



## Early-season movement dynamics of phytophagous pest and natural enemies across a native vegetation-crop ecotone



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### ABSTRACT

There is limited understanding about how insect movement patterns are influenced by landscape features, and how landscapes can be managed to suppress pest phytophage populations in crops. Theory suggests that the relative timing of pest and natural enemy arrival in crops may influence pest suppression. However, there is a lack of data to substantiate this claim. We investigate the movement patterns of insects from native vegetation (NV) and discuss the implications of these patterns for pest control services. Using bi-directional interception traps we quantified the number of insects crossing an NV/crop ecotone relative to a control crop/crop interface in two agricultural regions early in the growing season. We used these data to infer patterns of movement and net flux. At the community-level, insect movement patterns were influenced by ecotone in two out of three years by region combinations. At the functional-group level, pests and parasitoids showed similar movement patterns from NV very soon after crop emergence. However, movement across the control interface increased towards the end of the early-season sampling period. Predators consistently moved more often from NV into crops than vice versa, even after crop emergence. Not all species showed a significant response to ecotone, however when a response was detected, these species showed similar patterns between the two regions. Our results highlight the importance of NV for the recruitment of natural enemies for early season crop immigration that may be potentially important for pest suppression. However, NV was also associated with crop immigration by some pest species. Hence, NV offers both opportunities and risks for pest management. The development of targeted NV management may reduce the risk of crop immigration by pests, but not of natural enemies.

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### 1. Introduction

While there is increasing recognition that phytophagous pest management based on the activity of predatory arthropods and parasitic wasps requires a landscape approach (Cronin and Reeve, 2005; Chaplin-Kramer and Kremen, 2012), the development of landscape-scale pest management strategies is still in its infancy (Schellhorn et al., 2008). Studies examining the relationship between landscape-scale features on pest suppression are becoming more common (Bennett and Gratton, 2012; Caballero-López et al., 2012; Chaplin-Kramer and Kremen, 2012). However,

there is still limited understanding about which factors influence the spatial and temporal distribution of arthropod-mediated ecosystem services, and how these can be manipulated to suppress pests. The movement of pests and natural enemies is common (Rand et al., 2006; Thomson and Hoffmann, 2013), however we know little about the behavioural responses of arthropods to edges and ecotones. This movement is often described as the spillover of natural enemies from natural areas into cropping areas or vice versa (Rand et al., 2006). Understanding how landscape features may facilitate or impede movement can provide important information about immigration to crops and have implications for the management of arthropod-mediated ecosystem services (Kremen, 2005).

Agricultural landscapes can be considered as a collection of 'patches' with different land uses and disturbance levels. Crop

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habitats tend to be ephemeral, frequently disturbed, and recolonised throughout the growing season (Wissinger, 1997). In contrast, natural vegetation (NV) is more stable and can function as reservoirs of natural enemies (Bianchi et al., 2012; Letourneau et al., 2012), but potentially also of pests (Van Emden, 1965; Zhang et al., 2007; Al Hassan et al., 2013). Immigration from NV to crops involves the crossing of an ecotone, and species can have specific responses to different ecotones (Duelli et al., 1990; Duelli and Obrist, 2003). The contrast in vegetation types found on each side of an ecotone may be perceived differently by each species (Ries and Debinski, 2001). Therefore we cannot assume that all species will move easily from a remnant NV patch into a nearby crop. Quantifying the composition of the arthropod communities moving across a NV/crop ecotone can provide novel insights into the function of these habitats in supporting pests and their natural enemies, and suggest which species can easily access resources in both these habitats.

The relative timing of pest and natural enemy arrival in crops is considered a key factor for the effectiveness of natural enemies in suppressing pest populations (e.g. Settle et al., 1996). Theory suggests that the timing of natural enemy arrival in crops can be influenced by the distance between the crop and source habitat (Bianchi et al., 2009), and the dispersal ability of natural enemies relative to that of the pests (Sivakoff et al., 2012). This implies that pest populations in crops far from natural enemy source habitats have an increased time window for unchecked build-up compared to crops near source habitats (Ekbom et al., 1992; Bianchi et al., 2010). However, empirical evidence of how timing of arrival is influenced by landscape context is scant (Petersen 1999; Alomara et al., 2002). Here, we use bi-directional interception traps to measure the activity of flying insects across the NV/crop ecotone, relative to a control crop/crop interface. In the early part of the cropping season, in two distinct agricultural regions, traps were placed on these different interfaces. Our aims are three-fold. Firstly, we characterise the insect community at the NV/crop ecotone relative to a control interface. Secondly, we assess the direction of movement across the ecotone, and use this to indicate whether NV is a net exporter of pests, predators or parasitoids during the early stage of the growing season. Thirdly, we explore species-specific behaviour across the ecotone and between two regions which have a different cropping season phenology.

## 2. Methods

Our study was conducted in two regions in Australia: a temperate and a sub-tropical region with both autumn-sown cereals. In both regions the field dimensions, crop-types and NV patches were mapped in a 7 km radius circular area using aerial images and ground-truthing. The temperate region in New South Wales (NSW) was located near the town of Young (−34.422 S, 148.460 E, Appendix A) and 16% of the area consisted of NV dominated by *Eucalyptus melliodora*, *E. macrocarpa*, *E. blakelyi*, and *Acacia* spp. The crops included autumn-sown cereals and canola (25%) interspersed with managed pastures (51%). The sub-tropical region in Queensland (QLD) was located near the town of Pittsworth (−27.716 S, 151.635 E, Appendix A) and contained 15% NV dominated by *E. orgadophila*, *Acacia harpophylla* and *Casuarina cristata*. This region had year-round cropping (21%) that included autumn-sown cereals (wheat and barley) and, summer cropping (cotton and sorghum). Unmanaged pastures (19%) and fallow land (43%) were other important landscape elements.

