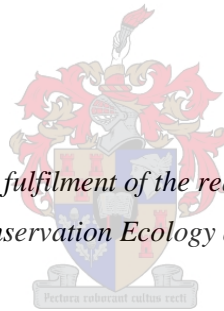


The effects of agriculture and alien plants on natural communities of plants, insect herbivores and parasitoids

by
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Declaration

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Abstract

Habitat transformation and invasions by non-native (alien) plants are two of the most concerning drivers of global environmental change. These factors cause biodiversity declines that disrupt species interactions, with cascading effects throughout ecosystems. On farmlands, this has implications for the provision of ecosystem services and disservices by insects, including crop damage by herbivores, some of which are crop pests, and pest control by natural enemies. In this study, I investigated how plants, insects and their interactions involved in these processes are affected by habitat transformation and alien plants in the Kruger to Cayons Biosphere Region, South Africa.

I first determined whether insect pests spill-over from habitats transformed for agriculture into surrounding natural vegetation in a fragmented landscape. Patches of preserved natural vegetation alongside farmlands are believed to be the source of crop pests and farmers manage the natural vegetation as a form of pest control. Using a case study with fruit flies (*Ceratitidis* spp.), cultivated mango (*Mangifera indica*, Anacardiaceae) and the marula tree (*Sclerocarya birrea*, Anacardiaceae) as a host species in nearby natural vegetation, I showed that pests appear to spill-over in the reverse direction, from crop fields to natural vegetation when mango is out of season. Marula fruit alongside mango farms were 25 times more likely to be infested by *Ceratitidis* than in the distant vegetation. *Ceratitidis* appears to spill-over into natural vegetation when marula replaces mango as the most apparent resource in the landscape. Marula may represent an important reservoir for *Ceratitidis* to maintain its population between crop seasons, but this may depend on seasonality and the relative timing of marula-mango fruiting.

Secondly, I investigated the interactive effects between habitat transformation and alien plants on the structure and composition of communities of plants, herbivores and parasitoids, and their interactions such as herbivory. Insect herbivores and parasitoids were reared from native and alien seeds collected along transects in mango fields, natural vegetation and disturbed margins, and the % alien seed abundance was determined for each transect. Mango fields had the lowest abundance and diversity of plants, herbivores and parasitoids. Across the landscape, high alien seed abundance was associated with lower herbivore and parasitoid species richness. Seed herbivory was lowest in mango fields and was influenced by interactive effects between habitat transformation and alien plants, with high and low alien seed abundance associated with high and low herbivory in mango fields and natural vegetation, respectively. In showing that habitat transformation and alien plants have both independent and interactive effects throughout this food web, this research is important for predicting future declines among plants, insects and their interactions in agricultural landscapes.

Managing the negative effects of habitat transformation and alien plants requires co-operation between farmers and conservationists in an area-wide approach. Farmers should manage pests and alien plants in crop fields to limit their dispersal into surrounding natural habitats. Conservation efforts should focus on improving habitat quality in agricultural landscapes by promoting natural vegetation alongside farms, and limiting harmful activities in crop fields, such as the use of pesticides and mowing. By reducing impacts on native plants, insects and their ecological interactions, these efforts will contribute to long-term sustainability of agriculture in the future.

Opsomming

Habitat verandering en indringer spesies is twee van die hoof drywers van globale omgewings veranderinge. Hierdie faktore veroorsaak dalings in biodiversiteit wat spesie-interaksies ontwig, en die gevolge kan gesien word regdeur ekosisteme. Op plaaslande het dit implikasies vir die voorsiening van ekosisteme dienste deur insekte. Dit sluit in gewaskade deur herbivore, waarvan sommige oes peste is, en plaagbeheer deur natuurlike vyande, parasitoïed perdebye ingesluit. In hierdie studie, bespreek ek die invloed van habitat transformasie en indringer plante op die interaksies tussen plante en insekte in die Kruger to Cayons biosfeer, Suid Afrika.

Ek het eers bepaal hoe grond transformasie die oordrag van peste en plae tussen plase en natuurlike areas binne gefragmenteerde landskappe beïnvloed. Daar word geglo dat die natuurlike beweiding langs bewerkte lande die bron is van peste en plae. Dus, probeer boere om die natuurlike lande langs hul bewerkte lande te beheer vir plaagbeheer. Deur gebruik te maak van vrugte vlieë (*Ceratitis* spp.), gekultiveerde mango (*Mangifera indica*, Anacardiaceae) asook die Marula boom (*Sclerocarya birrea*, Anacardiaceae) as gasheer spesies in nabygeleë natuurlike areas, is daar 'n gevallestudie opgestel. Dit het bewys dat die teenoorgestelde waar is; die peste en plae se oorloopgevolge vind plaas vanaf die bewerkte landerye na die natuurlike omgewing. Marula vrugte langs mango boorde het 'n 25 keer groter kans om deur *Ceratitis* besmet te word as die wat in afgeleë gebiede gevestig is. Dit dui daarop dat dit onwaarskynlik is dat natuurlike areas die bron is van vrugtevlieë vir mango velde, en lê klem op die negatiewe gevolge wat landbou het op die gasheer-plaag interaksies tussen bewerkte lande en die natuurlike omgewing.

Gevolgtreklik, het ek die interaksie tussen habitat transformasie en indringer plante op gemeenskappe van plante, herbivore en parasitoïds, en hul interaksies soos saad predasie, ondersoek. Mango boorde het 'n kleiner verskeidenheid herbivore en parasiete as natuurlike beweidinge en versteurde habitat marges gehad. Oor die landskap, toenemende hoeveelhede van uitheemse saad het dalings veroorsaak in herbivoor en parasitoïed spesierykheid. Saad predasie deur herbivore was die laagste in mango boorde, beïnvloed deur interaktiewe effekte tussen habitat transformasie en indringerplante, soos dat hoë uitheemse saad oorfloed is wat verband hou met hoë saad predasie in mango velde en lae saad predasie in natuurlike areas. Deur te bewys dat habitat transformasie en indringer spesies beide onafhanklike en interaktiewe verhoudings het in die voedsel-web, kan die plant- en insek-bevolkings dalings in die toekoms voorspel word vir die landbou bedryf.

Beheer van die negatiewe effekte van habitat transformasie en indringer spesies verg samewerking tussen boere en natuurbewaarders. Boere moet peste en indringer plant spesies op hulle bewerkte lande beheer om die verspreiding na omliggende natuurlike areas te verminder. Natuurbewaarders moet fokus op die bevordering van die natuurlike landskappe deur om die natuurlike plantlewes langs bewerkte landerye te bevorder, en skadelike aktiwiteite in bewerkte landerye, soos die gebruik van plaagdoders en gras sny, te beperk. Deur die impak op die inheemse plante, insekte en hulle ekologiese interaksies te verminder, sal hierdie pogings bydra tot die volhoubaarheid van die landbou in die toekoms.

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Table of Contents

Declaration.....	ii
Abstract.....	iii
Opsomming.....	iv
Acknowledgements.....	v
List of Appendices.....	viii
Chapter 1. General Introduction.....	1
1.1. The effect of global environmental change (GEC) on multi-trophic systems	1
1.2. Habitat transformation for agriculture as a driver of GEC.....	2
1.2.1. Local-scale impacts on plants, herbivores and natural enemies.....	2
1.2.2. Habitat diversity, landscape complexity and effects on pests and natural enemies	2
1.2.3. Between-habitat spill-over in heterogeneous landscapes.....	4
1.2.4. <i>Ceratitidis</i> fruit flies and infestation of crop and non-crop host plants.....	6
1.3. Alien plant invasions impact plant, herbivore and natural enemy communities.....	7
1.4. Interactive effects of GEC drivers on plants, herbivores and natural enemies	8
1.5. Concluding remarks and problem statement.....	9
1.6. Aim of this study.....	10
1.7. Thesis structure and outline	11
1.8. References.....	12
Chapter 2. Spill-over of insect pests between natural vegetation and crop fields: a test using <i>Ceratitidis</i> spp. fruit flies, mango and a native savanna tree species	18
ABSTRACT.....	18
2.1 INTRODUCTION	18
2.2 MATERIALS AND METHODS.....	21
2.3 RESULTS	26
2.4 DISCUSSION.....	37
2.5 REFERENCES	44
Chapter 3. Interactive effects between land-use transformation and alien plants in driving community changes among plants, herbivores and parasitoids	48
ABSTRACT.....	48
3.1 INTRODUCTION	48
3.2 METHODS AND MATERIALS.....	51
3.3 RESULTS	57

3.4 DISCUSSION	65
3.5 REFERENCES	72
Chapter 4. Thesis synthesis	76
4.1 Spill-over of insect pests from crop fields into surrounding natural vegetation	76
4.2 Interactive effects between habitat transformation for agriculture and alien plants	77
4.3 The effects of agriculture and aliens on plants, herbivores and parasitoids.....	78
4.4 Overall management and conservation recommendations.....	78
4.5 Study strengths and limitations	79
4.6 Further research.....	80
4.7 References.....	82
Appendix.....	84

List of Appendices

Appendix I. Description of study site and farm management procedures in the Kruger to Canyons Biosphere Region (K2C), Limpopo Province, South Africa.....	83
Appendix II. Map of the agricultural landscape and three farms where marula fruit were collected and pheromone trapping was conducted outside of Hoedspruit, Limpopo Province, South Africa.....	85
Appendix III. Total abundance of marula fruit in three ripeness categories observed and collected in the natural vegetation alongside mango fields and in the distant vegetation in the early (2015) and late (2014, 2015) seasons.....	87
Appendix IV. GLMM results determining the effect of season on plant, herbivore, parasitoid abundance and richness, and herbivory.....	87
Appendix V a-c. Backward simplification and selection of GLMMs fitted with abundance and species richness of a) plants b) herbivores and c) parasitoids as response variables, and land-use type and % alien seed abundance as fixed effects.....	88
Appendix VI. Comprehensive list of alien and native plant species sampled in mango fields, natural vegetation and along margins in April-May and June-July.....	90
Appendix VII. Backward simplification and selection of GLMMs fitted with seed herbivory as response variable, and land-use type and % alien seed abundance as fixed effects.....	94
Appendix VIII. Significant differences between land-use types in terms of seed herbivory.....	94

Chapter 1

General introduction

1.1. The effect of global environmental change (GEC) on multi-trophic systems

Human activity is driving rapid and dramatic changes to natural environments worldwide (Vitousek 1994; Pimm et al. 2014). This global environmental change (GEC) disrupts habitat conditions for natural biota and has driven widespread and often irreversible biodiversity losses across a wide array of ecosystems (Wilcove et al. 1998; Chapin et al. 2000). Since biodiversity is connected within complex food webs, species declines may have cascading effects throughout entire ecosystems that disrupt species interactions, driving secondary extinctions between and within trophic levels (Memmott et al. 2007). This “trophic collapse” has implications for ecosystem structure, stability (according to the diversity-stability debate, McCann 2000) and interaction-based ecosystem functions, including provision of ecosystem services (ES), the ecological processes that contribute to human well-being (Swift, Izac & van Noordwijk 2004; Butler, Vickery & Norris 2007; Winfree & Kremen 2009). In agricultural systems, biodiversity is managed to optimize the provisioning ES, such as the production of food and fuel, and regulating ES, including pollination and pest control (Zhang et al. 2007).

Recognizing that species interactions form the backbone of ecosystems (Fontaine et al. 2011), ecologists have become increasingly focused on how species interactions respond to GEC and biodiversity declines (Thies & Tscharntke 1999; Roschewitz et al. 2005; Thies, Roschewitz & Tscharntke 2005; Bianchi, Booij & Tscharntke 2006; Zaller et al. 2009). Of particular concern is the deterioration of interactions provided by insects in agroecosystems that link biodiversity, productivity, and ecosystem stability (that is, the resistance and resilience of the farmland ecosystem to further disturbance and collapse) (Valladares, Salvo & Cagnolo 2006). Some insects offer ecosystem disservices (EDS) on farmlands by regulating plants, causing crop damage as pests and incurring costs of around \$7.3 billion in crop losses per annum (Oerke 2006). Other insects are natural enemies of these pests, such as predators and parasitoids, which benefit humans by regulating pest populations through natural pest control.

A break-down in the interactions between crop pests, their predators and parasitoids is therefore detrimental to biological pest control, crop productivity and global food security (Thies & Tscharntke 1999; Thies, Steffan-Dewenter & Tscharntke 2003), requiring increased use of pesticides, which threaten the long-term economic and environmental sustainability of the agroecosystem (Naylor & Ehrlich 1997). Exploring the impacts of different GEC factors on pest-natural enemy communities will enhance our ability to predict and manage ecosystem changes, conserve ecosystem services and ensure long-term sustainability of agriculture in the future.

1.2. Habitat transformation for agriculture as a driver of GEC

1.2.1. Local-scale impacts on plants, herbivores and natural enemies

Agriculture already dominates 40 – 50% of Earth's terrestrial habitats (Chapin et al. 2000) and will see the loss of one third of remaining natural biomes in the future, predominantly in developing countries (Vitousek 1994; Tilman et al. 2001; Söderström, Kiema & Reid 2003). Transforming land-use for agriculture simplifies complex ecosystems by replacing diverse plant assemblages in the natural vegetation with dense stands of crop monocultures (Altieri 1999; Krebs et al. 1999). This is coupled with intensification of human activity and input on farmlands, such as increased application of agrochemicals, such as herbicides and pesticides, to maximize crop yield and economic outputs (Benton, Vickery & Wilson 2003). Under these conditions, habitat diversity is decreased and this is associated with greater ecosystem instability and consequently, a lowered capacity to recover (that is, return to an equilibrium state) after further ecological disturbance (see review by (McCann 2000). Herbivores and their natural enemies have closely evolved with each other and the plants they feed upon, so habitat degradation can be expected to be associated with local species extinctions among herbivores and natural enemies (Awmack & Leather 2002).

The economic and ecological value of agroecosystems is not only measured by disturbance alone but also high productivity and hence, resource availability (Tscharntke et al. 2005). When crops are in season, the concentration of plant biomass on farmlands enhances herbivore host searching and crop damage ('resource concentration hypothesis', (Root 1973), which exacerbates existing pest problems or drives other herbivore insects to pest status (Altieri & Letourneau 1982; Andow 1983). Disturbed habitats often lose the inherent ability to self-regulate these pests because natural enemies are generally more susceptible to disturbance than herbivores (Chaplin-Kramer et al. 2011). The specialization of enemy diets (particularly among parasitoids) (Holt et al. 1999) and their high trophic ranking (Holt 1996) make them disproportionately sensitive to changes within communities at lower trophic levels (Kruess & Tscharntke 1994; Zhang et al. 2007). However, this notion has been challenged (Mikkelsen 1993) and the susceptibility of species to extinction has been linked to other factors besides trophic ranking, such as body size, dispersal ability, resource specialization and population density (Gard 1984). Nevertheless, an overwhelming body of evidence highlights the negative effect of agricultural land-use on natural enemies, with density and diversity substantially lower in monocultures than in diversified systems, including polycultures (see quantitative review by Andow 1991).

1.2.2. Habitat diversity, landscape complexity and the effects on pests and natural enemies

In contrast to the negative effect of plant diversity loss on natural enemies, herbivores often have a higher abundance in monocultures than in diverse vegetation, including agroecosystems containing in-crop weeds (Altieri 1999). Diverse vegetation increases the structural complexity of the

environment, making it more difficult for herbivores to locate and remain on the crop, thereby increasing “associational resistance” to pest attack (Root 1975). In-crop weeds may increase host diversity for more species of herbivores on farmlands, which may generally be considered undesirable among farmers, but may actually increase the interspecific competition and apparent competition, mediated through shared enemies, within the herbivore community (Langer & Hance 2004). Furthermore, increasing in-crop diversity may also promote biocontrol by providing a greater diversity of alternate insect hosts for a wider variety of natural enemies (Norris and Kogan 2009).

Diversifying agricultural fields also increases the availability of complementary resources used by natural enemies, including floral resources, such as pollen and nectar, and sites for breeding, nesting, overwintering or as refuges from disturbance (Landis, Wratten & Gurr 2000). This has led many conservation biological control management schemes to maintain or introduce plant diversity both at the farm scale (van Veen, Memmott & Godfray 2006) and at the landscape scale by increasing landscape complexity (Rand, van Veen & Tscharntke 2012), that is, the amount of natural habitat in agricultural landscapes (Thies and Tscharntke 1999). Managing landscapes in this way is part of an increasingly recognized agroecological scheme to enhance desired biodiversity components, particularly those that provide important ecosystem services to farmers, in agricultural landscapes. The approach aims to counteract trophic collapse and ecological meltdown by restoring elements of biodiversity that have been lost in response to human disturbance (Altieri 1999). In particular, agroecologists attempt to stabilize insect communities in agricultural landscapes by introducing vegetational structures, such as margins, hedgerows, fencerows and woodlots, and by promoting habitat diversity and landscape mosaics (Altieri & Nicholls 2004).

Several studies have documented the positive effect of increasing habitat diversity on the abundance and diversity of natural enemies in agricultural systems (e.g. Bianchi et al. 2006, Chaplin-Kramer et al. 2011). This effect has been linked to strong bottom-up controls of parasitoid communities by herbivore prey, which also respond positively to the increased diversity of plant hosts in natural vegetation. Landscape complexity is believed to have a greater effect on natural enemies than to pests, with generalist natural enemies being more sensitive than specialists to habitat diversity and landscape complexity (Chaplin-Kramer et al. 2011). This is likely considering that generalists may rely on alternate prey or complementary resources found between different habitats throughout the growing season (Tscharntke et al. 2005, Rand et al. 2006). Enhanced effects of landscape complexity on parasitoids may be accounted for by lower resource complementarity among parasitoids and strong bottom-up control, detected through correlations between parasitism rates and pest density (Costamagna, Menalled & Landis 2004).

Furthermore, while landscape complexity has driven increased parasitism rates in some systems (Bianchi, Booij & Tscharntke 2006), parasitism may be offset by enhanced pest colonization across

complex landscapes, resulting in no net effect on pest populations and plant damage overall (Roschewitz et al. 2005). Increasing in-crop diversity has a similar effect on pests, with only 50% of herbivore species considered in a quantitative review (Andow 1991) being consistently less abundant in polycultures than in monocultures. In this way, habitat heterogeneity appears to have little effect on herbivores at the landscape-scale, likely because host resources are spatially heterogeneous at this level. Furthermore, herbivores are generally more susceptible to bottom-up control (such as resource concentration, Root 1973) than top-down control, and the higher abundance of generalist enemies in more diverse landscapes may have as much impact on herbivores as the lower abundance in more simplified landscapes.

Overall, enhanced plant diversity in and around farmlands may be positive or negative for farmers, in that the alternate habitats and hosts may supply natural enemies or pests to the farms, or attract them elsewhere. There may also be indirect effects on different trophic levels, with enhanced vegetation supporting fourth trophic level species that attack natural enemies of crop pests (Rand, van Veen & Tschardtke 2012). The types of plants included in the surrounding natural vegetation or among in-crop may also provide resources that differentially favour pests and natural enemies (Gurr, Wratten & Luna 2003). Despite these inconsistencies, biodiversity has been used successfully in agricultural landscapes to promote natural enemies and suppress pests and, in some cases, crop damage (Landis et al. 2000; Gurr, Wratten & Luna 2003).

1.2.3. Between-habitat spill-over of pests and natural enemies in heterogeneous landscapes

In heterogeneous landscapes with intensively-managed fields interspersed amongst patches of natural vegetation (Tschardtke & Brandl 2004), biodiversity is not independent between the adjacent habitats and may spill-over across margins, resulting in a large portion of earth's biodiversity occurring in agroecosystems (Pimentel et al. 1992) (termed "associated biodiversity", (Vandermeer & Perfecto 1995). This spill-over of biodiversity has been well-documented in many landscapes, including those modified for agriculture (see review by Blitzer et al. 2012). Spill-over is most frequently considered in the direction that influences the functioning of agroecosystems i.e. from natural vegetation to farmlands. Farmers benefit from spill-over of generalist natural enemies from the natural vegetation to subsidise their diets in crop fields, where they enhance biocontrol of pests, particularly at the start of the crop season (Tschardtke, Rand & Bianchi 2005). However, natural vegetation is also commonly considered an important reservoir of agricultural pests, particularly if close relatives to the crop are present in the vegetation (Norris & Kogan 2009). This long-standing belief encourages removal of natural vegetation and in-crop weeds as a form of cultural pest control (Herzog & Funderburk 1986). This practice may actually exacerbate pest problems by eliminating "alternative" host resources for natural enemies of pests in and surrounding the crop fields.

Such management practices do not consider that spill-over is driven by spatio-temporal patterns and fluctuations in resource availability, and that consumers generally shift from high to low productivity systems (Polis, Anderson & Holt 1997). Indeed, there is great potential for insects to accumulate in agroecosystems and disperse into natural vegetation, where they enhance their top-down control of native hosts (Rand & Louda 2006), though only three studies have investigated these dynamics among herbivores to date (Mckone et al. 2001; Kaiser, Hansen & Müller 2008; Squires, Hermanutz & Dixon 2009). In all three cases, herbivores shifted from agricultural crops to native plants in adjacent natural patches, where they reduced plant abundance and seed set (< 60% in some cases).

Relative to spill-over in the direction from natural vegetation to agriculture, spill-over of functionally important insects providing ES in the direction from agriculture to natural vegetation is largely underrepresented in the literature. Consequently, there is no consensus on whether agroecosystems or natural vegetation presents a source for insects in human-modified landscapes (Tschardtke, Rand & Bianchi 2005). As such, it is difficult to advocate natural vegetation in these landscapes for the promotion of ES, such as conservation biological control, particularly since natural vegetation is widely considered a source of agricultural pests.

This has likely contributed to the belief that a ‘land-sparing’ approach to conservation, that is, setting aside dedicated areas for conservation, essentially separating land for nature and farming, is best for optimizing agricultural production and meeting global demands for food. Indeed, because of the depauperate biodiversity in farmlands, with many species unable to survive on even the most sustainable farms, setting aside land specifically for these species is essential for conservation (Kleijn et al. 2011). However, the land-sparing approach suggests that increased intensification on farmlands will then sustain high production levels, limiting human encroachment into surrounding vegetation (which can then be set aside solely for conservation) (Phalan et al. 2011). While this approach does have benefits for conservation and securing global food availability at a superficial level, increasing agricultural yields without considering the effect on biodiversity in farmlands may compromise ecosystem functionality and resilience in these systems (Tschardtke et al. 2012).

Land-sharing, which sees the integration of conservation areas and farmlands into agricultural landscapes, presents a more sustainable approach through its promotion of wildlife-friendly agroecosystems that provide ecosystem services beyond food production (Tschardtke et al. 2012). This approach acknowledges that both wild and introduced biodiversity in agricultural landscapes provide important functions (including natural pest control), without the environmental degradation associated with agricultural intensification and consequent threats to agricultural sustainability.

The land-sparing vs. land-sharing debate hinges on the argument that crop production is both threatened and supported by wild biodiversity (Kleijn et al. 2011). Even though several studies have shown that high levels of biodiversity are of high short- or long-term functional importance in

farmlands (Tscharntke et al. 2005) and are positively correlated with crop production (Perfecto & Vandermeer 2010), conventional agricultural practices, including application of pesticide, are still frequently used in agroecosystems and threaten beneficial, non-target insects (Tscharntke et al. 2012). An unbiased understanding of how biodiversity spills-over and functions between farmland and natural habitats may highlight the value of natural vegetation and its intrinsic biodiversity to farmers when integrated into heterogeneous landscapes. This may promote the land-sharing approach in these landscapes, and ultimately, may ensure more sustainable management practices on farms in the future.

1.2.4. *Ceratitis* fruit flies and infestation of crop and non-crop host plants

Tephritid fruit flies of the genus *Ceratitis* are an ideal group for investigating how pests spill-over between agricultural fields and natural vegetation because of their polyphagous lifestyles, which allows them to use of a wide array of both cultivated and wild fruit trees as hosts (Annecke & Moran 1982). Among the species found in Africa, *Ceratitis cosyra*, commonly referred to as the mango fruit fly, is the least polyphagous species (Copeland & Wharton 2006) but is considered one of the most devastating pests on cultivated subtropical fruit, particularly mango, in sub-Saharan Africa where it is endemic (Annecke & Moran 1982; Vayssières, Sanogo & Noussourou 2007). An average of between 20 – 30% of mango crop in Africa may be lost to *C. cosyra* per year (up to 75% in some countries, Vayssières, Korie & Ayegnon 2009), which reduces the suitability of the fruit for export and affects the price of locally-sold produce (Lux et al. 2003).

C. cosyra has a largely Afro-tropical biogeographic range, which includes several countries in East and West Africa (list of studies in these areas referenced by Vayssières, Korie & Ayegnon 2009), and South Africa (De Meyer, Copeland & Lux 2002). In some African countries, *C. cosyra* has a wider distribution than other *Ceratitis* species (Copeland & Wharton 2006), but in South Africa, the species is limited to the North-Eastern part of the country (De Villiers et al. 2013). These distribution patterns appear to be determined by the availability of host plants for *C. cosyra* (and not by climatic conditions, which is the case for two other species in South Africa, *C. capitata* (Mediterranean fly) and *C. rosa* (Natal fly)) (De Villiers et al. 2013). Several lists have been compiled of the plant species that host *C. cosyra* in South Africa and throughout sub-Saharan Africa (see White & Elson-Harris 1992; De Meyer, Copeland & Lux 2002). Besides mango, *C. cosyra* is also known to use other fruit crops, including but not limited to guava (*Psidium guajava*), avocado (*Persea americana*) and orange trees (*Citrus sinensis*) as hosts in different seasons of the year.

In the North-Eastern part of South Africa, the distribution of *C. cosyra* is limited by that of its wild host, the marula tree (*Sclerocarya birrea*) (Holt 1977; De Villiers et al. 2013), although mango and other cultivated hosts, including citrus and passion fruit (*Passiflora edulis*) also occur in the area. Throughout Africa, marula is considered an important reservoir for *C. cosyra*, also frequently called

the marula fly, when mango is out of season (Copeland & Wharton 2006). The pests are believed to maintain their populations on marula until the crop is back in fruiting, but the year-round breeding of *C. cosyra* has currently not been documented. Nevertheless, *C. cosyra* is believed to be able to survive as adults through winter, and temporal variations in its population size and phenology depend on host resource availability (Vayssières, Sanogo & Noussourou 2007; De Villiers et al. 2013). Investigating how marula is used as a host for *C. cosyra* when mango is fruiting and when it is out of season will improve our understanding of how agriculture affects pest-wild plant interactions, and allow us to determine the role of marula as a reservoir for pests in agricultural landscapes.

1.3. Alien plant invasions impact plant, herbivore and natural enemy communities

Biotic invasions are the successful introduction of non-indigenous taxa into ecosystems outside of their native ranges. Accelerated human activities and movement have led to increased prevalence of alien species worldwide with few ecosystem types free of their influence today (Mack et al. 2000; Chytry et al. 2008). Alien invasions, second only to habitat loss in driving global biodiversity declines (Wilcove et al. 1998), are as much of a driver of environmental change as a symptom thereof (Hulme 2006). Human-altered habitats, including those transformed for agriculture, are often highly susceptible to invasion (Pauchard & Alaback 2006) as biodiversity declines and loss of species interactions translate into poor ecological resilience and resistance to further environmental change and perturbation (i.e. poor “ecological memory”, (Bengtsson et al. 2003). Furthermore, agricultural intensification also removes abiotic barriers against invasion by increasing availability of limiting resources, such as light, water and soil nutrients for alien plants (Hobbs & Huenneke 1996).

Invasions by alien plants, though less threatening to global biodiversity than alien consumers (Gurevitch & Padilla 2004), elicit complex and highly variable impacts on recipient ecosystems (Kulmatiski, Beard & Stark 2006). Most concerning of these effects is the displacement of native plant species and the consequent changes in the structure and stability of the invaded communities (Chornesky & Randall 2003). This effect is driven either indirectly through the disruption of abiotic processes, such as fire regimes, nutrient cycling and hydrology, or directly through allelopathy or competition with native plants in local habitats (for a South African example, see (Le Maitre et al. 1996). Besides the effects on native plants, alien plants also threaten biodiversity on higher trophic levels, including insects, by eliciting direct or indirect effects from the bottom-up (Heleno et al. 2009).

