Perspectives in Ecology and Conservation 15 (2017) 18–24

ABECO
ASSOCIAÇÃO BRASILEIRA DE CIÊNCIA ECOLÓGICA E CONSERVAÇÃO

Perspectives in ecology and conservation

Supported by Boticário Group Foundation for Nature Protection

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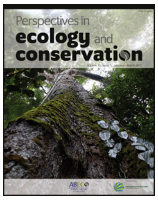

Research Letters

Positive responses of flower visiting bees to landscape heterogeneity depend on functional connectivity levels

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ARTICLE INFO

Article history:
Received 15 November 2016
Accepted 6 March 2017
Available online 27 March 2017

Keywords:
Functional ecological corridors
Landscape effects
Pollination
Bee richness and abundance
Atlantic forest

ABSTRACT

Landscape changes can lead to bee species loss, what impairs proper landscape level pollination processes, impacting both nature conservation and human welfare. Although landscape heterogeneity can rescue bee communities from collapsing, these insects seem sensitive to reduced functional connectivity, hindering pollen transfer among plants. Our objective was to verify which of these two factors, landscape heterogeneity or functional connectivity, can better explain variations of bee abundance and richness in a fragmented Atlantic Forest region. We sampled flower-visiting bees in 12 landscapes with varying heterogeneity and functional connectivity measured using a Functional Ecological Corridors framework. Both richness and abundance were affected by landscape factors, reaching its highest levels at intermediate levels of functional connectivity in highly heterogeneous landscapes, indicating the existence of strong regime shifts in the system. In low-forested landscapes, conservation actions for pollinating bees should focus on implementing diversified environments with high quality which are interspersed among each other and with native vegetation.

Introduction

Human made landscape changes are among the most important drivers of species extinction, leading to the loss of important ecological processes (Laurance et al., 2002). However, there are still only few studies which try to understand landscape changes effects on key ecological processes, such as seed dispersal and predation (Galetti et al., 2013), herbivory (Banks, 1998) and pollination (Andrieu et al., 2009). Among these processes, animal mediated pollination has been recognized as the one with greater and more direct impact over human populations and wellbeing (Potts et al., 2016). Pollinating insects have major economic value, since at least 35% of worldwide food crops directly depend on them (Klein et al., 2007), annually generating U$ 577,00 billion in environmental services (Potts et al., 2016).

The most important pollinating insects are bees, which are directly responsible for the maintenance of native plant diversity, since several plants depend on them to guarantee their reproduction (Ollerton et al., 2011). Nevertheless, these insects are very sensitive to environmental changes, specially to intensive land use and land change (Kennedy et al., 2013; Viana et al., 2012). Increases in landscape changes led to a worldwide decline in bee pollinators richness and abundance, which is even worse in tropical areas, where the proportion of animal pollinated plants is higher, when compared to temperate regions (Ollerton et al., 2011). This decline has severe consequences to natural ecosystems and agricultural production (Carvalheiro et al., 2010; Garibaldi et al., 2013).

Recent studies show that in landscapes with low remaining natural vegetation cover, pollinators richness and abundance, as well as agricultural productivity, may be rescued by high environmental heterogeneity (Kennedy et al., 2013; Moreira et al., 2015; Pryke et al., 2013). More heterogeneous landscapes allow greater resource diversity within the individuals foraging ranges, as well as varying environmental conditions and niche availability which allow a greater amount of interactions between plants and floral visitors (Fabian et al., 2013; Moreira et al., 2015). Landscape simplification has thus been termed as one of the major reasons for the decline of pollinators abundance (Viana et al., 2012).

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http://dx.doi.org/10.1016/j.pecon.2017.03.002

However, pollinators usually do not perceive their landscapes as binary habitat-non-habitat systems, but use distinct landscape units in different ways and with differential survival costs (Moniem and Holland, 2013). In this sense, landscape heterogeneity should be functionally approached, considering not only landscape composition, but also its configuration and the actual effects of different kinds of environments for each studied species or process (Fahrig et al., 2011). In landscapes that have already been highly changed by human interference, native land cover types are commonly substituted by low quality inhospitable environments that are not accessed by bees. In fact, Kennedy et al. (2013) modeled landscape structure effects on bee communities and suggested that for each 10% increase of high quality habitats, bee abundance must increase about 37%. Since pollinators must move through the landscape to gather needed resources, the quality of different land units may change their flux among patches (Slancarova et al., 2014). These processes can deeply change landscape functional connectivity for pollinators, directly influencing their populations and maybe even hindering pollen transfer and overall pollination effectiveness (Vögeli et al., 2010).