### 2.1. Sampling design

Bi-directional flight interception traps (Southwood and Hendersen, 2000) were used to compare the direction and

intensity of insect flight activity at the NV/crop ecotone relative to the crop/crop interface (Appendix A). These traps were used to measure the number of insects intercepted on both sides of the trap while they were flying from one habitat patch to another over weekly periods. The data were used to make inferences about the movement patterns at the community, functional group and taxon level. Within each region there were six trapping sites: three ecotone sites and three control interfaces. The location of each trapping site was independent in terms of not sharing field boundaries with other sites. The straight-line distance between sites ranged from ~500 m to 8 km (Appendix B). In 2010, cereal fields consisted of wheat in NSW and either wheat (two sites) or barley (four sites) in QLD; in 2011 all fields were wheat.

There were six traps per region, and each trap had two collection bottles (on each side of the trap), therefore there were 24 samples per time period. At each time period the bottles were open for 5–8 days. Sampling commenced at cereal crop planting and continued over two winter cropping seasons; QLD July–November 2010 and July–August 2011, NSW May–November 2010 and May–August 2011. Samples were collected every two weeks for 5–8 sample periods (QLD 9 – 2010 and 5 – 2011, NSW 8 – 2010 and 8 – 2011), giving a total of 360 samples. Two samples (both in NSW) were discarded because the trap was damaged by cattle. Samples were labelled as “NV” (NV/crop ecotone, insects moving from NV into crops), “crop” (NV/crop ecotone, insects moving from the crop and entering NV), or “control” (crop/crop, insects moving from a crop field to another crop). The samples of the crop/crop interface consisted of insects moving between crops from both directions and received the same label. Therefore, there was double the number of samples at each time point for the control than for either the NV or crop treatments.

As there was large variation in crop growth development rates between the two regions it was necessary to standardise the sampling dates to ensure we were focussing only on the samples collected in the early-season growth period of the crop. Growth Degree Days (GDD) at each site was calculated using the equation:

$$GDD = \frac{(T_{\max} + T_{\min})}{2} - T_{\text{base}}$$

where  $T_{\max}$  is the daily maximum temperature,  $T_{\min}$  is the daily minimum temperature and  $T_{\text{base}}$  was set at 0 °C. When temperatures were below 0 °C,  $T_{\min}$  was converted as  $T_{\min} = T_{\text{base}}$  (McMaster, 1997). Temperature data were collected from nearby weather stations to calculate GDD. Daily GDD value from the date of crop planting was summed to provide an accumulated GDD value (referred to as AGDD hereafter). When no information on the planting date was available, this date was estimated as 10 days prior to crop emergence. AGDD was used as a proxy for time and then to select samples to analyse that were within 0–900 AGDD (this reduced the total number of samples from 360–211). AGDD values between 0–900 were considered in the early stage of crop development as this roughly corresponds to the period up to stem elongation of cereal crops.

### 2.2. Insect sampling

The bi-directional interception traps (Sante Traps, Lexington, KY) were made out of fine mesh material and had a black mid-vane (165 cm length, 178 cm height at front, 104 cm height at back) that functioned as an interception trap. One end was supported with a tent pole and had two collection bottles half filled with 70% ethanol (~250 ml and ~5 ml of detergent). Insects flying from one direction hit the mid-vane and climbed upwards entering the collection bottle, while insects flying from the other direction were captured on the opposite side (Appendix A). Traps were positioned along the ecotone or control interface regardless of prevailing wind

direction. Certain flying insect species (e.g. honeybees) can avoid this trap, and are captured in very low numbers. Therefore, we draw no conclusions about those species here.

Each sample was returned to the laboratory, sieved through a fine mesh strainer (0.5 mm), and the remaining insects sorted under a stereo microscope (10–50× magnification). Grain pests

and their natural enemies were counted and identified (Bailey, 2007). This species list included (but was not limited to) important aphid pests (Aphidae), ladybeetle adults (Coccinellidae), hoverfly adults (Syrphidae), brown lacewing adults (*Micromus* sp.), and a range of parasitic wasps identified to genus (Appendix B). Adult Lepidoptera (moths and butterflies) were excluded because these

**Table 1**  
Results of GLMM analysis of insects moving across a native vegetation (NV)/crop ecotone relative to a crop/crop interface. Flying insects were collected in bi-directional interception traps. 'Crop' and 'NV' represent samples from a NV/crop ecotone, and 'control' represent samples from a crop/crop interface. The GLMM included the factors 'ecotone', time represented as 'AGDD', and 'region' as fixed effects, and 'trap' as a random effect. A *p*-value of <0.02 was considered significant (bold) (Also see Appendix B). NA indicates the factor was not included in the final model as it did not explain any additional variation in the data, a dash indicates that factor was not relevant in the model (e.g. 'region' term not necessary when species only collected in one region).