Directly, aliens may subsidize the resources available to herbivores, promoting population increases and attack rates on native plants and crops (Boppré 1991). This is not always the case, however, and there is also substantial support for lower herbivore survival and fitness on alien plants (see meta-analysis by (Hengstum et al. 2014). The lack of consensus has been linked to differences in herbivore diet specialization and phylogenetic relatedness among alien and native hosts (Proches et al. 2008;

Bezemer, Harvey & Cronin 2014). For example, alien plants may be subject to greater herbivory than their native congeners in invaded habitats, since they lack intrinsic defences against specialist herbivores that coevolved among the native plants (and this limits their invasion, “biotic resistance hypothesis”, see meta-analysis by (Levine, Adler & Yelenik 2004). Alternatively, distantly-related alien plants may be released from native specialist herbivores (“enemy release hypothesis”, (Keane & Crawley 2002), which may facilitate alien plant invasion by increasing herbivory on native plants (by increasing “apparent competition” with the native plants, Holt 1977).

Rather than directly impacting higher trophic levels, aliens may also elicit an indirect response by altering the structure and composition of the native plant community. For example, Heleno et al. (2009) observed lower overall plant diversity in highly invaded areas than in those dominated by native species and this promoted high variability in seed production and gaps in the resource availability for herbivores between seasons. Seed herbivore biomass declined under these conditions and local species extinctions were also observed. The loss of native hosts for specialized herbivores also drives increasing generalization of the insect community. Replacement of specialists by generalists in this way may have no net effect on herbivore abundance in highly invaded communities (Heleno et al. 2009).

The few studies to date that consider natural enemies (Harvey & Fortuna 2012) suggest that their response to aliens is highly species-specific and consequently, is determined by specific life history and morphological traits. For example, endoparasitoids are limited by the nutritional history of their insect hosts; if the quality and availability of a herbivore’s plant host is reduced through competition with alien plants, this in turn reduces the suitability of the herbivore as a host for its specific parasitoid (Bukovinszky et al. 2008). This may drive declines among specialist parasitoids and generalization of the enemy community (Rand, van Veen & Tschardtke 2012). Since generalists are not as strong regulators of herbivores as specialists, this increases herbivore load on native plants (and crops in invaded agroecosystems) (Tschardtke & Brandl 2004). Alternatively, if aliens provide a rich source of complementary resource for natural enemies, this may promote their populations and increase top-down control, providing a source of ‘enemy release’ for alien plants or crops (Harvey, Bukovinszky & van der Putten 2010).

1.4. Interactive effects of GEC drivers on plants, herbivores and natural enemies

Clearly, the response of plant, herbivore and parasitoid interactions to GEC varies greatly under the influence of different drivers. This variability is often linked to differences in species assemblages, specialization of natural enemies and the environmental context considered in different studies (see review by (Tylianakis et al. 2008). However, interactive effects between drivers of GEC that frequently co-occur, such as habitat disturbance and alien invasions, may also be responsible. (Didham et al. 2007) suggest that the interplay between several drivers may exacerbate or mitigate the

effects of each driver acting independently on biodiversity and ecosystems. For example, invasive aliens may not be the greatest threat to native biodiversity if the invasion is merely a symptom of habitat destruction (Vitousek et al. 1997). Understanding the relative importance and effect pathways of different drivers of GEC when interactive effects are operating has important implications for mitigating ‘main effects’, those driven by the dominant factor, on communities and ecosystems (Didham et al. 2007).

Unfortunately, our current knowledge of this interplay is limited because the vast majority of studies to date only consider single drivers of GEC independently. Consequently, it is difficult to accurately separate and generalize the effects of different drivers on biodiversity and species interactions (Didham et al. 2007). The few studies that consider combined effects of several GEC parameters on plant, herbivore and parasitoid communities only consider climate change along with N deposition (Binzer et al. 2012; de Sassi, Lewis & Tylianakis 2012) or combined components of climate change, such as high CO₂ levels, increased temperature and drought (Dyer et al. 2013; Romo & Tylianakis 2013).

These studies suggest that complex mechanisms are involved in the interactive effects between drivers at the species and community level. For example, temperature and nitrogen enrichment had interactive effects on herbivorous insects, with temperature driving increased peak abundance among individual species but nitrogen levels mediating this effect by altering species-specific developmental and phenological responses to temperature (de Sassi, Lewis & Tylianakis 2012). These non-additive (positive and negative) effects drove homogenization of herbivore communities and large increases in herbivore biomass. Interestingly, these trends were moderated by changes in the plant community, with increasing alien plant cover being the strongest determinant of herbivore abundance, even at highest temperatures and levels of nitrogen enrichment.

Currently, interactive effects between habitat transformation and alien invasions have only been investigated at the species-level among vertebrates in freshwater ecosystems (Light & Marchetti 2007; Hermoso et al. 2011). Applying a multi-trophic approach to determine the response of plants and insects to these two factors will thus be an important contribution to GEC research. In particular, elucidating the relative impacts on herbivores and natural enemies will inform our current and future understanding of pest outbreaks and biological control in disturbed habitats, particularly agroecosystems.

1.5. Concluding remarks and problem statement

Global biodiversity declines and environmental changes have accelerated in response to human activity, such as habitat transformation for agriculture and alien plant invasions. This has cascading impacts throughout ecosystems that disrupt the provision of ecosystem services by insects, such as

herbivory and pest control, which are costly or beneficial to farmers. These services are well-known to emerge from natural vegetation alongside farmlands and farmers remove the natural vegetation (in addition to mowing and spraying in-crop weeds with herbicides) as a form of pest control to prevent pests from spilling over and damaging the crop. However, these practices may actually be harmful to farmers as the source of natural enemies for pest control may also be removed in this process.

There is a large gap in the literature regarding insect spill-over in the reverse direction from crop fields into natural vegetation and it remains largely unknown whether farmlands are in fact, the source of pests for surrounding habitats. Further research in this area will inform conservationists firstly of the impacts of agriculture on natural plant, insect and enemy communities and secondly, whether natural vegetation is indeed the source of pests or pest control for farmers.

The effects of agricultural land-use and alien plant invasion have been widely investigated among plants, insect herbivores and natural enemies. Community responses between studies are highly variable and there is little consensus on whether these human-driven factors increase or decrease species richness and abundance on each trophic level. The disparity has been linked to differences in biotic and abiotic components between field-level studies, but also the fact that interactive effects among global change drivers may be at play. There is, in fact, great potential for interactive effects on ecosystems but the majority of studies to date only consider independent effects of single drivers. Considering that alien plants are frequently associated with disturbed habitats, there is great scope for investigating the combined effects of these drivers on biodiversity, particularly that involved in provision of ecosystem services such as plants, insects and natural enemies.

1.6. Aim of this study

This study focuses on two broad-scale topics in the field of global environmental change, namely spill-over dynamics in landscape fragmented by habitat loss and combined, interactive effects of habitat transformation and alien plant invasion that frequently co-occur in human-dominated systems. In addressing these two areas, I use a multi-trophic approach that considers effects on communities of plants, herbivores and natural enemies, specifically parasitoids, and their ecological interactions, such as herbivory. These effects are investigated at a broad spatio-temporal scale with local scale responses combined across a landscape and between different seasons from 2014 – 2015. These components contribute to the over-arching aim of this study:

To investigate community-level effects of two drivers of global change, namely habitat transformation for agriculture and alien plant invasion, on multi-trophic systems of plants, herbivores and parasitoids.

I address this aim using two empirical, observational studies in the Kruger to Canyons (K2C) Biosphere Region between two large protected areas, the Kruger National Park and Blyde River

Canyon. Study sites were in a transition zone in central K2C region outside Hoedspruit, where habitat transformation is permitted, provided that the activities thereafter are sustainable. The area is driven economically by agricultural and conservation activities and is a major producer of a wide variety of fruits, including mango (*Mangifera indica* L.).

The multi-trophic approach of this study will be beneficial in informing our understanding of human impacts at both the community and ecosystem level. Focus on the response of trophic interactions will also improve our understanding of how human activity disrupts ecosystem functions, allowing us to better predict and manage these effects in the future. This research will be particularly beneficial to conservationists and landscape ecologists who aim to promote landscape heterogeneity while preserving biodiversity and ecosystem stability. For farmers, I aim to investigate the importance of natural vegetation for the provision of alternate pest hosts and natural enemies for biological pest control in crop fields.

1.7. Thesis structure and outline

In chapter 2, I address the long-held belief that natural vegetation is a source of herbivorous pests for surrounding crop fields in a heterogeneous landscape. Using a case study, I investigate whether pests and their parasitoids spill-over instead in the reverse direction i.e. from crop fields into natural vegetation. Specifically, I use polyphagous *Ceratitis* spp. fruit flies and their parasitoids as study subjects to determine how insect abundance and infestation of a native host in the natural vegetation, the marula (*Sclerocarya birrea* Hochst. subsp. *caffra* Kokwara), is affected by proximity to cultivated mango crops (*Mangifera indica* L.). For unbiased assessment of spill-over between habitats, I also consider the potential for the natural vegetation to indeed be a source of *Ceratitis* for mango fields by investigating *Ceratitis* abundance in mango fields at varying distances from the natural vegetation.

In chapter 3, I investigate the combined effects of local habitat transformation and alien seed abundance on the structure and composition of plant (seed), seed herbivore and parasitoid communities, and seed herbivory in an agricultural landscape, including mango crop fields, natural vegetation and disturbed habitat margins. The design of this study is based on that of an unpublished study by L.G. Carvalheiro that also investigated plant-herbivore-parasitoid dynamics in the central K2C region from July to September, 2008. All farms and local sample sites in this current study are a subset of those sampled by Carvalheiro.

Chapters 2 and 3 were written as stand-alone research papers and repetition of information, including that presented in this introductory chapter, is regrettably unavoidable. In chapter 4, I present a summary and general discussion of key findings in each research chapter. I also highlight the contribution of these findings to their respective fields, present management recommendations and propose areas for future research.

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Chapter 2

Spill-over of insect pests between natural vegetation and crop fields: A test using *Ceratitis* spp. fruit flies, mango and a native savanna tree species

ABSTRACT

In fragmented landscapes, farmers believe that natural vegetation alongside farmlands is the source of insect pests for agricultural crops. However, the current understanding of how insects spill-over between these habitats is strongly biased, with insect dispersal mostly documented from natural vegetation into crop fields but not in the reverse direction. This chapter presents one of the few studies to date to consider pest and natural enemy spill-over in the reverse direction, from crop fields into natural vegetation. In the Kruger to Canyons Biosphere Region of South Africa, I investigated whether fruit infestation of the native marula tree (*Sclerocarya birrea* subsp. *caffra*, Anacardiaceae) by polyphagous *Ceratitis* spp. fruit flies and its parasitoids in natural vegetation is affected by proximity to fields of a crop in the Anacardiaceae family, mango (*Mangifera indica*). I reared *Ceratitis* from marula fruits to compare *Ceratitis* infestation close to and far from the crop, and compared *Ceratitis* abundance in mango fields and nearby natural vegetation using pheromone traps. Marula was up to 25 times more likely to be infested alongside mango fields than in distant vegetation. *Ceratitis* accumulated in natural vegetation, particularly at margins with crop fields, when marula had completely replaced the crop as the most apparent host resource in the landscape. *Ceratitis* may spill-over to marula to maintain its population outside of mango season, but the role of marula as a pest reservoir may depend on seasonality and temporal variation in mango-marula fruiting. Management of *Ceratitis* in heterogeneous landscapes requires an area-wide approach that targets different habitats according to crop and non-crop resource availability.

2.1 INTRODUCTION

Agriculture is already responsible for the majority of habitat transformation on Earth (Zhang et al. 2007) and is rapidly expanding to meet global demands for resources, particularly food (Thrupp 2000). Habitat loss and fragmentation associated with this expansion promotes mosaic landscapes with patches of natural vegetation interspersed between intensively managed farmlands (Benton, Vickery & Wilson 2003). These adjacent habitat types are not spatially or temporally independent and spill-over of biodiversity and its associated ecosystem services (ES) and disservices (EDS) can occur between them (see reviews by Tscharntke et al. 2005; Rand, Tylianakis & Tscharntke 2006; Blitzer et al. 2012).

In natural vegetation, diverse plant assemblages support rich communities of trophic consumers, such as insect herbivores (some of which may also be crop pests), and their natural enemies (i.e. predators and parasitoids). These insects may migrate from natural vegetation into adjacent farmlands in response to strong resource gradients between habitats in heterogeneous landscapes (Root 1973), a process which has been widely documented to date (for review, see Norris & Kogan 2009) and (Blitzer et al. 2012). For example, Aluja et al. (1996) observed the highest abundance of *Anastrepha*

fruit flies in non-crop vegetation at close proximity to mango orchards, suggesting that pest populations are driven outside of farmlands and that alternative plant hosts in natural vegetation can act as pest reservoirs when the crop is out of season. Plant species that are close taxonomic relatives of the crop display ‘associational susceptibility’ and are particularly vulnerable to infestation by crop pests (Barbosa et al. 2009).

Associational susceptibility is possible in the Kruger to Canyons (K2C) Biosphere Region of South Africa where mango farmlands (*Mangifera indica* L., Anacardiaceae) are interspersed with patches of savanna vegetation containing other members of the Anacardiaceae, and fields of other subtropical fruit crops. Mangoes in this region are infested by three species of *Ceratitis* fruit fly (Diptera: Tephritidae), namely the Mediterranean fruit fly (*C. capitata* (Wiedemann)), the Natal fly (*C. rosa* Karsch) and the Marula fly (*C. cosyra* (Walker)) (Grové, De Beer & Joubert 2006), which cause the greatest damage to economically-valuable soft fruits in the African tropics (De Meyer et al. 2008). Before fruit ripening, *Ceratitis* spp. oviposit their eggs beneath the skin of the mango, where the larvae then hatch and feed on the fruit tissue (Pena, Mohyuddin & Wysoki 1998; Manrakhan & Addison 2007). The larvae then drop to the soil, where they pupate and finally emerge as adult flies (Pena, Mohyuddin & Wysoki 1998).

All three *Ceratitis* species are polyphagous, being hosted by up to 882 crop and non-crop species in their African ranges (Copeland et al. 2002, 2006), many of which occur in the natural vegetation alongside mango fields in the K2C. One notable host includes the indigenous marula tree, *Sclerocarya birrea* (A. Rich) Hochst. subsp. *caffra* (Sond.) Kokwara – a keystone species of the lowveld savanna throughout Sub-Saharan Africa (Shackleton et al. 2002; Shackleton, Botha & Emanuel 2003). As relatives within the Anacardiaceae, marula and mango display similar life cycles, with fruiting seasons overlapping, though not completely, between November and April (Nghitoolwa, Hall & Sinclair 2003). Marula is dioecious and females produce fruit similar to mango with a large pit and a thick, soft exocarp (Nerd & Mizrahi 2000; Chirwa & Akinnifesi 2008). The fruits are known to host larvae of several invertebrate species, but host only one species of the three *Ceratitis* species infesting mango in the region, *C. cosyra* (Mwatawala et al. 2009).

Marula is considered an important reservoir for *C. cosyra* outside of the mango fruiting season in Sub-Saharan Africa (Copeland et al. 2006), which leads farmers to control non-crop hosts in natural vegetation at the start of the mango season (Mwatawala et al. 2009). On mango farms in the K2C, practices to control potential *C. cosyra* infestation involve burying, incinerating and removing marula fruits from natural vegetation surrounding farmlands (P. Malherbe, pers. comm.). Removing large amounts of marula may have unintended biological consequences for the ecosystem, firstly by eliminating alternate hosts for *C. cosyra* that may provide the mango crop with ‘associational resistance’ (Barbosa et al. 2009) to fruit fly infestation and inhibit pest attack. Indeed, there is

substantial evidence to support how higher levels of plant diversity, including alternate hosts for specialized herbivores, prevent pest outbreaks in agroecosystems (see review by Andow 1991). Secondly, marula may also present more oviposition sites and an overwintering habitat for natural enemies of *Ceratitis*, including parasitoid wasps, and act as a source of natural pest control during mango fruiting season. Other studies have observed dispersal of natural enemies from native, non-crop weeds along field margins into crop fields in spring (Thomas, Wratten & Sotherton 1992; Cottrell & Yeargan 1999). These natural enemies may provide adequate biological control to farmers if colonization of the crop is substantial following migration into the crop fields (Thomas, Wratten & Sotherton 1992). Therefore, removal of marula alongside mango farms may eliminate a source of natural enemies and threaten natural control of *Ceratitis* in crop fields when mango is in season.

However, instances of removing alternate hosts of natural enemies have also been beneficial to farmers in some instances. For example, a groundcover species in hops fields (*Humulus lupulus* L.) is commonly infested with the hop aphid (*Phorodon humuli* Schrank) and when cut, encouraged the dispersal of aphid predators onto the crop, resulting in limited crop-aphid infestation (Goller, Nunnenmacher & Goldbach 1997). Similarly, the timely removal of marula when *Ceratitis* is first detected in crop fields may also promote migration of natural enemies onto the mango in this way, providing mango with “associational resistance” (Barbosa et al. 2009) against infestation by fruit flies. Overall, the expected effects of marula removal on *Ceratitis* in mango fields are conflicting, and to establish whether this management practice is beneficial or harmful to farmers requires improved understanding of the role of marula as a source or alternate host for *Ceratitis* in this landscape.

The majority of studies to date have focused on biodiversity spill-over in the direction from natural vegetation to farmlands (for review see Blitzer et al. 2012). This biased understanding of spill-over between habitats makes it difficult to challenge the belief that natural vegetation is a source of crop pests, rather than a source of alternate hosts that inhibit pest infestation of the crop in agricultural landscapes. Only three studies to date have investigated pest spill-over in the reverse direction from crop fields to natural vegetation (Blitzer et al. 2012), yet it seems entirely possible that pests may disperse from the relatively resource-rich, high productivity habitat represented by monoculture crops into surrounding vegetation (Tschardt et al. 2005).

In this study, I investigated the effect that mango farms have on the infestation of marula by *Ceratitis* and the presence of parasitoid wasps as natural enemies in adjacent natural vegetation. I reared *Ceratitis* from marula fruits during the early and late marula fruiting season to address the following question: (i) Does the infestation of marula by *C. cosyra* differ between the natural vegetation alongside mango fields and in the distant vegetation far from mango fields? To determine whether *Ceratitis* accumulates within mango fields and at marula trees in natural vegetation during the late season, I used pheromone trapping to ask: (ii) Does *Ceratitis* abundance differ between the mango

fields and natural vegetation? Both fruit rearing and pheromone trapping were then used to address the following questions: (iii) Is *Ceratitis* abundance in natural vegetation affected by distance from mango fields, and by distance into mango fields from natural vegetation? And (iv) Is infestation of marula by *C. cosyra* in natural vegetation adjacent to mango fields affected by proximity to the crop?

2.2 MATERIALS AND METHODS

2.2.1 Study design in the natural vegetation

In the Kruger to Canyons Biosphere Region (see Appendix I for site description), sampling was conducted on three mango farms, namely Bavaria Fruit Estates, Mohlatsi and Venden, and two control sites in Hoedspruit. The farms were selected for the close proximity of the mango fields to large patches of natural vegetation (min. area ≈ 1.1 km x 500 m), typically separated by a 10-25 m margin. I selected 15 marula trees in natural vegetation adjacent to mango fields at Bavaria and ten at Mohlatsi and Venden (see Appendix II for site maps). All trees were at least 40 m apart and at distances of 20-300 m from mango fields. The position of each tree was recorded using a GPS (eTrex10®, Garmin International, Inc., USA) to determine the distance of each tree to the mango crop on each farm.

For control sites, I selected two areas of natural vegetation that were at distances of 1.3 – 6.2 km from mango or other fruit plantations in the Hoedspruit region. These sites were residential conservation estates, Raptor's View and the Hoedspruit Wildlife Estate. The control sites were included to observe whether densities of *Ceratitis* and their natural enemies infesting marula are affected by nearby mango as source of *Ceratitis* fruit fly. At each control site, I selected five marula trees that were distributed randomly on each estate and at least 35 m apart.

2.2.2 Fruit collection

Marula fruit are round or oval drupes, approximately 30 – 40 mm in diameter, which are green when immature and yellow with ripening on the ground following abscission from the tree (Nerd & Mizrahi 2000). Fruits were collected in two rounds in late summer, first during early marula fruiting season (late January, 2015) and again 31 – 32 days later during peak marula fruiting season (late February, 2015). During the early season, mango fruits were still present in the adjacent crop fields on Bavaria and Venden, but not on Mohlatsi. By the late season, all mango fruits had been harvested and all fallen fruits had been cleared from the ground on all farms.

In each round of sampling, I collected 30 fruits from each marula tree where possible, depending on the availability of the fruits. Twenty of the fruits were from the ground below the tree and were divided into two categories of ripeness based on their colour. The categories were “fallen, unripe” (FU) (n=10), identified as green-white fruits, and “fallen, ripe” (FR) (n=10), identified as yellow

fruits. Ten green fruits were also collected from within the canopy of each tree and were categorized as “unfallen, unripe” (UU). Across all farms and ripeness categories, 757 fruit were sampled in the early season and 966 in the late season. The total number of fruit recorded and collected on each farm within each ripeness category is presented for both sample seasons in Appendix III. To determine whether marula fruit ripeness and availability affects the infestation rates of marula by *C. cosyra* in natural vegetation, the total number of fruit within the tree canopy, the number of FU and FR fruit around the tree base and the number of fruiting trees within a 20 m radius around each sampled tree were recorded.

The onset of the wet season was later in 2014 (February – March) than in 2015 (November – December), resulting in later mango harvesting in 2014 and variable timing of mango harvesting relative to marula fruiting between years. To investigate how the relative fruiting times affect marula infestation by *Ceratitis*, I included data from a pilot study conducted in the late marula fruiting season (mid-March) in 2014 in this study. This small-scale study was carried out on Bavaria Fruit Estates when mango fruits were still present in crop fields, and did not include any control sites. Thirty-five marula trees were selected in natural vegetation alongside mango fields, with a minimum of 40 m between each tree. No UU fruits were sampled in this study, but fifteen fruits were collected within both FU and FR ripeness categories where possible, yielding a total of 508 fruits. For each sampled tree, the distance to the mango crop, and the number of fruiting marula trees within a 20 m radius of the tree were recorded.

2.2.3 Fruit processing and insect rearing

Fruits collected in both 2014 and 2015 were placed into individual polystyrene cups filled to a depth of 2 cm with commercially-available, dry and sterile sand, which provided a suitable substrate for pupation of *Ceratitis* larvae emerging from the marula fruit (Yuval & Hendrichs 2000). A piece of chiffon was placed over the top of each cup and secured with an elastic band to allow air to pass easily in and out of the cup, preventing the accumulation of metabolic heat known to hinder larval development of some *Ceratitis* species (Caceres 2002). Cups were kept in a closed room at ambient temperature (27 – 35 °C) for 28 – 31 days, the maximum duration of the *Ceratitis* life cycle (Hill 1983), before cups were checked for insect emergence. The sand in each cup was sifted through by hand and the total number of dead insects per cup, including *Ceratitis* adults and undeveloped pupae, and parasitoid wasps were counted and collected. *Ceratitis* adults that were still alive were also collected into 70% ethanol and added to the total insect count per cup. Totals per cup yielded total *Ceratitis* and parasitoid wasps emerging per fruit per sample season. All individual fly and wasp specimens were identified to species and genus level, respectively, and stored in 70% ethanol for reference. These are housed at the South African National Biodiversity Institute (SANBI) in Cape Town, South Africa.

2.2.4 Pheromone trapping

Investigating how mango farming affects *Ceratitis* and parasitoids in natural vegetation also requires understanding of *Ceratitis* and enemy populations in mango fields. However, rearing *Ceratitis* flies from mango in closed containers is difficult because the larvae die in the fluid of the fermenting fruit before being able to pupate (T. Carroll and W. Lammers, pers. comm.). Therefore, *Ceratitis* abundance in the mango was quantified using pheromone traps.

Sensus™ traps equipped with Pherolure bait specific to *Ceratitis* species (Insect Science (Pty) Ltd, South Africa) and Dichlorovos poison tablets were set up along two parallel 200 m transects, no less than 100 m apart, on each farm. Traps were positioned at 0 m, 10 m, 50 m, 100 m and 200 m away from the natural vegetation along each transect (sensu Lammers et al. unpublished data), yielding a total of 30 traps (see Appendix II for trap setup between habitats). Since the abundance of flies reared from marula cannot be compared with those collected in traps, I also set up pheromone traps at each sampled marula tree in the natural vegetation (n=30). This included only ten of the 15 trees sampled on Bavaria, which were selected such that their distances increased as evenly as possible from the mango fields. Traps were set up in late February, 2015 and left for two weeks before collection. The abundance of *Ceratitis* in each trap was recorded and all specimens were identified to species.

2.2.5 Data analysis

Does marula infestation by *C. cosyra* and its parasitoid wasps differ between natural vegetation alongside mango fields and in vegetation far from mango fields?

To account for the excess zeros in the *C. cosyra* abundance data collected using fruit rearing experiments, I used zero-altered hurdle models (see overview in Zuur et al. 2009). These models assume that all zeros encountered in the data are ‘true zeros’ and did not result from design or observer error. This was likely the case, given that: 1) fly emergence from fruit was only checked after the maximum known time required for the *Ceratitis* life cycle had passed and 2) counts of any un-emerged pupae were included in the total *Ceratitis* count. To choose between zero-altered negative binomial (ZANB) and Poisson models (ZAP), Akaike Information Criteria (AIC) were used. The ZANB model had the lower AIC and was considered a better fit of the data. The use of a negative binomial error distribution also eliminates the need to log-transform count data (which is not recommended, (O’Hara & Kotze 2010).

Hurdle models consider that marula infestation has two components: 1) the event of an infestation (presence or absence of *Ceratitis*) and 2) the extent of the infestation (the abundance of *Ceratitis*) i.e. there are “hurdles” that a fruit has to overcome to be infested with fruit flies, after which other factors may determine the degree of infestation. The hurdle model uses a binary zero-inflated model

(binomial error distribution with logit link) to identify what determines the likelihood of an infestation (*Ceratitis* presence vs absence). It then applies a zero-truncated count model (negative binomial with log link) to identify what determines the intensity of the infestation (*Ceratitis* abundance), once infestation has occurred. The zero-truncated count model uses count data where fly abundance per fruit > 0 i.e. in the event that a fly is present.

Separate ZANB models were used to assess whether *C. cosyra* infestation per marula fruit in natural vegetation alongside mango fields differed from that at control sites in the early and late fruiting seasons in 2015 only. The model included fruit ripeness, fruit abundance per ripeness category, and the number of fruiting trees within a 20 m radius of the sampled tree to determine the importance of marula fruit availability and ripeness in this effect. In the early season, only five unripe fruits (UU) were infested by a single *Ceratitis* fly each. Since these cases could not contribute to the abundance component of the ZANB model (i.e. abundance > 1), UU fruit were excluded from the early season model. Fruit from all ripeness categories were considered in the late season.

For simplification of all ZANB models, I used likelihood ratio tests in the process of backward selection for each of the binary and count models, assuming independence of their error distributions (*sensu* (Tambo & Abdoulaye 2012). These analyses were performed using the `pscl` package (Jackman et al. 2015) in R v3.1.2 (R Core Team, 2014).

Wasp abundance data were highly zero-inflated with only 15 fruits hosting wasps. A minimum of ten observations per parameter included in mixed effects model is required in a zero-inflated data set (i.e. 40 observations required in this case) (Bolker et al. 2009) so wasp abundance could not be modelled in this study and only observational results are presented.

Does *Ceratitis* abundance differ between mango fields and adjacent natural vegetation?

Generalized Linear Mixed Effects Models (GLMMs) were used to investigate whether overall *Ceratitis* abundance and abundance of each species collected in pheromone traps differed between mango fields and adjacent natural vegetation. GLMMs account for the spatial and temporal variation that may be introduced by sampling across different farms and at different times (Royle & Dorazio 2008). I included overall *Ceratitis* abundance and abundance per species as dependent variables in separate models, with farm and date of trap collection as random effects. Habitat type, a binary factor for mango fields and adjacent natural vegetation, was included as a fixed effect in the model.

Is *Ceratitis* abundance affected by distance into adjacent natural vegetation from mango fields and vice versa?

GLMMs were also used to address whether overall *Ceratitis* abundance and abundance per species collected in pheromone traps in each vegetation type were affected by distance to the adjacent habitat. I included distance of each trap to the adjacent habitat type (i.e. distance to the mango fields in the natural vegetation and vice versa) in each model above according to the following model structure:

Ceratitis abundance ~ Habitat type * Distance to adjacent habitat + (1|date) + (1|farm)

For all GLMMs, I considered Poisson or negative binomial error distributions with intrinsic log-link functions to account for non-normality of the count data. The negative binomial distribution was a better fit based on AIC model selection. I also considered random intercept and random slope models, evaluating which random effects structure provided a better fit of the data using AIC values (Zuur et al. 2009). The random intercept model had the lowest AIC and was selected as the model of better fit. Models were fitted using package lme4 (Bates 2005) or glmmADMB with model correction for zero-inflation of *C. rosa* abundance (Bolker et al. 2012).

