Natural vegetation benefits synergistic control of the three main insect and pathogen pests of fruit crop in southern Africa

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Summary

1 Most studies of the potential for natural habitat to improve agricultural productivity have been conducted in transformed, temperate regions, but little is known of the importance of agroecosystem services in biodiverse developing countries.

2 Natural vegetation may promote the density and/or diversity of natural enemies of crop pests, but the strength of the effect varies, and few studies directly measure concurrent impacts on pest density. Considering multiple pest species within the same agroecosystem may help explain why some pests are more affected than others by landscape complexity. Here, we investigated multiple pest species (leaf-galling flies, three species of Tephritidae fruit fly and pathogenic fungi *Fusarium spp.*) and their enemies in cultivated mango *Mangifera indica*, in North-Eastern South Africa.

3 The density of generalist Tephritidae fruit flies increased with distance from natural vegetation during harvesting months, and predation rate of pupae sharply decreased from ~50% at the edge with natural vegetation to 0% at 250m into the crop. Parasitism rates of the cryptic, gall-forming fly increased with proximity to natural vegetation but pest density was unrelated to distance from natural vegetation. Incidence of the fungal pathogen disease increased with distance from natural vegetation, possibly due to decreased predation of commensal mites.

4 Although the relationship with distance to natural vegetation was significant for all species considered, the strength of this relationship varied across pest species and type of natural enemy studied, suggesting the benefits of natural vegetation depends on each natural enemy species' ability to disperse into the agricultural environment.

5 *Syntheses and applications.* Our results suggest that natural vegetation is a net source of natural enemies in a region of South Africa that still contains much of its natural biodiversity. However, the decline in natural enemies, and increase in pests, with distance from natural habitat indicates that this biocontrol is limited by natural enemy dispersal. In landscapes like these that are still dominated by natural habitat, conservation biocontrol can still be improved by management aimed at providing corridors of key plants and habitat elements into to the crops, to facilitate natural enemy dispersal.

Keywords: agroecology, *Ceratitis*, conservation biological control, ecosystem services, integrated pest management, mango malformation disease, natural enemies, natural vegetation, pest control

Introduction

Native predators and parasitoids can contribute significantly to control of insect pest populations, a process known as ‘conservation biological control’ (Thies *et al.* 2011). The presence and state of local natural habitat could be instrumental in supporting this ecosystem service, because species at higher trophic levels are generally more sensitive to land-use intensity and habitat fragmentation than the insect pests they attack (Chaplin-Kramer *et al.* 2011). A recent meta-analysis found a positive effect of proximate natural/semi-natural vegetation on the intensity of pest suppression by native predators and parasitoids (i.e., natural enemies; Veres *et al*. 2013). However, natural enemy effectiveness can be unrelated to, or even negatively affected by, proximate natural habitat (Macfadyen *et al.* 2009; Thies *et al.* 2011; Shackelford *et al.* 2013), because natural enemy effectiveness is influenced by the crop type of the agroecosystem, the geographic location and the ecology of both pest and natural enemy.

To date, most studies relating land-use to pest suppression have been conducted in developed, ecologically-transformed temperate regions, particularly Europe and North America (Chaplin-Kramer *et al*. 2011; Shackelford *et al.* 2013; Veres *et al.* 2013). Therefore, the importance of natural habitat for ecosystem service provision remains poorly understood where habitat complexity remains high (Tscharntke *et al.* 2012). In complex landscapes, natural vegetation harbours greater, more diverse populations of service-providing species associated with greater agricultural yields (Tscharntke *et al.* 2005; Bianchi *et al.* 2006). A recent review hypothesised that ecosystem services in complex habitats (>20% untransformed) may be no stronger than in simple habitats (1-20% untransformed), although the authors conceded this may not apply outside of temperate ecosystems and called for more studies in high diversity regions (Tscharntke *et al.* 2012). Ultimately, to provide predictive, trait-based hypotheses linking landscape composition and biological control efficiency, quantitative analyses of real systems from many different habitats and geographic locations are required (Thies *et al.* 2011).

Our study system is situated within the subtropical, biologically-diverse Kruger to Canyons Biosphere in South Africa, ~55% of which is intact vegetation, unimpacted by human development (Mucina & Rutherford 2006; Coetzer *et al.* 2013). Our target crop, mango *Mangifera indica* (L.) [Anacardiaceae], is economically important in the region, and the dominant tropical fruit produced globally (FAO 2003). Previous analysis of our study system found that productivity (kg of mangos per tree) declined with distance from natural vegetation (Carvalheiro *et al.* 2010). This decline in yield was only partly explained by concurrent reductions in pollinator diversity and density, and we hypothesise that there is an additional effect of natural vegetation on pest densities. There is a dearth of studies identifying the effect of proximate natural vegetation on multiple pest and natural enemy species within the same agroecosystem (Veres *et al.* 2013). Given that natural vegetation can be a source of pests and natural enemies, it is important to evaluate both pest densities and natural enemy activity to ascertain the net effect of natural vegetation on conservation biological control (Chaplin-Kramer & Kremen, 2012).

Natural vegetation may benefit natural enemies by increasing local habitat heterogeneity or by acting as a population reservoir that increases local density and resistance to environmental stochasticity (Macfadyen *et al.* 2011). Landscape complexity may also benefit natural enemies by providing food sources (e.g. pollen, nectar, & protein and lipids from other insects) or by providing shade and shelter (Heimpel & Jervis 2005). Reservoirs of predators and parasitoids in natural vegetation are only effective if individuals can disperse to the target pests (Hossain *et al.* 2002; Werling & Gratton 2010). Similarly, vegetation that provides shelter or nutrition is only beneficial to pest control if it is sufficiently close to target pest populations (Vollhardt *et al.* 2010). Thus, with increasing distance into agricultural fields, natural enemy density and diversity should decrease, resulting in reduced pest control. This effect could have contributed to the productivity declines found in Carvalheiro *et al.* (2010).

Herein, we consider the effect of proximity to natural vegetation on the conservation biological control of two types of Dipteran pest and a fungus on cultivated mangos . We consider a suite of closely-related Tephritidae fruit flies (*Ceratitis spp.*), the non-native Mango leaf-gall-forming fly *Procontarinia matteiana* and a pathogenic fungus *Fusarium sp.*. Using these three pest types, whose control depends upon different groups of natural enemies, we ask (i) does the density of these pests/pathogens increase with distance from natural vegetation, and (ii) for the insect pests, does this correspond to a decline in natural enemy action with distance from natural vegetation?

Methods

Field site

We carried out pest, pathogen and natural enemy surveys on sections of a mango farming estate (~2km^2 in size) bordering large areas of natural vegetation that are occasionally grazed by cattle. The vegetation type in this area is “Granite Lowveld” savanna, dominated by large *Acacia (Senegalia) nigrescens* (Oliver) [Fabaceae] and *Sclerocarya birrea* (A.Rich) [Anacardiaceae] (Mucina & Rutherford 2006).

The estate is split into blocks of mango trees, each ~70 x 150 m block contains trees of a single cultivar, within a grid of non-native *Casuarina sp.* trees serving as windbreaks. Pest, pathogen and natural enemy surveys were conducted across multiple blocks bordering the natural vegetation; see below for detailed methods. Natural vegetation is separated from the crop by narrow paths and the windbreak; so the nearest mango trees are ~20 m from the natural vegetation edge. Within mango blocks, the herbaceous cover is dominated by non-native agricultural weeds (e.g. *Tridax procumbens* (L.) and *Bidens pilosa* (L.) [Asteraceae]).