Taxa	Distribution used in model <sup>e</sup>	Ecotone	AGDD	Region	AGDD <sup>2</sup>	Int (ecotone × AGDD)	Int (ecotone × region)	Int (AGDD × region)	Matches hypothetical model no. <sup>f</sup>	
Pest functional group	NB2	<0.001	<0.001	<0.001	NA	0.08342	NA	<0.001	7	
Predator functional group	NB2 zi	<0.001	0.729	<0.001	NA	NA	NA	<0.001	3	
Parasitoid functional group	NB2	<0.001	<0.001	<0.001	NA	0.0038	NA	<0.001	8	
Both regions (multiple years)										
Pests	<i>Acyrtosiphon</i> spp. <sup>c</sup>	NB2	0.013	<0.001	<0.001	NA	0.0100	<0.001	<0.001	8
	<i>Rhopalosiphum padi</i>	NB2	0.002	0.001	<0.001	NA	NA	NA	<0.001	7
	<i>Rhopalosiphum rufiabdominalis</i>	NB2	0.002	<0.001	0.007	NA	0.0080	NA	0.0305	8
	<i>Nysius vinitor</i>	NB2	0.048	0.253	0.001	0.0531	0.1257	NA	0.0044	1
Predators	<i>Micromus</i> sp.	NB2 zi	0.061	0.537	<0.001	NA	NA	NA	No	1
	<i>Melangyna</i> ( <i>Austrosyrphus</i> ) sp.	NB2	<0.001	0.479	<0.001	NA	NA	NA	<0.001	3
	Coccinellidae multiple species	NB1	0.076	0.026	0.004	NA	NA	0.2579	No	1
Parasitoids	<i>Diadegma</i> sp. B.	P	0.025	0.439	0.064	NA	NA	NA	<0.001	1
	Microgastrinae	NB2	0.317	0.185	0.024	NA	NA	NA	<0.001	1
	<i>Netelia</i> sp.	NB1 zi	<0.001	<0.001	<0.001	NA	0.0791	NA	0.0011	7
	Aphidiinae	NB2	0.020	0.239	<0.001	NA	0.0153	NA	0.0011	4
Both regions (only one year)										
Pests	<i>Rhopalosiphum maidis</i>	NB2	<0.001	0.061	<0.001	NA	0.4619	NA	0.0018	3
	<i>Therioaphis trifolii</i> <sup>d</sup>	NB2 zi	0.001	0.006	<0.001	NA	0.0131	0.0614	<0.001	8
NSW only										
Pests	<i>Creontiades dilutus</i>	NB1	0.885	0.057	–	NA	NA	–	–	1
	<i>Myzus persicae</i>	NB2	0.107	0.004	–	NA	0.2603	–	–	5
Predators	<i>Nabis kinbergii</i>	P zi	0.903	0.611	–	NA	No	–	–	1
Parasitoids	<i>Ichneumon promissorius</i>	P	<0.001	0.011	–	0.0292	0.039	–	–	7
QLD only										
Pests	Green sow thistle aphid	P zi	0.591	0.005	–	NA	NA	–	–	5
	Brown sow thistle aphid <sup>a</sup>	NB2	0.950	0.050	–	0.108	NA	–	–	1
	<i>Metopolophium dirhodum</i> jassids (leafhoppers) <sup>b</sup>	NB2	0.411	0.216	–	0.010	NA	–	–	1
		linear (log 10)	<0.001	0.011	–	0.0119	NA	–	–	7
Predators	<i>Mallada</i> sp.	P	0.518	0.088	–	NA	NA	–	–	1
	Rove beetles (Staphylinidae)	NB1 zi	0.160	0.015	–	0.0282	0.0946	–	–	5
	<i>Simosyrphus grandicornis</i>	NB2	0.649	0.019	–	NA	0.2381	–	–	5
	<i>Sphaerophoria macrogaster</i>	NB2	0.730	<0.001	–	NA	0.2449	–	–	5

<sup>a</sup> Interaction between AGDD × AGDD<sup>2</sup> *P* = 0.0191.

<sup>b</sup> Interaction between AGDD × AGDD<sup>2</sup> *P* = 0.050.

<sup>c</sup> Interaction between ecotone × AGDD × region *P* = 0.025.

<sup>d</sup> Interaction between ecotone × AGDD × region *P* = 0.034.

<sup>e</sup> The GLMM model distributions included negative binomial 1 and 2 (NB1, NB2) or Poisson (P), with zero inflation (zi).

<sup>f</sup> Refers to the hypothetical models outlined in Appendix B, Table 1.

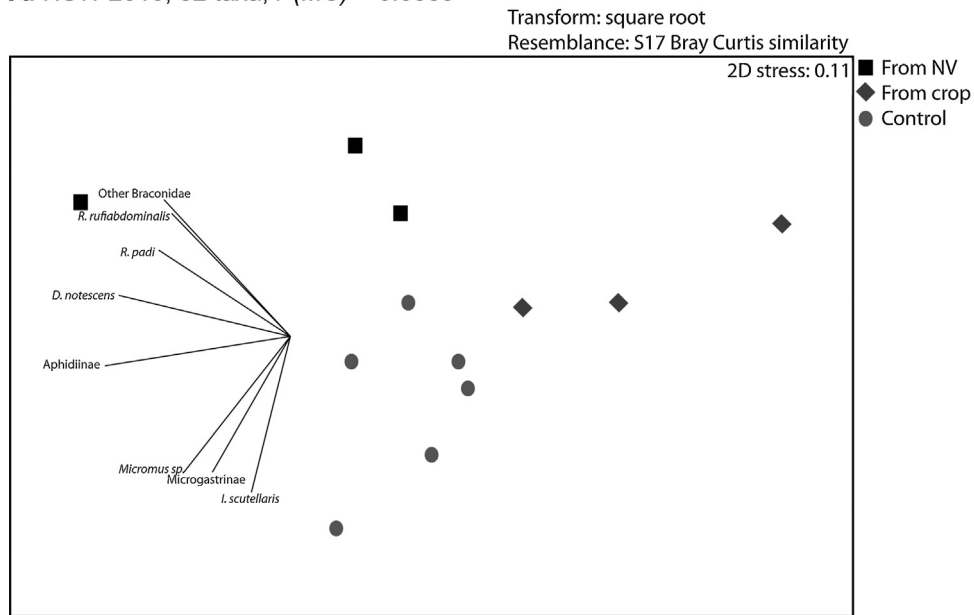
specimens cannot accurately be identified in ethanol. Each taxon was grouped into one of three functional groups: pests, predators or parasitoids (Appendix B).