Throughout model selection of all GLMMs, residual normality and overdispersion were checked by plotting residuals against fitted values and explanatory variables. Explanatory variables were also assessed for collinearity (Zuur et al. 2009). Likelihood ratio tests, AIC and Akaike weights were used to identify optimal models during the process of backward model simplification. The proportion of variance explained by fixed effects (marginal R^2) and fixed and random effects (conditional R^2) was also calculated as measures of goodness-of-fit for each model (using the method for random intercept models provided by Nakagawa & Schielzeth 2013). All GLMMs were fitted and simplified using package lme4 in R v3.1.2 (R Core Team 2014) at a significance level of $\alpha = 0.05$.

Is *C. cosyra* infestation of marula fruit affected by distance to the mango crop?

ZANB models were used to investigate whether marula infestation by *C. cosyra* is affected by distance from mango fields into adjacent natural vegetation between seasons and years. I modelled infestation rates as a function of distance to mango, the number of fruiting trees within a 20 m radius of the sampled tree and fruit ripeness. The model included data collected in both 2014 and 2015, so fruit ripeness was limited to the two categories considered in 2014 (FU and FR), with UU fruit from the 2015 dataset excluded. Since fruit abundance within each ripeness category was not recorded in 2014, this factor was also excluded from the model. Model selection was again performed using likelihood ratio tests in the process of backward selection for each of the binary and count models using the pscl package (Jackman et al. 2015) in R v3.1.2 (R Core Team 2014).

2.3 RESULTS

Does marula infestation by *C. cosyra* and its parasitoid wasps differ between natural vegetation alongside mango fields and in vegetation far from mango fields?

A total of 3580 *Ceratitis* flies emerged from the 1728 fruit collected during 2015. Of these, 3195 (89.3%) were adults and could be identified to species, while the remaining 385 (10.8%) were undeveloped pupae, but contributed to the *Ceratitis* total count. All but one of the flies to emerge from the marula fruit were *C. cosyra*, with a single *C. capitata* individual emerging from a fallen, ripe fruit on Bavaria at close proximity (22 m) to the mango fields.

Marula fruit in natural vegetation adjacent to mango fields were up to 24 – 25 times more likely to be infested by *Ceratitis* than marula in the distant vegetation in both seasons (Table 2.1). Note that model coefficients reported in Table 2.1, which were calculated using the intrinsic log-link function in the negative binomial GLMMs, have been reverse transformed (natural exponent: e^x) in this text. *Ceratitis* emerged from only 0.7% and 0.6% of fruit collected in the distant vegetation (5.2 – 6.2 km away from mango fields) compared to 20.8% and 21.2% of fruit collected from natural vegetation alongside mango fields in the early and late season, respectively.

While proximity to mango increased the likelihood of fruit infestation, proximity to mango did not significantly affect the intensity of fruit infestation (abundance of *Ceratitis* per fruit) (Table 2.1). Nevertheless, mean *Ceratitis* abundance (\pm standard error) emerging per marula fruit was slightly higher in natural vegetation adjacent to mango fields than in the distant vegetation in both the early (2.68 ± 0.26) and late (2.35 ± 0.21) seasons (Fig. 2.1). In the distant vegetation, 11 and 5 *Ceratitis* individuals emerged from a single fruit per season, yielding mean fly abundance per fruit of 0.08 ± 0.08 and 0.03 ± 0.03 in the early and late season, respectively.

Table 2.1. Parameter estimations from maximum likelihood tests and fit statistics of the ZANB model for the early and late marula fruiting season in 2015. Data include fruit from the natural vegetation alongside mango fields and at control sites. The early season model includes data for fallen unripe (FU) and ripe (FR) fruit only (n = 370), with the intercept corresponding to FU fruit at control sites. The late season model includes fruit from all three ripeness categories, including unfallen unripe (UU) and FU and FR (n = 971), with the intercept representing UU fruit at control sites. ‘-’ = factor not included in model, () = standard error of coefficient, Sig = level of significance and ‘n.s.’ = non-significance at $\alpha = 0.05$.

Parameter	Early season		Late season	
	Coefficient	Sig	Coefficient	Sig
<i>Binomial hurdle component of model (Ceratitis presence)</i>				
Intercept	-4.79 (1.05)	p < 0.001	-8.46 (1.43)	p < 0.001
Adjacent to mango	3.13 (1.03)	p < 0.01	3.17 (1.02)	p < 0.01
FU fruit ripeness	-	-	3.49 (1.02)	p < 0.001
FR fruit ripeness	1.43 (0.26)	p < 0.001	5.00 (1.01)	p < 0.001
No. fruiting marula trees	0.15 (0.09)	n.s.	-0.07 (0.07)	n.s.
UU fruit abundance	0.002 (0.0005)	p < 0.01	0.0005 (0.001)	n.s.
FU fruit abundance	-0.005 (0.007)	n.s.	-0.004 (0.002)	n.s.
FR fruit abundance	-0.007 (0.008)	n.s.	0.001 (0.0005)	p = 0.013
<i>Zero-truncated negative binomial component of model (Ceratitis abundance)</i>				
Intercept	2.26 (0.68)	p < 0.001	1.31 (1.10)	n.s.
Adjacent to mango	-0.24 (0.69)	n.s.	0.74 (0.82)	n.s.
FU fruit ripeness	-	-	-0.15 (0.75)	n.s.
FR fruit ripeness	0.25 (0.13)	n.s.	0.26 (0.74)	n.s.
No. fruiting marula trees	0.004 (0.05)	n.s.	0.03 (0.05)	n.s.
UU fruit abundance	0.0005 (0.0002)	n.s.	0.0007 (0.0007)	n.s.
FU fruit abundance	0.003 (0.004)	n.s.	-0.0008 (0.001)	n.s.
FR fruit abundance	0.0005 (0.006)	n.s.	0.0004 (0.0003)	n.s.
Log likelihood	-658.1		-893.8	

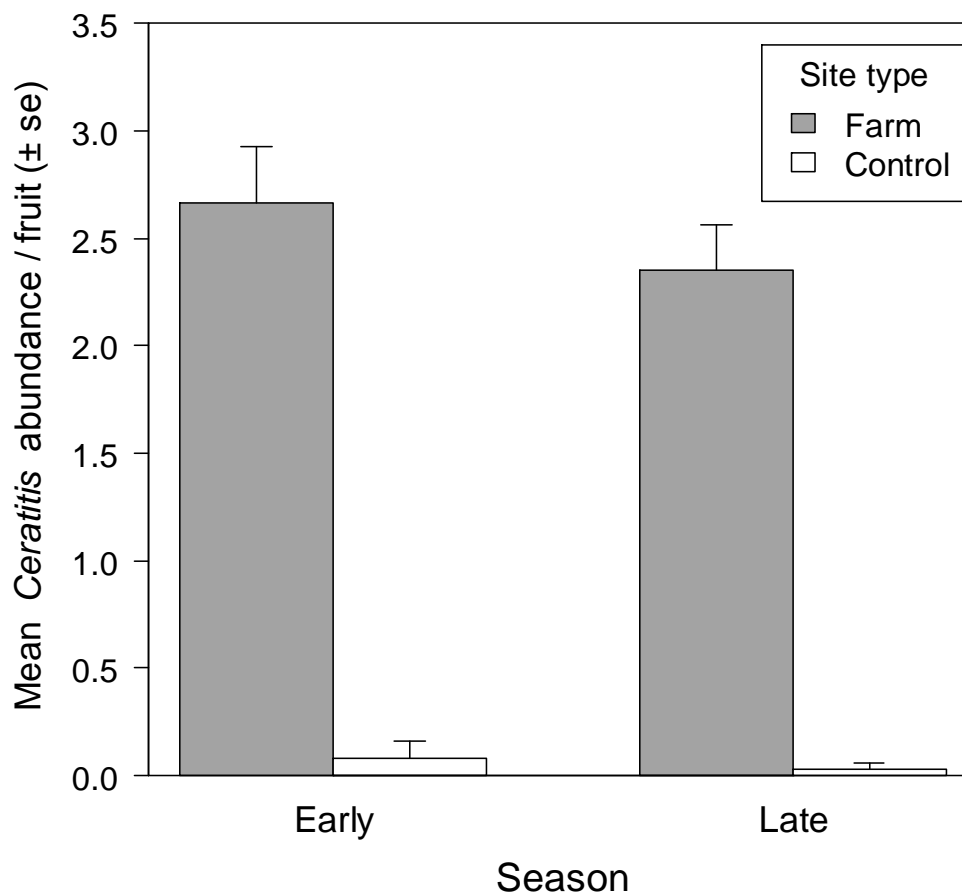


Figure 2.1. Mean *Ceratitis* abundance (\pm s.e.) emerging per marula fruit in the natural vegetation alongside mango fields (“Farm” site) (n = 622, 808) and in the distant vegetation (“Control” site) (n = 135, 163) in the early and late season in 2015 only.

Fruit ripeness, fruit abundance and fruiting marula tree abundance

In the early season, ripe fruit on the ground (FR) were 4.2 times more likely to be infested on average than unripe fruit on the ground (FU) (Table 2.1, Fig. 2.2). In the late season, FU and FR fruit on the ground were 32.8 and 148.4 times more likely to be infested by *Ceratitis* than unripe fruit within the marula tree canopy (UU). The intensity of infestation per marula fruit was similar for all ripeness categories in both seasons.

Total fruit abundance within the different ripeness categories per tree was a significant determinant of the likelihood of fruit infestation by *Ceratitis*, but not infestation intensity per fruit (Table 2.1). The likelihood of *Ceratitis* infestation per fruit increased with increasing abundance of unripe fruit within the tree canopy (UU) in the early season and ripe fruit on the ground (FR) in the late season. The number of surrounding fruiting marula trees did not affect either the likelihood or intensity of fruit infestation by *Ceratitis* (Table 2.1).

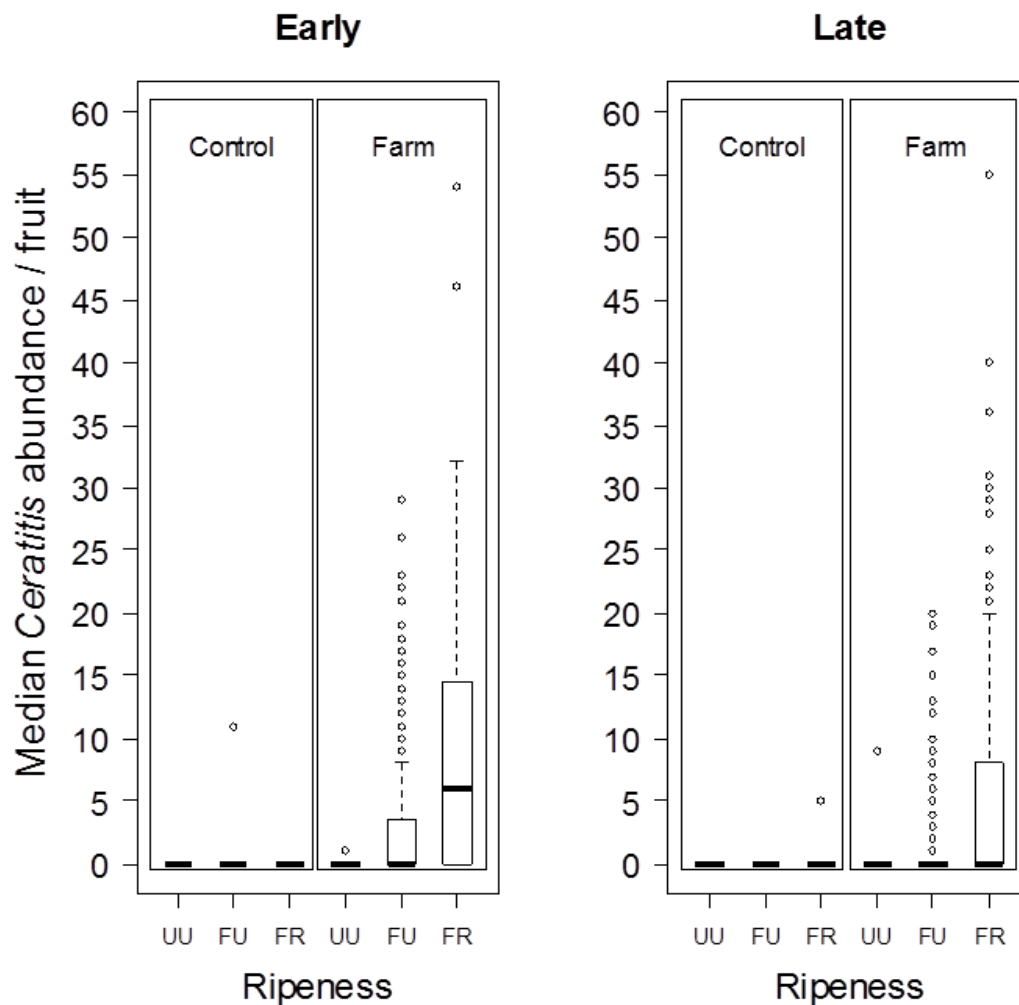


Figure 2.2. Median *Ceratitis* abundance emerging from fruit in three ripeness categories: ‘unfallen, unripe’ (UU), ‘fallen, unripe’ (FU) and ‘fallen, ripe’ (FR), from marula trees in the natural vegetation alongside mango fields (“Farm”) and in the distant vegetation (“Control”) in the early (n=757) and late season (n=971) in 2015 only.

Parasitoid wasp abundance

Two species of parasitoid wasp emerged from all fruit collected in 2014 and 2015, namely *Fopius* sp. and *Opius* sp. (Hymenoptera: Braconidae). A total of 60 wasps emerged from fruit across both site types and seasons, with only 9 emerging from samples in 2014. In 2015, all 34 wasps in the early season emerged from fruits collected in the natural vegetation adjacent to mango fields, with no wasps emerging from fruit in the distant vegetation (Fig. 2.3). In the late season, more wasps emerged from fruit in the distant vegetation (n=13 from a single fruit) than adjacent to mango fields (n=4 from 3 fruits).

Parasitoids emerged from 0% and 0.61% of fruit collected in the distant natural vegetation compared to 1.7% and 0.4% of fruit collected in the natural vegetation adjacent to mango fields in the early and late season, respectively. In 2015, the majority of the wasps (75.6%) emerged from ripe fruit on the

ground (FR), followed by unripe fruit on the ground (FU) (24.5%). Zero wasps emerged from unripe fruit within the tree canopy (UU). All 9 wasps from fruit collected in 2014 emerged from FR fruit at close proximity to mango fields (though no fruits were sampled in the distant vegetation).

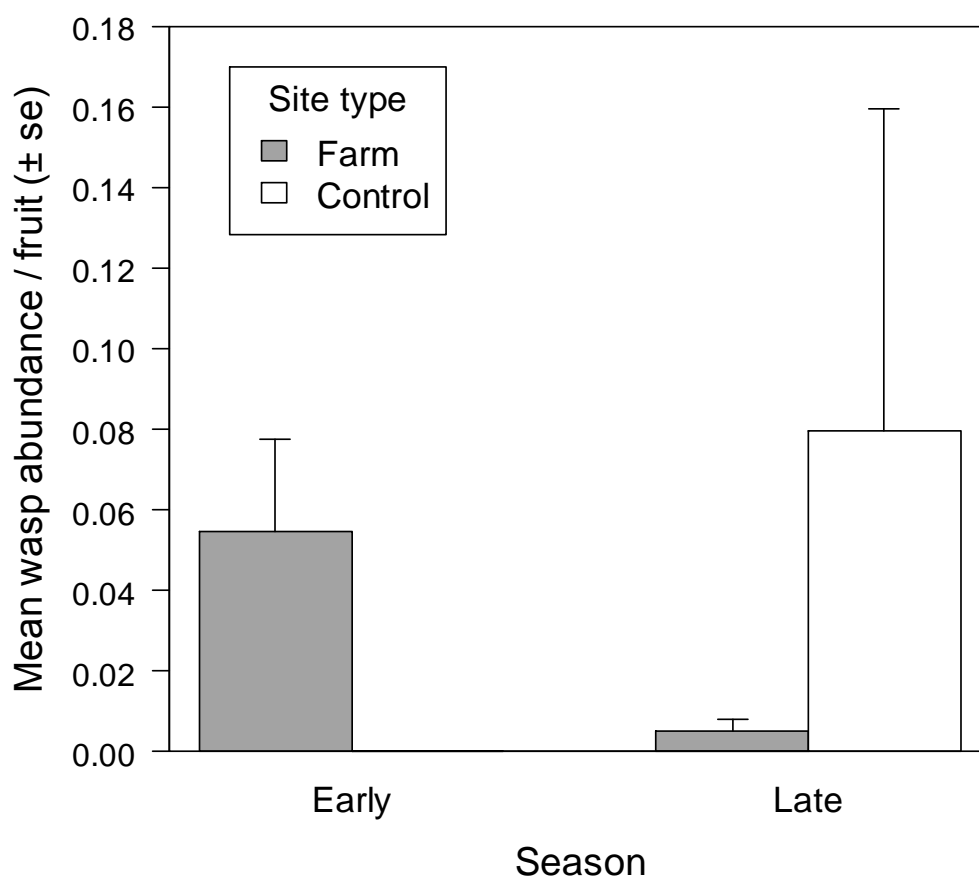


Figure 2.3. Mean parasitoid abundance (\pm se) emerging per marula fruit in the natural vegetation alongside mango fields (“Farm”) (n = 622, 808) and in the distant vegetation (“Control”) (n = 135, 163) in the early and late season (2015 only).

Does *Ceratitis* abundance differ between mango fields and adjacent natural vegetation?

Three traps in the natural vegetation were disturbed during the study and analyses are based on samples collected in 27 traps in natural vegetation and 30 traps in mango fields. A total of 735 *Ceratitis* flies were collected, of which 24.5% and 75.5% occurred in mango fields and in adjacent natural vegetation, respectively. Overall *Ceratitis* abundance was significantly higher in natural vegetation than in mango fields (Table 2.2, Fig. 2.4). For the overall *Ceratitis* abundance model, 70.9% and 99.8% of the variance could be accounted for by the fixed effects, and fixed and random effects, respectively.

Table 2.2. Effect of habitat type (HAB) (mango fields and adjacent natural vegetation) and distance to the adjacent habitat type (m) (DIST) on total *Ceratitidis* abundance (a) and abundance of each of the three *Ceratitidis* species (b – d) in the late marula fruiting season.

Abundance	HAB	DIST	HAB x DIST	d.f.	AIC	Akaike weighting
(a) All <i>Ceratitidis</i> species						
Model 1	n.s.	n.s.	n.s.	7	343.56	0.37
Model 2	p < 0.001	p = 0.05	-	6	343.07	0.63*
Null model	-	-	-	4	361.17	p < 0.0001
(b) <i>C. cosyra</i>						
Model 1	p < 0.001	n.s.	n.s.	7	319.09	0.34 *
Model 2	p < 0.001	n.s.	-	6	319.39	0.39 *
Model 3	p < 0.001	-	-	5	320.65	0.27
Null model	-	-	-	4	336.52	p < 0.0001
(c) <i>C. capitata</i>						
Null model	-	-	-	5	150.43	p = 0.539
(d) <i>C. rosa</i>						
Model 1	n.s.	n.s.	p < 0.001	8	86.73	0.99*
Model 2	n.s.	p = 0.026	-	7	97.27	0.007
Null model	-	-	-	5	100.30	p < 0.001

P-values are significance of variables obtained from likelihood ratio tests. 'n.s.' denotes non-significance at $\alpha = 0.05$. '-' indicates terms excluded from each model. AIC and Akaike weightings of each model are presented, with lowest AIC values indicating models of best fit. Akaike weightings (0 – 1) represent the probability that the model is the best approximating fit (*). When AIC values differ by < 2 and Akaike weightings differ by < 0.05, models are said to fit equally well (*sensu* Seymour et al. 2015). Equations for models of best fit are presented below.

(a) Mango: Model 2 $e^{0.67 (\pm 0.71) - 0.31 (\pm 0.15) \times \text{DIST}}$; Natural vegetation: Model 2 $e^{0.002 (\pm 0.70) - 0.0006 (\pm 0.15) \times \text{DIST}}$

(b) Mango: Model 1 $e^{0.0037 (\pm 0.765)}$ Model 2 $e^{0.0039 (\pm 0.762)}$; Natural vegetation: $e^{-0.0084 (\pm 0.738)}$ Model 2 $e^{-0.0089 (\pm 0.746)}$

(d) Model 1 $e^{0.32 (\pm 0.34) - 0.66 (\pm 0.38) \times \text{DIST} - 0.09 (\pm 0.00001) \times \text{DIST (HAB)}}$

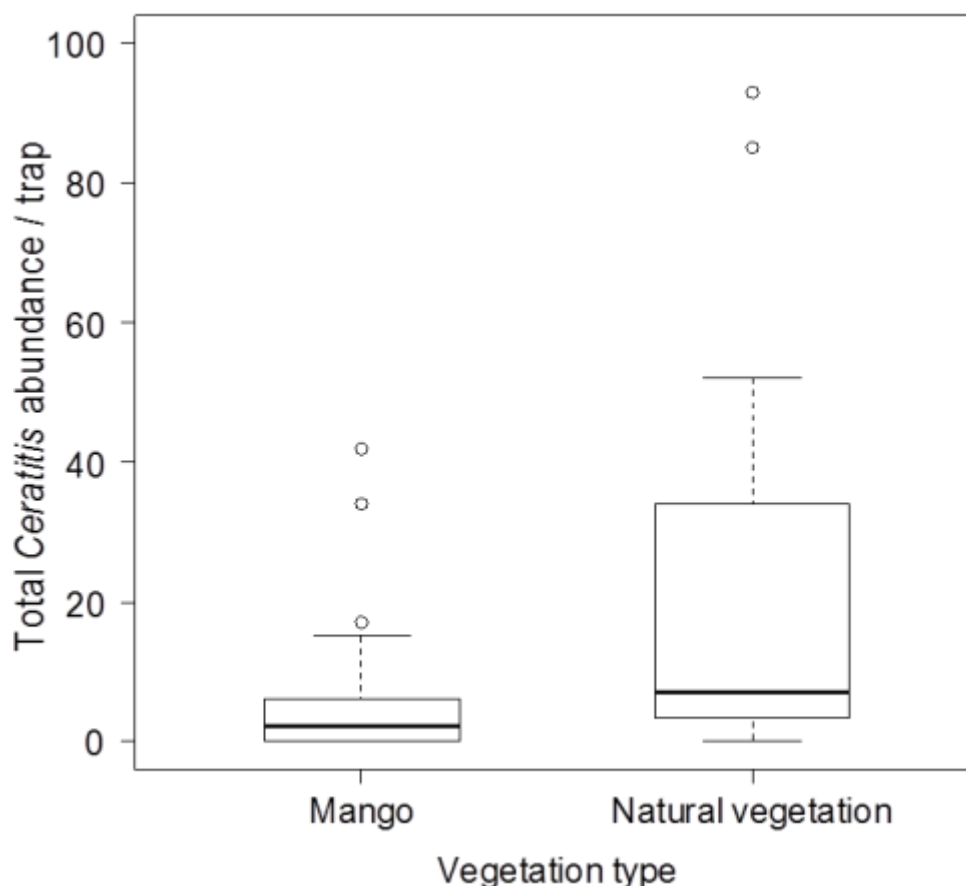


Figure 2.4. Median total *Ceratitis* abundance collected per trap between mango fields (n=30) and adjacent natural vegetation (n = 27). The two outlier traps in the natural vegetation yielded 78 and 93 *Ceratitis* specimens.

Three species of *Ceratitis* were captured in traps in both habitats, namely *C. cosyra*, *C. capitata* and *C. rosa*. The marula fly, *C. cosyra*, was the most abundant species captured overall in both habitats (89.5% of total fly captures). Of the 658 *C. cosyra* specimens captured, 79.8% and 20.2% occurred in natural vegetation and mango fields, respectively. Average *C. cosyra* abundance per trap (\pm standard deviation) was significantly higher in natural vegetation (19.4 ± 25.6) than in mango fields (4.4 ± 8.1) (Table 2.2, Fig. 2.5). Fixed effects, and both fixed effects and random effects accounted for 72.3% and 99.95% of variance in the final model, respectively.

C. capitata and *C. rosa* only made up 6.8% and 3.7% of the total overall captures, respectively. *C. capitata* abundance per trap did not differ significantly between mango fields (0.8 ± 1.8) and adjacent natural vegetation (1.0 ± 1.7). Random effects including farm and date of collection are more likely to have influenced the abundance of this species (Table 2.2). In fact, 60% of *C. capitata* were found on Venden farm, especially in mango fields, while zero were collected on Mohlatsi.

Although 85.2% of total *C. rosa* captures occurred in mango fields, abundance per trap was not significantly different between mango fields (0.77 ± 1.33) and adjacent natural vegetation, where four flies were captured in a single trap (Table 2.2, Fig. 2.5). Fixed effects and both fixed and random effects accounting for only 23.6% and 31.1% of the variation in *C. rosa* abundance per trap.

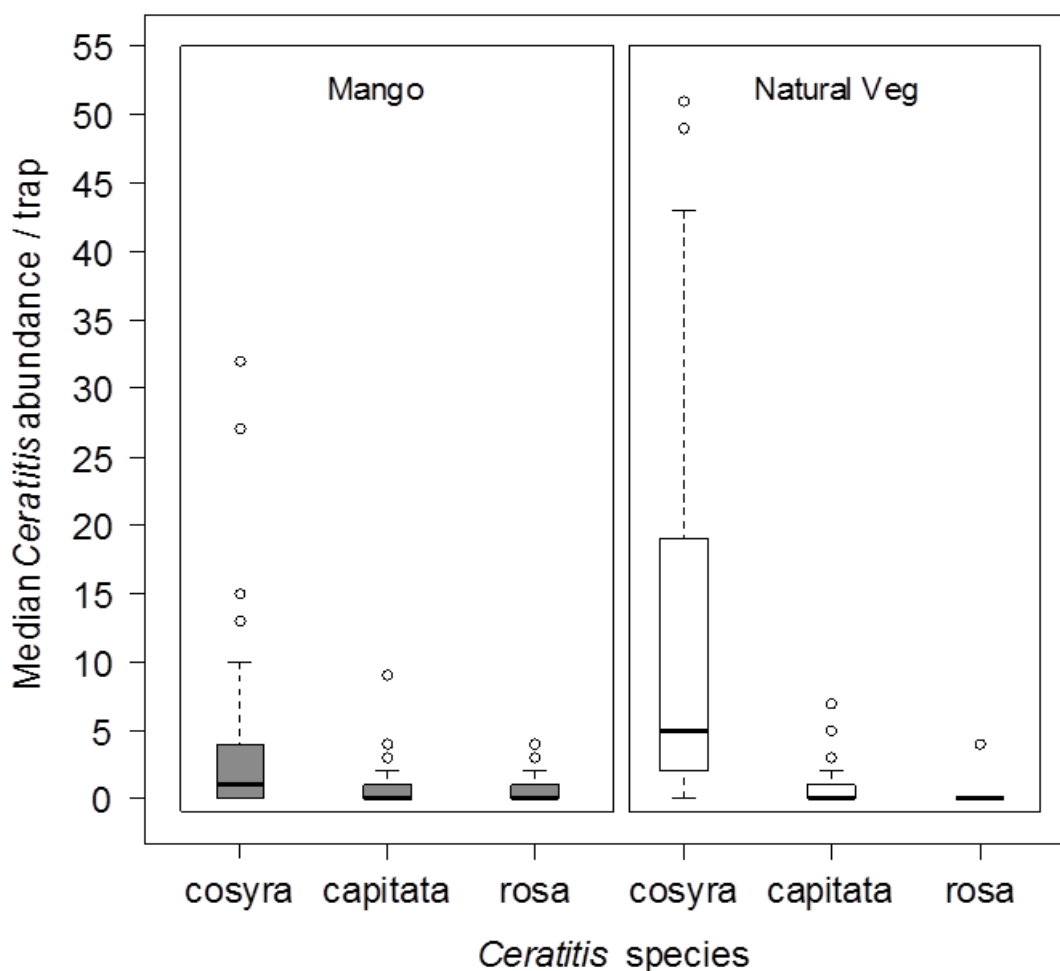


Figure 2.5. Median *Ceratitis* species abundance per trap in mango fields (n=30) and adjacent natural vegetation (n=27). Two outliers have been removed from the natural vegetation, where 93 and 78 *C. cosyra* flies emerged from single traps (at 84 m and 168 m from the mango crop).

Is *Ceratitis* abundance affected by distance into adjacent natural vegetation from mango fields and vice versa?

