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# Turnover in bee species composition and functional trait distributions between seasons in a tropical agricultural landscape

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ABSTRACT

A comprehensive understanding of how spatial variation across landscapes regulates local abundances and species richness also needs to consider possible temporal changes in such relationships. In many tropical areas, the contrast between dry and rainy season is pronounced and the types and distributions of the main floral resources differ (herbs vs trees). This shift in resources could result in different pollinator abundances, species richness and trait compositions between seasons, as well as in how these components are spatially distributed. We compared the bee species composition between dry and rainy season in an agricultural mosaic landscape in southwestern Ethiopia, and analyzed it in relation to forest cover. We sampled bees for 67 days in the dry season and 86 days in the rainy season with pan and vane traps in 28 homegardens covering a gradient from low to high tree cover in the surrounding area. We found a clear shift in species composition between seasons, with more small bee species and more below-ground nesting bees in the rainy season compared to the dry season. The distribution of height at which the bees were foraging shifted between seasons with a higher proportion of the bees foraging at tree level in the dry season. Bee abundance and richness were generally positively affected by higher forest cover surrounding the homegardens, but there were no clear interaction effects between seasons, in contrast to our hypothesis. The clear turnover in species composition between seasons and the positive effect of forest cover show that mechanisms acting both at spatial and temporal scales are important in regulating local bee communities.


## 1. Introduction

Landscape composition and complexity are repeatedly found to affect the local number of species and their abundances across agricultural landscapes (Benton et al., 2003; Tscharntke et al., 2012; Shackelford et al., 2013). However, conditions across landscapes change over the season, affecting spatial patterns of species richness, density and population performance (Tylianakis et al., 2005; Miguet et al., 2013; Riedinger et al., 2014). This change is especially relevant for short-lived organisms such as insects. Several studies on the interaction between spatial and temporal drivers have focused on between-year patterns (e.g. Thies et al., 2008; Zhao et al., 2013), while studies on intra-annual patterns have mainly focused on the effects of mass flowering crops (e.g. Kovacs-Hostyanszki et al., 2013). There are very few studies conducted during longer time periods across a year that directly target whether land-use composition have differing impacts on species communities in different seasons (but see Tylianakis et al., 2005). This question is especially interesting in tropical areas where there is a high activity of most species groups throughout the year, despite seasonal variation in precipitation and temperature. In this study, we examined the interactive effect of rainy and dry season and forest cover on bee species composition in a tropical agro-ecological landscape in southwestern Ethiopia.

Bees are recognized as important pollinators for both crops and wild plants worldwide (Klein et al., 2007; Potts et al., 2010). In an agricultural system, a higher bee diversity often provides more stable and effective pollination services, resulting in higher and more stable yields (Klein et al., 2003a; Hoehn et al., 2008; Garibaldi et al., 2011). Bees depend on food and nesting resources for survival and reproduction, and a higher diversity and abundance of these resources generally corresponds to higher bee diversity and

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abundance (Potts et al., 2003, 2005; Grundel et al., 2010). However, depending on region and species traits, bees respond differently to different habitats and at different spatial scales. A worldwide meta-analysis found, when evaluating nesting traits, that above-ground nesters (honeybees excluded) respond more negatively to isolation from natural or semi-natural habitats compared to below-ground nesters (Williams et al., 2010). In another study, pollinator visitation rates on crops decreased faster with distance from natural/semi-natural habitats in tropical compared to temperate regions, and also slightly faster for social than for solitary bees (Ricketts et al., 2008). In tropical agro-ecosystems, vicinity to indigenous forest is often found to have a positive impact on bee abundance and diversity (Klein et al., 2003b; Ricketts, 2004; Brosi et al., 2008; Gemmill-Herren and Ochieng, 2008), which may not always be the case in temperate regions (Winfree et al., 2007). Nearby forests may have a more positive effect on pollinators in the tropics since tropical forests provide more resources in terms of nectar and pollen when compared to forests in temperate regions that tend to be more dominated by wind-pollinated tree species (Ollerton et al., 2011). A higher proportion of tropical bee species may also depend on forest habitats for nest construction (e.g. using resins, tree cavities) (Michener, 2007). On the other hand, the importance of forest habitat to bees may not be the same in all tropical areas. A study by Hagen and Kraemer (2010) from western Kenya suggested that structurally rich farmland supports bee communities in the natural forest rather than the opposite. Moreover, Brosi et al. (2007) found no effect of distance from forest on bee diversity or abundance in Costa Rica. However, they found a strong shift in bee community composition, with more native sting-less bees close to forest and a higher abundance of exotic honeybees in areas far from forests (Brosi et al., 2007).