2.3. Data analysis

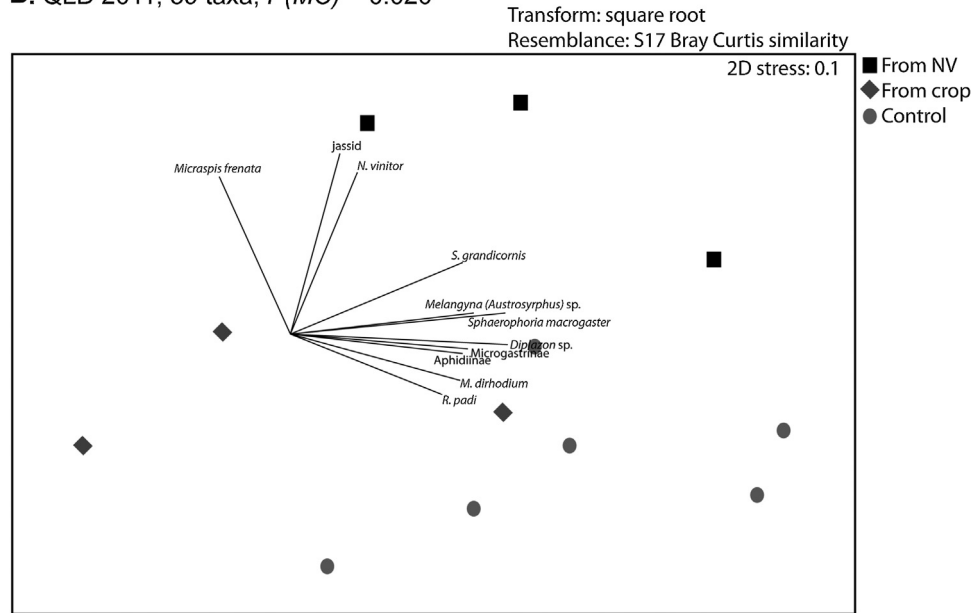
The composition of the insect community at the ecotone and control interface was visualised using non-metric multidimensional scaling (NMDS) in PRIMER 6 (v 6.1.13) (Clark and Gorley, 2006). A matrix of total abundance of each taxon found in each treatment (NV, crop, control) was constructed for each year (2010, 2011) and region (NSW, QLD) for a total of four matrices. Abundance was square-root transformed (to down-weight common species) and a Bray Curtis (also known as Sorensen)

similarity matrix was created. A randomization test was used to assess the optimal number of dimensions for NMDS ordination. A permutational analysis of variance using PERMANOVA+ (v 1.0.3) (Anderson et al., 2008) was used to test for differences in community composition between ecotone and control. Type III partial sums of squares were derived with Monte Carlo simulations involving the unrestricted permutation of the raw data (9999 permutations). Pair-wise comparisons were then made between replicates of the NV, crop and control treatments. Comparisons with  $P(MC) < 0.1$  were considered significant. For the cases where significant community structuring was found, the taxa were separated into functional groups (pests, predators and parasitoids) and the analysis repeated at this finer resolution.

