



A major subtropical fruit pest accumulates in crop fields and spills over to a wild host



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ABSTRACT

Wild plant species are often considered a source of crop pests in mixed landscapes but this view rarely considers pest spillover in the opposite direction (from crop fields to natural vegetation), or spatiotemporal variability in resources between crop and wild habitats. We investigate how infestation of mango crop (*Mangifera indica*, Anacardiaceae) and a related wild host (marula, *Sclerocarya birrea*, Anacardiaceae) by a major subtropical fruit crop pest (*Ceratitis cosyra*, Diptera: Tephritidae) varies with distance from the boundary between crop and natural vegetation. We determined how infestation of marula is associated with proximity to mango crops at field and landscape scales over two fruiting seasons on three farms in north-eastern South Africa. This is one of few studies to date to consider pest spillover from crop fields to natural vegetation and the only one performed in a biodiverse region with relatively little habitat transformation. Over three sampling periods, *C. cosyra* infestation of marula always decreased with distance from mango fields. At the landscape scale, marula alongside crop fields were 30 times more likely to be infested than in distant vegetation (1.3–6 km from mango), suggesting that spillover occurs from crop fields to natural vegetation. During late mango and marula fruiting, twice as many flies infested marula than mango. However, over the two months post-mango fruiting, up to 25 times more *C. cosyra* were trapped in mango fields than in bordering natural vegetation. Although pests spillover from crop fields into natural vegetation to use marula as an alternate host, biological control in the natural vegetation may eliminate this habitat as a pest reservoir outside the crop season. Other nearby crops may be more important than wild hosts for maintaining *C. cosyra* out of mango season. Landscape planning should consider proximity and arrangement of fields containing crops that host shared pests at different times of the year.

1. Introduction

Agriculture has fragmented natural ecosystems worldwide, leaving mixed landscapes with patches of natural vegetation interspersed among human-managed agroecosystems (Benton et al., 2003). Biological communities in these landscapes are spatially and temporally dynamic (Thies et al., 2005); if consumer species are supported by resources in both crop and non-crop patches, they may move freely between the two habitats (Tscharrntke et al., 2005). This spillover has been widely studied, with much focus on its effect on ecosystem

services and disservices in agroecosystems (Blitzer et al., 2012; Rand et al., 2006). Many insect herbivores are crop pests responsible for large-scale production and economic losses in agricultural systems (Oerke, 2006), so understanding insect spillover informs how habitat transformation affects ecological functioning in these systems.

Studies on spillover have tended to focus on movement of pests from natural vegetation to crop fields because this research is of most interest to farmers. Over 100 studies reviewed by Norris and Kogan (2009) show that natural vegetation is a source of insect herbivores that shift into crop fields. In natural vegetation, host plants are dispersed, making

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them difficult for pests to locate, but crop monocultures provide a concentrated resource on which pests may accumulate in high densities (Root, 1973). Crops are only available at certain times of the year, however, and resource alteration after crop harvesting often forces pests onto alternate hosts in nearby natural vegetation (Altieri and Letourneau, 1982).

Spillover from crop fields to natural vegetation is far less understood; a recent review by Blitzer et al. (2012) identified only three studies that investigated spillover in this direction (Kaiser et al., 2008; Mckone et al., 2001; Squires et al., 2009). Nevertheless, spillover from crop fields to natural vegetation is likely common given that many insect herbivores are polyphagous habitat generalists (Tscharrntke et al., 2005), with many using both crops and wild plants as hosts (Norris and Kogan, 2009). Such spillover suggests that wild hosts may act as a refuge for pests outside the crop season (Mckone et al., 2001).

Opposing predictions have been made for whether insect pests shift from habitats of low to high resource concentration (i.e. from natural vegetation to crop) or vice versa, with evidence of pest spillover across the crop-non-crop interface suggesting that natural vegetation can be either a source or a sink (a population “reservoir” or secondary host source) in mixed agricultural landscapes (reviewed by Tscharrntke et al., 2005). Cultural pest-control schemes often target wild hosts in natural vegetation by managing or removing wild plants before the crop season, without considering these conflicting findings and the broader spatiotemporal dynamics of mixed agricultural landscapes (Herzog and Funderburk, 1986). Removing alternate hosts in surrounding natural vegetation can reduce crop-pest infestation by encouraging dispersal of natural enemies into crop fields, promoting biological pest control (e.g. Cottrell and Yeargan, 1999). However, some wild hosts may provide crops with “associational resistance” to infestation by retaining pests in natural vegetation (reviewed by Barbosa et al., 2009), where predation rates can be higher (Henri et al., 2015). Removing these wild hosts may encourage pest spillover onto nearby crops.