Study species and their surveillance

***1. Tephritidae fruit flies* (Ceratitis spp.)**

Locally, mangos are infested by three closely-related *Ceratitis* species: the Marula fly *C. cosyra* (Walker), the Mediterranean fly *C. capitata* (Wiedemann), and the Natal fly *C. rosa* (Karsch). Tephritid fruit flies are considered the most economically important insect pest of mango globally (Chin *et al.* 2010). Females lay eggs under the fruit’s skin. The larvae eat the flesh and pupate in the soil. Larvae are vulnerable to parasitoid wasps, whereas the sessile pupae are vulnerable to generalist predators (Chin *et al.* 2010; Ovruski *et al.* 2000). Natural vegetation could be a source of *Ceratitis* and their natural enemies, as all three *Ceratitis* spp. are polyphagous (see

De Meyer *et al.* 2002). Estate employees surveyed *Ceratitis* spp. density over four mango fruiting seasons (December-April, 2009-2013), using 29 Sensus™ adult fly traps containing Capilure™ (River Bioscience Ltd, Port Elizabeth, SA). Single traps were placed in alternate blocks of mango trees and monitored/reset every two weeks. Traps were placed 80m (n=9), 240m (n=7), 400m (n=6) & 560m (n=7) away from the mango-natural vegetation boundary. Traps were used in 8 cultivars with their relative representation reflecting the estate as a whole (Kent: 16; Tommy Atkins (TA): 9; Sensation: 8; Heidi: 4; Keitt: 4; Joa: 1; Manzanillo: 1; Shelly:1). To test for the effect of natural vegetation on adult fly density, we performed a Generalised Linear Mixed Effect Model (GLMM) with the following structure:

*Total fly count per trap ~ Distance of trap from natural vegetation * Month of survey + (1+Distance| Year / Month) + (1| Block number) + (1| Cultivar of block) + (1| Observation level factor), family = poisson.*

An observation-level random factor was included to account for high levels of extra-poisson variance associated with count data (Harrison 2014).

We reared *Ceratitis* clutches from mangos from 12 different tree blocks between March and April, 2013 (n=64; 33 ‘ripe’, 31 ‘unripe’); obtaining at least 5 mangos in every 25m band (e.g. 0-25, 25-50, etc.) up to a distance of 300m from the mango-natural vegetation boundary (measured using Garmin eTrex10® GPS device, Southampton, UK). Mangos were stored in separate, perforated plastic bags with a portion of sand. Bags were checked daily for fly pupae for two weeks following mango collection. Pupae were separated into eppendorf tubes (with small holes for air-flow) and monitored for one month after pupation; eclosing flies or parasitoids were recorded and identified. Pupae which failed to eclose within a month were presumed dead, either due to parasitism or other causes; proportion of pupae failing to eclose was calculated on a 'per mango' basis. We considered mango ripeness as a fixed effect in our analyses as studies have shown fruitfly parasitoids prefer ripe mangos (Eben *et al.* 2000). Ripeness was assessed by the predominant colour of the mango at collection; ripe mangos were ≥50% orange and unripe mangos >50% green. To test for an effect of distance to natural vegetation on proportion of fly larvae successfully becoming adults, we performed a GLMM using the following structure:

*Proportion of pupae eclosed per mango ~ Host mango distance from natural vegetation * Host mango ripeness* + *(1*| *Day of mango collection)* + *(1+Distance*| *Block)* + *(1*| *Observation level factor), family = binomial.*

We placed cohorts of eight fly pupae at 300, 150 and 10m into natural vegetation, and 250, 150 and 10m into the estate, from the border between the two environments. Cohorts were placed along three parallel transects running perpendicular to the border between April and May, 2013. The study ran for three weeks with one cohort being placed at each transect point each week, totalling three cohorts per transect point (n=48). For each cohort, we recorded the proportion of pupae that survived for 48 hrs. Pupae were considered predated if they were missing upon return or showed obvious signs of feeding damage. We collected samples of predators if predation was observed. All observed predators were ants, which were identified by Caswell Munyai (University of Venda). To test for the effect of distance from the natural/agricultural environment border on fruitfly pupae predation, we performed a GLMM using the following structure:

Proportion of cohort predated ~ Distance of cohort from border + *(1+Distance*| *Date)* + *(1+Distance*| *Transect)* + *(1*| *Observation level factor), family = binomial.*

2. Mango leaf gall fly (Procontarinia matteiana)

Mango leaf gall fly *Procontarinia matteiana* (Kieffer and Cecconi), lays eggs on young mango leaves, the larvae bore into the leaf tissue, creating leaf-galls in which the larvae pupate to emerge as adults (Mahmood, Mahmood & Razaq 2013). The gall fly appears to be primarily controlled by the specialist parasitoid *Chrysonotomyia pulcherrima* (Kerrich) (Waite 2002). In the absence of the parasitoid, high gall fly densities cause substantial reductions in mango crop (Augustyn *et al.* 2013). There is no documented evidence of *P. matteiana* persisting on native vegetation in South African savanna, nor records of native natural enemies attacking the gall fly.

We collected mango leaves across four parallel transects running perpendicular to the border between natural and managed environments, two transects each within the cultivars Kent and TA. Leaves were collected at distances of 0, 10, 50, 100 & 200 m from natural vegetation between March and June 2013. At each distance, we surveyed two leaves below head-height and two above from the same tree. We accounted for gall age by picking leaves with at least five galls exhibiting a characteristic dark spot without signs of insect eclosure (4-10 weeks old [Augustyn *et al*. 2013]). Leaves were randomly chosen until the requisite numbers fulfilling sample criteria were obtained. Leaves were frozen for 24hrs before data collection. Number of galls on each leaf was recorded and five randomly-chosen galls were dissected. The contents were classified as either: *C. pulcherrima*, *P. matteiana*, or Unidentifiable. To test for an effect of natural vegetation on gall fly infestation, we performed a GLMM with the following structure:

*Sum gall count on two leaves ~ Distance of tree from natural vegetation * Cultivar + (1+Distance|Date collected) + (1+Distance|Leaf height) + (1+Distance|Transect) + (1| Observation level factor), family = poisson.*

To test for an effect of natural vegetation on gall fly parasitism, we performed a GLMM with the following structure:

*Proportion galls containing parasitoids per tree ~ Distance of tree from natural vegetation * Cultivar + (1+Distance|Date collected) + (1+Distance|Transect) + (1| Observation level factor), family = binomial.*

3. Pathogenic mango malformation fungus (Fusarium sp.)

Mango malformation disease (MMD), caused by one or more fungi in the genus *Fusarium, is* of growing concern: infection is irreversible and it has now been described in most mango-growing countries (Chakrabarti 2011). Mango flowers are small and occur in large numbers within inflorescences. The disease causes malformed inflorescences, which do not fruit; yield losses up to 86% have been recorded (Chakrabarti 2011).

In August 2013, we surveyed five parallel transects running perpendicular from the natural vegetation boundary ~300 m into mango; each transect was in a different block of cultivar Kent. Within each transect, eight mango trees were selected at distances of 5, 9, 15, 27, 51, 99, 195 and 303 m from the edge. For each tree, total number of inflorescences and number of malformed inflorescences were counted. Only inflorescences displaying the typical cauliflower appearance of advanced MMD were scored as malformed. To test for an effect of natural vegetation on MMD severity, we performed a GLMM using the following structure:

Proportion of malformed inflorescences per tree ~ log Distance from natural vegetation + (1+logDistance|Transect number), family = binomial.