A. NSW 2010, 32 taxa,  $P(MC) = 0.0039$



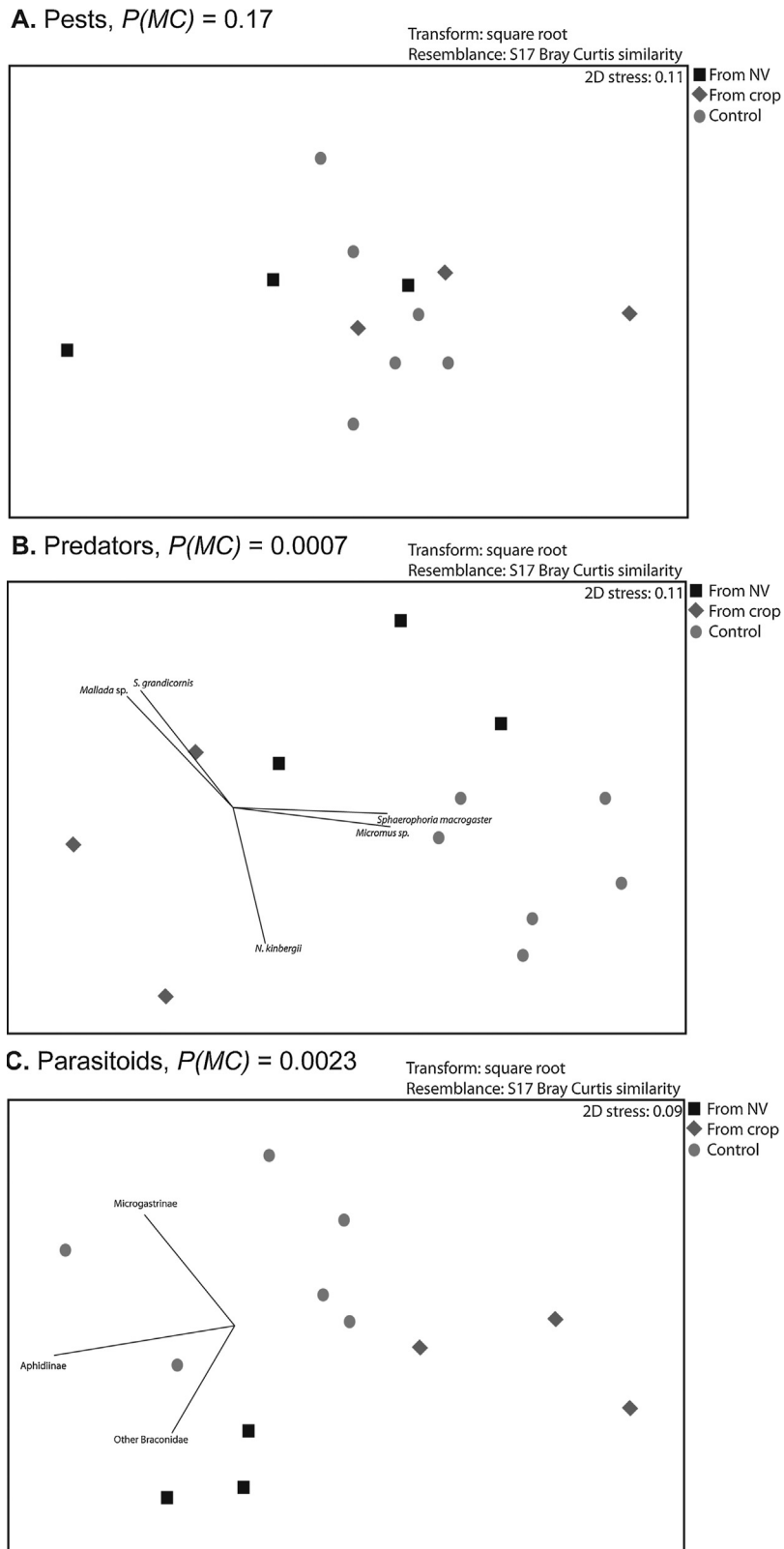
B. QLD 2011, 39 taxa,  $P(MC) = 0.020$



**Fig. 1.** Multi-dimensional scaling plots showing differences in insect communities moving from native vegetation (NV) into crops, and from crops into NV, in comparison to a crop/crop interface, which serves as a control. Flying insects were collected in bi-directional interception traps placed on a NV/crop ecotone in NSW 2010 (A), and QLD 2011 (B). The significance level from a PERMANOVA is shown. The data were square root transformed and a Bray Curtis similarity measure was used. The vectors (black lines) show taxa with a Spearman correlation >0.7.

Prior to NMDS analysis each of the four matrices were tested for spatial autocorrelation of samples using a combination of similarity measures and regression analysis to test whether the composition of insect communities were related to the

proximity of traps (Appendix C). Some degree of spatial autocorrelation was observed in the QLD 2010 samples and these samples were therefore discarded for the NMDS analysis (Appendix C).



**Fig. 2.** Multi-dimensional scaling plots showing differences in functional groups moving from native vegetation (NV) into crops, and from crops into NV, in comparison to a crop/crop interface, which serves as a control. Samples are from NSW in 2010. Flying insects were grouped into pest (A), predator (B) or parasitoid (C) functional groups. The vectors (black lines) show Spearman correlation >0.7. For details see Fig. 1.

A series of generalised linear mixed effects models (GLMM) were used to test hypotheses regarding the movement of functional groups and individual taxa in relation to ecotone (Appendix C). The glmmADMB package in R (v 2.15.0) was used to develop a range of GLMM as basic linear regression models following Bolker et al. (2009, 2011). Log<sub>10</sub> transformation of the response variables rarely resulted in normally distributed data (except for jassids in QLD, Table 1). Therefore, each untransformed response variable was included in the full model. Fixed effects were 'ecotone' (NV, crop, or control), time expressed as the 'AGDD' value (0–900), and 'region' (NSW, QLD). A random effect 'trap' was included in every model to account for the non-independence of repeated measures over time. The interactions between the three fixed effects were included in the full model, and later excluded if not significant (based on AIC). An additional fixed effect quadratic term (AGDD<sup>2</sup>) was introduced into the models to improve the fit. The response variables consisted of the abundance of the three functional groups (pests, predators and parasitoids) or individual taxon (species or genera). A cumulative count of 10 specimens per taxon was used as the criterion for inclusion in the analysis. Inferences about the fixed model parameters were made using the 'Anova' function in the 'car' package (Fox and Weisberg, 2011), which produces an analysis of deviance with chi-square type II tests. A conservative *p*-value (<0.02) for ecotone effects was used to assess significance. Using the final model, we derived region and ecotone specific predictions of insect movement across time (AGDD between 0 and 900). Each GLMM represented a hypothesis regarding the amount of movement across the ecotone relative to the control and the direction of movement across the ecotone (Appendix C). For those species that showed a significant ecotone effect the predicted mean numbers moving across the ecotone and control (averaged across the whole sampling period) was ranked. The raw data from each sample for the three main functional groups is shown in Appendix D.

