, 2014; Marrero et al., 2016). In addition, agricultural land management can favor exotic plants (Marrero et al., 2014), which usually compete strongly with natives (Bjerknes et al., 2007; Muñoz and Cavieres, 2008; Stout and Morales, 2009; Morales and Traveset, 2009; Montero-Castaño and Vilà, 2012; Gómez et al., 2014).

Although exotic plants could be the only resource for pollinators in some agroecosystems (Nicholls and Altieri, 2013), little is known about their potential effects on other plants in the community. Exotic plants can disrupt mutualistic interactions between native plants and their pollinators and thus influence plant fitness (Traveset and Richardson, 2014). Grass et al. (2013) found increased pollinator visitation rates on native plants and decreased visitation to exotic plants with increasing exotic abundance and land-use intensity in agroecosystems. In addition, the functional diversity of pollinators in agroecosystems decreases with increasing relative exotic plant abundance, affecting pollination and the stability of plant-pollinator assemblages (Grass et al., 2014). However, nothing is known about the effects that agricultural land management and the presence of exotic plants have on pollen transport in agroecosystems.

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Limited space on the pollinator's body might restrict transported pollen loads, so that adding pollen of one species reduces the amount of pollen of another species (Mitchell et al., 2009). By negatively affecting specialist pollinators and promoting generalized pollinators that carry multi-specific pollen (Kremen et al., 2007; Fischer and Lindenmayer, 2007; Grass et al., 2013; Marrero et al., 2014; Weiner et al., 2014; Vanbergen, 2014; but see Vázquez and Simberloff, 2002), agricultural land management may lead to increased deposition of heterospecific pollen in floral stigmas (Marrero et al., 2016), increasing the pollination niche overlap among plants (Mitchell et al., 2009) and ultimately hampering fruit and seed production (Morales and Traveset, 2008; Ashman and Arceo-Gómez, 2013; Arceo-Gómez and Ashman, 2011a,b, 2016). Exotic species are often supergeneralists (Aizen et al., 2008; Vilà et al., 2009; Traveset and Richardson, 2014) with broad niches (Vázquez, 2006), which could lead to increased overlap in the pollination niche among plants in the invaded communities. High levels of pollination niche overlap might affect plant reproduction in general and even the yield of crops. For example, Montero-Castaño et al. (2016) showed that some mass flowering crops can influence pollinator patterns in the surrounding landscape by competing with native plants for generalist pollinators.

Here we evaluate how agricultural land management influences pollen transport by pollinators in the Argentine Pampas, a highly transformed region that has experienced a strong intensification of agricultural land management during the last two centuries (Medan et al., 2011). Although data are available on plant-pollinator interactions and composition of stigmatic pollen loads in this system (Marrero et al., 2014, 2016), some studies suggest that the analyses of pollen transported by pollinators could contribute to a better understanding of the effects of agricultural intensification. For example, the deposition of heterospecific pollen on stigmas was shown to be unrelated to the interspecific movements of pollinators and their degree of specialization (Fang and Huang, 2016). Moreover, in a community the plants that act as heterospecific pollen donors are not the same that act as receptors (Fang and Huang, 2013). We can thus expect that the diversity of pollen transported by pollinators and the pollination niche overlap among plants are also greater in agricultural land management. Teasing apart these effects of agricultural land management on pollen transport by pollinators and the resulting niche overlap among plants is essential for a mechanistic understanding of the effects of agricultural practices on pollination services. To this end, we studied the pollen transport networks, which quantify the interactions between plants and pollinators through the amount of pollen grains transported by pollinators (Forup and Memmott, 2005). This type of networks represents a useful approach to study pollination niches of plants, providing information about which pollinator species carry pollen of which plant species, and are thus more accurate than visitation networks to study pollen flow in communities (Forup and Memmott, 2005).

We compared pollen transport networks from fragments under agricultural management (agricultural fragments) with fragments where these practices had been abandoned for several years or were under conservation-aimed land management (restored fragments). We hypothesized that, by promoting the invasion by exotic plants and the predominance of generalized plant-pollinator interactions, agricultural land management would lead to increase diversity of pollen transported by pollinators and increased pollination niche overlap among coexisting plants. Thus, we predicted that (i) agricultural fragments would have greater diversity of pollen transported by floral visitors, (ii) agricultural fragments would have greater pollination niche overlap among plants, and (iii) pollination niche overlap would be positively related to the presence of exotic species.

2. Materials and methods

2.1. Study sites

The study was carried out at three sites along a 700 km transect located at 36°S in Buenos Aires and La Pampa provinces, Argentina. From east to west, the sites were located in Estancia Las Chilcas (hereafter referred to as 'LC'), Estancia San Claudio ('SC') and Estancia Anquilóo ('AN') (see Supporting information for a detailed description of the study sites). The predominant land use varied among sites as a function of precipitation and soil types (see Fig. S1 in Supporting information). In LC, extensive cattle production on semi-natural pastures was predominant and no agrochemical or farm machinery was used during this study. The main entomophilous crop found at this site was bird's-foot trefoil (*Lotus tenuis*). In SC, cropping is predominant under a mixed farming system (although there was extensive cattle production), where herbicides and pesticides are frequently and intensively used. The main crops found at this site were soybean (*Glycine max*), maize (*Zea mays*) and, to a lesser extent, sunflower (*Helianthus annuus*) and alfalfa (*Medicago sativa*). Lastly, production in AN was mixed farming, with a predominance of extensive cattle production and controlled grazing. Here, the agricultural fragments were sown with alfalfa and weeping lovegrass (*Eragrostis curvula*) as forage.

In LC and SC, restored fragments were enclosures with permanent fences which have not been cultivated or grazed for the last 3 and 20 years, respectively. In AN, restored fragments were sites with a conservation-aimed land management where cattle have been absent from September until April during the last 30 years, the time of the year when sampling was carried out. In these fragments, farm managers conserved the woody elements of the vegetation intentionally, including many entomophilous species (*Prosopis caldenia*, *Condalia microphylla* and *Geoffroea decorticans*, among others), although cattle trampling may have affected the entomophilous herbaceous plants. It is important to emphasize that woodland clearance traditionally has been the greatest modification undertaken by human beings in this region, thus making access for cattle easier and obtaining larger grazing areas (González-Roglich et al., 2012).

At each site, two restored and two agricultural fragments of 1 ha each one were selected (except for LC, where only one appropriate restored area was found; see Marrero et al., 2014 for more details on the study sites). The restored and agricultural fragments in each site were located at least 500 m apart in order to guarantee their independence. Although some bee species are known to fly much larger distances (Beekman and Ratnieks, 2000), smaller bees and/or some flies (which dominated our visitor assemblages) typically fly distances shorter than 500 m (Zurbuchen et al., 2010; Rader et al., 2011). Unlike the cattle production sites (LC and AN), the field margins in SC (4% of total area) were included in the cropping areas as they are a landscape elements of the agroecosystem and are generally considered to be important biodiversity reservoirs (Olson and Wäckers, 2007; Torretta and Poggio, 2013; Hodara and Poggio, 2016). Although our study fragments were located in three distant areas with rather different plant and pollinator assemblages, the structure of the plant-pollinator networks (e.g., overall generalization) was similar among fragments (Marrero et al., 2014). For this reason we think that fragments from different sites can be used as replicates to carry out this study.

2.2. Floral visitors and vegetation surveys

Monthly samplings in the eleven fragments were performed from November to March (2010–2011). Two 50 m × 2 m transects were placed randomly in each fragment to estimate the abundance of flowers or inflorescences of entomophilous plants and their