Statistics

All Generalised Linear Mixed Effect Models (GLMM) were performed in R (R Core Team 2014) using glmer in the lme4 package (Bates *et al*. 2014). Initial exploration to assess GLMM assumptions were performed following guidelines in Zuur *et al*. (2010). Prior to analyses we assessed the data for collinearity using pairwise scatterplots to assess fixed effect correlations >0.7 (Dormann *et al*. 2013). Random slope analyses were used for transect effects due to high type I error rates of GLMM random intercept analyses, where distance effects were unlikely to be consistent between transects (Barr *et al*. 2013). The Minimum Adequate Model was established via log-likelihood ratio comparisons using Maximum Likelihood approximation, for which X^2 results indicating significance are reported; fixed effect parameters were estimated using Restricted Maximum Likelihoods. GLMM models account for pseudoreplication in time and space, where survey dates and locations were included as random effects (Bates 2010). Observation level random factors were included to account for overdispersion, identified by greater than expected variation with all models, and to improve R^2 estimation accuracy (Harrison 2014). Poisson error structures were used for count data and binomial error structures for proportion data. We also assessed variance explained by the models, reporting marginal R^2 values for fixed effects alone and conditional R^2 for both fixed and random effects (Johnson 2014).

Results

i) Does the density of pests/pathogens increase with distance from natural vegetation?

Tephritid fruit flies

Multi-year trapping suggested that the relationship between adult fly counts and distance from natural vegetation varied significantly with month, with fly density decreasing with distance from natural vegetation in December (slope= -0.00063x) and January (-0.00065x), the reverse being true in February (0.00020x), March

(0.00033x) and April (0.00035x) (X^2_5 = 16.644, $P < 0.01$; R^2 marginal = 0.08; R^2 conditional = 0.83; Fig 1).

Mango leaf gall fly

Gall counts per tree were not significantly related to distance from natural vegetation (X^2_1 = 1.39, P = 0.24; Fig 2a). However, there were significantly more galls on TA than Kent trees (X^2_1 = 11.25, $P < 0.001$; R^2 marginal = 0.18; R^2 conditional = 0.24; Fig 2b).

Pathogenic fungi (Fusarium *spp.*)

The proportion of malformed inflorescences per tree increased with distance from natural vegetation (X^2_1 = 10.61, P = 0.001; R^2 marginal = 0.28; R^2 conditional = 0.34; Fig 3). Only one of the 40 trees surveyed exhibited no MMD; on average 17% of inflorescences were malformed.

ii) Does mortality of dipteran pests decline with distance from natural vegetation?

Successful tephritid fruit fly emergence

The proportion of pupae not eclosing decreased with distance from natural vegetation in green (unripe) mangos, the opposite was true in orange (ripe) mangos (interaction term; X^2_1=8.72, $P < 0.01$; R^2: marginal = 0.21, conditional = 0.52; Fig 4). The negative relationship between distance and fly mortality in unripe mangos was ~three times as steep as the positive effect of distance for ripe mangos, suggesting the distance effect was stronger on larvae in unripe mangos.

Predation of tephritid pupae placed in soil

Mortality rates of fly pupae were highest in natural vegetation and lowest in mango, and intermediate at the border between the two environments (X^2_1=9.97, P = 0.001; R^2: marginal = 0.51, conditional = 0.92; Fig 5). *Pheidole cf megacephala* (big-headed ant), was the only visually verified predator.

Mango leaf-gall fly

Rates of gall parasitism were significantly lower in trees further from natural vegetation ($X^2_1 = 6.69$, $P < 0.01$; R^2 Marginal = 0.07, R^2 Conditional = 0.42; Fig 6), but did not vary between Kent and TA cultivars ($X^2_1 = 2.21$, $P = 0.14$).

Discussion

Biological control services provided by natural vegetation in this study system.

This is one of the few studies considering 'conservation biological control' of multiple pest and natural enemy species in the same study system simultaneously, and the only one performed in a relatively untransformed, biodiverse subtropical region (Chaplin-Kramer *et al*. 2011). Our results suggest that natural vegetation characteristic of 'Granite Lowveld' provided a net positive pest control service to mango growers, that was significantly reduced by ~200m into the crop (average pest mortality was 25-80% lower compared to the edge). Across studied pest, predator and pathogen species in this study, benefits declined with distance from natural vegetation, supporting hypotheses that beneficial ecosystem services are limited by dispersal distance from source vegetation (Hossain *et al.* 2002; Werling & Gratton 2010). Similar studies performed in temperate countries suggest that benefits of natural vegetation dissipate by ~80 m into the agricultural environment (Collins *et al.* 2002; Thomson & Hoffman, 2013); compared to 200 m herein. It is unclear whether this difference is because of the limited spatial scale considered in prior studies or because of greater immigration by service providing organisms into agroecosystems in high complexity landscapes (Bianchi *et al.* 2006). Tscharntke *et al.* (2012) hypothesised that conservation management practices are less effective in high complexity regions; however, strong dispersal limitation could explain potential for natural vegetation patches within crops to improve ecosystem service provision (Carvalheiro *et al.* 2012).

In this study, we observed distance-dependent effects of natural vegetation on mortality and infestation severity by pests known to cause significant reductions in mango yields, which could account for declines beyond those associated with pollination loss (Carvalheiro *et al*., 2010). However, as observed in prior studies, there was significant variability in the strength of the effect of natural vegetation across study species (Chaplin-Kramer *et al.* 2011; Thies *et al.* 2011; Shackelford *et al.* 2013). Below, we discuss possible mechanisms behind distance effects in each focal species.

Tephritid Fruit Flies (*Ceratitis spp.*)

Natural vegetation can be a source of both pests and natural enemies (Chaplin-Kramer & Kremen, 2012; MacFadyen & Muller 2013). *Ceratitis spp*. use a wide range of native species as host plants (De Meyer *et al*. 2002). Early in mango harvesting season (December and January) we observed higher densities of adult flies close to natural vegetation (Fig. 1). This suggests that host plants within natural vegetation may provide nursery sites for *Ceratitis spp.* outside the mango growing season. Pest population increases generally preceed significant natural enemy-driven mortality (Chaplin-Kramer & Kremen, 2012; MacFadyen & Muller 2013). Later in the season (February, March and April) adult fly counts were lower closer to natural vegetation (Fig 1). In March and April, juvenile fly mortality was greater near natural vegetation (Figs 4 & 5); suggesting that natural enemies could have driven this negative relationship between proximity to natural vegetation and adult fly density. Across all months, mean fly counts increased with distance from natural vegetation (Table 1), suggesting that, on balance, natural vegetation favours natural enemies over Tephritidae pest populations as predicted elsewhere (Chaplin-Kramer *et al*. 2011). The relatively shallow slopes for adult fly count with distance could have arisen because of the high number of zero-values (counts where there were no flies) which reduced average fly-count, thus underestimating the strength of distance effects. Alternatively, shallow slopes could indicate a weak effect of natural vegetation on fly density or an effect that was only weakly limited by dispersal.

The effect of proximity to natural vegetation on mortality of larvae and pupae reared under controlled conditions could have been caused by parasitoids prior to collection of fruits from orchards. After collection, all fruit, larvae and pupe were treated identically. Parasitoid wasps ovipositing in *Ceratitis spp*. larvae are well documented (Ovruski *et al.* 2000); however, we only reared a single, Opinine parasitoid wasp during the study. This may be because parasitoid development generally takes longer (Courtney Moxley, personal communication, February 2015), extending beyond our field season or, alternatively, that larval and pupal mortality was caused by a currently unknown agent (e.g., a pathogen). Greater pupal predation in natural vegetation compared to within the crop suggests that highly effective natural enemies within natural vegetation could not inhabit crop fields despite prey being available. *Pheidole cf megacephala* was the only predator observed, seen carrying study pupae away on multiple occasions. Although we found consistent effects of natural vegetation on pest mortality, few causative agents were identified, limiting conclusions on the relative importance of natural enemy density or biodiversity (Tscharntke *et al*. 2005). This gap highlights the need for network ecology analyses that identify key biological control agents and the habitat features that aid their dispersal into agricultural environments.