A major pest of mango (*Mangifera indica* L. Anacardiaceae), the mango fruit fly, *Ceratitis cosyra* (Walker) (Diptera: Tephritidae), also uses marula fruits (*Sclerocarya birrea* (A. Rich) Hochst., Anacardiaceae) in nearby natural vegetation. *Ceratitis cosyra* is polyphagous, using 33 other crop and non-crop species as hosts throughout Sub-Saharan Africa (De Meyer et al., 2002). Mango and marula fruiting overlap between November and April and consequently, marula is considered an important reservoir for *C. cosyra* (Copeland et al., 2006). Marula is often managed by farmers at the start of mango season by spraying auxins to facilitate early marula ripening, followed by burial, incineration or removal of fruits from natural vegetation on farmlands.

Relative timing of the onset of mango and marula fruiting varies between years, likely because marula fruiting is more coupled to rainfall than mango, which receives irrigation throughout the year. This variation results in marula fruiting earlier than mango in some years but later in others. Given that the net direction of spillover depends on spatiotemporal dynamics in productivity between habitats (Ries et al., 2004), marula could be either a source or reservoir for *C. cosyra*, depending on relative resource availability between habitats between seasons.

We investigated fruit infestation in mango and marula at increasing distances from the habitat margin in crop fields and natural vegetation, respectively, at field and landscape scales. Since related host species display increased susceptibility to infestation when they occur in close proximity (Barbosa et al., 2009), we expected that marula fruit infestation would be highest in natural vegetation nearest to mango fields. In three periods varying in relative marula-mango resource availability, we asked:

1. How is marula fruit infestation in natural vegetation associated with distance to nearby mango fields (field scale)?
2. How is marula infestation associated with proximity to mango fields at the landscape scale?

3. Does *C. cosyra* accumulate in mango fields or natural vegetation at the end of the crop fruiting season?

2. Methods and materials

2.1. Study site and species

The study was conducted on three mango farming estates (Bavaria Fruit Estates, Mohlatsi and Venden) in the Kruger to Canyons Biosphere Region, a biodiverse area of north-eastern South Africa, of which half is set aside for conservation (Coetzer et al., 2010). Mango are farmed in single cultivar blocks (~70 × 150 m) separated by a single row of *Casuarina* sp. trees serving as windbreaks. Other subtropical fruits, including several *Citrus* spp., passion fruit (*Passiflora edulis*) and avocado (*Persea americana*) are also cultivated on these farms over the year. Farms practise conventional pest control using chemical pesticides throughout the year.

The farms have patches of natural vegetation alongside some crop fields, with the habitats separated by a 10–25 m margin. The natural vegetation is “Granitic Lowveld” savanna, dominated by woody *Acacia* spp. and *S. birrea* (marula) (Mucina and Rutherford, 2006). Marula is dioecious; females bear small fruits (mass = ~20 g) with a large pit and soft, fleshy skin when ripening on the ground.

Ceratitis cosyra is endemic to sub-Saharan Africa where it can cause up to 73% losses to the annual mango crop in some countries (Vayssières et al., 2009). Adult flies damage fruits by ovipositing their eggs beneath the fruit skin, where larvae hatch and feed, later dropping to the soil to pupate and eclose as adults (Hill, 1983).

2.2. How is marula fruit infestation in natural vegetation associated with distance to nearby mango fields?

2.2.1. Fruit collection and processing

In natural vegetation alongside mango fields at the three farms we sampled fruit from randomly distributed marula trees (> 40 m apart) at various distances (4–275 m) from the field-natural vegetation margin. From 15 trees at Bavaria and 10 trees at Mohlatsi and Venden, we collected up to 20 fruits from the ground surrounding each tree, wherever possible (range: 1–20 fruits per tree). We sampled in three periods differing in relative availability of marula and mango: 1) Late marula/late mango fruiting (March 2014, $n = 302$ marula fruits); 2) Early marula/peak mango fruiting (January 2015, $n = 304$); 3) Late marula/post-mango (30 days later, February 2015, $n = 605$), when mango fruiting had ended and crop fields had been cleared of all fruit. Bavaria was the only farm sampled in 2014, while all farms were sampled in both seasons in 2015.

Marula fruits were placed into individual polystyrene cups with ~4 cm depth dry, sterile sand as a substrate for fly pupation, covered with chiffon secured with an elastic band to prevent emerged adult flies from escaping while permitting air flow. Cups were stored at ambient temperature (~27 °C) for at least 35 days before adult flies were counted and identified as *C. cosyra*. Larvae and pupae that failed to develop and eclose were considered dead due to parasitism or other causes and could not be identified to species. These were assumed to be *C. cosyra* and included in total fly count per fruit.

2.2.2. Data analysis

We ran two separate generalized linear mixed effects models (GLMMs) to investigate how distance from the habitat margin is associated with 1) the likelihood of marula infestation by *C. cosyra* and 2) infestation intensity. GLMMs are suitable for analysing non-normal data that are pseudo-replicated in space and time (Bolker et al., 2009).

The likelihood of marula infestation was investigated using a binomial GLMM (with logit function) and *C. cosyra* presence/absence per fruit as the response variable. Infestation intensity was investigated

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