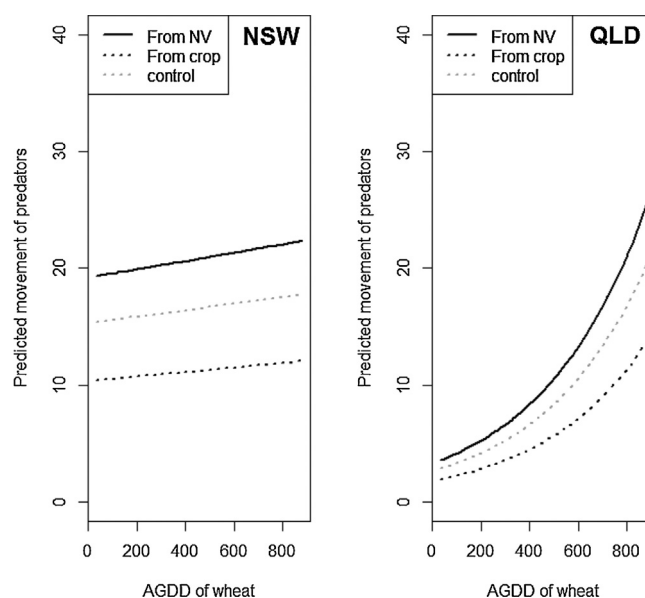
### 3. Results

The 211 analysed samples contained 7406 pest, 2861 predator, and 1689 parasitoid individuals. The average number of taxa per sample was  $24 \pm 1$  SEM, and ranged from 13 to 43 taxa. The community-level analyses suggest that the insect communities moving across the control interface were different to those moving across the ecotone, however this pattern was only observed in two out of three cases. NMDS plots showed three clearly separate clusters in NSW 2010, suggesting that insect communities moving from NV were different to communities moving from the crop or between crop/crop interfaces (Fig. 1a). Similar clustering of insect communities was observed in QLD in 2011 (Fig. 1b), but not in NSW 2011 (data not shown). The lack of structuring in the QLD 2010 samples is confounded by some spatial autocorrelation of samples and were therefore discarded from this analysis (Appendix B). NSW and QLD had region-specific taxa that were influential in the formation of the clustering pattern; only the oat aphid *Rhopalosiphum padi*, *Aphidiinae* parasitoids and *Microgasterinae* parasitoids were abundant in both NSW and QLD (Fig. 1). The PERMANOVA analysis supported the structuring of the ordination pattern according to ecotone in NSW 2010 ( $P(\text{MC})=0.0039$ ) with significant differences between NV and control ( $P(\text{MC})=0.025$ ), and crop and control ( $P(\text{MC})=0.026$ ), and a marginally significant difference between NV and crop ( $P(\text{MC})=0.062$ ). For QLD 2011 ( $P(\text{MC})=0.020$ ) there was a marginally significant difference between NV and control ( $P(\text{MC})=0.072$ ), and crop and control ( $P(\text{MC})=0.058$ ), and a non-significant difference between NV and crop ( $P(\text{MC})=0.11$ ). These results demonstrate that in both these cases the communities moving across the NV/crop ecotone were different from those moving across the crop/crop interface.

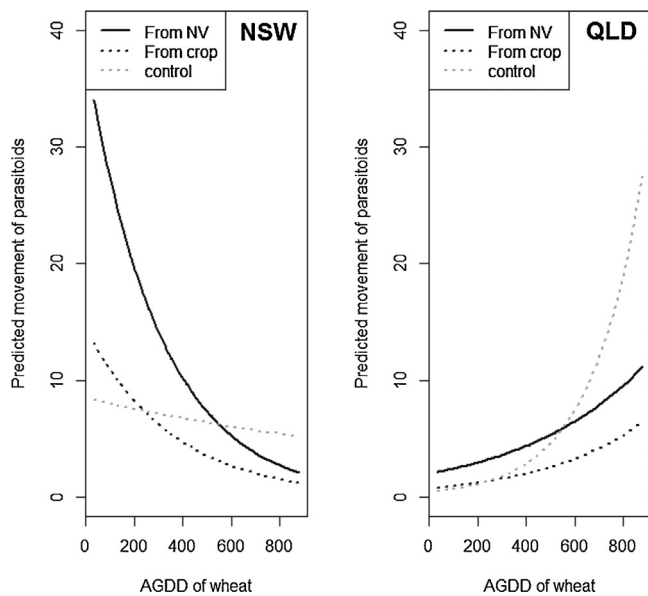
#### 3.1. Functional group response to ecotone

Cases with a significant ecotone effect at the whole community-level were further explored by placing taxa into functional groups. For NSW 2010 we found significant clustering in relation to movement across the ecotone for the predators and parasitoids, but not for pests (Fig. 2). All pair-wise comparisons were significant for predators (NV and control  $P(\text{MC})=0.031$ , NV and crop  $P(\text{MC})=0.047$ , crop and control  $P(\text{MC})=0.002$ ) and parasitoids (NV and control  $P(\text{MC})=0.029$ , NV and crop  $P(\text{MC})=0.022$ , crop and control  $P(\text{MC})=0.021$ ). The movement of damsel bugs (*Nabis kingbergii*) was influential for the ordination of samples along the vertical axis (separating samples moving from NV from those moving from crop and control), and the brown lacewing (*Micromus* sp.) along the horizontal axis (separating samples moving from NV and control from those moving from crop) (Fig. 2b). In the parasitoid functional group, five out of six of the controls had a higher abundance of *Microgasterinae* (in comparison to NV, Fig. 2c). The presence of higher numbers of *Aphidiinae* contributed to the separation of samples along the horizontal axis (Fig. 2c). In QLD 2011, pests showed significant structuring ( $P(\text{MC})=0.0078$ ), but the structuring of predators ( $P(\text{MC})=0.092$ ) and parasitoids ( $P(\text{MC})=0.065$ ) was only marginally significant.