Mango Leaf Gall fly *Procontarinia matteiana*

Benefits of natural vegetation tend to be much weaker for specialist (e.g., parasitoids) than generalist natural enemies (Chaplin-Kramer *et al.* 2011; Rand *et al.* 2012). This may partly be because specialist natural enemies are less likely to have population reservoirs in the natural environment, particularly if the preferred prey/host is a specialist feeder itself (Shackelford *et al.* 2013). However, parasitism rates of mango leaf gall fly by its parasitoid were significantly higher closer to natural vegetation despite there being no records of the pest or the parasitoid persisting on species other than mango (Fig 6). Increased parasitism closer to natural vegetation may have resulted from direct provisioning effects; for example, flowers provide nectar and pollen for local parasitoids, increasing their longevity and parasitism rates (Heimpel & Jervis 2005). We did not find a concurrent, significant effect on gall density (Fig 2), either because the effect of increased parasitism was too weak to affect local gall fly populations, or because of population effects of high local parasitism being evenly distributed over the area through fly dispersal.

Whereas landscape complexity is generally correlated with natural enemy density, its effect on pest density is far more variable (Chaplin-Kramer *et al.* 2011; Veres *et al.* 2013). Our study, in conjunction with others, suggests two pest traits that may be important. Firstly, densities of pest species primarily controlled by a single, relatively specialist natural enemy, such as *P. matteiana* and *Empoasca vitis* in viticulture systems, were not reduced by the presence of proximate semi-natural vegetation (Van Helden, Pain & Pithon 2008). This is despite positive effects on respective natural enemies, *C. pulcherrima* in this study and *Trichogramma spp.* in viticulture systems (Thomson & Hoffman, 2010). Similarly, studies of other pest species controlled by few natural enemy species, such as cereal aphids, find little evidence of benefits to control associated natural enemy diversity (MacFadyen *et al.* 2009). Comparatively, pest species attacked by multiple natural enemies (e.g., *Ceratitis* spp. in this study), are more prone to control associated with biodiverse systems, where natural enemy complementarity and redundancy are supported by proximate natural vegetation, and thus associated with reduced pest density (Tscharnkte 2005). Secondly, densities of hidden pest species, for which there may be fewer potential natural enemy species, such as *P. matteiana* herein or stem-weevils *Ceutorhynchus spp.* in oil-seed rape, do not respond to natural vegetation proximity (Zaller *et al.* 2008). Further studies of multiple pests within the same study system whose control is dependent upon a broad or narrow range of enemies is required to elucidate the degree to which biodiversity could explain variation in response of pest species to landscape complexity (Chaplin-Kramer *et al.* 2011; Veres *et al.* 2013).

Mango Malformation Disease *Fusarium spp*.

Severity of mango malformation disease (MMD) increased significantly with distance from natural vegetation. The percentage of malformed inflorescences increased from 10% on mango field edges to ~40% at 250m into the crop (Fig 3). Spread of the disease within estates is thought to occur via cutting (Kumar, Singh & Beniwal 1993) but severity of MMD has also been shown to correlate with density of mango bud mite *Aceria mangiferae* (Sayed) (Gamliel-Atinsky *et al.* 2010; Lindquist, Sabelis & Bruin 1996). It is possible that predators originating from natural vegetation reduce *A. mangiferae* density, reducing severity of MMD closer to natural vegetation; the likelihood of which should be the subject of further study. MMD is a growing problem globally (Chakrabarti 2011) and was a topic of concern during personal communication with local farmers. We found that over a third of inflorescences (maximum ~60%) were infected at ~250m into the agricultural environment. Because we only scored severe advanced stages of malformation these figures are likely an underestimation.

Factors other than proximity to natural vegetation

Average variance in pest or natural enemy presence explained by distance effects in this study was 22%. Spatial and temporal influences were marked, given that random factors (which captured position and date) explained a further 27% of the variation. This may be because ecosystem service provision often originates from a particular or small group of species or microhabitats (Bianchi & Wäckers 2008; De Meyer *et al*. 2002), which are not ubiquitous or uniformly dispersed spatially or temporally within the natural environment. Thus, some of the variance explained by spatial and temporal random effects may have arisen from unequal distances to key plant species, which occur at different densities and change over the season, because of differing phenologies. We would also expect some spatial and temporal autocorrelation associated with pest population dynamics and dispersal. *Fusarium spp.*, which cause MMD, is particularly slow spreading, and its incidence (not severity) may exhibit strong spatial aggregation (Gamliel-Atinsky *et al.* 2010).

We found a significant effect of tree cultivar on mango leaf gall fly infestation, corroborating previous studies (e..g. Augustyn *et al*. 2013). Different cultivars also flower and fruit at different times of year, altering spatial aggregation of pests/pathogens and natural enemies, and we found a significant effect of month on the relationship between natural vegetation proximity and adult fruit fly density (Fig 1). We tried to limit our investigations to the Kent cultivar and have included tree cultivar as a random or independent model variable when this was not possible. However, there may be additional effects unaccounted for, such as type of cultivar in adjacent blocks.

Limitations and future studies

All of our data were collected on a single but sizeable (~ 2km^2) estate bordering a large area of natural vegetation. We used GLMMs including date and position as random effects to account for repeated transect sampling, and future extension of this work over more estates and a wider geographic range are required to test the generality of our results. At present we cannot distinguish whether weak distance effects were due to weak effects of natural vegetation or lack of dispersal limitation. Future studies could address this by quantifying effects of species mobility on the interaction between natural and managed environments.

Conclusions

Our findings suggest that part of the decline in mango productivity with distance from natural vegetation that cannot be explained by declines in pollination alone (Carvalheiro *et al*. 2012) are attributable to changes in densities of adult *Ceratitis spp*. during key mango harvesting months, and severity of Mango Malformation Disease; both of which impact mango productivity (Chakrabarti, 2011; Chin *et al.* 2010). This corroborates previous studies suggesting that natural vegetation is only important within an effective distance and that the scale of habitat structure is important in determining ecosystem service strength (Hossain *et al.* 2002; Tscharntke *et al*. 2005; Bianchi & Wäckers 2008; Werling & Gratton 2010).

It has been hypothesised that management aimed at generally increasing biodiversity conservation will have little impact on the ecosystem service of pest control in complex landscapes with high proportion of intact biodiversity (Tschartke *et al.* 2012). However, our results indicate that in such landscapes, conservation biocontrol is limited by natural enemy dispersal and can be improved by providing corridors of key plants and habitat elements in crop fields to facilitate movement into fields.

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Table 1. Average and standard error of *Ceratitis* spp. fly counts across all blocks, months and years.

Distance from natural vegetation (m)	80	240	400	560
Mean adult count (+/- s.e.)	1.62 (+/- 0.09)	1.77 (+/- 0.12)	2.19 (+/- 0.15)	2.24 (+/- 0.14)

Fig legends

Fig 1. Counts of all adult *Ceratitis spp.* flies caught in Census™ traps against distance from the natural/agriculture environment border. Data are separated according to month of collection to illustrate the interaction between month and distance. Lines illustrate median values +/- 1s.d. Equations are poisson glm fits of median values.

