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# Pollination limitation despite managed honeybees in South African macadamia orchards

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ABSTRACT

There is growing demand for pollination services in agricultural production, which contrasts with declines of wild and managed pollinator populations. Macadamia (*Macadamia integrifolia)* is a mass-flowering crop that depends on pollination services and is increasingly cultivated in South Africa. We studied the crop's pollination in South African orchards considering variation in landscape context and the spatial arrangement of managed honeybees (*Apis mellifera*). We conducted pollination experiments and pollinator observations on macadamia trees along a distance gradient from orchard edges that bordered either near-natural or human-modified habitats. In addition, we mapped position and density of honeybee apiaries at orchard-level. Nut set of macadamia trees strongly relied on animal-mediated pollination: pollinator exclusion reduced the initial nut set (3 weeks after pollination) by 80% and the final nut set (15 weeks after pollination) by 54%. Supplemental hand-pollination of otherwise untreated flowers increased initial and final nut set by 66% and 44%, respectively, indicating substantial pollination limitation. The landscape context only weakly affected pollinator visitation to macadamia trees, with reduced visitation closer to orchard edges bordering human-modified habitats. Furthermore, we observed almost no wild pollinator species. Instead, honeybees constituted 99% of all visits, whereby honeybee visitation rates increased with a tree's connectivity to apiaries. However, neither initial nor final nut was related to visitation rates, and the final nut set was actually reduced where honeybee colony density was high, with a predicted 50% reduction in final nut set between the lowest and highest colony densities. Our study demonstrates a strong pollination limitation in South African macadamia orchards, where managed honeybees fail at delivering the increasing need for pollination services. Indeed, increasing their colony densities may further limit their pollination efficiency. A pollination management that also includes non-*Apis* managed pollinators and wild pollinators is possibly needed to increase nut set and provide solutions for increasing pollination service demands. In intensive macadamia orchards, this can also necessitate the need for more pollinator-friendly management practices, including habitat restoration and reduced pesticide application.

## 1. Introduction

Pollination by animals enhances the quantity, quality and stability of production from 70% of the world's leading food crops (Klein et al., 2007; Ricketts et al., 2008). While the global production of crops that depend on pollination is increasing (Lautenbach et al., 2012) both wild and commercial pollinators are under pressure (Potts et al., 2010). Agricultural expansion commonly happens at the expense of natural habitats, threatening wild pollinator populations (Kremen et al., 2002; Potts et al., 2010). In turn, production of many animal-pollinated crops increasingly relies on managed species, in particular honeybees (Apidae; especially the Western honeybee *Apis mellifera*, L.). However, honeybees often show low pollination efficiency, and yields of most animal-mediated crops are still largely dependent on wild pollinators

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regardless of honeybee abundance (Garibaldi et al., 2013). Solely relying on managed honeybees for crop production thus may result in pollination limitation.

Pollination limitation, i.e., the occurrence of reduced fruit or seed production because of temporally or spatially limited pollination services, is likely to be particularly pronounced in large orchards of mass-flowering crops. Macadamia (Proteaceae; commercially most important species: *Macadamia integrifolia* and *M. tetraphylla*) is an economically important food crop of which production in South Africa in 2014 surpassed that of Australia, making South Africa the world's largest macadamia nut producer (Department of Agriculture Forestry and Fisheries South Africa, 2015) despite the plant having its native range in Australia. Notably, nut set in macadamia trees strongly depends on pollination by wild bees and managed honeybees (Heard and Exley, 1994). Cross-pollination among the outcrossing cultivars appears to be particularly important (Trueman, 2013).

Pollination services in agroecosystems are usually strongly affected by the surrounding landscape. Services often decline with an increase in landscape simplification and agricultural expansion (e.g. Ricketts et al., 2008; Shackelford et al., 2013). In contrast, proximity of agricultural areas to natural habitats can increase on-farm pollinator abundance and richness as well as crop pollination (Blanche et al., 2006; Carvalheiro et al., 2010; Chacoff and Aizen, 2006; Garibaldi et al., 2011). Especially for central-place foragers, such as bees, the distance between the nest and nectar-providing flowers is crucial and can be an important determinant for successful pollination (Gathmann and Tscharntke, 2002; Ricketts, 2004; Kremen et al., 2007). Visitation rates therefore are likely to decrease with increasing distance from field edges bordering essential habitats, leading to spatial variation in pollination services in large orchards (Klein et al., 2003a,b; Morandin and Winston, 2005).