Overall *Ceratitis* abundance decreased with increasing distance to the adjacent habitat in both mango fields and natural vegetation, but this effect was only marginal (Table 2.2, Fig. 2.6). *C. cosyra* and *C. capitata* abundances were not affected by distance to the adjacent habitat types but *C. rosa* abundance in mango fields decreased significantly with distance from the adjacent natural vegetation (Fig. 2.6). In natural vegetation, *C. rosa* was only captured in a single trap at close proximity to mango fields (22 m) and distance effects could not be evaluated.

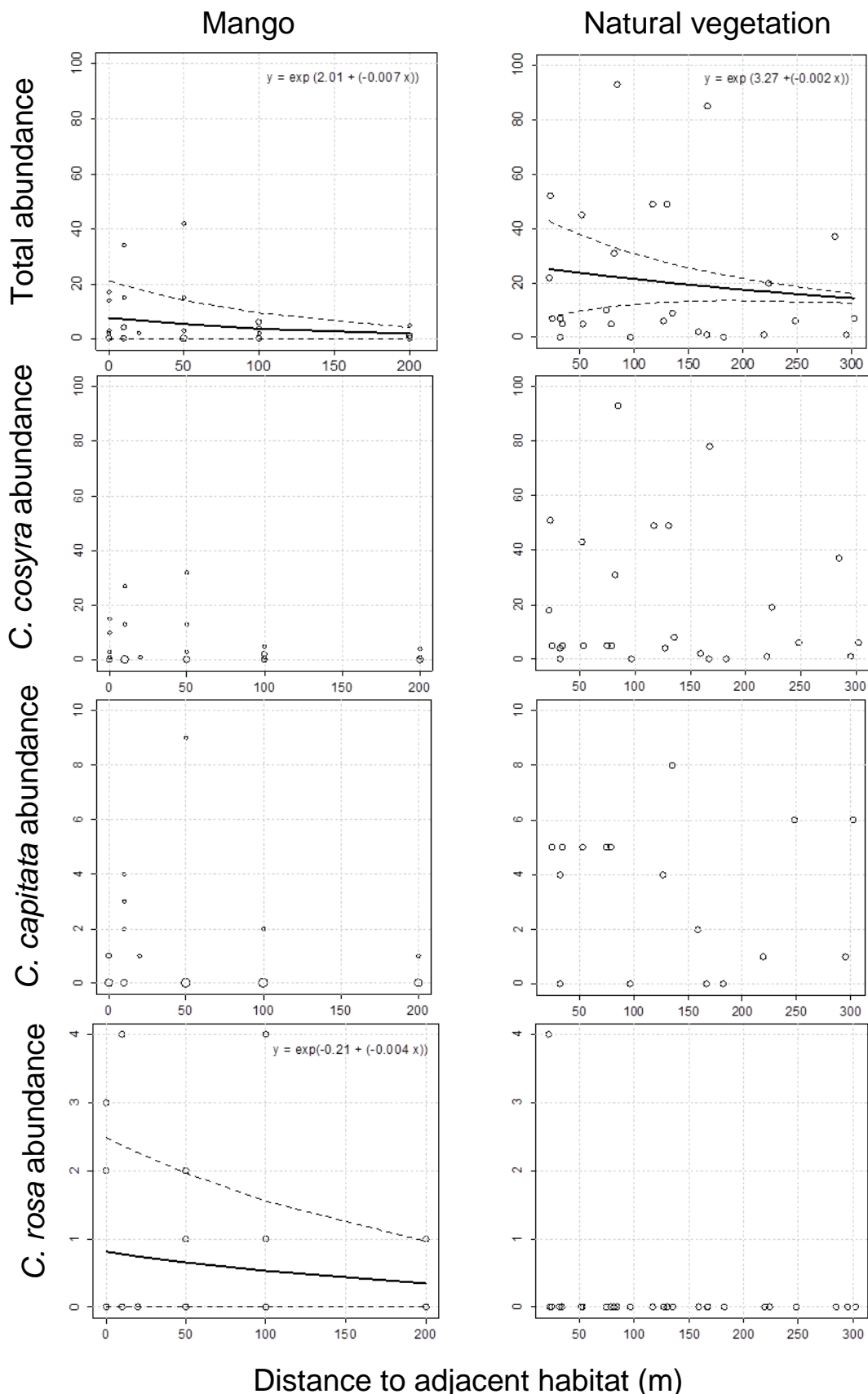


Figure 2.6. Overall *Ceratitis* and species abundance collected in pheromone traps at distances from the adjacent habitat (m) in mango fields (n = 30) and in natural vegetation (n = 27). Equations and lines are negative binomial glm fits of mean values (\pm sd) for each habitat (without random effects, unlike models in Table 2.2). Point size is weighted by frequency of flies captured per distance point.

Is *C. cosyra* infestation of marula fruit affected by distance to the mango crop?

In the 2014 study, a total of 695 *C. cosyra* flies emerged from 507 fruit collected from natural vegetation adjacent to mango fields. This dataset was analysed with a subset of the 2015 dataset which included 3550 *Ceratitis* flies emerging from 909 FU and FR fruit (UU excluded) from natural vegetation alongside mango fields in both early and late seasons.

In both seasons in 2015, marula fruits were less likely to be infested by *Ceratitis* with increasing distance from the mango crop (Table 2.3), but this effect was not observed in 2014. Distance to the mango crop also affected the intensity of *Ceratitis* infestation per fruit in the late season of 2015, with the abundance of *Ceratitis* emerging per fruit decreasing with distance from mango fields (Table 2.3, Fig. 2.7).

Fruit ripeness, fruit abundance and fruiting marula tree abundance

Ripe fruit on the ground (FR) were 3.9 and 4.4 times more likely, on average, to be infested than unripe (FU) in the early and late season of 2015, respectively. In the late season of 2014, FR fruit were only 2.7 times more likely to be infested on average than FU fruit.

The abundance of *Ceratitis* flies emerging per fruit was 1.3 and 1.5 times greater on average for FR fruit than FU fruit in the early and late season of 2015, respectively (Table 2.3). Fruit ripeness had no effect on the intensity of *Ceratitis* infestation per fruit in 2014. The number of surrounding fruiting marula trees did not determine the likelihood or the intensity of fruit infestation by *Ceratitis* in any of the three sample seasons.

Table 2.3. Parameter estimations from maximum likelihood tests and fit statistics of the ZANB model for the late marula fruiting season in 2014 (n = 507), and the early and late season in 2015 (n = 304, 605, respectively). Data include fruit collected in the natural vegetation alongside mango fields. For all models, only fruit within the FU and FR ripeness categories were included. The intercept corresponds to FU fruit at 0 m from mango fields. () = standard error of coefficient, Sig = level of significance, ‘n.s.’ denotes non-significance at $\alpha = 0.05$.

Parameter	2014		2015			
	Late season		Early season		Late season	
	Coefficient	Sig	Coefficient	Sig	Coefficient	Sig
<i>Binomial hurdle component of model (presence of Ceratitidis)</i>						
Intercept	-1.57 (0.23)	p < 0.001	-0.50 (0.24)	p < 0.01	-1.36 (0.22)	p < 0.001
Distance to mango (m)	-0.002 (0.001)	n.s.	-0.004 (0.002)	p = 0.028	-0.004 (0.001)	p = 0.014
FR fruit ripeness	0.99 (0.22)	p < 0.001	1.37 (0.25)	p < 0.001	1.49 (0.21)	p < 0.001
No. fruiting trees	0.04 (0.07)	n.s.	0.15 (0.08)	n.s.	-0.07 (0.06)	n.s.
<i>Zero-truncated negative binomial component of model (abundance of Ceratitidis)</i>						
Intercept	1.81 (0.18)	p < 0.001	2.34 (0.14)	p < 0.001	2.24 (0.13)	p < 0.001
Distance to mango (m)	-0.002 (0.0008)	n.s.	-0.001 (0.0008)	n.s.	-0.001 (0.0007)	p = 0.033
FR fruit ripeness	0.09 (0.18)	n.s.	0.29 (0.12)	p = 0.019	0.38 (0.13)	p < 0.01
No. fruiting trees	0.006 (0.06)	n.s.	0.007 (0.036)	n.s.	0.04 (0.04)	n.s.
Log likelihood	-575.3		-628.8		-878.3	

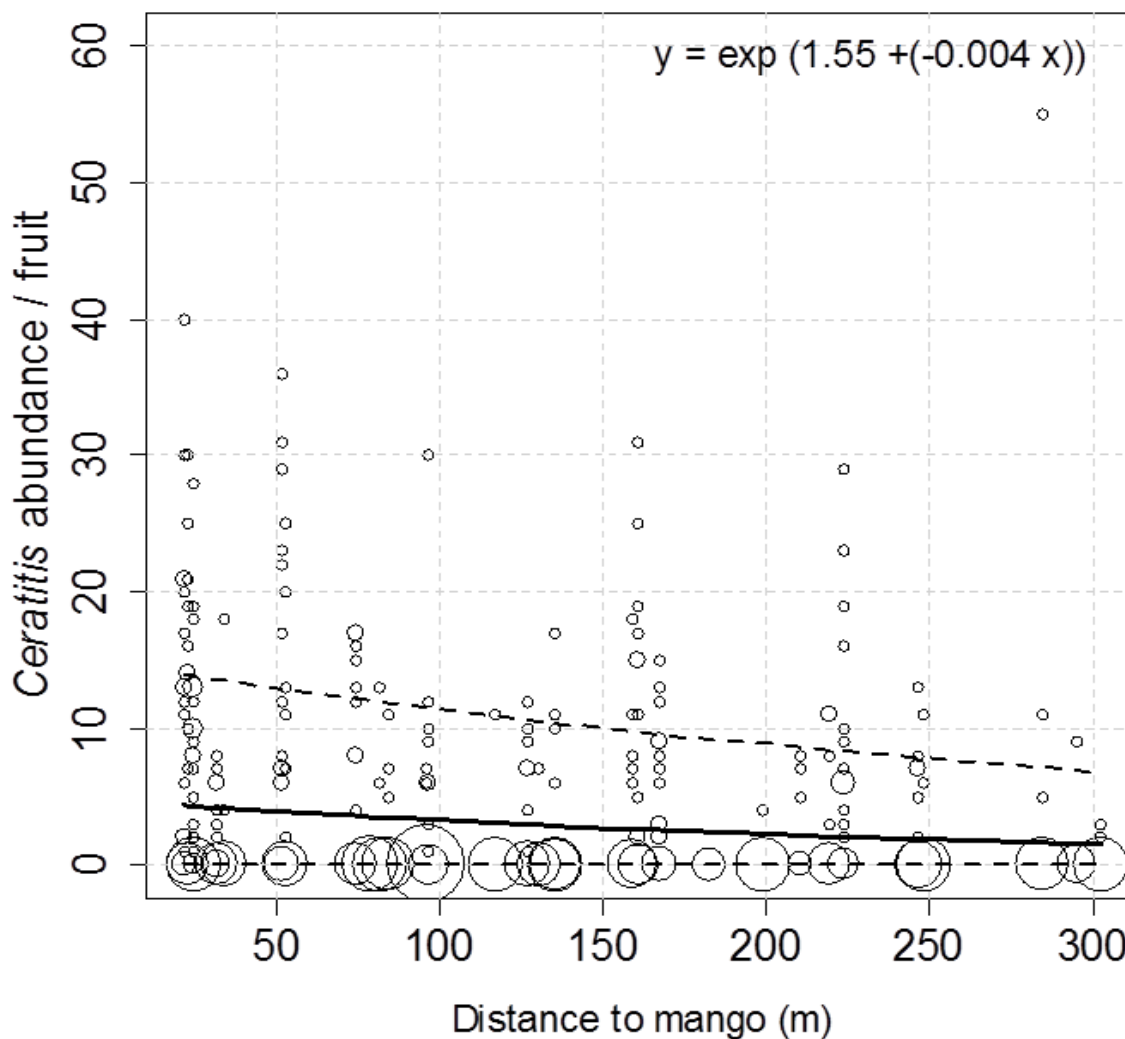


Figure 2.7. Abundance of *C. cosyra* emerging per fruit (FU and FR ripeness categories only) (n=605) at increasing distance from the mango crop in the late marula fruiting season (2015). Lines represent mean \pm sd predicted abundance from best fit model. Equation was calculated using glm.nb models for each vegetation type. Point size is scaled according to frequency of flies per distance point.

2.4 DISCUSSION

This study presents one of the few examples to date of how agriculture affects spill-over of a crop pest associated with a native plant host in a heterogeneous landscape. I considered the economically important fruit fly genus *Ceratit*s and its infestation of marula (*Sclerocarya birrea* subsp. *Caffra*) in natural vegetation alongside mango fields (*Mangifera indica* L.) in a major conservation area in South Africa, the Kruger to Canyon (K2C) Biosphere Region. At the end of mango fruiting season, *Ceratit*s abundance accumulated in the natural vegetation at close proximity to mango fields but not in distant vegetation. Below, I relate my findings to spill-over effects in response to host availability shifts and discuss the implications for conservation.

***Ceratitis* spill-over in response to shifts in resource availability**

Marula fruit alongside mango farmlands were approximately 25 times more likely to be infested by *Ceratitis* fruit flies than fruits collected far from the mango crop at the end of the mango fruiting season (late season). This finding may suggest that *Ceratitis* spills-over from mango fields to natural vegetation at the end of mango season when marula replaces mango as the most apparent resource in the landscape. Crop monocultures represent an abundant and apparent resource in agricultural landscapes (Root 1973), on which herbivorous insects like *Ceratitis* proliferate to reach pest status. At the end of the mango fruiting season, the concentration of fruit resources shifts in the landscape as marula comes into season, creating a strong productivity gradient from mango fields to natural vegetation (Rand, Tylianakis & Tschamntke 2006). *Ceratitis* appears to respond to this gradient by diffusing out of crop fields to find suitable oviposition sites among marula in natural vegetation. Spill-over of *Ceratitis* from mango fields into adjacent natural vegetation is further supported by the accumulation of *C. cosyra* and overall *Ceratitis* abundance in natural vegetation rather than mango fields in the late marula season when all mango fruit had been removed from the farmlands.

***Ceratitis* spill-over in response to “associational susceptibility”**

Higher infestation of marula alongside mango fields than in distant vegetation may also be linked to “associational susceptibility” (hereafter, AS), that is, the indirect plant-plant interaction that increases the likelihood that marula is detected and vulnerable to herbivory by *Ceratitis* due to close proximity to mango (Barbosa et al. 2009). Besides dependence on plant-specific traits, AS is also influenced by the relative abundance of the interacting plants, particularly the relative concentration of their resources for pests (Barbosa et al. 2009). With monoculture crops, such as mango, representing a large resource to support a high abundance of pests (Marques, Price & Cobb 2000), AS is likely in the direction from the mango crop to marula, which presents a comparatively low-density resource for *Ceratitis*, both near to and away from the farm.

Though AS at the landscape scale remains largely unexplored, its effect over large distances is likely limited by the dispersal scale of the focal pest (Grez & Gonzalez 1995). With immobile (poorly dispersive) herbivores expected to be influenced by small-scale changes in plant composition and mobile insects exhibiting no response to small-scale habitat fragmentation (Banks 1998), it follows intuitively that small-scale plant associations (rather than landscape-scale interactions) should impact herbivores displaying poor dispersal ability (Barbosa et al. 2009). *Ceratitis* flies are relatively poor dispersers, remaining mostly within tens of metres but up to 400-700 m from the point of emergence from hosts (though *Ceratitis capitata* may disperse up to 9.5 km in some instances, (Meats & Smallridge 2007). Consequently, distant marula (5.2 – 6.2 km away from mango) may be unlikely to experience AS with the mango crop as strongly as marula alongside the mango fields, despite the availability of mango at the landscape scale. However, *Ceratitis* has been known to colonize large

areas (50 – 80km²) in search of oviposition sites (Eskafi & Kolbe 1990) and landscape AS may occur if critical resources for *Ceratitis* are available in the distant natural vegetation, or, in other cases, if overwintering survival is enhanced in these habitats (Barbosa et al. 2009). Assuming that provision of these resources is substantial alongside the mango farms, this may eliminate the need for *Ceratitis* to disperse into the distant vegetation.

***Ceratitis* “population cycling” and marula as an alternate host**

However, high *Ceratitis* abundance and marula infestation alongside mango fields may suggest that this resource is a suitable alternate host for *Ceratitis* when mango goes out of season, without the need to disperse into the distant vegetation. Due to the polphagous diets and broad host ranges of many *Ceratitis* species, this cycling between hosts, termed “population cycling”, is a life history trait commonly observed among *Ceratitis* fruit flies (Headrick & Goeden 1996 and references therein). Among species that do not diapause, population cycling is believed to be critical in maintaining fly populations throughout the year. In South Africa, the seasonal phenology of the three important *Ceratitis* species, including *C. cosyra*, is determined by the availability of host plants (De Villiers et al. 2013). *C. capitata* has been shown to disperse between areas in response to spatial and temporal shifts in host resource availability throughout the year (Annecke & Moran 1982). Home gardens are also shown to be important refuge sites for *C. capitata* and *C. rosa* in agricultural landscapes (De Villiers et al. 2013).

In this study, the high abundance of trapped *Ceratitis* and high fruit infestation alongside mango fields in the late season suggests that *C. cosyra* uses marula as an alternate host when mango goes out of season. Monocultures are believed to induce area restricted movement of herbivores, making pests less likely to leave fields when the crop is in season (Holmes & Barrett 1997), but with the loss of the crop-host resource, *C. cosyra* likely spills over into natural vegetation where it can use marula as an alternate host. By maintaining their populations in these reservoirs outside of the crop season, pests may then re-establish on farms when the crop is fruiting again, and cause substantial crop damage and economic losses throughout the season (Headrick & Goeden 1996).

Although *Ceratitis* does appear to shift hosts from mango to marula at the end of mango season, marula may not necessarily represent the source of *Ceratitis* for mango at the start of the next crop season. In an agricultural landscape where several crops are farmed alongside each other, shifts in the availability of major apparent resources may be limited to between crop species, rather than between crops and plant hosts in the natural vegetation. In the case of the K2C, *Ceratitis* is known to use several *Citrus* spp. (see De Meyer, Copeland & Lux 2002; Meats & Smallridge 2007)) during the winter months (May – August) when mango and marula are out of season. *Ceratitis* may accumulate again on the farmlands during this season when the *Citrus* crop replaces mango (and marula) as the abundant host resource. In this way, farmlands, rather than natural vegetation may be major reservoirs

of *Ceratitis* throughout the year as the interplay between mango and citrus maintains the pest population across the landscape. Marula may then be important in population cycling of *C. cosyra* in this landscape, maintaining its populations between crop fruiting seasons, especially if marula remains in season after mango harvesting has ended, as was the case in this study. Together, the wild and crop-plant system may present a temporally stable resource to maintain *Ceratitis* populations in this landscape. This area requires further investigation to determine the relative importance of marula and other crops in supporting *Ceratitis* outside of the mango season.

Seasonal shifts in relative mango and marula fruiting affects *Ceratitis* spill-over

The importance of marula as an alternative host for *Ceratitis* may depend on the temporal availability of marula relative to that of mango across the landscape. In 2015, higher infestation of marula close to mango fields, decreasing with distance into natural vegetation, may suggest that *C. cosyra* spills-over from mango into natural vegetation when marula replaces mango as the most abundant host resource in this landscape. However, this effect was not observed in 2014, when the start, peak and end of mango and marula season overlapped, likely due to earlier onset of rainfall (50 -100 mm, December 2013) than in the current study (10 – 25 mm, drought period, November 2014 – April 2015). In fact, another study using pheromone trapping on Bavaria Fruit Estates from March – April, 2014 (Lammers et al., unpublished data) observed that *Ceratitis* accumulated in mango fields rather than in natural vegetation at the end of the mango fruiting season, unlike in this current study. Considering the combined results of these studies, *Ceratitis* may not spill-over into natural vegetation (and host-shift to marula) if mango is still fruiting and available as the concentrated resource in the landscape. Other studies have observed low dispersal of *Ceratitis* into surrounding habitats when the crop was still available (Prokopy, Duan & Vargas 1996; Papadopoulos, Katsoyannos & Nestle 2003).

In the 2014 study by Lammers et al., *Ceratitis* flies were also trapped in the mango fields in early May, two months after mango and marula season had ended. Traps in the natural vegetation at this time were unsuccessful in trapping *Ceratitis*. These findings may suggest that *Ceratitis* may survive in mango fields up until the citrus crop comes into season (May – August), without the need for marula to act as an alternative host in the landscape. *Ceratitis* may then disperse into nearby citrus fields to use the crop as a host over winter, but this requires further research. Findings in this current study suggest that *Ceratitis* spills-over from mango fields into nearby natural vegetation, but that the role of marula in providing mango with a source of pests at the start of the next season depends on the relative timing of marula and the mango crop, as well as the role of citrus in *Ceratitis* population cycling in this landscape.

Habitat margins as important reservoir sites for *Ceratitis*

Habitat margins appear to be particularly important reservoir sites for *Ceratitis* at the end of mango and marula season, with trapped *Ceratitis* abundance decreasing with distance from margins in both natural vegetation and mango fields. A major driver of this effect in crop fields may be the use of chemical pesticides (neonicotinoids and organophosphates). Mango farms in the K2C use pesticides to control *Ceratitis* populations before, during and even after mango fruiting season, with Bavaria Fruit Estates, for example, spraying in mango fields almost every month in a year (J. du Preez, pers. comm.). Pesticides may accumulate in the middle of fields and less towards the field edges, accounting for the decline in *Ceratitis* abundance further into mango fields.

Agricultural disturbance may also account for high *Ceratitis* abundance at close proximity to mango fields in natural vegetation, due to loss of natural pest control. Diverse plant assemblages in the natural vegetation support a diversity of natural enemies that provide natural biological control of insect herbivores and pests (Thies & Tschardtke 1999; Bianchi, Booij & Tschardtke 2006; Gardiner et al. 2009) but specialized species on higher trophic levels, like parasitoids, are known to be particularly sensitive to disturbance (Holt 1996; Chaplin-Kramer et al. 2011). Disturbance such as pesticide use may threaten these natural enemies, weakening top-down control of *Ceratitis* in and near to mango fields. Indeed, Henri et al. (2015) observed higher *Ceratitis* pupal predation in natural vegetation than in mango fields, suggesting that natural enemies cannot colonize the disturbed habitat, despite the availability of *Ceratitis* as prey.

In natural vegetation, parasitoids may be threatened at close proximity to mango fields, resulting in lower top-down control and higher *Ceratitis* infestation of marula at habitat margins. Generalist enemies, such as ants, which forage for *Ceratitis* pupae within the soil, have displayed increasing activity with distance into natural vegetation alongside mango farms in the K2C (Nakagawa & Schielzeth 2013; Henri et al. 2015). The higher abundance of parasitoids observed in the distant vegetation (in the late season only) than alongside mango fields may also suggest that natural control of *Ceratitis* may be less effective at habitat margins. However, since overall parasitoid abundance was low in this study, definitive conclusions cannot be made about the role of parasitoids in controlling *Ceratitis* populations between habitats. Determining the importance of marula as a host for parasitoids and as a source of natural pest control, and the vulnerability of this ecosystem service to pesticides in adjacent crop fields requires further research.

Nevertheless, margins appear to be important reservoir sites for *Ceratitis* at the end of the fruiting season. This is congruent with the traditional view that margins are a source of pests and crop losses (Van Emden 1965). Resultantly, habitat margins are often severely managed as a form of pest control, despite their potential as a source of natural enemies of crop pests (e.g. higher pupal predation at margins than in mango field centres, Henri et al. 2015). Also, the accumulation of pests and higher

marula infestation at the margin in the late season provides further evidence that *Ceratitidis* may spill-over from mango fields, relying on marula as an alternate host for population cycling when the crop is out of season.

The effect of marula ripeness and availability on *Ceratitidis* infestation

Abscised and ripe fruits (FR) were most likely to be infested by *Ceratitidis* in natural vegetation adjacent to mango fields. While immature and mature green fruits still remaining on trees have been associated with higher abundances of *Ceratitidis* elsewhere (Gikonyo, Lux & Nemeje 2005; Sciarretta & Trematerra 2011), the increasing chance of infestation with fruit ripeness may be expected since ripe fruit have had the longest exposure to gravid *C. cosyra* females. Odours released by ripe fruit are also detected as short-range olfactory stimuli by females to signal the suitability of hosts for larval survival and development (Yuval & Hendrichs 2000; Gikonyo, Lux & Nemeje 2005).

In both early and late seasons of 2015, fruit abundance within the ripeness category that made up the greatest proportion of total fruit in each season, increased the likelihood of *Ceratitidis* infestation. Since a larger fruit resource would present an enhanced olfactory stimulus, fruit abundance likely played a greater role in directing *Ceratitidis* to fruiting trees, rather than influencing oviposition events *per se*. This accounts for why UU fruit abundance increases infestation events, even though FR fruit are preferred for oviposition in the early season. Furthermore, if the size of the fruit resource per tree alone is sufficient to attract *Ceratitidis* females to potential hosts, this would account for why the number of surrounding fruiting trees had a negligible effect on fruit infestation in either season. Several other studies, however, confirmed that host tree abundance and fruit availability do indeed influence population size and distribution of *C. capitata* (Vera et al. 2002; Sciarretta & Trematerra 2011).

Conclusions and perspectives for conservation

This study demonstrates how mango farmlands affect *Ceratitidis* dynamics in adjacent natural vegetation. I have shown how *Ceratitidis* appears to spill-over from crop fields, where populations accumulate when the crop is in season, to natural vegetation when alternative hosts, such as marula become the most ‘apparent’ host resource in a heterogeneous landscape. In particular, the likelihood of marula infestation by *C. cosyra* alongside mango fields is high, likely due to increased associational susceptibility of marula to infestation at the habitat scale. Although marula may also experience associational susceptibility at the landscape scale, since *Ceratitidis* may disperse over large distances, marula infestation was notably lower in the distant vegetation. This suggests that marula directly alongside the crop may present a substantial alternate resource to support *Ceratitidis* populations, without the need for flies to disperse over large distances when the crop goes out of season.

Ceratitis accumulated in the natural vegetation at the end of mango season to utilize the available marula resource. Fruit flies may shift hosts between seasons as a form of “population cycling” to maintain its populations throughout the year without overwintering. Further research is required to determine whether *Ceratitis* shifts from marula to citrus crops in this landscape, and therefore, whether marula acts as an important pest reservoir between mango and citrus seasons. Nevertheless, this study highlights how marula acts as an important alternate host for *Ceratitis* when mango goes out of season but the role of marula as a pest reservoir likely depends on seasonality and the relative timing of mango-marula fruiting between years.

The results highlight the spill-over of *Ceratitis* from mango fields into natural vegetation at the end of the crop season. Fruit flies may shift hosts across this landscape to maintain their populations throughout the year and the role of marula in this process appears to depend on seasonality and temporal variation in crop-non-crop fruiting. Managing mobile, polyphagous *Ceratitis* in this landscape may require an area-wide approach that targets different habitats, particularly habitat margins, depending on seasonal availability of different host resources (De Villiers et al. 2013). Co-operation among conservationists and farmers is required to optimize farm productivity and ensure agricultural sustainability, while mitigating the negative effects of agriculture on natural ecosystems in heterogeneous agricultural landscapes.

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Chapter 3

Interactive effects between land-use transformation and alien plants in driving community changes among plants, herbivores and parasitoids

ABSTRACT

Habitat transformation and biotic invasions are the two greatest threats to global biodiversity but their relative and interactive impacts on multi-trophic systems are largely unknown. On farmlands, transformation and invasion may disrupt native plant-insect communities, with consequences for species interactions such as herbivory. This study investigates the combined effects of land-use transformation and alien plants on communities of plants (represented by seed abundance), seed herbivores and parasitoids in crop fields, habitat margins and natural vegetation. Crop fields had equal alien and native seed species richness but aliens contributed up to 85% of the total seed abundance, suggesting that crop fields can represent areas of high alien propagule pressure. Insect herbivores and parasitoids were reared from seeds collected in each habitat to determine how land-use and the relative abundance of alien vs. native seeds affect plant and insect abundance and richness. Crop fields had approximately 10, 25 and 12 times fewer seeds, herbivores and parasitoids, respectively than the natural vegetation. High % alien seed abundance was associated with low seed herbivore and parasitoid species richness across the landscape, with parasitoids being the most severely affected. In crop fields, the proportion of seeds infested by herbivores was 75% lower than natural vegetation but seed herbivory was patchy across the landscape, with incidences of high seed infestation (up to 90% of seeds infested) in all three habitats. Disturbance in agricultural habitats should be mitigated to reduce risk of invasion and interactive negative effects of habitat change and alien plants on plants and insects at the habitat and landscape scale. This will ensure long-term sustainability of ecosystem services in agricultural landscapes that benefit farmers, including natural pest control, and promote ecosystem stability and functioning.