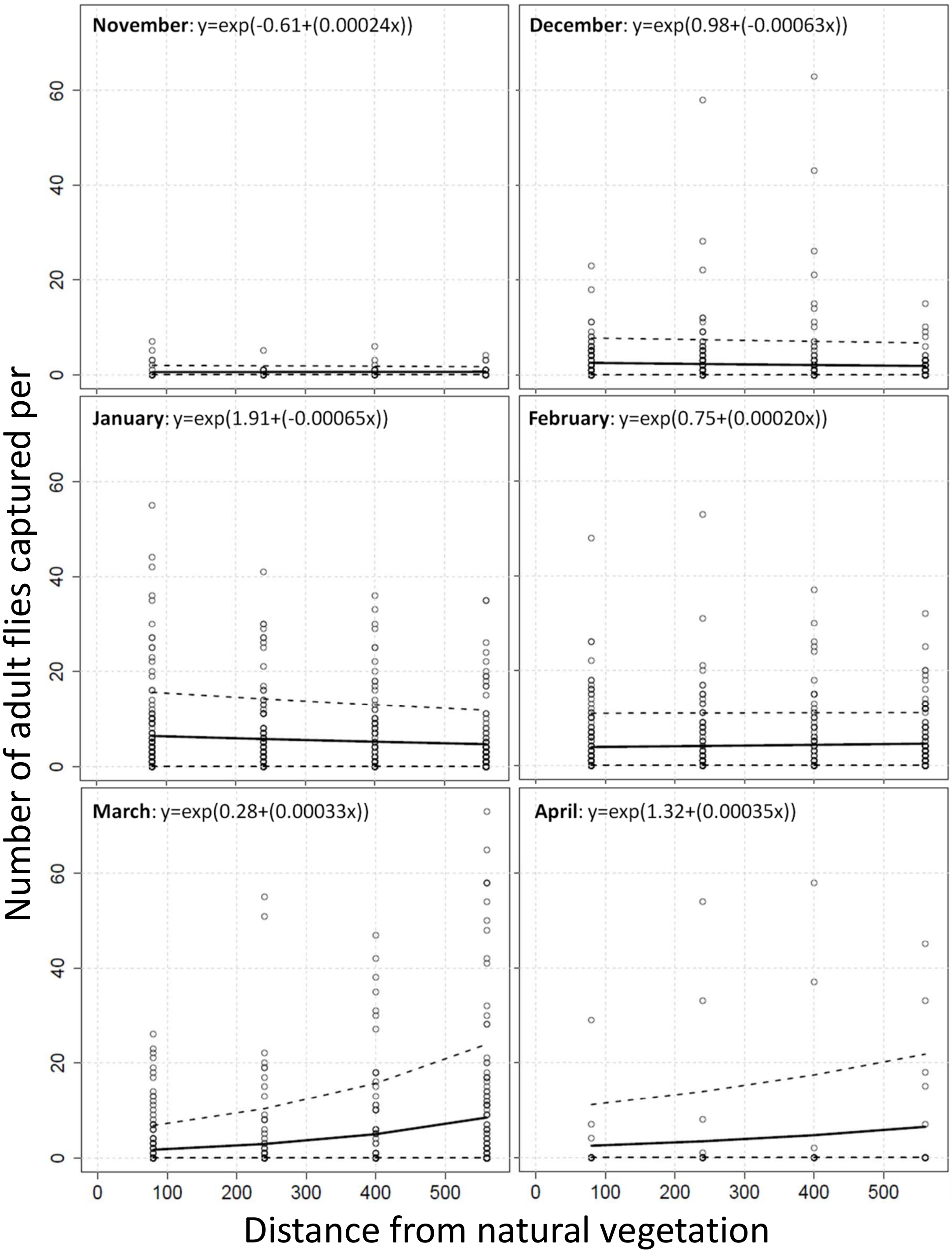
Fig 2. (a) Leaf gall counts per tree against the log(distance) of the tree from natural vegetation. (b) Leaf gall counts per tree for each cultivar studied.

Fig 3. Proportion of inflorescences per mango tree that exhibited pathogenic flower malformation against the log(distance) of the tree from natural vegetation. Lines and equations illustrate model best fit +/- 1s.e.

Fig 4. Proportion of reared *Ceratitis* pupae not eclosing against the distance of the host mango from natural vegetation, for (a) ripe and (b) unripe mangos. Lines and equations illustrate model best fit +/- 1s.e. Point size is weighted by log(number of pupae collected from sampled mangoes).

Fig 5. Proportion of *Ceratitis* pupae predated within 48 hrs against distance from the natural/agriculture environment border. Negative distances represent distance into natural vegetation and positive ones indicate distance into the estate. Lines illustrate model best fit +/- 1s.e. Point size is weighted according to the number of points at that value; i.e. number of cohorts for which that particular proportion of pupae were predated at that distance across all replicates and transects.

Fig 6. Proportion of parasitised galls per tree against the log(distance) of the tree from natural vegetation. Lines and equations illustrate model best fit +/- 1s.e.


November: y=exp(-0.61+(0.00024x))
December: y=exp(0.98+(-0.00063x))
January: y=exp(1.91+(-0.00065x))
February: y=exp(0.75+(0.00020x))
March: y=exp(0.28+(0.00033x))
April: y=exp(1.32+(0.00035x))
0
20
40
60
0
100
200
300
400
500
Number of adult flies captured per
Distance from natural vegetation

662

663 Fig 1

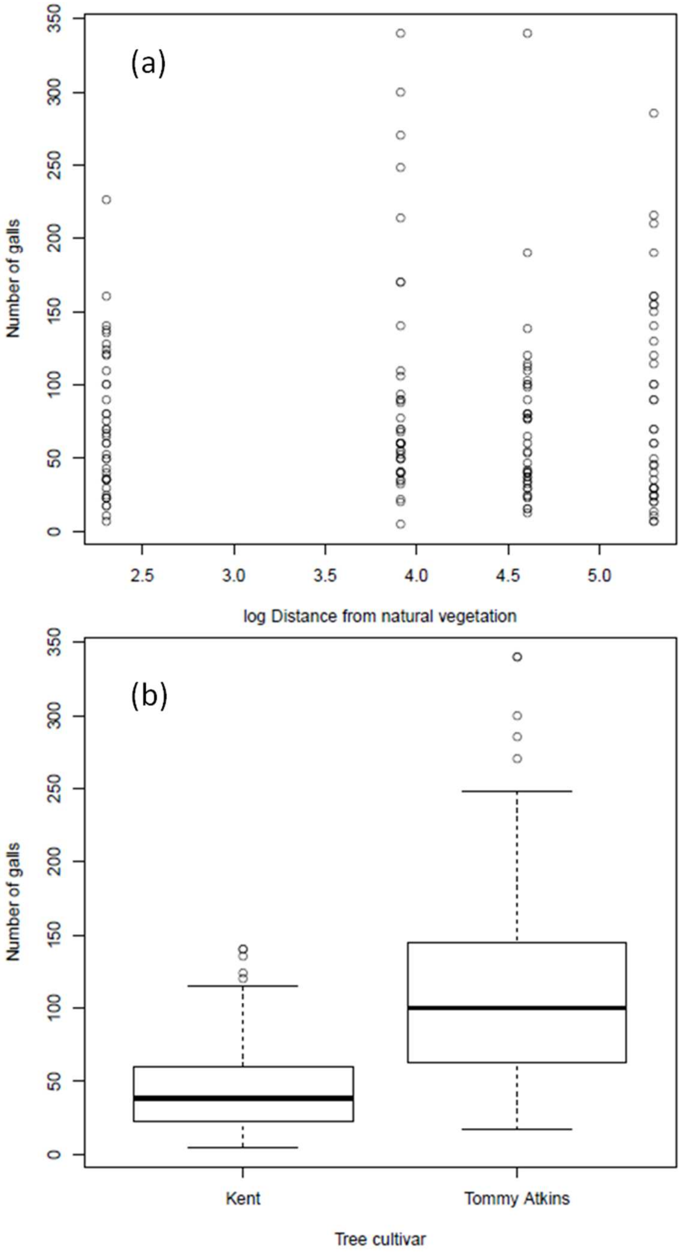

(a)
Number of galls
0
50
100
150
200
250
300
350
2.5
3.0
3.5
4.0
4.5
5.0
log Distance from natural vegetation
(b)
Number of galls
0
50
100
150
200
250
300
350
Kent
Tommy Atkins
Tree cultivar