If pollination services by wild pollinator species are limited, farmers may increasingly rely on pollination by domesticated pollinators, commonly honeybees. However, pollination services by honeybees can also be spatially limited, depending on the density and spatial arrangement of apiaries within orchards (Cunningham et al., 2016). On first sight this may seem counterintuitive given the high spatial mobility of honeybees (Beekman and Ratnieks, 2000). Nevertheless, an over-abundance of resources from mass-flowering crops can result in restricted foraging ranges of honeybees. This has recently been shown in mass-flowering almond orchards (Cunningham et al., 2016): pollen-collecting activity of honeybees decreased with distance from apiaries. Honeybee activity was further influenced by colony density, which resulted in decreased nut set of almond trees at densities lower than 6.8 colonies per ha. It remains unclear whether such density-dependent effects on crop pollination are generalizable. Moreover, if honeybees are the sole pollinators in large orchards, their foraging behaviour may counteract efficient cross-pollination because they repeatedly exploit the same, most accessible resources. In fact, studies in almond orchards have shown that wild pollinators are needed to frequently disturb honeybees during foraging, resulting in enhanced movement rates of honeybees between the interplanted cultivars and thus enhanced pollination effectiveness (Brittain et al., 2013). A similar positive role of wild bees on honeybee pollination effectiveness was found in sunflower seed production (Greenleaf and Kremen, 2006). Given the high reliance of nut set in macadamia cultivars on outcrossing, absence of wild bees may severely limit the effectiveness of honeybee management for crop pollination.

Here, we study pollination services in South African macadamia orchards. We use pollination experiments to discern the role of animal-mediated pollination for nut set, as well as pollen limitation. In addition, we identify the role of landscape context and honeybee management for pollination services. Specifically we address the following questions: (I) Is there evidence for substantial pollen limitation in commercial South African macadamia orchards? (II) How much do wild pollinators and managed honeybees contribute to flower visitation and nut set? (III) How do the spatial arrangement of apiaries and the landscape context influence pollinator visitation rates and nut set?

## 2. Materials and methods

### 2.1. Study region and design

We conducted our study in the Levuvhu Valley at the southern foothills of the Soutpansberg, 20 km east of Makhado, Limpopo Province, South Africa (23° 3′ 0″ S, 29° 54′ 0″ E). The Levuvhu Valley is dominated by extensive monocultures of macadamias (*M. integrifolia*, *M. tetraphylla* and hybrids), pecan nuts (*Carya illinoinensis*), avocados (*Persea americana*), bananas (*Musa* spp.), pines (*Pinus* spp.) and gum trees (*Eucalyptus* spp.). The orchards are interspersed with remnants of natural bush and savannah. The adjacent Soutpansberg Mountain Bushveld is mostly covered by natural bush with few pine and gum tree plantations. The region is characterized by a tropical dry to moist climate, with a rainy season in summer from November to April, and annual rainfall of about 960 mm. Daily temperatures range between 15 and 40 °C and between 0 and 25 °C in summer and winter, respectively (Taylor et al., 2013).

In August 2015 we selected six commercial macadamia orchards in the region, which were situated on five farms with 8–16 year old trees (orchard size: 77.7 ha ± 71.6 ha [mean ± SD]; min = 11.0 ha; max = 210.3 ha). Farmers grew altogether five different cultivars of *M. integrifolia* (246, 788, 741, 816, 814) and one hybrid of *M. integrifolia* and *M. tetraphylla* (695 = Beaumont; in the following also referred to as 'cultivar'). Cultivars were planted in blocks or varied per tree row, resulting in a spatially diverse mosaic of cultivars allowing for cross-pollination. To assess the effect of landscape context on pollinator activity within farms, we identified two edges with strongly contrasting bordering habitat composition in every orchard. These edge types were classified as either 'near-natural' or 'human-modified', depending on the composition of the adjacent habitat types (Fig. A1 in Supplementary materials). The most important natural habitat for wild pollinators in our study, natural bush and savannah, made up on average 80% [SD: ± 18%] of the habitat bordering the Macadamia orchards at natural edges. In contrast, natural bush and savannah made up only 27% ± 19% of the adjacent vegetation at human-modified edges.

### 2.2. Study species and pollination experiments

*Macadamia integrifolia*, *M. tetraphylla* and their cultivars are the only economically important species within the genus *Macadamia*. All are at least partially self-incompatible and cross-pollination among cultivars results in highest yields (Sedgley, 1983; Trueman, 2013). The inflorescences are pendant racemes bearing 100 to 300 single flowers; one tree can bear up to 2500 racemes per flowering season (Trueman and Turnbull, 1994). The flower stigma becomes receptive a few days after ripe pollen by the same inflorescence has been produced. Fertilization occurs within 1 week after anthesis, followed by immature fruit drop during the first 7–15 weeks after pollination (Sedgley, 1983). Full nut ripening can take up to 24 weeks.

We experimentally determined the contribution of pollinators to nut set as well as pollen limitation of macadamia trees, applying three treatments: (I) bagging of racemes to prevent insect pollination, (II) marked but otherwise untreated racemes and (III) racemes open for pollination with supplemental hand pollination using pollen from a different cultivar.

To test for the contribution of pollinators to nut set, we bagged flowers to exclude flower visitors from access. At each edge type in every orchard we selected two trees, resulting in a total number of 24 trees. One tree was situated directly at the edge of the orchard, the second one in a distance of 15 m from the orchard edge (Fig. 1a). On each of these trees we bagged one to eight racemes with plastic gauze (mesh width 2 mm × 2 mm). One bag was lost during the experiment, resulting in a sample size of 23. The number of bagged racemes