3.1 INTRODUCTION

Human activity is driving changes to natural environments at an unprecedented rate, resulting in increased disruptions to ecosystems on a global scale (Chapin et al. 2000; Sala et al. 2000). Biological diversity is declining rapidly under these conditions (Olson et al. 2002) and habitat loss and fragmentation due to land-use change are considered the greatest drivers of this global environmental change (GEC) (Vitousek et al. 1997; Sala et al. 2000). In particular, natural habitats are being extensively transformed for agriculture to meet the growing demands for food as consumption of resources, inefficiencies in food distribution and the human population, already at 7.4 billion people (<http://www.populationmatters.org>), increase worldwide (Tilman et al. 2001).

Substantial and often irreversible loss of biodiversity on farmlands, already documented among several groups of organisms (Fahrig 2003; Tscharrntke et al. 2005; Butler, Vickery & Norris 2007; Koh & Wilcove 2008), drives a cascade of impacts through complex food webs by disrupting species interactions. This is believed to have implications for ecosystem stability, such as the ecosystem's ability to return to an equilibrium state after some perturbation event (termed "dynamic stability") or its ability to withstand change (known as "ecosystem resistance and resilience") (McCann 2000).

While the correlation between biodiversity and ecosystem stability hinges largely on the ecological scale at which biodiversity is considered, the response of different functional groups to disturbance and the strength of the interactions between species, experimental evidence and theory support that changes in community composition destabilize ecosystem dynamics and drive ecosystem collapse (McCann 2000 and references therein).

These unstable communities often display a lowered capacity for withstanding further disturbance, such as the invasion by non-native species (hereafter “alien” species) (Chapin et al. 2000; Brooker 2006; Suttle, Thomsen & Power 2007). Traditionally, simplified communities, including those on cultivated lands, are believed to be more susceptible to alien invasions due to enhanced fluctuations in population densities (hypothesis proposed by Elton 1958). Furthermore, habitat transformation eliminates natural physical and environmental barriers, such as landscape features, habitat quality and microclimate conditions, which previously excluded aliens from the habitat under normal ecological conditions (Parendes and Jones 2000). Human disturbance may also remove biotic barriers, such as native competitor species, which usually limit the effectiveness of intrinsic alien traits (e.g. dispersal mechanism, seed production and viability) and propagule pressure (i.e. the availability of propagules for invasion) alone in driving plant invasion (Parendes and Jones 2000).

Alien species invasions have accelerated with increased human globalization and are second only to habitat transformation as a threat to global biodiversity (Wilcove et al. 1998; Mack et al. 2000; Sala et al. 2000). They contribute substantially to native species declines and hence, ecosystem stability, but also disrupt ecosystem stability through the addition (that is, invasion) of the alien species themselves to communities. Through effects on biodiversity and ecosystem stability, aliens may also disrupt ecosystem function, including a broad range of ecological processes that are shaped by ecosystem composition and dynamics associated with species interactions (Vitousek et al. 1997, Strayer 2012).

Considering the frequent co-occurrence of land-use change and alien plant invasions in ecosystems worldwide, these factors are believed to have great capacity to interact and elicit synergistic or additive impacts on global diversity, species interactions and ecosystem structure and function (Didham et al. 2007). Nevertheless, these two drivers of GEC are often considered and investigated independently (Fazey, Fischer & Lindenmayer 2005). Consequently, the relative impacts of these two drivers on species interactions at the landscape scale is poorly known, despite the increasing focus on multi-trophic systems in the GEC literature (e.g. plant-pollinators, Lopezaraiza-Mikel et al. 2007, Aizen et al. 2008, Carvalheiro et al. 2010; plant-seed predators, Rand & Louda 2006; host-parasitoid, Kruess and Tschardtke 2000). This limited understanding hinders conservation and management across several ecological scales because species interactions form the intrinsic link between biodiversity and ecosystem functions, particularly the provision of important ecosystem services (ES)

and disservices (EDS) (Vitousek et al. 1997). These include ecological processes that are beneficial or harmful to human economic and social activities (Pimm et al. 1995).

In agriculture, insects are essential components in the provision of ES and EDS (Losey & Vaughan 2006). Herbivorous insects contribute to economic losses on farmlands by reducing crop productivity and damaging crop products, but may also control weeds, reducing competition with the crop for abiotic resources as a result. Insects at higher trophic levels, such as parasitoid wasps, are natural enemies of herbivores, some of which are agricultural pest species. Understanding the relative importance of GEC drivers and their interactive effects on plants and insects may help to focus GEC management and conservation efforts in agricultural landscapes, to limit the decline of ES and ensure ecosystem stability in agroecosystems and surrounding habitats.

To my knowledge, this is the first study to consider the effects of both land-use and alien plant invasions on plant and insect communities in a landscape transformed for agriculture. I investigated how communities of seeding plants, seed herbivores and parasitoids respond to these two drivers of GEC in the Kruger to Canyons (K2C) Biosphere Region, South Africa. Before considering these effects, I first determined whether land-use type and alien plant invasions interact at the plant level by addressing the following question: How does land-use affect alien seed abundance and richness?

Contrasting land-use types in an agricultural landscape were investigated, including mango crop fields and preserved patches of natural vegetation. Margins between these two habitat types were also included because ruderal areas, roadsides and trails are known to be important channels for alien dispersal (Brothers & Spingarn 1992; Parendes & Jones 2000). Based on the existing evidence for how disturbance facilitates invasion, I expected the most disturbed land-use type, mango fields, to have the highest alien seed abundance and richness in this landscape.

I then investigated how the structure and composition of plant and insect communities respond to the two GEC drivers at the landscape scale. I reared insect herbivores and their parasitoid wasps from seeds collected in the vegetation types to address the following question: How do land-use type and alien plants affect the abundance and species richness of i) plants (represented by seed), ii) seed herbivores and the proportion of seeds they infest, and iii) parasitoids?

Alien plants often lack specialist natural enemies in their introduced ranges (which facilitates their invasion: 'enemy release hypothesis', reviewed by Keane & Crawley 2002). Furthermore, specialized organisms are likely to be more susceptible to ecological disturbance (Kruess and Tscharntke 1994). Therefore, I expected increasing alien plant invasion to be associated with lower seed herbivore species richness as specialists are lost, particularly in mango fields. Generalists may replace specialists, so although there may be a decrease in number of herbivorous insect species, there may be no net change in abundance in highly invaded areas (Heleno et al. 2009). Therefore, I also expected

no change in herbivore abundance and seed infestation (herbivory) with increasing propagule pressure and hence, among land-use types.

Parasitoids should be more susceptible to land-use change and increasing alien plants because they are more specialized than seed herbivores (Chaplin-Kramer et al. 2011) and are found at higher trophic levels (Holt 1996). I expect that the loss of specialist herbivores (predicted above) may represent the loss of specific hosts for parasitoids, which would in turn drive declines in parasitoid richness. Assuming generalist parasitoids are also lost in response to disturbance, I also expect parasitoid abundance to decline with increasing invasive species' seed abundance and to be lowest in the mango fields.

3.2 METHODS AND MATERIALS

3.2.2 Study design

In the Kruger to Canyons Biosphere Region (see Appendix I for site description), sampling was conducted on four mango farms (3 – 14 km apart), namely Bavaria Fruit Estates, Grovedale, Moriah and Mohlatsi. On each farm, a focal mango field in close proximity to natural vegetation was selected. Sampling was conducted within a 1 km radius of this central field on each farm, hereafter referred to as a 'zone' (Fig. 3.1). I sampled in two non-overlapping zones on the two larger farms (Bavaria and Moriah, mean farm size $\sim 8.5\text{km}^2$) and in one zone on each of the two smaller farms (Grovedale and Mohlatsi, $\sim 1.6\text{ km}^2$). Within each zone, I selected plots to represent three land-use types: 1) Mango fields (MNG), in which in-crop weeds grew in 2.5 m-wide corridors between rows of mango trees, 2) natural vegetation (NTL), typical of the surrounding savanna vegetation and displaying little to no human disturbance and 3) margins (MAR), typically observed between the mango fields and natural habitats along roadsides, fence lines or rows of *Casuarina* sp. windbreaks. The vegetation in MAR plots contained species from both MNG and NTL areas and had obvious signs of human disturbance, including soil erosion and frequent mowing.

I sampled along at least three 30-m linear transects that were ≥ 30 m apart in each land-use type, yielding a total of 18, 19 and 20 transects in the MNG, NTL and MAR vegetation, respectively. Sampling was conducted along the same set of transects during two seasons after mango harvesting, from April to the end of May, and from June to the end of July. I sampled in two seasons to determine whether effects observed in this study may be generalized across broader temporal scales (see Fazey, Fischer & Lindenmayer 2005).

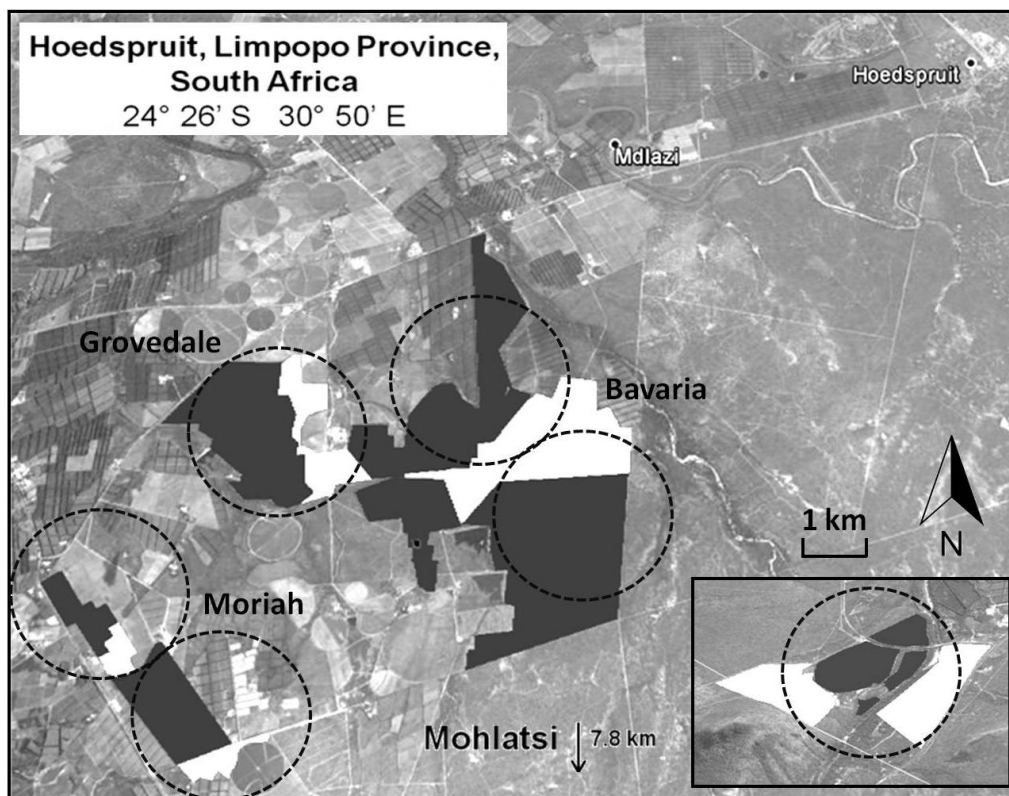


Figure 3.1. Map of the study region in the Kruger to Canyons Biosphere Region near Hoedspruit, Limpopo Province, South Africa. Highlighted areas show the sampled area on four mango farms, with Mohlatsi depicted in the inset. Dark grey areas denote mango fields (MNG) on each farm (citrus and other crop fields excluded) and white areas denote patches of natural vegetation (NTL) alongside or between mango fields. Margins (MAR) were sampled within or on boundaries between MNG and NTL. Circles indicate 1 km-radius zones in which transects were sampled in each of the three land-use types on each farm.

3.2.3 Plant community sampling

Along each transect, a sample of seeds (>20, where possible) was collected from every seeding/fruitletting plant species (excluding grasses) that occurred within 2 m on each side of the transect line. In cases where species were highly abundant and sampling every individual was impractical, seeds were sub-sampled within a 3 x 4 m area containing the species along the transect (which I term a seed ‘batch’). For every plant species encountered per transect, I recorded: 1) total seed abundance per individual/batch and 2) the total abundance of seeds collected per individual/batch. This information enabled calculation of overall expected densities of seeds, herbivores and parasitoids for each transect. All plants were identified to species and it was noted whether each species was native or alien.

3.2.4 Rearing insects from seed samples

Seed samples were transferred to envelopes that were sealed with tape to prevent the loss of any insects after emergence from the seeds. Fleshy fruits (such as *Cucumis* sp., *Strychnos* sp. or *Ficus* sp.) were placed in plastic tubs containing commercially-available, dry and sterile pool sand as a substrate for insect pupation. The tubs were covered with a piece of chiffon secured with an elastic band, to prevent insects from escaping, while also allowing for aeration of the sample to prevent samples from rotting and affecting insect emergence.

The seed samples collected in both seasons were stored together in a closed room at ambient temperature (25 – 31 °C) and checked for insect emergence after an average of 290 days from collection. This was the maximum amount of time allowed due to time constraints, but some insects may still have emerged up to a year after seed collection (L. G. Carneiro, pers. comm.). Nevertheless, most insects would have emerged in the initial 290 days and because all samples were compared after similar amounts of time had elapsed, insect communities are still comparable. All emerged insects were counted, identified to Order and assigned to morphospecies.

Wasps (Hymenoptera) were identified to Family by L. Mokubedi at SANBI using identification keys provided by Goulet and Houber (1993). Specimens were then classified as seed herbivores or parasitoids using biological descriptions of each Family provided by Goulet and Houber (1993). Wasps whose biology was unknown, that were polyphagous, or could not be identified to Family due to poor specimen quality were included in both herbivore and parasitoid analyses. These specimens only represented a small portion of the total sample in each season (AM: 1.01%; JJ: 0.57%). All insect specimens were preserved in 80% ethanol for reference and are housed at SANBI, Cape Town, South Africa.

3.2.5 Data analysis

All quantitative plant and insect data were multiplied up to give estimates of total abundance within each transect for analysis. For the plant community, I determined the total alien and overall seed abundance by summing across all individuals/batches of alien and all species. For the insect community, I calculated the total abundance per morphospecies expected to emerge from all seeds observed on each transect, using the total abundance emerging from all sampled seeds and the sampled seed: total seed abundance ratio. This was to ensure that insect abundance was standardized to the area of the transect to be comparable in analyses. I summed across morphospecies to determine the total abundance of insects expected to emerge overall per transect.

To account for the hierarchical design of this study with transects nested within zones and farms, mixed effects models were used for all statistical analyses (Gelman & Hill 2006; Zuur et al. 2009). A

summary of all fitted models, the data used in each case and outliers excluded, are presented in Table 3.1. Prior to model-fitting, all data were evaluated for outliers and to determine the distribution of the data. Data that were normally distributed were analysed using Gaussian linear mixed effect models (LMMs). In cases where the data were not normally distributed, generalized linear mixed effects models (GLMMs) were used. These models use intrinsic link functions that negate the need for data transformations, which are often not recommended for ecological datasets, especially count data (O'Hara & Kotze 2010).

Explanatory variables were assessed for collinearity before models were fit (Zuur et al. 2009). Some models included season as a fixed factor, with transect nested within zone and farm as random effects ("Season fixed", Table 3.1). In cases where separate models were fit for April-May and June-July (see below), another model was fit thereafter in each case to determine the effect of season on each response variable. These models included season as a fixed effect and transect, nested within zone and farm as random effects, to account for the repeated sampling on the same set of transects between seasons. Model selection and results are presented in Appendices V, VII and VIII.

How does land-use transformation affect alien seed abundance and richness?

Binomial GLMMs were used to determine whether the proportion of the total seeds that were alien differed among the three land-use types. The models included land-use type and season as fixed effects and transect nested within zone and farm as random effects. Total seed abundance per transect was also included as a scaled fixed factor in each model to account for the variability in total seed abundance among transects.

The difference in species richness of aliens and the proportion of alien relative to native seeds (A:N) among the three land-use types was also evaluated. Counts of alien species were analysed using GLMMs with Poisson error structure. The A:N species richness data were also counts of alien species but were analysed using Poisson GLMMs that included native plant species counts as an offset in each model (Zuur et al. 2009). Transects containing no native species were excluded (n=3). Both alien and A:N species richness models included land-use type and season as fixed effects and transect nested within zone and farm as random effects. An observation-level random effect with a unique level for each data point (i.e. the length of the data set) was included in each model to deal with overdispersion (see Harrison 2014).

Table 3.1. Summary of error structure and the data, including the values of excluded outliers, used in each fitted model. “Between seasons” model results are presented in Appendix IV.

Response variable	Model	Data	Error structure	Transects (n)	Outliers
<i>Seed abundance</i>					
Alien plants	Season fixed	Proportion	Binomial	114	-
<i>Seed species richness</i>					
Alien plants	Season fixed	Count	Poisson	114	-
A:N plants	Season fixed	Proportion	Poisson + offset	111	Native = 0
<i>Seeding plant community</i>					
Abundance	April-May	Count	Negative binomial	57	-
	June-July	Count	Negative binomial	57	-
	Between seasons	Count	Negative binomial	114	-
Sp. richness	April-May	Count	Gaussian	57	-
	June-July	Count	Gaussian	57	-
	Between seasons	Count	Poisson	114	-
<i>Herbivore community</i>					
Abundance	April-May	Count	Negative binomial	56	3497
	June-July	Count	Negative binomial	55	5053, 12452
	Between seasons	Count	Negative binomial	111	
Sp. richness	April-May	Count	Gaussian	57	-
	June-July	Count	Negative binomial	57	-
	Between seasons	Count	Poisson	114	-
Herbivory (insects per seed)	April-May	Proportion	Binomial	57	-
	June-July	Proportion	Binomial	55	1.38, 1.79
	Between seasons	Proportion	Binomial	112	
<i>Parasitoid community</i>					
Abundance	April-May	Count	Negative binomial	57	-
	June-July	Count	Negative binomial	54	535, 1049, 2817
	Between seasons	Count	Poisson	113	
Richness	April-May	Count	Negative binomial	57	-
	June-July	Count	Negative binomial	57	-
	Between seasons	Count	Poisson	114	-

How do land-use type and alien seed abundance affect overall plant seed, seed herbivore and parasitoid communities?

The effect of alien seed abundance in the three land-use types was investigated for the plant, herbivore and parasitoid communities separately in each season. Abundance and species richness were the two community traits investigated as response variables in each case, with proportion of seeds containing herbivores (i.e. herbivory) also considered for the seed herbivore community. All models included % alien seed abundance, land-use type and the interaction between the factors as fixed effects, and zone nested within farm as random effects.

For analysis of seed, herbivore and parasitoid abundance, GLMMs with Poisson and negative binomial error structure were both considered. In all cases, negative binomial GLMMs had lower AIC values and less overdispersion among residuals than the Poisson models, and were considered the models of better fit. For species richness, LMMs or GLMMs with Poisson or negative binomial error structure were considered based on the distribution of the count data in each case. Random intercept and random slope models were both considered for abundance and richness models and evaluated using AIC values (Zuur et al. 2009). In all cases, random intercept models had lower AIC values and were selected as the models of best fit. All Poisson, negative binomial and normally distributed models were evaluated in each case using AIC values and the error structures of the models of best fit (lowest AIC) are presented in Table 3.1. Model selection for all abundance and richness models is presented in Appendix Va - c.

For herbivory, binomial GLMMs were fitted with the proportion of seeds infested by herbivores per transect as the response variable. The models also used total seed abundance per transect as a weighted variable to account for variability in total seed abundance among transects.

Selection of all models involved evaluation of residual normality and overdispersion by plotting residuals against fitted values and explanatory variables. Likelihood ratio tests, Akaike Information Criteria (AIC) and Akaike weights were used to identify optimal models during the process of backward model simplification. Models with a lower AIC and higher weighting denoted models of better fit (Burnham & Anderson 2002). The proportion of variance explained by fixed effects (marginal R^2) (R^2_m) and both fixed and random effects (conditional R^2) (R^2_c) were also calculated as measures of goodness-of-fit for each model (using the method for random intercept models, Nakagawa & Schielzeth 2013). All models were fitted and selected using packages lme4, nlme and glmmADMB in R v3.0.1 at a significance level of $\alpha = 0.05$ (R Development Core Team 2014).

3.3 RESULTS

How does land-use transformation affect alien seed abundance and richness?

Approximately 149 700 and 128 050 seeds in total were observed in April-May and June-July, of which 24 290 and 16 350 were collected in each season, respectively. Overall, this represented 175 plant species within 43 families, of which 33 (19%) were alien (see Appendix VI for comprehensive species list). The number of alien species overall was approximately equal between April-May and June-July (28 and 27, respectively).

3.3.1 Alien seed abundance

In both seasons, aliens contributed the most to total seed abundance in mango fields than in either the natural vegetation ($z = 5.28$, $p < 0.001$) or the margins ($z = 4.63$, $p < 0.001$) (Fig. 3.2), with no difference between seasons ($\chi^2 = 1.12$, $p = 0.29$). However, land-use type and random effects accounted for little of the variance in proportional alien seed abundance in both seasons ($R^2_c = 0.03$, $R^2_m = 0.03$).

Alien seed abundance was lowest in natural vegetation in both seasons but in some transects, aliens comprised between 93 - 97% of the total seed abundance (Fig. 3.2). Consequently, alien seed abundance was not different between natural vegetation and margins in both seasons ($z = 1.18$, $p = 0.24$). When the few outliers (AM: $n = 1$, JJ: $n = 4$) were excluded (1.5 times the IQR above the 3rd quartile, Crawley 2007), alien seed abundance was significantly lower in natural vegetation than along margins in both seasons ($z = 2.14$, $p = 0.03$) ($R^2_m = 0.03$, $R^2_c = 0.03$), with no difference between seasons ($\chi^2 = 0.69$, $p = 0.41$).

3.3.2 Alien species richness

Of the 33 alien species observed overall across the landscape, 21, 23 and 20 occurred in the mango fields, margins and natural vegetation. In both seasons, the number of alien species in mango fields (mean, ~ 4 species) was significantly greater than along margins (~ 2 species) ($z = 2.14$, $p = 0.03$) but approximately equal to that in natural vegetation ($z = 0.34$, $p = 0.73$). Overall, alien species richness was higher in the three land-use type in April-May than June-July ($\chi^2 = 4.05$, $p = 0.04$, $R^2_m = 0.78$, $R^2_c = 0.88$). The proportion of alien to native species that were seeding at the time of sampling was highest in mango fields, with an average of approximately one alien species observed per native species in both seasons (1.09 ± 0.22). Margins displayed significantly lower alien:native species richness (0.56 ± 0.12) than mango fields in both seasons ($z = 2.76$, $p < 0.01$) and natural vegetation (0.92 ± 0.20) was more similar to mango fields ($z = 0.47$, $p = 0.64$) than to margins ($z = 2.39$, $p = 0.02$, $R^2_m = 0.69$, $R^2_c = 0.76$).

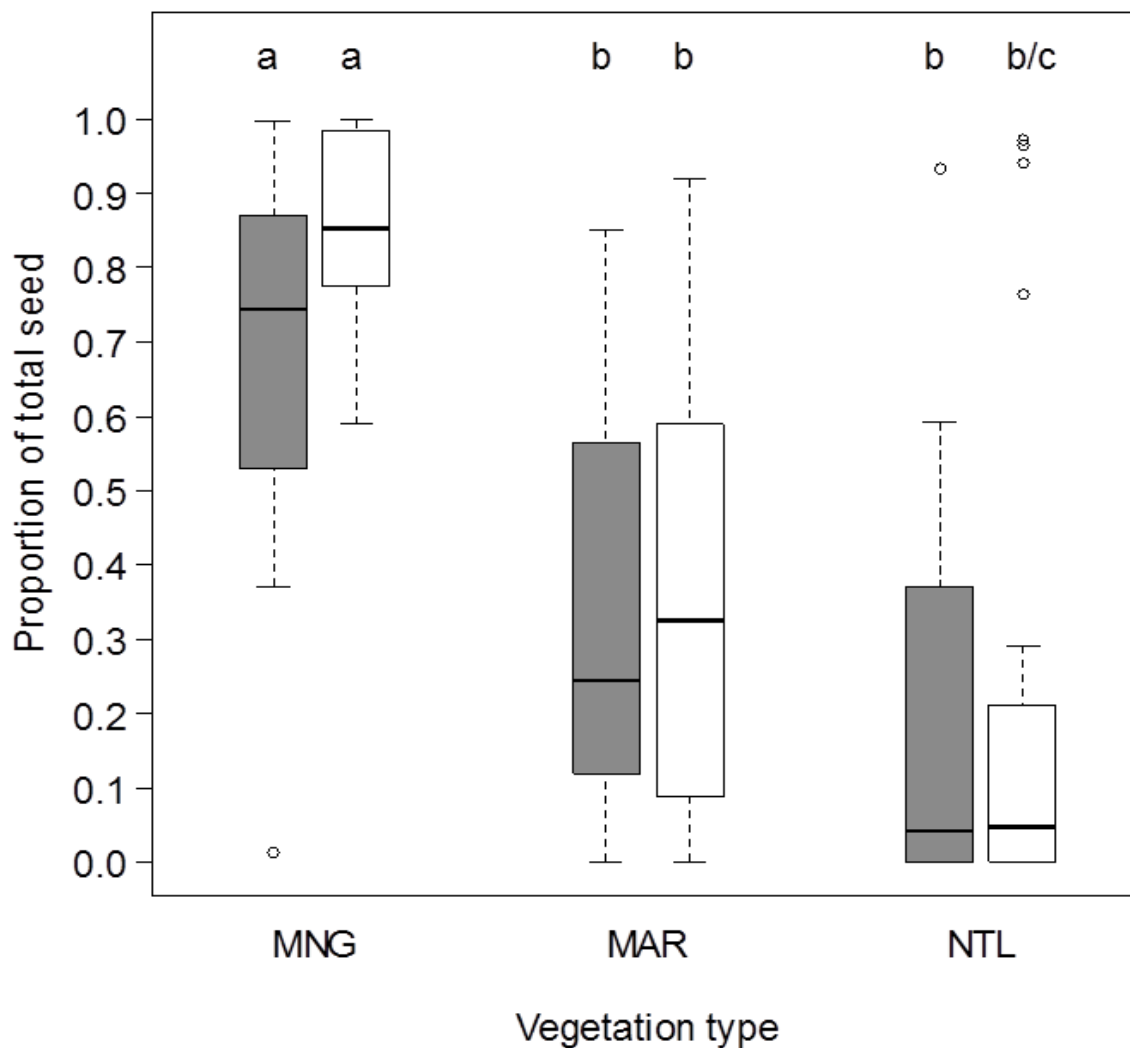


Figure 3.2. Contribution of alien plants to the total seed abundance per transect between mango fields (MNG) (18, 18), margins (MAR) (20, 20) and natural vegetation (NTL) (19, 19) in April-May (grey) and June-July (white). Symbols above boxplots denote significant differences between habitats between seasons. Two options are presented for NTL for analysis: b) including outliers and c) excluding outliers.

How do land-use type and alien seed abundance affect overall plant seed, seed herbivore and parasitoid communities?

3.3.3 Plant seed community

In both seasons, alien seed abundance did not have an effect on overall seed abundance and species richness (Appendix Va). Seed abundance and richness were both significantly higher in April-May than in June-July (Appendix IV).

Mango fields displayed the lowest seed abundance among all three land-use types in April-May ($R^2_m = 0.99$, $R^2_c = 0.99$) and June-July ($R^2_m = 0.99$, $R^2_c = 0.99$) (Fig. 3.3). Mango fields had 2 - 4 times

fewer seeds than margins from April-May to June-July and up to ~ 10 times fewer seeds than in natural vegetation in June-July only (Table 3.2). Similarly, margins had significantly lower seed abundance than natural vegetation in June-July only, but this difference was only marginally significant (Fig. 3.3, Table 3.2).

Species richness was only influenced by land-use type in June-July ($R_m^2 = 0.10$, $R_c^2 = 0.10$) (Table 3.2). In this season, mango fields again had up to ~ 4 times fewer plant species than in the natural vegetation. Plant species richness along the margins was not different from that in either the mango fields or natural vegetation.

