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Review

The influence of local and landscape scale on single response traits in bees: A meta-analysis

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ABSTRACT

Assessments of environmental drivers that regulate the functional composition of various organisms have become more frequent in the ecological literature, as this approach establishes a more direct connection between community structure and ecosystem functions. Bee response traits, such as sociality, body size, nest location, nest behaviour, and dietary specialization, have been reported in empirical studies that examine the role of land use intensity in functional diversity. However, empirical studies include different descriptors measured at different spatial scales, producing poor generalizations. Processes operating at different scales may have different effects depending on the response traits considered in the analysis. In this meta-analysis, we provide a quantitative assessment of the role that the structural complexity of habitats at local and landscape scales plays in the richness and abundance patterns of bees, considering different response traits. As indicated through this meta-analysis, the descriptors of structural complexity at the local scale explained more of the richness and abundance of bees with distinct response traits than the descriptors at the landscape scale. In addition, high management intensity has a negative effect on the different response traits. Below-ground nesting bees and social bees showed different abundance trends, which suggest a mechanism denominated 'response diversity'. This result suggests that the adoption of hybrid management strategies at the local scale could support the richness and abundance of different bees with distinct response traits in agroecosystems. These distinct response traits can be an important ecological pattern that contributes to the development of management strategies that maintain, in space and time, bees with distinct response traits. However, we should analyse the communities in terms of clusters of response traits, considering the possible synergies and trade-offs between these traits.

1. Introduction

Assessing the diversity of functional traits found in a particular biological community has been reported as a more direct way to establish a connection between biodiversity and ecosystem functioning than an approach focusing only on taxonomic diversity (Díaz and Cabido, 2001; Hooper et al., 2005; Díaz et al., 2007; Gagic et al., 2015). There are two dimensions related to functional traits: response and effect traits. The effect traits mediate the species contribution to ecosystem functioning and affect the species provision of ecosystem services (Wood et al., 2015). The presence or occurrence of a given species that possesses an important functional trait in a space-time snapshot may depend on environmental filters that can act in selecting that species (Díaz et al., 2007). However, the relative importance of each environmental driver depends on the response trait that is being evaluated, and the identification of relevant traits within a given context is a major challenge (Laliberte et al., 2010).

Functional response traits are traits that mediate the response of species abundance or occurrence in relation to environmental filters (Violle et al., 2007; Laliberte and Legendre, 2010), such as microclimate changes, vegetation complexity, landscape structure (Forrest et al., 2015; Le Feon et al., 2016; De Palma et al., 2015). Functional

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response traits are related to morphological, physiological or behavioural characteristics that define the distribution of organisms in space and time (Kremen and M'Gonigle, 2015; Gagic et al., 2015; Wood et al., 2015). Thus, functional composition in a community is determined by response traits (Ricotta and Moretti, 2011). For bees, the most important pollinator group (Klein et al., 2007), sociality, body size, nest location, nest behaviour and dietary specialization are the primary response traits used to explain community structure in agroecosystems (Rader et al., 2014; Ahrenfeldt et al., 2015; Warzecha et al., 2016), and some empirical studies have focused on mechanistic explanations to determine the influence of distinct environmental predictors on the diversity of these bees according to their response traits (Klein et al., 2003a; Le Feon et al., 2016). The evaluation of which response traits are more likely to explain the loss of species in scenarios, such as intensive farming regimes, can be an important step in promoting mitigation actions (Bartomeus et al., 2017). However, we lack general quantitative information on bee richness and abundance with different response traits in agroecosystems (but see Williams et al., 2010).

The studies that evaluated the diversity of bees according to their response traits in agroecosystems vary in terms of the spatial scale and the predictors used (Bommarco et al., 2010; Rader et al., 2014; Baños-Picón et al., 2013). Ecological processes operating at different spatial scales complement each other in explaining the structure of a particular community, but the relative importance of these processes may vary according to the response trait considered in the analysis (Klein et al., 2008; Forrest et al., 2015; Martins et al., 2015; Ekroos et al., 2013). Ground nesting bees, for example, are strongly affected by management intensity of field crops, largely benefitting from open areas with low humidity content (Ngo et al., 2013). On the other hand, large social bees, which move small distances to forage and form small colonies, are more influenced by landscape heterogeneity (Ekroos et al., 2013), indicating that this group is more influenced by ecological processes at large spatial scales than local spatial scales (Aguirre-Gutiérrez et al., 2016). Light intensity best explains the abundance and richness of solitary bee species that nest on the ground in agroforestry systems in the tropical zone (Klein et al., 2003a; Klein et al., 2008). Other studies show that the richness of plant and flower abundance at a local scale are the predictors that best explain variation in richness and abundance of these bees (Albrecht et al., 2007), as well as the grassland coverage percentage in the landscape (Woodcock et al., 2013). These papers taken together show that the identity of these traits and the spatial scale approach are key aspects to understanding the influence of land use on the pattern of functional diversity in agroecosystems (Brittain et al., 2013; Aguirre-Gutiérrez et al., 2016). Quantitatively contrasting these different parameters and spatial scales of observation has not been well reported. In addition, explanations for the variation in the response of bees with different response traits have not been well defined.