Additionally, some authors even suggest that important extinction thresholds for plant-pollinator interaction networks should occur between 50 and 60% of native vegetation loss (Fortuna et al., 2013; Keitt, 2009). For the Atlantic Forest, there is evidence that crucial regime shifts influencing pollinating bee abundance occur in landscapes with about 40% of remaining forest (Ferreira et al., 2015). Although connectivity must be crucial to maintain proper landscape level pollination in such a forest depleted system, there are still only few empirical studies focusing on this aspect and even less which use a functional approach (Viana et al., 2012). Here, we aimed to evaluate the influence of functional landscape connectivity on the richness and abundance of flower visiting bees in a region with severely fragmented Atlantic Forest, in which remaining patches rarely cover more than 40% of the area. These forests are embedded within several different land use types with varying resources and survival costs for bees.

We hypothesized that flower visiting bee richness and abundance in forest patches should increase with landscape diversity because more different resources might be closely available in those landscapes, increasing foraging efficiency. Additionally, bee richness and abundance on flowers might also increase with functional connectivity, what leads to higher biological fluxes throughout the landscape. Also, we believe that these two landscape factors, heterogeneity and functional connectivity, might jointly increase bee richness and abundance in highly connected heterogeneous landscapes, with homogeneous low connectivity landscapes presenting poorer communities with less individuals. This kind of functional approach will allow better understanding of the human impact on pollination processes at the landscape level, helping to improve landscape management strategies to create better sustainable landscapes where pollinators can be more resilient to environmental changes.

Methods

Study region and sampling locations

This study was conducted between Cantareira and Mantiqueira mountain ranges (Fig. 1) in the state of São Paulo, Brazil. This is an Atlantic Forest priority conservation area, since it can serve as an important biodiversity corridor between these two highly forested regions (Cantareira and Mantiqueira). Land cover is very heterogeneous, being originally covered by montane dense ombrophilus forests (Veloso et al., 1991). However, intense anthropogenic pressures converted most of this vegetation into silvicuture, agriculture, cattle fields, suburban real state and dense urban development.

In this region, we mapped 40 randomly distributed landscapes (circles with 2 km radius centralized in forest patches ranging from 15 to 25 ha). Using Google satellite images and 1:5000 scale aerial photography we classified land cover of each landscape. Then, based on field verifications we selected 12 landscapes with central forest patches in advanced regrowth stages, making sure that these landscapes formed a gradient of landscape heterogeneity. Bee sampling was then conducted in the central point of each of these landscapes (Fig. 1). To reduce spatial autocorrelation among sample points, the minimum distance between patches was 3 km (Zurbuchen et al., 2010). All selected landscapes had less than 40% of forest cover, below which structural landscape thresholds are expected (Andrén, 1994; Metzger and Décamps, 1997), making forest remnants smaller and more isolated from each other. Under such conditions, the spatial arrangement of landscape units shall become crucial for the survival of several native species (Fahrig, 1998), increasing the chances of connectivity and landscape level effects on the remaining biota (Fig. 1). We avoided correlation between forest cover and landscape diversity ($p = 0.27$). Mapping and landscape measures were done using QGis (v1.8.0 and 2.8.2) and Fragstats 4.0.

Biological data

At each selected forest patch we installed a regular hexagonal plot with 25 m sides located at least 50 m from any forest edge (modified from Taki and Kevan, 2007). Within each hexagon, we observed all understory flowering plants up to 2 m in height for 15 min and sampled all observed bee flower visitors using entomological nets. We consecutively repeated this sampling cycle for all flowering plants within the hexagon from 7:00 to 16:00 h.

Each hexagon was sampled in four nonconsecutive sunny and warm (21 to 31 °C) days, totaling 36 sampling hours per landscape, at the highest peak of understory flower availability in the region (Morelato LPC, personal communication), between October and November of 2014. Sampled bees were marked and individually stored in 92% ethanol. Bees were identified to the most possible specific taxonomic group by specialists and deposited at the Entomological Collection Prof. J.M.F. Camargo (RPSP) at the Biology Department from FFCLRP/USP. Bee richness and abundance were then calculated for each sampled landscape.

Landscape heterogeneity and functional connectivity

To measure landscape diversity and functional connectivity, we generated land cover maps with 10 m resolution by manually classifying Google satellite images using the OpenLayers plugin in QGis (http://www.openlayers.org). The landscape surrounding each focal patch was classified into 14 different land units (Table 1) within 2 km radii of sampling points. This distance was based on the average foraging distance of most bees (Zurbuchen et al., 2010). Within this radius, the percentage of forest varied from 11% to 39%, including both young and mature forests. The most common land-cover units were Open pastures (12–64%), Pastures with shrubs (4–31%) and Forestry (Eucalyptus; 2–26%). Agriculture, Urban areas and Rural villages were also significantly represented (Fig. 1).

We calculated landscape heterogeneity within these landscapes with the Shannon Landscape Diversity Index (SHDI), which equals minus the sum of the total landscape proportion of each land-cover unit multiplied by its natural logarithm. It increases when the number of different land-cover units increases and/or the proportional area of these units becomes more equitable (McGarigal et al., 2012). We used this index because it is sensitive to the occurrence