GLMMs were used to estimate the relationship between ecotone, region and time (AGDD), for the response taxa (species and species functional groups). For all three functional groups, the GLMMs indicated that there is a significant interaction between time (AGDD) and region, thus overall movement patterns of insects across time differed between the two regions (Table 1). In general, the movement of insects across the ecotone decreased in time in NSW, whereas it increased in time in QLD. However, we did find a consistent ecotone effect across the regions. For predators there was a consistently greater movement from NV into crops as compared to the control, and no interaction with time was detected (Fig. 3, Table 1). For parasitoids, the pattern was more complex, with clear regional differences in response to ecotone across the early season period (Fig. 4, Table 2). In NSW and QLD movement from NV was greater than the control between 0 and



**Fig. 3.** Movement patterns of insect predators across a NV/crop ecotone in comparison to a control interface. 'From NV' indicates insects moving from NV patches into cereal fields, 'From crop' are insect moving from cereal fields into NV patches, 'control' are the insects moving across a crop/crop interface. AGDD (accumulated growth degree days of wheat) is used as a measure of time. Back transformed predicted values from a GLMM are indicated by lines (Table 2).



**Fig. 4.** Movement patterns of parasitoids across a NV/crop ecotone in comparison to a control interface. AGDD (accumulated growth degree days of wheat) is used as a measure of time. For details see Fig. 3.

~550 AGDD, but in QLD movement across the control interface increased rapidly hereafter. In NSW pest movement from NV was higher between 0 and 600 AGDD, however after 600 AGDD there was little movement across both the ecotone and the control interface (Fig. 5, Table 2). In QLD the overall predicted values for pests suggest that movement from NV is higher than for the control for up to ~650 AGDD (Fig. 5, Table 2).

### 3.2. Species-specific response to ecotone

Individual taxa varied greatly in their response to ecotone (Table 1). For many taxa the GLMMs showed a significant region effect, and significant interaction between region and time (AGDD), and mostly a non-significant interaction between ecotone and region (Table 1). This suggests that whilst there are differences between the two regions in the extent of movement over time, a consistent pattern was observed in relation to ecotone. Out of the 25 taxa analysed, there was no significant ecotone effect for 15 taxa (Table 1), suggesting that these species exhibit similar movement dynamics across the ecotone and control interface. If we just consider the taxa that were common in the traps in both regions then eight out of 13 taxa showed no significant ecotone effect (Table 1).

**Table 2**

Summary of GLMMs for functional groups and insect taxa that showed a significant response to ecotone. Ticks indicate more movement from NV into crops as compared to crop/crop interfaces, crosses indicates increased movement across the crop/crop interface as compared to the NV ecotone. The rank of the predicted mean from the GLMM (Table 1) is provided for the entire sampling period (B) or part of the sample period (C) (see also Appendix B).

Taxa	Predicted values mean rank NSW	Conclusion NSW	Predicted values mean rank QLD	Conclusion QLD
B Pest functional group	NV > crop > control	✓	NV > control > crop	✓ (But control similar)
B Predator functional group	NV > control > crop	✓	NV > control > crop	✓
C Parasitoid functional group	0–600: NV > crop > control	✓	0–500: NV > control > crop	✓
C <i>Acyrtosiphon</i> spp.	400–900: control > NV = crop	✗	300–900: control > crop > NV	✗
B <i>Rhopalosiphum padi</i>	NV > control > crop	✓	NV > control > crop	✓
C <i>Rhopalosiphum rufiabdominalis</i>	0–600: NV > crop > control	✓	0–600: NV > crop > control	✓
B <i>Rhopalosiphum maidis</i>	Control > crop > NV	✗	Control > NV > crop	✗
C <i>Therioaphis trifolii</i>	0–200: NV > control > crop	✗	0–900: control > NV > crop	✗
B <i>Melangyna (Austrosyrphus)</i> sp.	NV > control > crop	✓ (But control similar)	NV > control > crop	✓ (But control similar)
B <i>Netelia</i> sp.	NV > crop > control	✓	NV > crop = control	✓
C <i>Aphidiinae</i>	0–450: NV > crop > control	✓	400–900: control > NV > crop	✗
B <i>Ichneumon promissorius</i>	Control > crop > NV	✗	–	–
B Jassids (leafhoppers)	–	–	NV > control > crop	✓