In a meta-analysis, Bommarco et al. (2010) reviewed the trends of three functional groups in response to a reduction in habitat area. However, the study was based on a set of data collected for five different types of habitats in Central Europe, decreasing our ability to make broader generalizations, in addition to limiting the findings to the specificities of a restricted set of habitat types.

Through this study, we aim to provide general quantitative information about the different responses of bees, according to distinct response traits in relation to descriptors of habitat and landscape in agroecosystems, discussing the implications of the use of these traits to explain and predict the presence of bees in these systems. In this manner, we asked the following questions: i) At the local scale, to what degree does the intensity of management and structural aspects of the habitat consistently affect the richness and abundance of bees with different response traits? ii) At the landscape scale, to what degree does the landscape structure consistently affect the richness and abundance of bees with different response traits?

2. Materials and methods

2.1. Literature search

To conduct this meta-analysis, we followed the PRISMA protocol (Moher et al., 2009). To identify studies in the literature that address the influence of land use for agricultural and/or the context the surrounding landscape on the functional diversity of bees in agroecosystems, we conducted a search in the database Scopus and Web of Science using the following keyword combinations: [functional diversity AND bees AND agroecosystem] OR [trait* AND bees AND agroecosystem] OR [functional diversity AND bees AND landscape] OR [functional diversity AND bees AND landscape composition] OR [functional diversity AND bees AND landscape configuration] OR [pollinator* OR functional diversity OR bee OR bees OR apoidea OR pollinator*] AND [fragmentation OR landscape composition OR landscape configuration OR land use type OR landscape OR soil use].

2.2. Protocol design

Studies included in this meta-analysis had to meet the following criteria: presented a variable response to functional diversity of bees in agroecosystems or some functional trait measure not synthesized by an index; included replication; reported the sample size; presented the mean and standard deviation for the type of habitat used for data collection (for studies using categorical predictor variables), or presented some statistics such as correlation and regression coefficients (for continuous predictor variables), as the effect size was calculated from this information (see below).

The studies assessing the functional diversity of bees considered different approaches ranging from the measurement of a single trait (e.g., body size or dietary specialization) to studies that consider the synthesis of information on different functional traits through functional diversity indexes (Ricotta and Moretti, 2011). Only studies that considered individual response traits were used in this meta-analysis. Some authors reported no statistical values with non-significant results. These authors were contacted to avoid bias in the meta-analysis from studies that did not report non-significant results (Winfree et al., 2009).

2.3. Grouping the data for meta-analysis: landscape and habitat descriptors

Because of the different approaches considered in the studies, we divided the data into different groups for the quantitative evaluation of the effect size of each subgroup. The studies were separated according to the type of approach used in the predictor variables: landscape or habitat scale. We used two categories to encompass studies conducted at the landscape scale: the proportion of crop area and the proportion of non-crop area. Studies that evaluated the influence of natural or semi-natural habitats (e.g., meadow in any proportion of radii from the point of sampling, proportion of home garden at a large scale, proportion of forest) at spatial scales wider than the habitat were included in the category "proportion of non-crop area". Studies that evaluated the influence of agriculture on the response variable were included in the "proportion of crop area". Accordingly, for many studies, the landscape structure was reported more than once, for example, measuring influence of crop and non-crop area. Therefore, "study" was included as a random variable in all mixed models (Shackelford et al., 2013) (see below). For studies that used more than one spatial scale to categorize the surrounding landscape, we chose the correlation coefficient with the greater value.

For the local scale, we used a similar approach such as described for the landscape scale. We reclassified the different measures used to describe structural complexity and the differences between agricultural intensities into three categories: structural complexity, resource availability and agricultural intensity. These categories reflect the different measures used in the original studies (empirical studies used in this