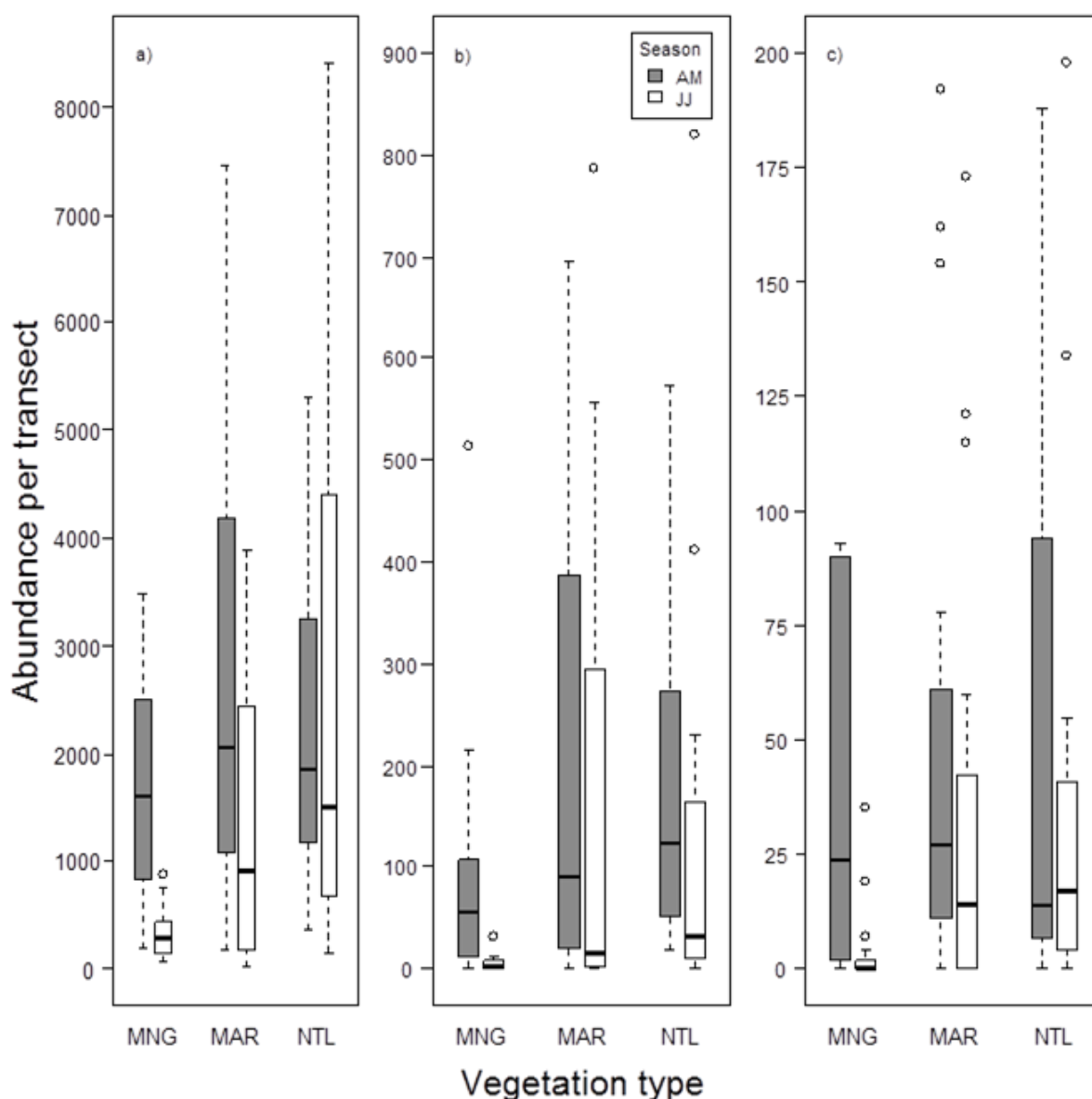


Figure 3.3. Abundance of (a) seeds, (b) insect herbivores and (c) parasitoids per transect in April-May (AM) and June-July (JJ) in mango fields (MNG), margins (MAR) and natural vegetation (NTL). Note that the scale of the abundance axis differs for each trophic level for improved visual clarity in each case.

Table 3.2. Pairwise comparison of the plant (seed), insect herbivore and parasitoid communities, including abundance and species richness, between mango fields (MNG), margins (MAR) and natural vegetation (NTL) in April-May and June-July. Δ Coeff (\pm se) values denote how many times smaller (-) or greater (+) the first land-use type is on average than the second in each pairwise comparison in terms of each parameter. Δ Coeff values have been reverse transformed (natural exponent e^x) to account for the intrinsic logit and log-link functions used to account for non-normality of data using GLMMs with poisson and negative binomial error structure.

	MNG-MAR		MNG-NTL		MAR-NTL	
	Δ Coeff (\pm se)	p-value	Δ Coeff (\pm se)	p-value	Δ Coeff (\pm se)	p-value
Plant community						
<i>Seed abundance</i>						
April-May	- 1.95 (1.29)	0.009 *	- 1.54 (1.30)	0.098	1.27 (1.29)	0.36
June-July	- 4.21 (1.38)	< 0.001 *	- 8.30 (1.40)	< 0.001 *	- 1.97 (1.39)	0.038 *
<i>Seed species richness</i>						
April-May	- 1.16 (1.33)	-	- 1.11 (1.35)	-	0.05 (1.31)	-
June-July	- 1.58 (1.09)	0.15	- 2.73 (1.11)	0.017 *	- 1.15 (1.08)	0.29
Herbivore community						
<i>Abundance</i>						
April-May	- 3.54 (1.56)	0.004 *	- 2.59 (1.58)	0.037 *	1.37 (1.56)	0.61
June-July	- 23.57 (1.81)	< 0.001 *	- 22.38 (1.77)	< 0.001 *	1.05 (1.73)	0.92
<i>Species richness</i>						
April-May	- 2.68 (1.51)	-	- 2.89 (1.54)	-	- 0.20 (1.50)	-
June-July	- 3.10 (1.41)	< 0.001 *	- 2.52 (1.42)	0.008 *	1.23 (1.36)	0.50
Parasitoid community						
<i>Abundance</i>						
April-May	- 1.20 (1.62)	-	- 1.26 (1.65)	-	- 1.05 (1.65)	-
June-July	- 8.13 (1.83)	< 0.001 *	- 9.82 (1.90)	< 0.001 *	- 1.21 (1.88)	0.77
<i>Species richness</i>						
April-May	- 1.00 (1.29)	-	- 1.00 (1.31)	-	1.00 (1.29)	-
June-July	- 2.97 (1.49)	0.007 *	- 4.74 (1.49)	< 0.001 *	- 1.60 (1.39)	0.16

P-values denote significant differences between land-use types (*) at $\alpha = 0.05$. In cases where the null models were the models of best fit (see Appendix Va-c), p-values are not reported and denoted with “-”. In cases where vegetation type was not included in the models of best fit but was significant in an alternative model (with higher AIC than optimal model), the p-values are presented in **bold**.

3.3.4 Seed herbivore community

A total of 2196 and 2541 insects from 259 and 129 morphospecies emerged overall from seeds collected in April-May and June-July, respectively. These abundances were extrapolated to 19 948 and 29 346 insects emerging from seeds overall in each season. Of these abundances, 78.28% and 80.54% were seed herbivores from five orders, namely Coleoptera (41.82%; 90.41%), Diptera (11.71%; 0.44%), Hemiptera (14.10%; 7.02%), Hymenoptera (4.49%; 1.31%) and Lepidoptera (26.12%; 0.09%).

Herbivore abundance was significantly lower in mango fields than along margins or in natural vegetation in both seasons (Fig. 3.3, Table 3.2), with the effect increasing significantly from April-May ($R^2_m = 0.97$, $R^2_c = 0.99$) to June-July ($R^2_m = 0.98$, $R^2_c = 0.99$) (Appendix IV). In June-July, mango fields had up to ~ 25 times fewer herbivores than either the natural vegetation or margins (Table 3.2). Proportional (%) alien seed abundance and its interaction with land-use type were not significant determinants of herbivore abundance (Appendix Vb).

The lowest species richness of herbivores emerging from seeds was observed in the mango fields, with ~ 3 times fewer species in this habitat on average than in either natural vegetation or along margins (Fig. 3.3, Table 3.2) but this effect was only observed in June-July. However, vegetation type only explained very little of the variation ($R^2_m = 0.013$, $R^2_c = 0.86$). Significantly more herbivore species on average emerged from seeds per transect overall in April-May (~7 species) than in June-July (~3 species) (Appendix IV).

In June-July, herbivore richness significantly declined with increasing alien seed abundance across all three habitats in the landscape (Fig. 3.4), with species richness declining by 70% (~4 species) on average from alien-free (0%) to alien-dominated (100%) habitats. Overall, the model that included only % alien seed abundance as a determinant of herbivore richness was a better fit than the model including land-use type, suggesting that % alien seed abundance may be a stronger determinant of herbivore richness at the landscape scale (Appendix Vb).

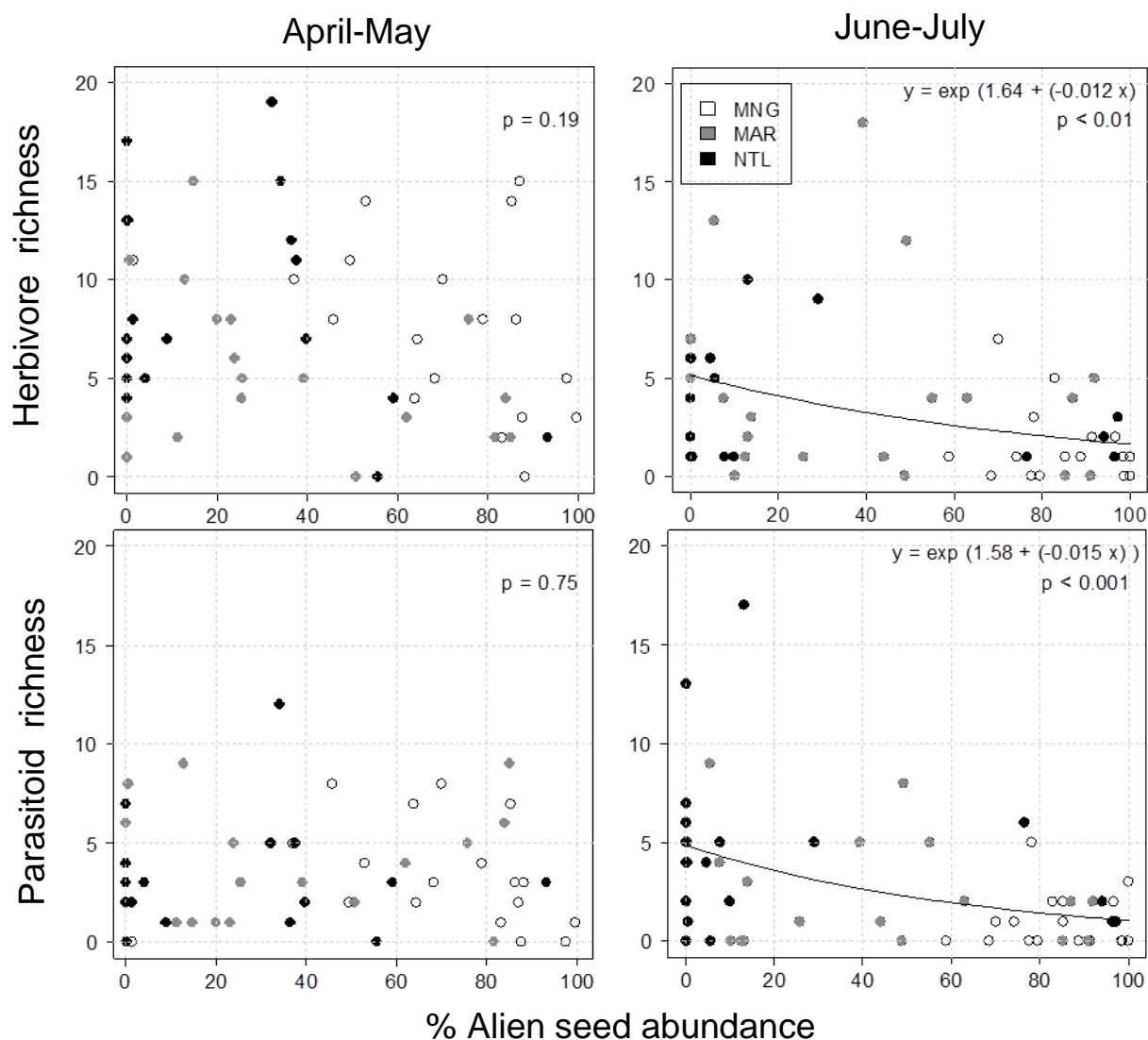


Figure 3.4. Effect of % alien seed abundance on herbivore and parasitoid species richness across the landscape in April-May ($n=57$, 57) and June-July ($n=57$, 57). The land-use type of each transect is also indicated, namely mango fields (MNG), margins (MAR) and natural vegetation (NTL). Equations and lines are negative binomial glm fits of mean herbivore and parasitoid species richness. The equations of the model of best fit and the significance of the effect in each case are presented.

3.3.5 Herbivore infestation of seeds

The average proportion of seeds infested by herbivores was significantly lower in June-July (7.2%) than in April-May (8.7%) (Appendix IV), with the lowest seed infestation in mango fields in both seasons (Fig. 3.5, Appendix VII). On average, 83% and 96% more seeds were infested along margins than in mango fields in April-May and June-July, respectively (Appendix VIII). Approximately 75% more seeds in the natural vegetation were infested than that in mango fields on average in both seasons. In April-May, seed herbivory was highest in natural vegetation but this was likely due to a single transect which had herbivores emerging from approximately every second (1.7) seed encountered (Fig. 3.5). The highest rate of herbivory then shifted to the margins in June-July, where approximately every seed (1.1) had an insect herbivore emerging in the most extreme case.

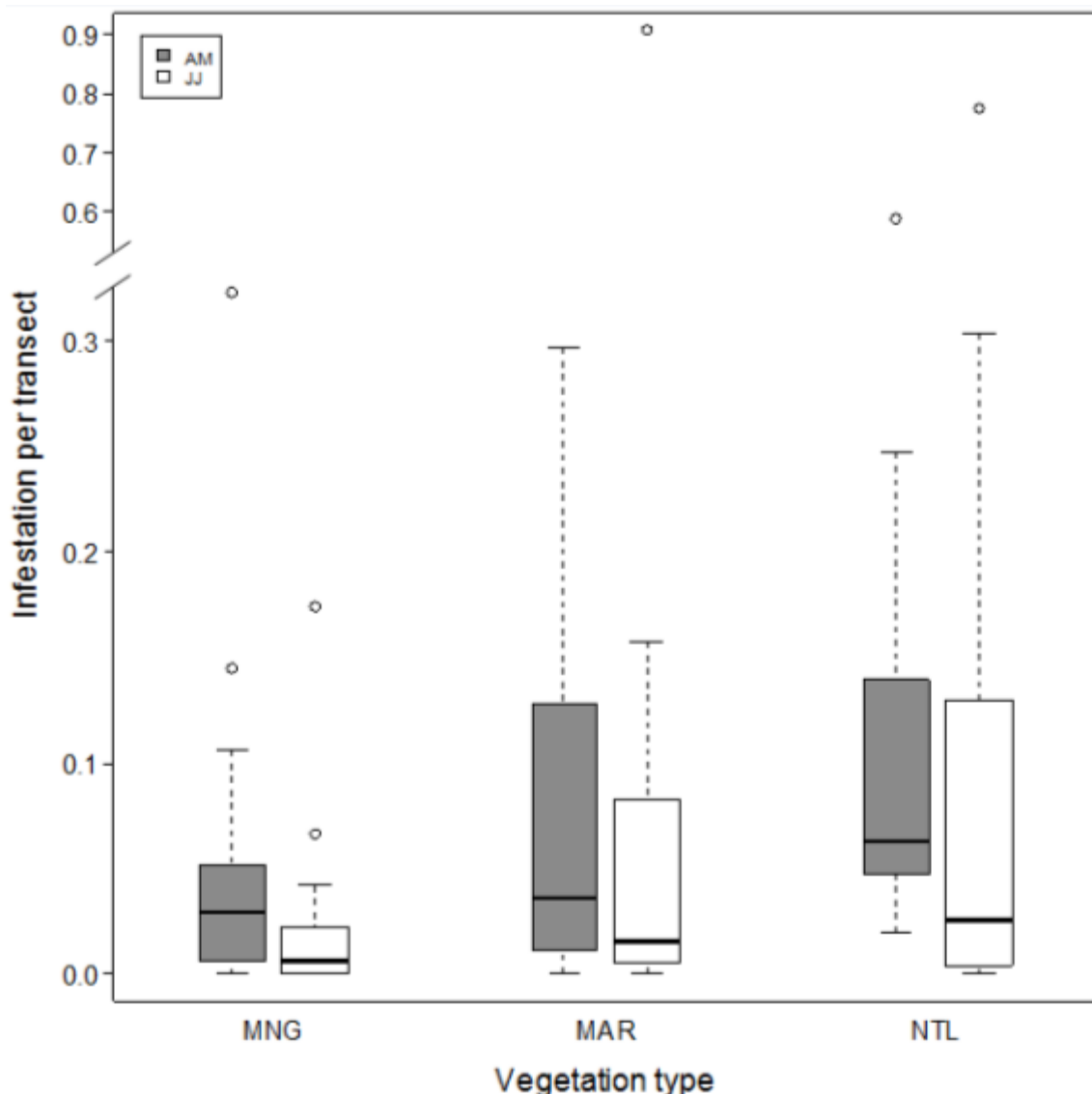


Figure 3.5. Proportion of seeds infested by herbivores per transect between mango fields (MNG) (18, 18), margins (MAR) (20, 19) and natural (NTL) (19, 18) vegetation, in April-May (AM) and June-July (JJ).

Land-use type also significantly influenced the effect of % alien seed abundance on seed herbivory in both seasons, though the interaction between these factors accounted for little variation in April-May ($R^2_m = 0.001$, $R^2_c = 0.02$) and June-July ($R^2_c = 0.005$, $R^2_m = 0.42$) (Fig. 3.6, Appendix VII). In mango fields, seed infestation increased with % alien seed abundance in April-May. The opposite effect was observed in the natural vegetation, where herbivory declined with increasing % alien seed in June-July. Along margins, the opposite effect to that in the mango fields in April-May was observed, with herbivory decreasing as the proportion of alien seeds increased (Fig. 3.6). However, the effect on margins in June-July was opposite to that observed in natural vegetation, with herbivory increasing as % alien seed abundance increased.

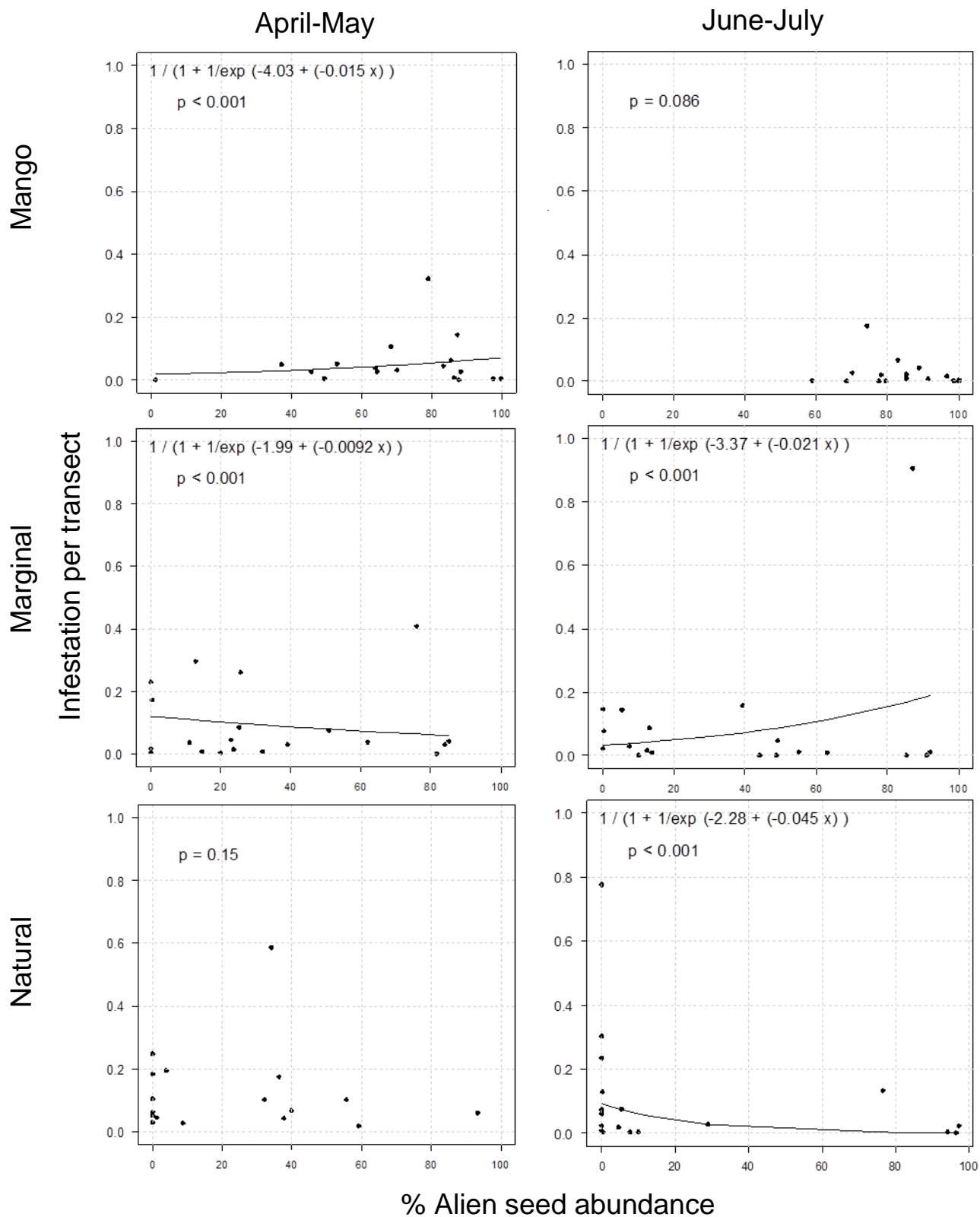


Figure 3.6. Proportion of seeds infested by herbivores per transect with increasing % alien seed abundance per transect between mango fields, margins and natural vegetation, in April-May and June-July.

3.3.6 Parasitoid community

Of the 23 Hymenopteran families observed, 18 were identified as parasitoids. These wasps made up 14.03% and 18.88% of the total insect abundance in April-May and June-July, respectively. The highest abundance of wasps was observed among the Chalcidoidea (64.29%; 94.55%) (particularly within families Pteromalidae and Perilampidae) and Ichneumonoidea (25.04%; 2.40%) in both seasons.

Parasitoid abundance was higher in June-July, while species richness was higher in April-May (Appendix IV). Land-use type influenced parasitoid abundance and richness only in June-July (Table 3.2, Fig. 3.3). Parasitoid abundance was up to ~ 10 – 12 times lower in mango fields than along margins and in natural vegetation ($R^2_m = 0.53$, $R^2_c = 0.99$). Both parasitoid abundance and richness were highest in natural vegetation but not significantly different from that along margins. The mango fields were the least species rich, with between 3 - 5 times fewer parasitoid species than the margins and natural vegetation ($R^2_m = 0.02$, $R^2_c = 0.89$) (Table 3.2).

As with herbivore richness, parasitoid richness declined as the % of alien plants increased overall (Fig. 3.4) but the effect on parasitoids was greater than on herbivores, with richness declining by ~ 4 species from alien-free (0% alien seed) to alien-dominated (100%) habitats. This effect was observed at the landscape scale as the interaction between % alien seed abundance and land-use type was not significant. Overall herbivore richness was positively correlated with parasitoid richness, though this effect was fairly weak, increasing from April-May (Spearman rank correlation, $r_s = 0.66$, $p < 0.001$) to June-July ($r_s = 0.69$, $p < 0.001$). As with herbivore richness, increasing % alien seed abundance was a stronger determinant of parasitoid species richness declines than was land-use type (Appendix Vc).

3.4 DISCUSSION

The combined effects of several drivers of global environmental change on multi-trophic systems of plants and insects are still largely unknown. This is the first study to investigate the effects of habitat transformation and alien plant invasion on communities of plants, seed herbivores and parasitoids in an agricultural landscape. Habitat transformation was the most important driver of change in abundance on all three trophic levels. Alien seed abundance drove declines only in herbivore and parasitoid species richness. Seed herbivory was influenced by interactive effects between habitat transformation and alien seed abundance across the landscape. In this section, I discuss the results with reference to my original questions and predictions, while also considering the limitations of the study and implications of my findings for conservation.

How does land-use transformation affect alien seed abundance and richness?

Land-use is considered one of the most important factors determining habitat susceptibility to alien invasion (Chytry et al. 2008), with disturbance playing a key role in this effect either directly by changing environmental condition or indirectly by increasing alien seed abundance (Vila and Inandez 2011). In this study, mango fields had the highest alien seed abundance among three land-use types in a heterogeneous agricultural landscape. Although alien plants were also observed in natural vegetation and margins between habitats, their species richness and contribution to total seed abundance was greatest in mango fields.

As predicted, high alien seed abundance in the mango fields appears to be driven by human impact in this land-use type. Disturbance in the mango fields is intense; changing landscape features, clearing natural vegetation for crop fields and on-going agricultural activities may facilitate invasion by exposing bare ground, increasing soil quality, and water, nutrient and light availability (conditions that also promote in-crop weeds) (Hobbs and Huenneke 1992, Parendes and Jones 2000). While native plant species may be poorly adapted to these conditions, the novel habitat may be more suitable for aliens to establish and invade (i.e. have low establishment limitation, Warren et al. 2011). This appears to be the case in the mango fields where alien: native species richness was highest on average across the landscape.

High A:N richness may also suggest that high alien seed abundance in mango fields may be sufficient for aliens to overwhelm and overcome biotic barriers against invasion, such as ecological resistance by native plant communities (Von Holle & Simberloff 2005). However, an important caveat in this study is that only plants that were seeding at the time of sampling, and not all present native and alien plants, are included in measures of species richness. Caution should thus be taken in interpreting A:N seed species richness, and the relative richness of all present aliens and natives (*sensu* Von Holle & Simberloff 2005) should provide an improved indication of ecological resistance and habitat susceptibility to invasion.

High overall alien seed abundance and richness suggest that mango fields represent an important alien propagule centre in this landscape and a source for invasion into surrounding land-use types (Parendes and Jones 2000). In fact, alien (and A:N) species richness in surrounding patches of natural vegetation closely resembled that in mango fields in this study. This result was unexpected considering that natural patches have been robust against invasion in other systems (e.g. Brothers and Spingarn 1992), where environmental conditions, such as poor light availability limits alien establishment in preserved forest fragments. However, this is more likely to be the case between margins and mango fields in this study, where rows of *Casuarina* sp. planted as windbreaks along many margins may have provided strong barriers against invasion by limiting light and water availability. This is reflected in the lowest levels of alien (and A:N) species richness and alien seed abundance along the margins. These results

were unexpected for margins, considering that they are often identified as suitable sites for invasion and channels for propagule dispersal in many landscapes (e.g. Parendes and Jones 2000; Pauchard and Alaback 2006).

High alien richness in the natural vegetation may be linked to landscape configuration; isolated patches of natural vegetation are more likely to be invaded than continuous wilderness areas (Vila and Inandez 2011, Thomas and Moloney 2015). The outlier transects that contributed to similar alien seed abundance between margins and natural vegetation were all sampled on Moriah, a farm with very small and isolated patches of natural vegetation often embedded between mango fields. Alien seed abundance in the natural vegetation was significantly lower than disturbed margins and mango fields (in June-July only) when these transects were excluded, suggesting that increasing isolation and the size of the natural vegetation patch may affect invasibility by increasing alien seed abundance from surrounding farms. Nevertheless, the natural vegetation appears to have strong resistance against invasion, as reflected in the poor availability of propagules, particularly in contrast to the mango fields. In the absence of habitat disturbance in this land-use type, abiotic barriers appear to be robust against alien invasion (Brothers and Spingarn 1992).

How do land-use type and alien seed abundance affect overall plant seed, seed herbivore and parasitoid communities?

Land-use transformation for agriculture saw declines in communities of plants (seeds), seed herbivores and parasitoids, with the effect being most marked for higher trophic levels. Up to 25 times fewer herbivores occurred in the mango fields than in the natural vegetation and along margins. This difference was particularly marked in June-July, likely in response to the onset of the dry season and human disturbance in the fields at the end of mango fruiting season, such as mowing and application of chemical pesticides. Besides the direct impact of insecticides, mowing appears to elicit an indirect effect by driving seed abundance and richness declines, which reduces host availability for herbivore infestation. This is reflected in the low levels of herbivory observed in the mango fields, particularly in June-July when all mango transects had been mowed.