Fig 2

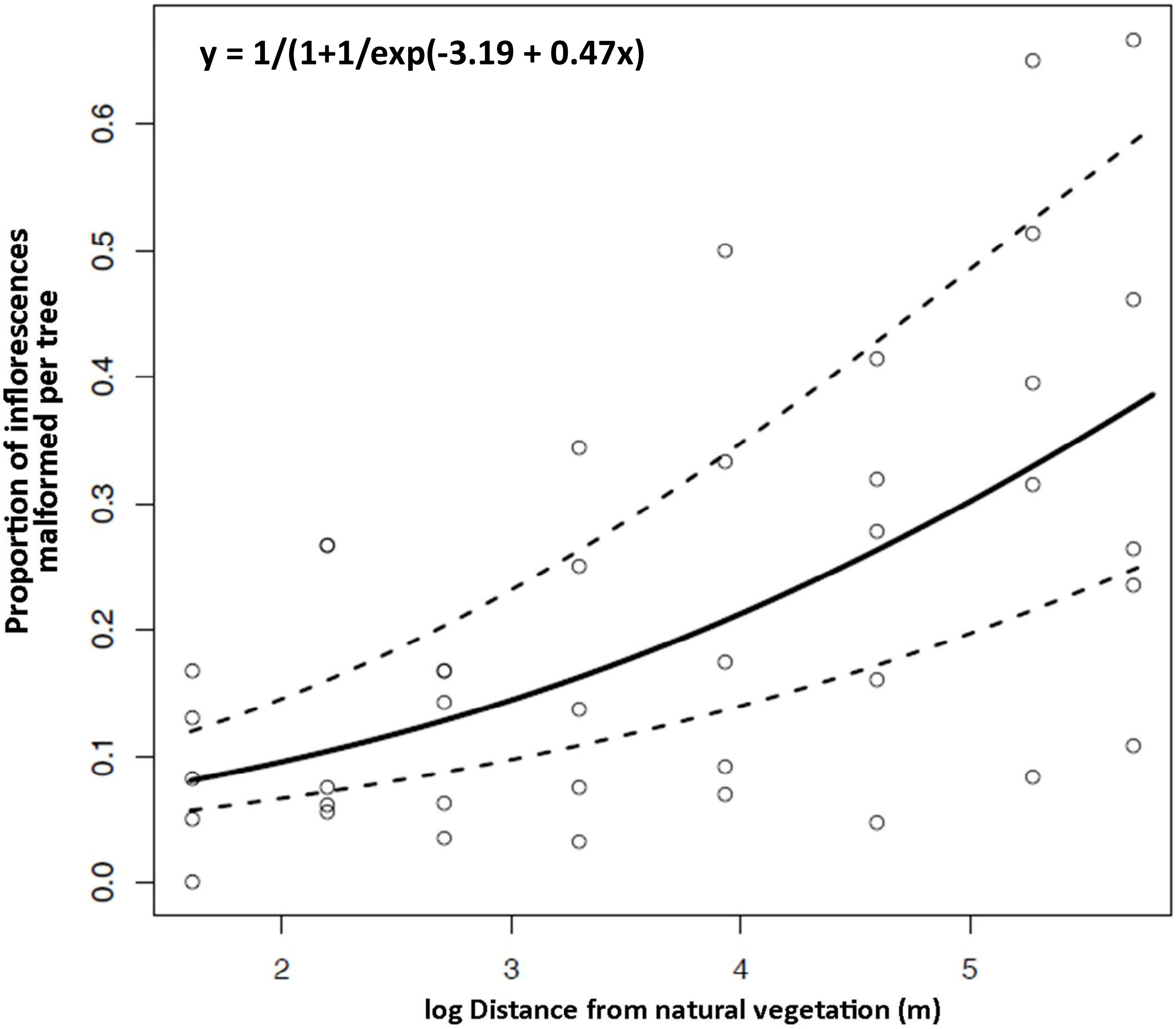

y = 1/(1+1/exp(-3.19 + 0.47x)
Proportion of inflorescences malformed per tree
0.0
0.1
0.2
0.3
0.4
0.5
0.6
2
3
4
5
log Distance from natural vegetation (m)