Bee species composition generally changes over a year (Heithaus, 1979; Oertli et al., 2005). Some species have very short flight periods and some species have longer ones. For example, whereas many solitary bee species have short flight periods and differ in their time of emergence, many social bee species are active throughout the year (Heithaus, 1979; Michener, 2007). Precisely when specific bee species are active and able to reproduce depends on factors such as the availability of food resources and local climate (Richards and Packer, 1995; Williams and Kremen, 2007; Forrest and Thomson, 2011; Frund et al., 2013). Tropical regions have more stable temperatures compared to temperate regions during a year, but precipitation can vary substantially, leading to large changes in the appearance of the landscapes and the resources available for bees. In Ethiopia in north-east Africa, the low precipitation during the dry season in addition to high grazing pressure results in dry, dusty landscapes. Drought and grazing reduces the number of flowering herbaceous plants at ground level, resulting in few available resources of nectar and pollen. However, many trees and fruit trees have their main flowering period at some point during the dry season, which in the agricultural landscape as well as in forests provide abundant but patchy food resources for nectar and pollen-feeding insects, at tree level (Fichtl and Adi, 1994). In contrast, during and directly following the rainy season the agricultural landscape is generally green and flourishing, with a high diversity of flowering herbaceous plants and annual crops (Fichtl and Adi, 1994). Since both the main food resource (trees and herbaceous plants) and its spatial distribution differ between dry and rainy seasons, a shift in the bee community and bee traits may be expected. For example, to utilize the patchy resources flowering trees provide in the dry seasons, high mobility may be advantageous. Since flight distances for bees are strongly correlated with size and especially inter-tegula distance (Greenleaf et al., 2007), it could be expected that larger species have an advantage and therefore are more common during the dry season.

Our study was conducted in a heterogeneous agricultural landscape in southwestern Ethiopia. The distance to larger forest blocks is seldom more than a few kilometers. However, on a local scale, the amount of forested areas varies. As in other parts of Ethiopia, the contrast between dry and rainy seasons is very pronounced. We had two overall aims with our study. First, we evaluated how the bee-community composition changes between dry and rainy season and whether this change is linked to species traits such as size (mobility) and nesting requirements. In addition to that, we investigated whether bees forage at different heights in the different seasons by using traps at both ground and tree level. Second, we assessed how the spatial variation in bee abundance, species richness and composition are affected by the amount of forest in the surrounding area and if the relationship differs between the dry and rainy seasons. We hypothesized that if food resources provide the main limiting factor for the bees, the forest should have the highest impact on bees in the dry season when most trees are flowering. On the other hand, if nesting resources is the main limiting factor, we hypothesize that forest structures should have the highest impact on bees in the rainy season, since wood provides above-ground nesting opportunities when below-ground nesting may be unfavorable due to the soil being wet. Furthermore, we evaluated whether the amount of forest in the surrounding affects bees on different spatial scales in the different seasons, which could be expected if species with different mobilities are active in different seasons.

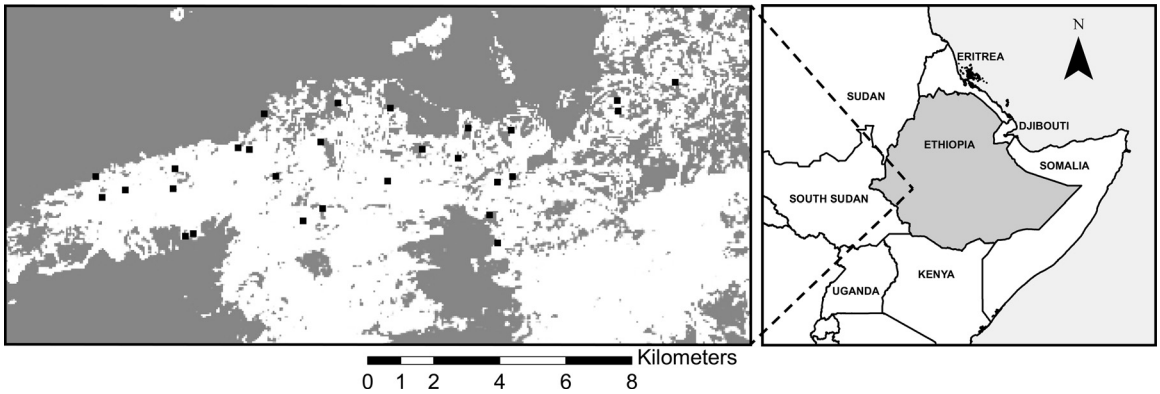


**Fig. 1.** Our study landscape in southwestern Ethiopia. The black squares denote the positions of the 28 homegardens where we passively collected bees with vane and pan traps. The gray areas in the landscape figure are forested areas and white areas are open land (e.g. agricultural land, grasslands, wetlands).