However, low herbivore abundance in the mango fields may also be linked to poor suitability of the available seed for insect infestation in both seasons. For example, almost all seed samples (92.5 - 98.86 %) from two common in-crop weeds occurring on almost all transects in the mango fields, *Tridax procumbens* and *Alternanthera pungens*, had no insects emerging. These two species are herbaceous perennials with small seeds (feathery or flat and papery, respectively) that may be unsuitable for infestation by most herbivores. In contrast, a wide variety of perennial shrubs and trees occurred in the natural vegetation and along margins, providing fleshy fruits, berries and pods (e.g. *Acacia* sp. (mostly native), *Grewia* sp. (native), *Melia azedarach* (alien), *Lantana camara* (alien)) that may present more habitable, nutrient-rich seed hosts for herbivores. This may be reflected in the

higher herbivore abundance, richness and seed herbivory in these two land-use types, compared to the mango fields.

However, considering that seed type and size may have influenced the abundance and type of herbivores emerging in this way, and these factors may have varied even within each habitat type, herbivore richness and abundance may be limited by the method of seed sampling in this study. The fact that seed type and size were not standardized between habitat types or considered as factors influencing herbivore infestation represents an important study limitation. Furthermore, the different life history traits among plant species, such as chemical defences against infestation and herbivory (Feeny 1975), may also have introduced great variation in the seed infestation between and within habitats. Consequently, insects sampled in this study may not provide a true representation of the herbivore and parasitoid species richness infesting the seeds between habitats. Future research would benefit from sampling seeds of the same type or size, or from considering these factors, including plant defences against infestation, in analyses. The relatively low herbivore abundance in the mango fields is not congruent with my prediction that increasing alien seed abundance would drive no net change in abundance as generalists replaced specialists. Indeed, herbivore richness was lowest in mango fields where alien seed abundance was highest and, since herbivores with specialized diets will not select aliens as hosts, the remaining species are likely to be generalists that can incorporate aliens into their diets (Keane and Crawley 2002). This is suggested by increasing herbivory with alien seed abundance in the mango fields (in April-May).

However, the large decline in overall herbivore abundance between the mango and natural vegetation type may suggest that generalists cannot compensate for the loss of specialist abundance in this habitat. This is in contrast to other studies that have observed no negative effect on generalists (e.g. Carvalho et al. 2010) and no net change in insect abundance as generalists apparently replace specialists (Heleno et al. 2009). Low herbivore abundance appears to translate into low seed herbivory in mango fields, with 75% fewer seeds infested than in the natural vegetation, likely due to intensive use of pesticides (with pesticides applied up to every month on some farms).

However, since insects were only identified to morphospecies, and the relative abundance of generalists and specialists therefore cannot be used to account for the low herbivore abundance in the mango fields, these conclusions require further analysis and support. Future research would benefit from further identification of insects to species level, if possible, to support this argument. Furthermore, the contribution of specialists and generalists to seed herbivory, even after species identification, may be difficult to assess considering that seed size and type (which may affect seed susceptibility to infestation) were not considered. The low abundance of herbivores in mango fields may not be attributed to land-use and disturbance alone, if seeds available to these insects are smaller and less suitable for infestation. Seeds in mango fields are likely to be unsuitable for infestation in this

way, considering that this habitat had the highest relative alien seed abundance and that pioneer (alien) species tend to have smaller seeds (see review by Pysek and Richardson 2007). Therefore, conclusions regarding differences in herbivore abundance, species richness and seed infestation are limited throughout this study by differences in the types, seed size, chemical defences of plant species sampled in the different habitats, as well as the level of identification of insects, which cannot be used effectively to support conclusions about generalists and specialists.

Regarding parasitoids, mango fields had up to 12 times fewer insects than in either the natural vegetation or along margins. Surprisingly, parasitoids did not appear to be as negatively affected by habitat type as herbivores (25 times fewer in mango fields), contrasting with theory that specialized groups on higher trophic levels are more susceptible to disturbance (Holt 1996, Chaplin-Kramer et al. 2011). This discrepancy may be accounted for by the fact that the parasitoids sampled in this study are larger, more generalist families. Therefore, the decline among herbivores with habitat type and disturbance may have been unlikely to elicit severe cascading bottom-up effects on the parasitoids, since the parasitoids could exploit a wide array of herbivore prey.

Parasitoids are also generally “temporal omnivores” and use both suitable hosts and other complementary, plant-derived resources for survival at different stages of their life cycles (Wäckers & Fadamiro 2005). This is likely to have influenced parasitoid abundance between habitat types, contributing to lower parasitoid abundance in mango fields. The availability of complementary resources may have differed between habitat types, with mango fields providing fewer nesting sites and food sources including pollen and nectar due to lower plant diversity among non-crop weeds. Fewer complementary resources in mango fields may have forced parasitoids to forage along margins or in natural vegetation, where they would also likely have encountered more hosts for oviposition (results in this study). This fact makes it difficult to conclude that lower parasitoid abundance in mango fields results from land-use disturbance alone.

Lower parasitoid abundance in mango fields is not necessarily harmful to farmers, who may only benefit from a few specialized species of parasitoid. Therefore, if the parasitoid abundance is comprised of species that benefit the farmer (i.e. as natural enemies of crop pests, such as fruit flies, for example), the preservation of these species, rather than a larger abundance of parasitoids in general that may also leave the crop fields in search of alternate resources, becomes the main conservation concern for farmers. Such conclusions can be drawn with further identification of the parasitoid species and confirmation of whether the species are beneficial as natural enemies of crop pests. Furthermore, the lack of an effect of habitat type on parasitoid species richness, while positive from a conservationist’s perspective, may only be beneficial to farmers if the parasitoid species present in the mango fields, or those in natural vegetation and margins that are capable of dispersing

into mango fields, are specific enemies of crop pests. Again, this requires further identification of parasitoids to be beneficial to farmers.

Caution should be taken in analysing the interactive effect between all land-use types and alien seed abundance on seed herbivory. Herbivory was generally low in all land-use types, with cases of an insect emerging every second seed or more frequently (>0.5 insect/seed) on only three transects throughout the entire study. Insect seed herbivory seems to be patchy across the landscape, with isolated cases of high herbivory (up to 90% seed infestation) occurring in all land-use types, in both seasons and with different % alien seed abundance. Since habitat fragmentation is known to impact herbivores (Kruess and Tschardt 2000; Valladares, Salvo & Cagnolo 2006; Blitzer et al. 2012), this patchiness may be explained by spatial effects at the landscape scale, such as farm size, fragment composition and fragment configuration in the landscape. Alternatively, resources are known to be patchy in fragmented landscapes (Gripengberg & Roslin 2005), and herbivory will depend on the distribution, type and quality of seed resources available in the different habitats (see review by Lewinsohn, Novotny & Basset 2005).

Increasing alien seed abundance was associated with declines in herbivore and parasitoid richness at the landscape scale in June-July when overall seed abundance and richness was lower than in April-May. This is expected as more specialist herbivore species are likely to be lost as aliens increasingly replace their specific hosts in the seed bank (Keane and Crawley 2002). This pattern appears to have bottom-up effects on parasitoid richness, which was positively correlated (66 – 69%) with herbivore richness. Indeed, the proposed loss of specialist herbivores appears to be mirrored in the loss of parasitoid diversity, likely because specific hosts are increasingly lost across the landscape. As expected, the parasitoid species decline (up to ~5 species) was greater than for herbivores (~3 species) likely because of greater specialization and vulnerability to disturbance on higher trophic levels (Holt 1996).

Concluding remarks

This study showed that habitats transformed for agriculture had the highest alien seed abundance across a heterogeneous landscape. While these two factors did not have synergistic effects on seed, herbivore and parasitoid communities, they both saw declines in species abundance and richness within all three communities. Land-use and alien seed abundance had combined effects on seed herbivory, however, which was patchy across the landscape. High abundance of alien seeds within cultivated fields suggests that agricultural land-uses represent major centres of alien propagule pressure for dispersal into surrounding habitats in fragmented landscapes. However, the invasiveness of aliens is species-specific (Rouget & Richardson 2003) and the potential for aliens to invade surrounding habitats depends on the alien species present in crop fields. Furthermore, species with invasive traits may also be present in the natural vegetation and along margins, and therefore, low

alien seed abundance does not rule these two land-use types out as potential centres for invasion into surrounding habitats. Determining which habitat type is the most invaded or susceptible to invasion was beyond the scope of this study and requires further investigation.

Increasing seed infestation with alien seed abundance in crop fields may also suggest that aliens are not 'released' from enemies in this habitat (Keane and Crawley 2002). Increased top-down control of aliens in this way may limit propagule pressure and the potential for aliens to become invasive in crop fields and in surrounding habitats, but this too requires further research. The depauperate communities of seeds, herbivores and parasitoids suggest that transforming habitats for agriculture threatens complex ecosystems and their functions, particularly those that benefit farmers, such as natural pest control. Plant and insect communities appear less disturbed in natural vegetation and along margins, suggesting that conservation in these habitats will ensure the long-term sustainability of ecosystem services such as pest control in agricultural landscapes.

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Chapter 4

Thesis synthesis

4.1 Spill-over of insect pests from crop fields into surrounding natural vegetation

In fragmented landscapes, biodiversity spills over between habitats transformed for agriculture and nearby patches of natural vegetation. Several reviews show that our understanding of this spill-over is biased and incomplete, with the vast majority of studies only considering dispersal of insects, particularly crop pests, from natural vegetation to crop fields but not in the reverse direction (Blitzer et al. 2012). This bias means that natural vegetation is considered a reservoir for agricultural pests and is often managed to prevent pests from spilling-over into farmlands and damaging crops (for example, see Aluja et al. 1996).

Indeed, Chapter 2 does present further evidence that natural vegetation may act as a reservoir for pests in an agricultural landscape. Accumulation of fruit flies at orchard margins have previously been considered as evidence of their dispersal from alternate hosts in surrounding vegetation to crop fields when mango is back in season (e.g. Aluja & Birke 1993, Aluja et al. 1996). Aluja et al. (1996) suggest that other fruit fly populations (*Anastrepha* spp.) are not endemic to crop fields, but rather that they shift seasonally between neighbouring natural vegetation, isolated wild host plants and other commercial orchards. Management practices encouraged in response to “host cycling” include intercepting fruit flies before spill-over between habitats. Similarly, steps should be taken to limit the apparent dispersal of *Ceratitis* from crop fields to natural vegetation observed in this study, thereby preventing *Ceratitis* from maintaining its populations on marula when mango is out of season. In turn, this will limit the dispersal of *Ceratitis* from natural vegetation into crop fields when other commercial hosts become available, such as citrus and mango, in different seasons throughout the year.

Aluja et al. (1996) suggest the use of baited traps to capture fruit flies before spill-over, particularly at the periphery of orchards where a large abundance of flies was observed. Since this is congruent with the findings of this current study, with *Ceratitis* accumulating at habitat margins between crop fields and natural vegetation, pheromone trapping may also be suggested as a means of limiting pest dispersal from mango fields at the end of the season. This approach has been successful in reducing fly infestation of fruit crops elsewhere (e.g. *Rhagoletis pomonella* infestation of apple, Prokopy et al. 1990).

Another study on mango farms in the K2C (Lammers et al. unpublished data) observed that *Ceratitis* adults may emerge from pupae in mango fields long after mango season has ended (early winter, May 2014). This may suggest that *Ceratitis* can survive in mango fields up until the citrus crop becomes available (May – July), without using marula as an alternative host between crop seasons. Therefore,

management schemes should focus on controlling *Ceratitis* between crop fields rather than in the natural vegetation, as marula may only play a role as a temporary, bridging resource between crop seasons. Henri et al. 2015 also found that parasitism of *Ceratitis* pupae is higher in natural vegetation than in mango fields, suggesting that natural vegetation is a source of pest control for farmers in this landscape.

Employing pheromone trapping at field margins presents a pest management approach that is also favourable to conservationists because it will reduce the need for insecticides in mango and other crop fields. This may, in turn, promote the spill-over of natural enemies from natural vegetation into crop fields, further improving pest control on the farms. Other environmentally-friendly methods of pest control can also be applied at field margins on mango farms to reduce pest spill-over into natural vegetation, such as mass release of parasitoids and sterile flies (Aluja et al. 1996).

4.2 Interactive effects between habitat transformation for agriculture and alien plants

Several studies have encouraged investigation into the relative effects of GEC drivers to avoid under- or over-estimating their net effects on biodiversity (Didham et al. 2007; Tylianakis et al. 2008). My study presents one of the few examples to consider the combined effects of two co-occurring drivers of GEC on multi-trophic communities. It is also a baseline study for how habitat transformation and alien plants impact on plant-insect interactions. In this case, both habitat transformation and alien plants negatively affected plant, seed herbivore and parasitoid community structure and composition, with interactive effects on seed infestation. This research is important for future predictions of how plant and insect communities and their interactions will respond to higher order effects of several GEC drivers in other ecosystems worldwide (Didham et al. 2007).

Besides improving our ability to predict GEC effects on this multi-trophic system, it may also inform current conservation efforts to mitigate these effects. Crop fields should be managed as centres of alien propagule pressure, to prevent aliens from infiltrating and invading surrounding natural habitats. The effect of alien seed abundance in driving declines in herbivore and parasitoid species richness is not limited to crop fields, however, and appears to occur at the landscape scale. Therefore, managing alien plants in the different habitats in this landscape may not be as successful in mitigating herbivore and parasitoid species richness declines as alien management at the landscape level. Managing aliens could include eradication and long-term control of species with high propagule pressure.

This study highlights that habitat transformation for agriculture has negative impacts on every level in multi-trophic food webs, particularly among the seed herbivores. Efforts to mitigate these negative effects at every trophic level should focus on promoting natural vegetation in agricultural landscapes, since this habitat supported the highest abundance and richness within all communities across the landscape. Alternatively, the quality of disturbed habitats could also be improved by decreasing the

intensity of agricultural practices, such as reducing pesticide application and promoting conservation biological control.

4.3 The effects of agriculture and aliens on plants, herbivores and parasitoids

Overall, this study aimed to determine the effect of agriculture and alien plants on natural communities of plants, insect herbivores and parasitoids. I observed negative effects of agriculture on the plant community, with the lowest seed abundance and diversity observed in habitats transformed for commercial mango farming, likely due to intensive practices such as herbicide application and seasonal mowing (Chapter 3). Agriculture also drove elevated infestation of nearby wild plants (i.e. *S. birrea*) used as alternative hosts by mango pests (Chapter 2). The plant community in mango fields was also the most invaded, with alien plant species making up the largest portion of the seed bank in this habitat (Chapter 3).

Insect herbivores were differentially affected, depending on whether they were seed predators of non-crop weeds or frugivorous pests of the crop and other wild fruits. Firstly, frugivorous pests (*Ceratitis* fruit flies) responded to the shifting seasonal availability of the mango crop by dispersing into the natural vegetation to use an alternative wild host (Chapter 2). Mango (and other crops), as a concentrated monoculture resource, likely drives the build-up of *Ceratitis* populations in this landscape, and the populations appear to be maintained by marula when mango goes out of season. In contrast, the seed herbivore community was negatively affected by agriculture, with comparatively lower herbivore abundance and diversity in mango fields than in surrounding natural vegetation (Chapter 3).

The parasitoid community was also threatened by agricultural land-use and was the least abundant and diverse in the mango fields, compared to either natural vegetation or habitat margins (Chapter 3). The specialized parasitoids of mango fruit flies were also rare alongside mango fields, but also in the distant vegetation, suggesting that the parasitoid distribution may be patchy in this landscape, rather than negatively impacted by agricultural activities (Chapter 2). This may also account for why parasitoids were less affected by agriculture and alien seed abundance than herbivores (Chapter 3). Overall, the effects on the insect communities are harmful to farmers and concerning to conservationists: firstly in terms of increased pest prevalence and lower capacity for natural pest control (which increases the need for harmful pesticides), and secondly in terms of lower biodiversity levels, which may have consequences for ecosystem stability and functioning (including other ES, like pollination and weed control).

4.4 Overall management and conservation recommendations

Considering that natural vegetation had the highest abundance and diversity on all three trophic levels, this habitat may provide a source of biodiversity and ecosystem services to nearby mango fields,

eliminating the need for intensive management practices on the farms. In particular, the high abundance and diversity of natural enemies may provide farmers with natural pest control (though this study did not determine whether parasitoids emerging from seeds were natural enemies of other mango pests). Other studies show that even small and isolated fragments of natural vegetation can support ecosystem services, including but not limited to pest control (Bianchi et al. 2006). This study highlights how diverse communities of herbivores and parasitoids can persist in a heterogeneous landscape with a land-sharing approach to conservation. Promoting the preservation of natural vegetation in mixed landscapes may ensure the long-term sustainability of mango farms, by replacing intensive inputs on farms with natural ecosystem services. This wildlife-friendly approach coincides with the goals of the Kruger to Canyons Biosphere Region, and presents economic and environmental benefits to both farmers and conservationists.

However, natural vegetation was also a reservoir for the mango pest, *Ceratitis* spp. in this study and, in this way, may present an undesirable element of the landscape for farmers. Nevertheless, a land-sharing approach to conservation can still be promoted in combination with an area-wide approach to pest management. Pest control at the field-level, such as the removal of natural vegetation and in-crop diversity, and the application of insecticides, is known to have cumulative effects on ecosystem functions at the regional scale (Turner and Gardner 1991), highlighting the need for management beyond the crop boundary (Shellhorn et al. 2008). An area-wide approach encourages collaboration among farmers that involves considering the temporal dynamics of pests in relation to the relative timing of crop hosts between monocultures (and nearby natural habitats where wild resources are available). Area-wide management applied on a large scale and in a synchronous manner has been successful in reducing pest populations and in increasing agricultural production in landscapes elsewhere (see review by Shellhorn et al. 2008). Methods of pest control adopted include the release of pheromones, mass trapping of pests, alternating the planting dates of crops and release natural enemies and sterile males at a large scale (Shellhorn et al. 2008). Such methods should be applied in a mosaic landscape such as in the K2C, where resources may be provided for pests throughout the year as crop resources shift spatially and temporally between farms throughout the year. This is particularly the case for economically-important *Ceratitis* species, which are strong dispersers and whose distributions are driven by availability of hosts (De Villiers et al. 2014).

4.5 Study strengths and limitations

Using a case study approach in Chapter 2, only marula is considered as a host for *Ceratitis* in natural vegetation even though other alternative plant host species were also observed in natural vegetation in this study (e.g. *Ficus* sp., *Opuntia* sp., *Strychnos* sp.) (De Meyer, Copeland & Lux 2002). Disregarding these other plant species may under-represent the effect of *Ceratitis* spill-over from crop fields; including other host species may have provided a broader context for how agriculture drives

pest spill-over into natural vegetation. However, since no *Ceratitis* emerged from alien and native seeds sampled in natural vegetation after mango and marula season in 2014 (Chapter 3, results not presented), I am confident that this case study with marula alone provides a reliable snapshot of the *Ceratitis* community and its use of plant hosts in the natural vegetation after spill-over from crop fields.

In Chapter 3, time and logistic constraints limited the number of transects sampled, the number of seeds that could be collected from each transect and the amount of time before seeds were checked for insects. Furthermore, sampling occurred over a period when only a portion of all plants present between habitats were seeding. Consequently, it is likely that my methods overlooked many herbivore and parasitoid species (a problem also highlighted by Heleno et al. 2009). The removal of seeds from transects may also have prevented further herbivore and parasitoid attack, further limiting the abundance and richness of emerging insects. However, this sampling bias occurred across all transects and is unlikely to have influenced my results, which were focussed on comparisons between habitats. Finally, since seeds were also sampled in two seasons and were left for approximately 290 days, I expect that a large majority of the insects to emerge from the seeds were sampled in this study.

Since insects emerging from seeds were only identified to morphospecies, lack of taxonomic clarity may have resulted in over- or under-estimations of true herbivore and parasitoid species richness in this landscape. Future research should identify insect species, possibly using DNA barcoding, to improve estimates of species richness and its response to GEC. This would also allow parasitoids to be linked to their specific herbivores, enabling investigations into the combined effects of GEC drivers on insect parasitism and natural pest control in agroecosystems.

4.6 Further research

Spill-over of *Ceratitis* in this study was in the direction from mango fields to natural vegetation in 2015 when marula fruiting started at the end of mango season. Contrasting results were observed in another study investigating *Ceratitis* dynamics in the K2C (April-May, 2014) (W. Lammers, unpublished data) in which marula and mango fruiting seasons overlapped completely and *Ceratitis* accumulated in the mango fields rather than natural vegetation at the end of the fruiting season. Future studies should investigate long-term *Ceratitis* spill-over between habitats and consider how shifts in host resources (and hence, *Ceratitis*) across the landscape may be linked to different relative timing of marula and mango fruiting (likely driven by variation in rainfall patterns) between years. This will provide a broader context for our understanding of how resource shifts drive pest spill-over between crop fields and natural vegetation.

Further research should also consider that *Ceratitis* may also shift between different crops in an agricultural landscape, rather than to or from hosts in natural vegetation *per se*. For example, *Citrus*

spp., passion fruit (*Passiflora edulis*) and avocado (*Persea americana*) crops, which are also known to support *Ceratitis* (De Meyer et al. 2002), grow alongside mango fields in the K2C and fruit over winter (May-July) when mango is out of season. It would be beneficial to determine whether *Ceratitis* uses these crops as a reservoir over winter and therefore, whether fruit flies shift between crops, rather than from natural vegetation to crop fields or vice versa.

In Chapter 3, I related patchy seed herbivory across the landscape to spatial effects, such as habitat fragment size, composition and configuration. Indeed, the response of insects to landscape elements depends largely on their dispersal ability, which in turn is governed by body size and trophic position (see review by Tscharntke & Brandl 2004). Further research into the landscape effects of habitat transformation on ES such as weed control (e.g. seed herbivory) and pest control should consider body size as factor that limits forage range among herbivores and parasitoids. Wasps collected in this study have already been measured and analysed in a preliminary study investigating how wasp body length differs between habitat type and distance to agricultural fields (L. Mokubedi and C. L. Seymour, SANBI).

Finally, plant, seed herbivore and parasitoid community data collected in this study can be used to construct empirical species interaction networks (i.e. food webs), which are useful ecological tools for investigating how GEC affects ecosystem function and stability (McCann 2000). This is achieved by quantitatively assessing the structure of the networks using a series of metrics derived from food-web theory, such as connectance, nestedness and modularity (Bascompte, Jordano & Olesen 2006). Using this approach, we can determine how alien plants infiltrate into plant-herbivore-parasitoid networks (e.g. Heleno et al. 2009) and interact with habitat transformation to disrupt the resilience of the ecosystem to further disturbance and network collapse.

4.7 References

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Appendix

Appendix Ia. Description of study site and farm management procedures in the Kruger to Canyons Biosphere Region (K2C)

The study was conducted in and around Hoedspruit, Limpopo Province in the central subregion of the Kruger to Canyons (K2C) Biosphere Region, South Africa (24° 26'S 30° 50'E). This is the largest biosphere area in South Africa and the third largest in the world registered under UNESCO (Coetzer et al. 2010).

The study area has low mean annual rainfall (566 mm) that is concentrated in summer (<http://en.climate-data.org>) and occurs on Archaean granite-derived soils (Shackleton 2002; Mucina & Rutherford 2006). The natural vegetation, characterized as “Granitic Lowveld”, is mixed, broad-leaved with a discontinuous overstory of deciduous, woody species (particularly of the Combretaceae and Mimosaceae), and a herbaceous layer dominated by dense C₄ grass communities (Mucina & Rutherford 2006).

Approximately half of the K2C bioregion is formally conserved, with the surrounding transition areas aimed at sustainable use of resources and socio-economic development of rural and suburban human settlements (Coetzer et al. 2010; Coetzer, Witkowski & Erasmus 2014). Considerable land use change has been observed in the K2C with fields for subsistence or commercial farming having replaced the natural vegetation (Coetzer et al. 2010). Farming in the area has shifted towards sub-tropical perennial crops, such as mango, citrus and passion fruit, in response to advances in irrigation methods and increased investment in this sector (Coetzer et al. 2010). Mango farming (*Mangifera indica* L.) in the area represents a major component of the sub-tropical fruit industry and foreign investment in South Africa (DAFF 2013).

Contrasting land-uses in the area have promoted a heterogeneous landscape with patches of natural vegetation interspersed among crop fields. All sampled farms in this study had patches of natural vegetation between their crop fields or alongside at least one boundary of the farmlands. Habitat types were typically separated by a 10-25 m margin, such as a road or fence line and single rows of *Casuarina* sp. trees serving as windbreaks. All farms practice conventional weed control on sampled fields, such as mowing and hand-slashing in-crop weeds and spraying herbicides (including RoundUp®), generally during mango flowering season and before weed seeding (August and December – February, respectively), and pest control with chemical pesticides throughout the year.

Pesticides include a variety of neonicotinoids and organophosphates, which are applied for the control of fungi, such as mildew, anthracnose, black spot and brown rot, and arthropod pests, such as thrips, mites, weevils, scales and fruit fly. In some instances, pesticides may be applied up to every month of

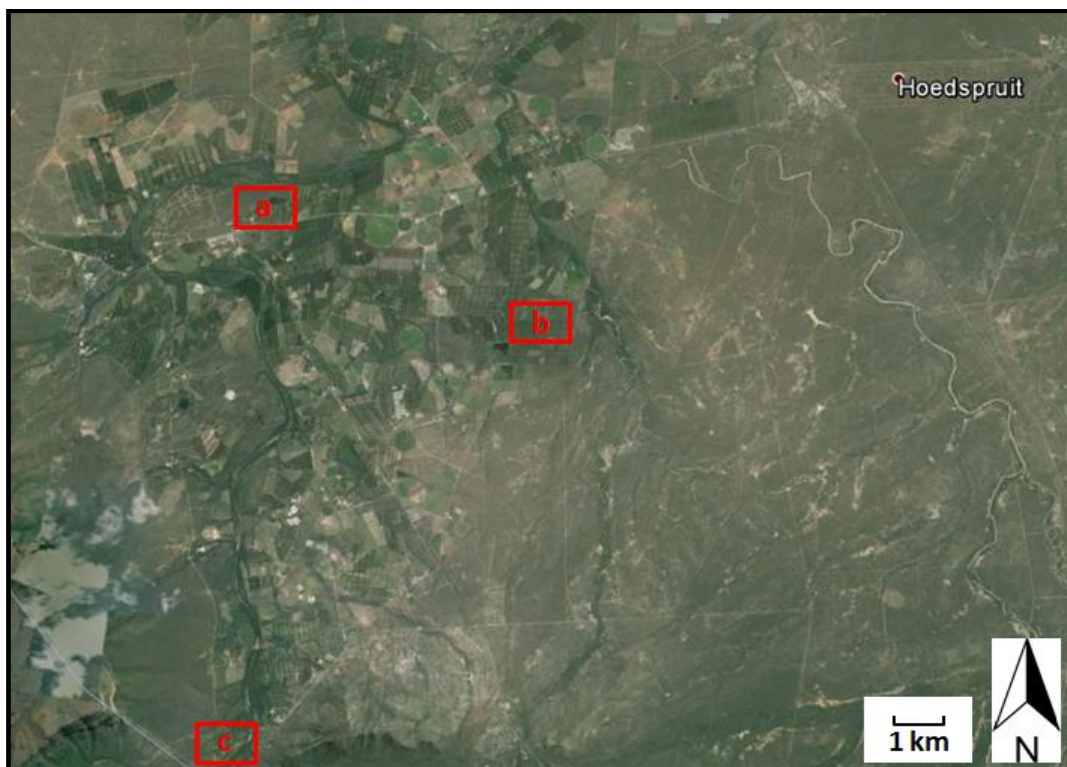
the year or more frequently, both during and outside the mango fruiting season. For example, fields sampled in Bavaria during this study had been sprayed every month from January 2013 – December 2014, excluding a three month period from March – May 2013 (post-harvesting, when normal weed control methods were still employed).