Fig 3

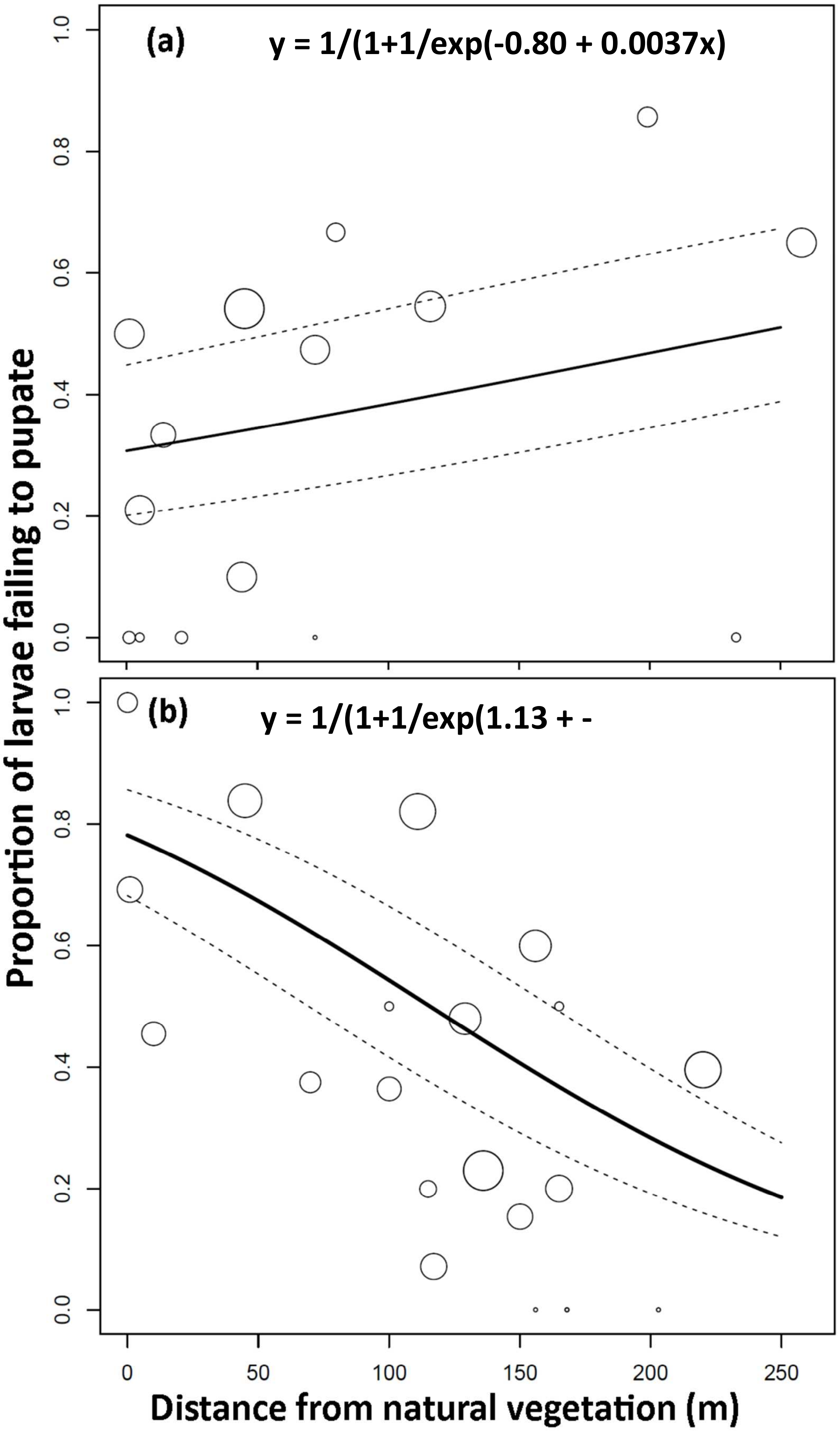

(a)
y = 1/(1+1/exp(-0.80 + 0.0037x)
(b)
y = 1/(1+1/exp(1.13 + -
Proportion of larvae failing to pupate
0.0
0.2
0.4
0.6
0.8
1.0
0
50
100
150
200
250
Distance from natural vegetation (m)

Fig 4

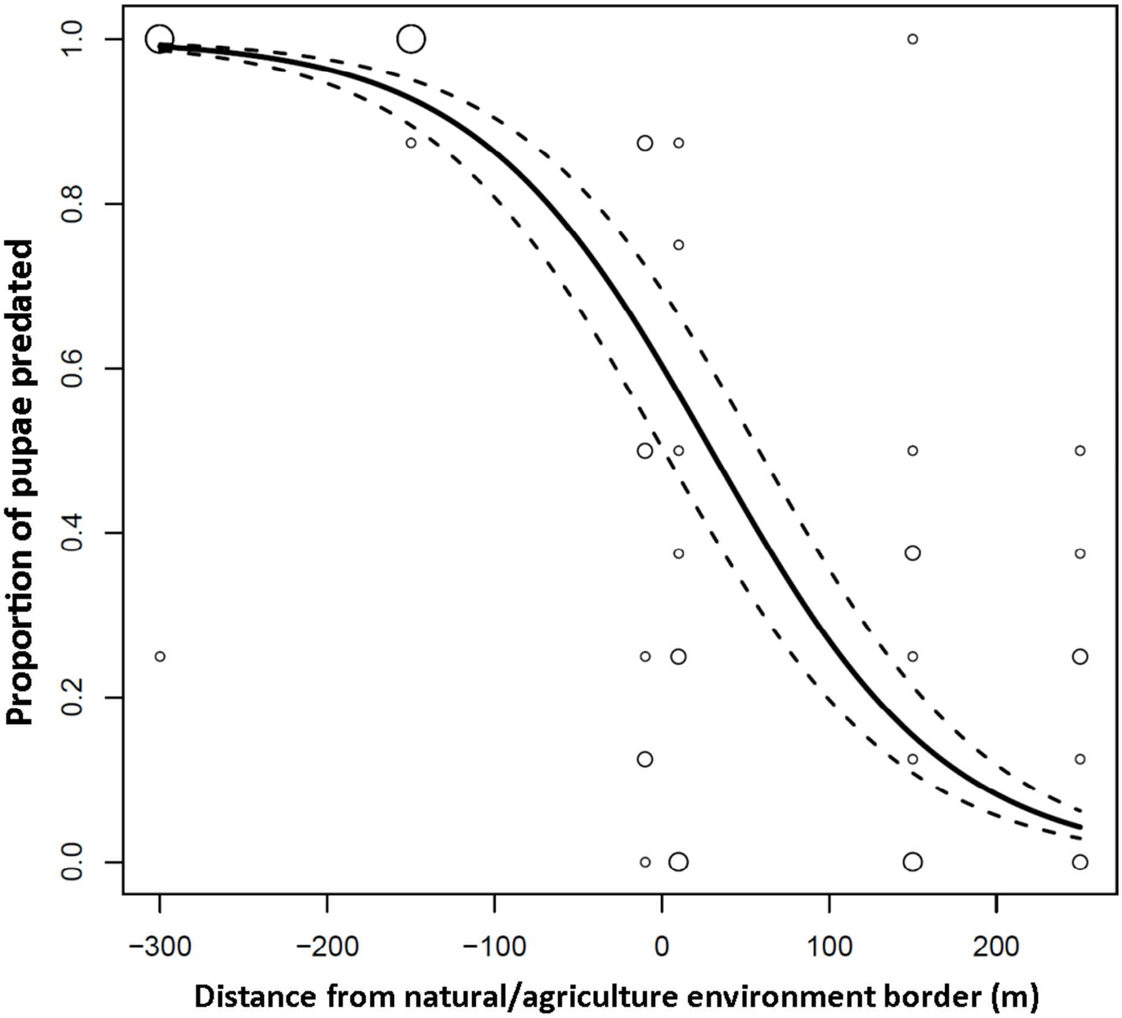

Proportion of pupae predated
0.0
0.2
0.4
0.6
0.8
1.0
−300
−200
−100
0
100
200
Distance from natural/agriculture environment border (m)

Fig 5.

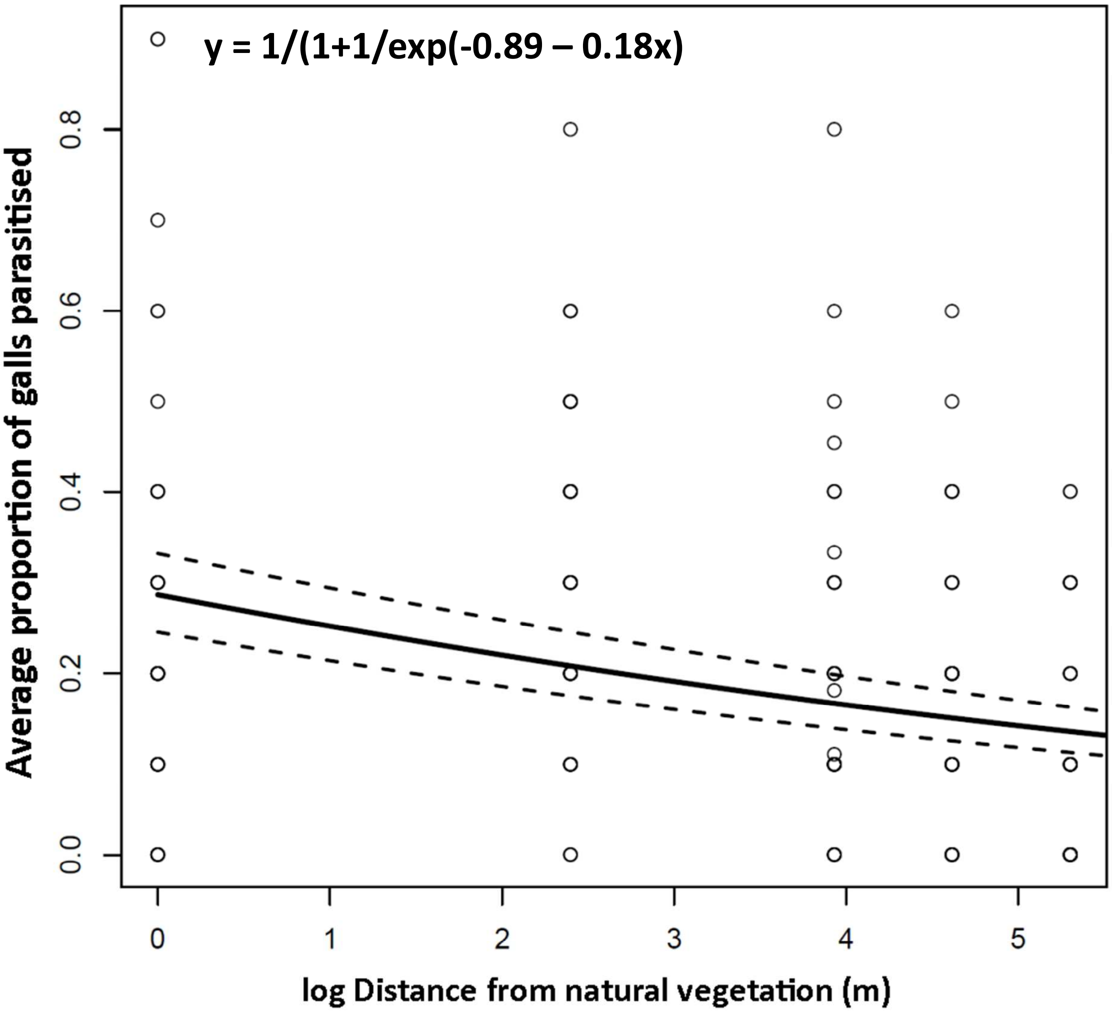

y = 1/(1+1/exp(-0.89 – 0.18x)
Average proportion of galls parasitised
0.0
0.2
0.4
0.6
0.8
0
1
2
3
4
5
log Distance from natural vegetation (m)

Fig 6.

Supplementary materials 1. Outputs of GLMER models applied to various data sets

Adult fly data

*glmer(Fly Count~Distance*Month+(1+Distance|Year:Month)*
+(1|Block)+(1|obs)+(1|Cultivar), family= poisson)

Random factor

Groups	**Variance**	**Std.Dev.**
Observation level	2.70E+00	1.6429641
Block	2.02E-01	0.4498547
Distance|Year/Month	5.03E-01	0.7095413
	7.16E-08	0.0002675
Cultivar	2.39E-01	0.4885443

Number of observations	2117	Groups	Observation	2117		
			Block	29	Year/Month	19
			Cultivar	8		

Fixed effects	**Estimate**	**Std.Error**	**Z-value**	**Pr(>|z|)**	
(Intercept)	-2.4869377	0.9007367	-2.761	0.005762	**
Distance	0.0010492	0.0014367	0.73	0.465225	
Month[December]	2.2935921	0.9438696	2.43	0.015099	*
Month[January]	3.2404589	0.9416189	3.441	0.000579	***
Month[February]	2.1397982	0.9440194	2.267	0.023409	*
Month[March]	0.3821232	0.9500778	0.402	0.687535	
Month[April]	0.0863817	1.1387376	0.076	0.939533	
Distance:Month[December]	-0.0024232	0.0014453	-1.677	0.093623	.
Distance:Month[January]	-0.002363	0.0014308	-1.651	0.098646	.
Distance:Month[February]	-0.0001987	0.0014342	-0.139	0.889821	
Distance:Month[March]	0.0026	0.0014546	1.787	0.073879	.
DistanceMonth[April]	0.0022794	0.0020005	1.139	0.254539	

AIC	BIC	logLik	deviance	df.resid
8702.3	8804.2	-4333.2	8666.3	2099

Pupae rearing data

*glmer(Survival~Distance*Ripeness+(1|Date.Day)+(1+Distance|Plot)*
+(1|Observation level), family=binomial)

Random effects

Groups	**Variance**	**Std.Dev.**
Observation level	3.94E-01	6.28E-01
Day of collection	2.51E-01	5.01E-01
Block of collection	5.83E-10	2.41E-05

Number of observations	64	Groups	Observation	64	Day	9
			Block	7		

Fixed effects	**Estimate**	**Std.Error**	**Z-value**	**Pr(>|z|)**	
(Intercept)	1.130935	0.513562	2.202	0.02766	*

Distance	-0.011007	0.003952	-2.785	0.00535	**
Ripeness[Ripe]	-1.926249	0.591277	-3.258	0.00112	**
Distance:Ripeness[Ripe]	0.014723	0.004892	3.009	0.00262	**

AIC	BIC	logLik	deviance	df.resid
169.8	189.2	-75.9	151.8	55

Pupae predation data

glmer(Proportion predated~Distance+(1+Distance|Transect)
+(1+Distance|Date cohort placed) + (1|Observation),family=binomial)

Random effects

Groups	**Variance**	**Std.Dev.**
Observation level	5.21E+00	2.28E+00
Distance|Date cohort placed	1.35E-09	3.67E-05
		1.01E-07
Distance|Transect	3.81E-10	1.95E-05
		6.42E-08

Number of observations	49	Groups	Observation	49	Date placed	7
					Transect	3

Fixed effects	**Estimate**	**Std.Error**	**Z-value**	**Pr(>|z|)**	
(Intercept)	0.419615	0.403388	1.04	0.298	
Distance	-0.014199	0.002857	-4.971	6.67E-07	***

Gall Density

glmer(Gall count~Cultivar+(1+logDistance|Date surveyed)+(1+logDistance|High.Low)
+(1|Observation level)+(1+logDistance|Transect),family=poisson)

Random effects

Groups	**Variance**	**Std.Dev.**
Observation level	3.83E-01	0.618714
logDistance|Date surveyed	5.07E-02	0.225062
	5.46E-03	0.075744
logDistance|Transect	1.62E-03	0.040235
	6.63E-05	0.008372
logDistance|High.Low	1.91E-03	0.043737
	9.18E-05	0.009584

Number of observations	199	Groups	Observation	199	Date surveyed	15
					Transect	4

Fixed effects	**Estimate**	**Std.Error**	**Z-value**	**Pr(>|z|)**	
(Intercept)	3.56002	0.09713	36.65	2.00E-16	***
Cultivar[TommyAtkins]	0.97299	0.12688	7.67	1.74E-14	***

AIC	BIC	logLik	deviance	df.resid
2038.6	2068.2	-1010.3	2020.6	190

Gall parasitoid density

glmer(Proportion parasitised~logDistance+(1+logDistance|Date surveyed)
+(1+logDistance|Transect)+(1|Observation level),family=binomial)

Random effects

Groups	**Variance**	**Std.Dev.**
Observation level	0.450315	0.67105
logDistance|Date surveyed	0.374802	0.61221
	0.008708	0.09332
logDistance|Transect	0.001855	0.04307
	0.002373	0.04872

Number of observations	199	Groups	Observation le	199	Date surveyed	15
					Transect	4

Fixed effects	**Estimate**	**Std.Error**	**Z-value**	**Pr(>|z|)**	
(Intercept)	-0.88904	0.21955	-4.049	5.13E-05	***
logDistance	-0.17858	0.05305	-3.366	0.000762	***

AIC	BIC	logLik	deviance	df.resid
745.1	774.8	-363.6	727.1	190

Malformed inflorescences

glmer(Proportion malformed~logDistance+(1+logDistance|Transect),family=binomial)

Random effects

Groups	**Variance**	**Std.Dev.**		
logDistance|Transect	0.02218	0.1489		
	0.1066	-1		
Number of observations	40	Groups	Transect	5

Fixed effects	**Estimate**	**Std.Error**	**Z-value**	**Pr(>|z|)**	
(Intercept)	-3.19025	0.27778	-11.485	<2e-16	***
logDistance	0.46885	0.07905	5.931	3.00E-09	***

AIC	BIC	logLik	deviance	df.resid
226.7	235.2	-108.4	216.7	35