Appendix IIb. Details of insecticide application on Bavaria mango fields during 2013

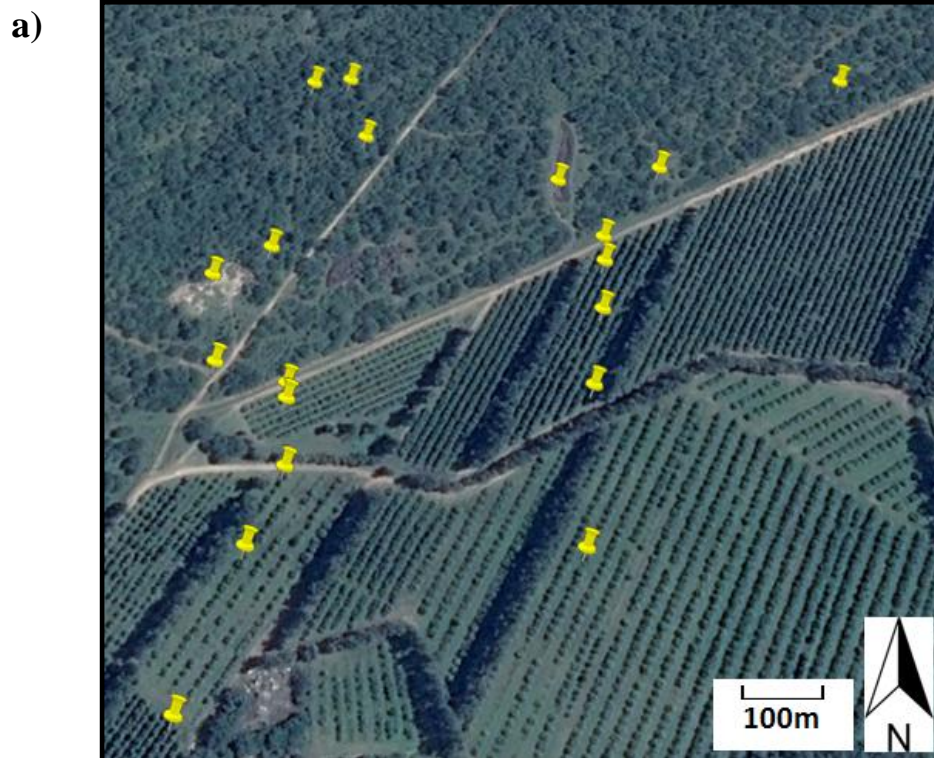
Pest targeted	Active chemical	Application frequency	Days withheld
Fruit fly	Mercaptothion Deltamehtrin	Monthly	10 - 28
Thrip	Thiamethoxam Phenyl-pyrazole	Monthly	7 – 43
Scale	Imidacloprid Pyriproxyfen	Monthly	2 – 212
Mite	Tetronic acid Bromopropilate	Monthly (or more frequently)	0 – 10

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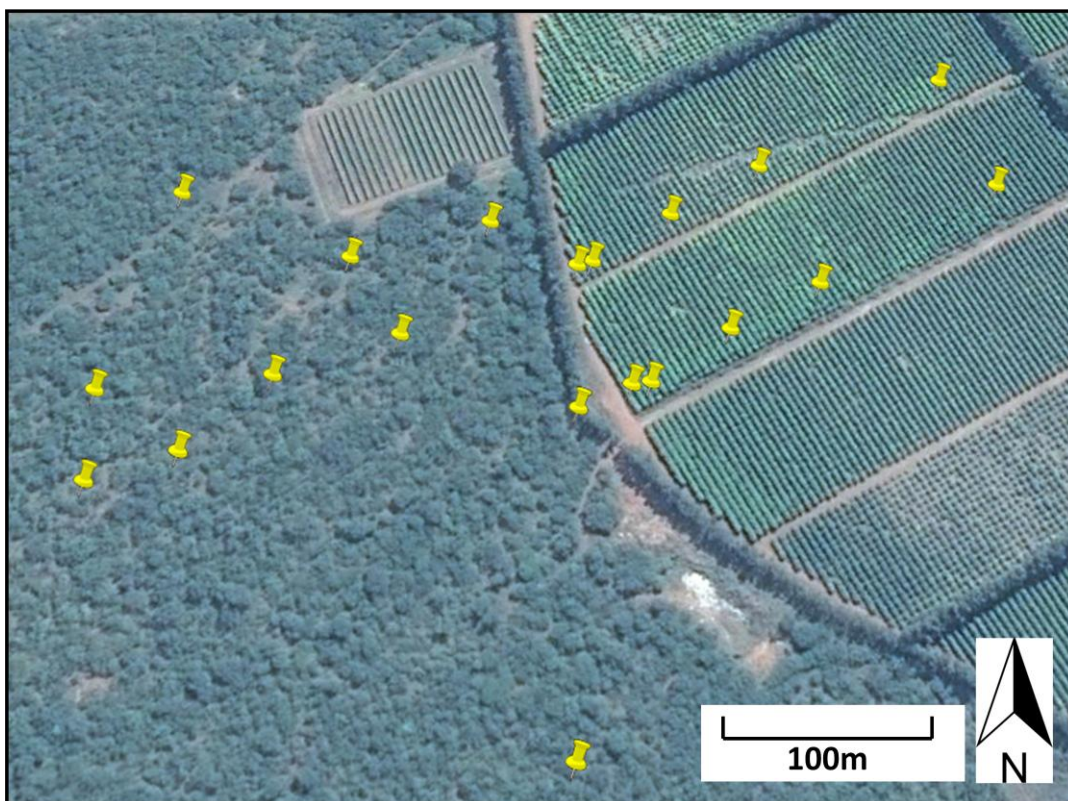
Appendix II. Map of the agricultural landscape where marula fruit were collected and pheromone trapping was conducted outside of Hoedspruit, Limpopo Province, South Africa. Highlighted areas denote sampled mango farms, namely a) Venden b) Bavaria Fruit Estates and c) Mohlatsi. Individual maps for each farm are presented below, with yellow markers indicating positions of pheromone traps in natural vegetation and mango fields (rows of trees arranged in fields). Markers in the natural vegetation correspond to positions of sampled marula trees.



b)



c)



Appendix II. cont.

Appendix III. Total abundance of observed and collected (Coll.) marula fruit in the natural vegetation alongside mango fields and in the distant vegetation (“Control”) in the early (2015) and late (2014, 2015) seasons. Abundance is reported for each fruit ripeness category, namely unfallen-unripe (UU), fallen-unripe (FU) and fallen-ripe (FR). “-” denotes cases where no fruit were collected or recorded.

Season	Ripeness	Site type / Farm							
		Bavaria		Mohlatsi		Venden		Control	
		Total	Coll.	Total	Coll.	Total	Coll.	Total	Coll.
Early 2015	UU	6147	151	1993	90	3465	78	2631	78
	FU	87	69	53	28	236	79	98	49
	FR	140	55	65	10	138	62	9	8
	Total		275		128		219		135
Late 2015	UU	2288	125	335	18	846	60	565	50
	FU	1058	147	159	65	671	81	471	89
	FR	5027	143	703	74	448	95	60	24
	Total		415		157		236		163
Late 2014	FU	-	255	-	-	-	-	-	-
	FR	-	252	-	-	-	-	-	-
	Total	-	507	-	-	-	-	-	-

Appendix IV. Effect of season on overall plant (seed), herbivore and parasitoid abundance, richness and herbivory across all land-use types between April-May and June-July.

	Model outputs			Season mean (\pm se)	
	p -value	Δ AICc	Δ Coeff (\pm se)	April-May	June-July
Seed plant community					
Abundance	0.049 *	-4.86	1.80 (1.23)	2626.44 (\pm 260.25)	2246.40 (\pm 431.82)
Sp. richness	p < 0.001 *	-21.53	1.36 (1.07)	10.35 (\pm 0.39)	7.63 (\pm 0.33)
Herbivore community					
Abundance	0.011 *	-4.54	- 2.80 (2.02)	1.37 (\pm 0.37)	11.18 (\pm 4.57)
Sp. richness	p < 0.001 *	-89.44	2.25 (1.09)	7.33 (\pm 0.46)	3.26 (\pm 0.34)
Herbivory per seed					
	p < 0.001 *	- 23 968	0.55 (0.50)	0.087 (\pm 0.011)	0.072 (\pm 0.016)
Parasitoid community					
Abundance	p < 0.001*	1.90	- 1.03 (2.18)	2.95 (\pm 1.30)	9.58 (\pm 6.40)
Sp. richness	0.034*	-14.40	-1.25 (1.25)	3.47 (\pm 0.26)	2.77 (\pm 0.32)

Appendix Va. Effect of land-use (L-U) and % alien seed abundance on total plant (seed) abundance and species richness in April-May and June-July.

		Land-use	% A seed	L-U : % A seed	Residual df	AIC	Weighted AIC
<i>Seed abundance</i>							
April-May	Model 1	0.24	0.95	0.87	9	1018.23	0.011
	Model 2	0.072	0.82	-	7	1014.52	0.16
	Model 3	0.043 *	-	-	6	1012.57	0.56
	Null model	-	-	-	4	1014.88	0.28
June-July	Model 1	p < 0.001 *	0.87	0.77	9	896.56	0.017
	Model 2	p < 0.001 *	0.66	-	7	893.07	0.22
	Model 3	p < 0.001 *	-	-	6	891.27	0.76
	Null model	-	-	-	4	915.56	0
<i>Seed species richness</i>							
April-May	Model 1	0.37	0.32	0.44	9	336.94	0.013
	Model 2	0.27	0.17	-	7	334.60	0.088
	Null model	-	-	-	4	331.46	0.9
June-July	Model 1	0.030 *	0.19	0.21	9	310.09	0.08
	Model 2	0.023 *	0.20	-	7	309.26	0.26
	Model 3	0.047 *	-	-	6	308.88	0.43
	Null model	-	-	-	4	311.00	0.23

P-values of fixed factors were obtained for each model using likelihood ratio tests. Significance was determined at the $\alpha = 0.05$ significance level and denoted with an asterisk (*). Non-significant terms excluded from subsequent models are denoted by “-”. Model fit was evaluated in each case using the Akaike Information Criteria (AIC) and Akaike weightings, with the lowest AIC values indicating optimal models (highlighted in **bold**). Akaike weightings represent the probability that the model is the best approximating fit, with largest values indicating optimal models.

Appendix Vb. Effect of land-use (L-U) and % alien seed abundance on herbivore abundance and species richness in April-May and June-July.

		Land-use	% A seed	L-U: % A seed	Residual df	AIC	Weighted AIC
<i>Herbivore abundance</i>							
April-May	Model 1	0.16	0.48	0.30	9	702.18	0.034
	Model 2	0.13	0.79	-	7	700.58	0.17
	Model 3	p = 0.028*	-	-	6	698.65	0.60
	Null model	-	-	-	4	701.84	0.195
June-July	Model 1	p < 0.01*	0.76	0.90	9	505.42	0.02
	Model 2	p < 0.001 *	0.33	-	7	501.64	0.30
	Model 3	p < 0.001 *	-	-	6	500.58	0.69
	Null model	-	-	-	4	518.49	0
<i>Herbivore species richness</i>							
April-May	Model 1	0.37	0.20	0.20	9	350.79	0.052
	Model 2	0.24	0.97	-	7	349.99	0.17
	Null model	-	-	-	4	348.45	0.78
June-July	Model 1	0.26	0.30	0.57	9	267.92	0.029
	Model 2	0.13	0.11	-	7	265.03	0.26
	Model 3	-	p < 0.01 *	-	5	265.15	0.43
	Model 4	0.005*	-	-	6	265.62	0.26
	Null model	-	-	-	4	272.20	0.015

Appendix Vc. Effect of land-use (L-U) and % alien seed abundance on parasitoid abundance and species richness in April-May and June-July

		Land-use	% A seed	L-U: % A seed	Residual df	AIC	Weighted AIC
<i>Parasitoid abundance</i>							
April-May	Model 1	0.98	0.97	0.99	9	576.72	0.002
	Model 2	0.62	0.78	-	7	572.73	0.029
	Null model	-	-	-	4	567.21	0.97
June-July	Model 1	0.025 *	0.11	0.057	9	388.64	0.19
	Model 2	0.066	0.64	-	7	390.37	0.18
	Model 3	0.0041 *	-	-	6	388.59	0.60
	Null model	-	-	-	4	395.57	0.03
<i>Parasitoid species richness</i>							
April-May	Model 1	0.88	0.78	0.72	9	277.65	0.003
	Model 2	0.78	0.51	-	7	274.31	0.031
	Null model	-	-	-	4	268.93	0.97
June-July	Model 1	0.43	0.37	0.91	9	249.30	0.017
	Model 2	0.16	0.084	-	7	245.48	0.25
	Model 3	-	p < 0.001 *	-	5	245.10	0.53
	Model 4	p < 0.01 *	-	-	6	246.47	0.21
	Null model	-	-	-	4	256.20	0.003

Appendix VI. Alien (A) and native (N) plant species sampled in mango fields (MNG), natural vegetation (NTL) and habitat margins (MAR) in April-May (AM) and June-July (JJ). **Note.** Plant morphospecies whose status was “Unknown” were not included in the estimation of % alien seed abundance and A:N species richness in analyses.

No.	Plant species	Season	A/N	Habitat
1	Morphospecies 22.2	AM	Unknown	NTL
2	Morphospecies 40.1	AM	Unknown	MAR
3	Morphospecies 41.1	JJ	Unknown	MAR
4	<i>Abrus precatorius</i>	JJ	N	MAR
5	<i>Abutilon fruticosum</i>	AM, JJ	N	MAR, NTL
6	<i>Acacia erubescens</i>	AM, JJ	N	MAR, NTL
7	<i>Acacia exuvialis</i>	AM, JJ	N	NTL
8	<i>Acacia karroo</i>	AM, JJ	N	MAR, NTL
9	<i>Acacia mearnsii</i>	AM	A	NTL
10	<i>Acacia mellifera</i>	JJ	N	NTL
11	<i>Acacia nigrescens</i>	AM, JJ	N	NTL
12	<i>Acacia nilotica</i>	AM, JJ	N	MAR, NTL
13	<i>Acacia robusta</i>	JJ	N	NTL
14	<i>Acacia tortillis</i>	AM, JJ	N	MAR, NTL
15	<i>Acalypha indica</i>	AM, JJ	N	MNG, MAR, NTL
16	<i>Acanthospermum hispidum</i>	AM, JJ	A	MNG, MAR
17	<i>Achrynthes aspera</i>	AM, JJ	A	MNG, NTL
18	<i>Acrotome hispida</i>	AM, JJ	N	MNG, MAR, NTL
19	<i>Aerva leucura</i>	AM, JJ	N	MAR, NTL
20	<i>Ageratum houstonianum</i>	AM, JJ	A	MNG, MAR
21	<i>Albizia harveyi</i>	AM	N	NTL
22	<i>Aloe zebrina</i>	AM, JJ	N	NTL
23	<i>Alternanthera pungens</i>	AM, JJ	A	MNG, MAR, NTL
24	<i>Amaranthus hybridus</i>	JJ	A	MAR
25	<i>Amaranthus powelli</i>	AM	A	MNG
26	<i>Amaranthus praetermissus</i>	AM, JJ	N	MAR, NTL
27	<i>Amaranthus spinosus</i>	AM	N	MNG
28	<i>Amaranthus viridis</i>	AM	N	MAR
29	<i>Barleria elegans</i>	AM, JJ	N	NTL
30	<i>Barleria senensis</i>	JJ	N	MAR
31	<i>Berkheya insignis</i>	JJ	N	NTL
32	<i>Bidens bipinnata</i>	JJ	A	MAR, NTL
33	<i>Bidens pilosa</i>	AM, JJ	A	MNG, MAR, NTL
34	<i>Boerhavia diffusa</i>	AM, JJ	A	MNG, MAR
35	<i>Bridelia cathartica</i>	AM, JJ	N	MAR
36	<i>Cassipourea filiformis</i>	AM	A	MAR
37	<i>Casuarina equisetifolia</i>	JJ	A	MNG
38	<i>Ceropegia stapeliiformis</i>	AM	N	MAR
39	<i>Chamaecrista absus</i>	AM, JJ	N	NTL
40	<i>Chamaecrista mimosoides</i>	AM	N	MNG, MAR, NTL
41	<i>Chenopodium carinatum</i>	AM, JJ	N	MAR
42	<i>Cleome monophylla</i>	AM, JJ	N	NTL
43	<i>Coccinia rehmannii</i>	AM	N	NTL
44	<i>Combretum apiculatum</i>	AM, JJ	N	MAR, NTL
45	<i>Combretum imberbe</i>	AM	N	NTL
46	<i>Combretum zeyheri</i>	AM, JJ	N	NTL
47	<i>Commelina benghalensis</i>	AM, JJ	N	MNG, MAR, NTL
48	<i>Commelina erecta</i>	AM	N	MNG, MAR, NTL

No.	Plant species	Season	A/N	Habitat
49	<i>Commiphora mollis</i>	AM	N	NTL
50	<i>Conyza bonariensis</i>	JJ	A	NTL
51	<i>Corallocarpus bainesii</i>	AM	N	MAR, NTL
52	<i>Corchorus asplenifolius</i>	AM	N	MNG, NTL
53	<i>Cordia ovalis</i>	AM, JJ	N	MAR, NTL
54	<i>Crabbea hirsuta</i>	AM, JJ	N	NTL
55	<i>Crassocephalum crepioides</i>	AM	N	MNG
56	<i>Crotalaria damarensis</i>	AM	N	MAR
57	<i>Crotalaria pallida</i>	AM	N	MAR
58	<i>Crotalaria sphaerocarpa</i>	AM, JJ	N	MNG, MAR, NTL
59	<i>Cucumis hirsutus</i>	AM, JJ	N	MAR, NTL
60	<i>Cucumis metuliferus</i>	AM, JJ	N	MNG, MAR, NTL
61	<i>Cucumis zeyheri</i>	AM, JJ	N	MAR, NTL
62	<i>Cyathula lanceolata</i>	JJ	N	MAR, NTL
63	<i>Cynanchum ellipticum</i>	AM, JJ	N	NTL
64	<i>Decorsea schlechteri</i>	JJ	N	MAR
65	<i>Delonix regia</i>	AM, JJ	A	MAR
66	<i>Dichrostachys cinerea</i>	AM, JJ	N	MAR, NTL
67	<i>Ehretia rigida</i>	AM, JJ	N	MAR, NTL
68	<i>Epilobium hirsutum</i>	AM, JJ	N	MNG, NTL
69	<i>Ethulia conyzoides</i>	AM	A	NTL
70	<i>Euclea crispa</i>	AM	N	MAR, NTL
71	<i>Euphorbia crotonoides</i>	AM, JJ	N	NTL
72	<i>Euphorbia heterophylla</i>	AM, JJ	A	MNG, MAR
73	<i>Euphorbia hirta</i>	AM, JJ	A	MNG, MAR
74	<i>Evolvulus alsinoides</i>	AM, JJ	N	MAR, NTL
75	<i>Felicia mossamedensis</i>	JJ	N	MNG
76	<i>Ficus sycomorus</i>	AM, JJ	N	MAR
77	<i>Flaveria bidentis</i>	AM, JJ	A	MNG, MAR, NTL
78	<i>Gossypium herbaceum</i>	AM, JJ	N	MAR, NTL
79	<i>Grewia bicolour</i>	AM, JJ	N	MAR, NTL
80	<i>Grewia flavescens</i>	AM, JJ	N	NTL
81	<i>Grewia hexamita</i>	AM	N	MAR, NTL
82	<i>Grewia monticola</i>	AM, JJ	N	NTL
83	<i>Grewia occidentalis</i>	AM	N	NTL
84	<i>Grewia retinervis</i>	AM	N	NTL
85	<i>Grewia villosa</i>	AM, JJ	N	NTL
86	<i>Helichrysum rugulosum</i>	AM	N	MNG
87	<i>Heliotropium ovalifolium</i>	AM, JJ	N	MNG, MAR
88	<i>Heliotropium zeylanicum</i>	AM, JJ	N	MAR
89	<i>Hermannia boraginiflora</i>	AM, JJ	N	MAR, NTL
90	<i>Hermstaedtia fleckii</i>	AM, JJ	N	MNG, MAR
91	<i>Hermstaedtia odorata</i>	AM, JJ	N	MAR
92	<i>Hibiscus micranthus</i>	AM, JJ	N	MNG, MAR, NTL
93	<i>Hibiscus platycalyx</i>	AM, JJ	N	MAR, NTL
94	<i>Hirpicium bechuanense</i>	AM, JJ	N	MAR
95	<i>Hypertelis bowkeriana</i>	AM, JJ	N	MAR
96	<i>Indigofera astragalina</i>	AM, JJ	N	MAR, NTL
97	<i>Indigofera colutea</i>	AM, JJ	N	MNG, MAR, NTL
98	<i>Ipomoea crassipes</i>	AM	N	MAR
99	<i>Ipomoea magnusiana</i>	AM, JJ	N	MNG, MAR, NTL
100	<i>Ipomoea obscura</i>	AM, JJ	N	MNG, MAR
101	<i>Ipomoea sinensis</i>	AM, JJ	N	MNG, MAR, NTL
102	<i>Ipomoea</i> sp.1	AM	Unknown	NTL

No.	Plant species	Season	A/N	Habitat
103	<i>Ipomoea</i> sp.2	JJ	Unknown	MNG
104	<i>Ipomoea</i> sp.3	JJ	Unknown	NTL
105	<i>Isoglossa delicatula</i>	JJ	N	NTL
106	<i>Jasminum fluminense</i>	AM, JJ	N	MAR, NTL
107	<i>Justicia flava</i>	AM, JJ	N	MNG, MAR, NTL
108	<i>Kalanchoe rotundifolia</i>	JJ	N	NTL
109	<i>Kyphocarpa angustifolia</i>	AM, JJ	N	MAR, NTL
110	<i>Lantana camara</i>	AM, JJ	A	MNG, MAR, NTL
111	<i>Lantana rugosa</i>	AM, JJ	N	MAR, NTL
112	<i>Leonotis leonurus</i>	JJ	N	MAR, NTL
113	<i>Leucas sexdentata</i>	AM	N	NTL
114	<i>Leucosphaera bainesii</i>	AM	N	MNG
115	<i>Lippia javanica</i>	AM	N	MAR
116	<i>Litogyne gariepina</i>	JJ	N	MNG
117	<i>Macrotyloma axillare</i>	AM, JJ	N	MNG, NTL
118	<i>Malvastrum coromandelianum</i>	AM, JJ	A	MNG, MAR, NTL
119	<i>Melhania prostrata</i>	AM, JJ	N	MAR, NTL
120	<i>Melhania rehmannii</i>	AM, JJ	N	NTL
121	<i>Melia azedarach</i>	AM, JJ	A	NTL
122	<i>Microcharis galpinii</i>	AM	N	NTL
123	<i>Monechma debile</i>	AM	N	NTL
124	<i>Monsonia angustifolia</i>	AM	N	NTL
125	<i>Nesea schinzii</i>	AM	N	MNG
126	<i>Nidorella auriculata</i>	AM	N	MAR
127	<i>Ocimum americanum</i>	JJ	N	NTL
128	<i>Ocimum gratissimum</i>	AM	N	NTL
129	<i>Oldenlandia herbacea</i>	AM	N	NTL
130	<i>Olea capensis</i>	AM, JJ	N	NTL
131	<i>Opuntia stricta</i>	AM, JJ	A	NTL
132	<i>Ormocharpum trichocarpum</i>	AM	N	NTL
133	<i>Oxalis corniculata</i>	AM, JJ	A	MNG
134	<i>Oxygonum sinuatum</i>	AM, JJ	N	MNG, MAR, NTL
135	<i>Pavonia burchellii</i>	AM, JJ	N	MNG, MAR, NTL
136	<i>Pegolettia senegalensis</i>	AM, JJ	N	MNG, MAR
137	<i>Pergularia daemia</i>	AM, JJ	N	MAR, NTL
138	<i>Phyllanthus angolensis</i>	AM	A	MNG, MAR, NTL
139	<i>Pseudoconyza viscosa</i>	AM	N	MNG
140	<i>Pupalia lappacea</i>	AM, JJ	N	MNG, MAR, NTL
141	<i>Rhynchosia caribaea</i>	AM	N	MAR
142	<i>Rhynchosia minima</i>	AM	N	MNG, MAR, NTL
143	<i>Richardia brasiliensis</i>	AM, JJ	A	MNG, MAR
144	<i>Ricinus communis</i>	AM, JJ	A	MAR, NTL
145	<i>Ruellia patula</i>	JJ	N	MAR, NTL
146	<i>Salpinctium schimperii</i>	AM, JJ	N	MNG, MAR, NTL
147	<i>Searsia chirindensis</i>	AM	N	NTL
148	<i>Seddera capensis</i>	AM	N	NTL
149	<i>Senecio othonniflorus</i>	JJ	N	MNG, MAR
150	<i>Senna italica</i>	AM	N	MAR
151	<i>Senna petersiana</i>	JJ	N	MAR
152	<i>Sesbania bispinosa</i>	AM, JJ	A	MNG, MAR, NTL
153	<i>Sida acuta</i>	AM	N	MNG, NTL
154	<i>Sida alba</i>	AM, JJ	N	MNG, MAR, NTL
155	<i>Sida cordifolia</i>	AM, JJ	N	MNG, NTL
156	<i>Sida dregei</i>	AM, JJ	N	MNG, MAR, NTL

No.	Plant species	Season	A/N	Habitat
157	<i>Sida rhombifolia</i>	AM, JJ	N	MNG, MAR, NTL
158	<i>Solanum americanum</i>	AM	A	MNG, NTL
No.	<i>Plant species</i>	Season	A/N	Habitat
159	<i>Solanum delagoense</i>	JJ	N	MAR
160	<i>Solanum retroflexum</i>	JJ	N	NTL
161	<i>Strychnos madagascariensis</i>	AM, JJ	N	NTL
162	<i>Tagetes minuta</i>	AM, JJ	A	MNG, MAR, NTL
163	<i>Tephrosia purpurea</i>	AM, JJ	N	MNG, MAR, NTL
164	<i>Tragia dioica</i>	AM	N	MAR
165	<i>Tribulus terrestris</i>	AM	N	MNG, MAR
166	<i>Tridax procumbens</i>	AM, JJ	A	MNG, MAR
167	<i>Triumfetta pentandra</i>	AM, JJ	N	MNG, MAR
168	<i>Verbena brasiliensis</i>	AM	A	NTL
169	<i>Vernonia colorata</i>	AM, JJ	N	MAR, NTL
170	<i>Vernonia fastigiata</i>	AM, JJ	N	MAR, NTL
171	<i>Vigna frutescens</i>	AM	N	NTL
172	<i>Waltheria indica</i>	AM, JJ	N	MNG, MAR, NTL
173	<i>Xanthium strumarium</i>	JJ	A	MNG
174	<i>Xenostegia tridentata</i>	AM	N	NTL
175	<i>Zinnia peruviana</i>	AM, JJ	A	MAR, NTL

Appendix VII. Effect of land-use (L-U) and % alien seed abundance on insect herbivore infestation per seed per transect in April-May and June-July.

	Land-use	% A seed	L-U : A% seed	Residual df	Δ AICc
April-May					
Model 1	p < 0.001	p < 0.001	p < 0.001	8	p < 0.0001 *
Model 2	p < 0.001	p < 0.001	-	6	- 304.85
Null model	-	-	-	3	- 2189.66
June-July					
Model 1	p < 0.001	p < 0.001	p < 0.001	8	p < 0.0001 *
Model 2	p < 0.001	p < 0.001	-	6	- 1019.33
Null model	-	-	-	3	- 2324.01

Fixed effects excluded from each model are denoted with a dash (-). Significance of each term was determined at $\alpha = 0.05$. Akaike Information Criteria (AIC) were used to evaluate goodness of fit for each model and to select the optimal model (highlighted in **bold**). Optimal models were those with the lowest AIC values. The difference in AIC between the optimal model and the other models are presented (Δ AICc). P-values marked with an asterisk (*) denote significant difference between the optimal model and the null model.

Appendix VIII. Pairwise comparisons of insect herbivore infestation of seeds per transect and the interaction with % alien seed abundance between mango fields (MNG), marginal (MAR) and natural (NTL) vegetation in April-May and June-July.

	MNG-MAR		MNG-NTL		MAR-NTL	
	Δ Coeff (\pm se)	p-value	Δ Coeff (\pm se)	p-value	Δ Coeff (\pm se)	p-value
<i>Vegetation</i>						
April-May	- 0.83 (0.51)	*	- 0.75 (0.51)	*	- 0.62 (0.51)	*
June-July	- 0.96 (0.57)	*	- 0.74 (0.58)	*	0.89 (0.53)	*
<i>Veg: % A seed</i>						
April-May	0.69 (0.51)	*	0.63 (0.51)	*	- 0.57 (0.51)	*
June-July	- 0.57 (0.58)	0.43	0.91 (0.58)	*	0.93 (0.52)	*

The pairwise differences in model coefficients for each land-use type (Δ Coeff \pm se) are presented, with asterisks (*) denoting significant differences at $\alpha = 0.001$. Δ Coeff (\pm se) values denote how many times smaller (-) or greater (+) the first habitat is on average than the second in each pairwise comparison in terms of each parameter. Δ Coeff values have been reverse transformed (natural exponent e^x) to account for the intrinsic logit and log-link functions used to account for non-normality of data using GLMMs with poisson and negative binomial error structure.