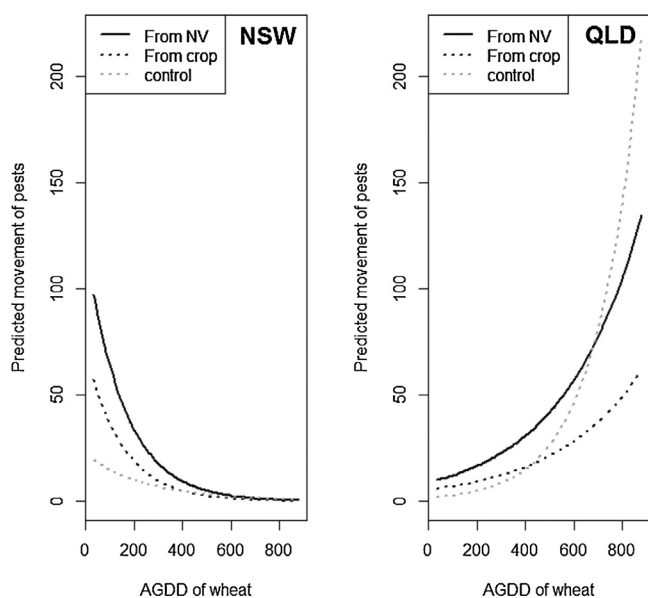
For most taxa there was a significant region effect (11 out of 13 taxa collected across both regions, Table 1), but this was not always related to the ecotone. For example, *Micromus* sp. showed much greater movement across both the ecotone and the control interface in NSW than in QLD at the same crop stage (Table 1). For the taxa whose movement patterns were significantly affected by ecotone (Table 2), the conclusions for each region were generally the same. The only exception were *Aphidiinae* parasitoids that showed more movement relative to the control from NV in NSW, but not in QLD (Table 2). Movement from NV was more prevalent for the parasitic wasp genus *Netelia* and the predatory *Melangyna* than vice versa, but not for the parasitic wasp *Ichneumon promissorius*. The pest aphids *R. padi* and *R. rufiabdominalis* showed greater movement from NV relative to the control, but *Acyrtosiphon* spp., *R. maidis* and *Therioaphis trifolii* did not (Table 2).

## 4. Discussion

Firstly at the community-level ecotones influence the movement of predators and parasitoids, and to lesser extent pests during the critical early-stage period. Secondly, predators were found to consistently move more frequently from NV towards crops (relative to the control) throughout the entire early-season period. Finally, whilst movement patterns across time differed for each region, the species-specific responses to ecotone were similar across the two regions. In theory, the relative timing of pests and natural enemies arriving in crop fields early in the season may influence pest population build-up and ultimately pest control (Ekbom et al., 1992; Ives and Settle, 1997; Chang and Kareiva, 1999). Overall, we found no time lag between the movement of pests and natural enemies into crop fields from NV. If the theoretical predictions about the timing of arrival hold, these crop fields should be well placed to suppress pest populations throughout the season.

### 4.1. Insect communities moving across the ecotone

There is a high contrast between NV and the adjacent crop fields in terms of vegetation structure and composition, which may limit movement across this ecotone for certain species (Ries and Debinski, 2001; Cunningham et al., 2013). Campbell et al. (2011) used flight interception traps to show that the movement of beetles across two ecotones with different degrees of contrast varied considerably. In the light of these results it is not surprising that we found significant differences between the insect communities moving across the ecotone and those moving across the crop/crop interface in NSW 2010 and QLD 2011. In NSW 2010, the



**Fig. 5.** Movement patterns of pests across a NV/crop ecotone in comparison to a control interface. AGDD (accumulated growth degree days of wheat) is used as a measure of time. For details see Fig. 3.

natural enemy communities showed clearer differences in response to ecotone than the pest communities. Given that many species rely on resources that can only be found in NV at this time of the year, one may anticipate differences in insect movement patterns between the ecotone and the control interface. Indeed, there are many species whose presence or abundance is influenced by the amount of natural and semi-natural areas in agricultural landscapes (Duelli and Obrist, 2003). In a literature review, Chaplin-Kramer and Kremen (2012) found that generalist natural enemies showed a positive response to landscape complexity (and the area of semi-natural habitats), while pests did not. Synthesising these findings with the results of our study suggest that natural enemies are more likely to forage for resources in and around NV than pests, and that natural enemies may therefore benefit more from NV than pests.

#### 4.2. Native vegetation as a net exporter of pests, predator and parasitoids

At crop planting during autumn, the vegetation in our study sites consisted of semi-perennial pastures and small NV patches (Appendix A). As bare fields provide little refuge and resources, the potential sources for insects are limited to a few habitat patches. At the functional group level we observed large numbers of predators moving from NV into the crop suggesting that predators are emigrating from NV. These patterns were consistent throughout the early season period. For parasitoids, the pattern was more complex, with more movement from NV very early in the sampling period in NSW (up to ~550 AGDD) than between the crop/crop interface. Later in the sampling period, NV still provided immigrants, but movement across the crop/crop interface outnumbered that of the ecotone (Fig. 4). This suggests that parasitoids may be better able to find suitable hosts in the crop fields because of higher host densities and a simpler vegetation structure (Vollhardt et al., 2008; Macfadyen and Muller, 2013). The pest functional group showed more movement from NV early in the cropping season (up to ~650 days). However, the significant effect of time and region suggests that movement patterns change across this early season time period, probably in response to the stage of the crop (Mesa et al., 2013). A better

understanding of the plant–pest–natural enemy relationships (Stephens et al., 2006; Isaacs et al., 2009) may lead to management strategies that facilitate the movement of natural enemies, but impede that of pests.

#### 4.3. Species-specific ecotone movement behaviours

Not all pest and natural enemy species were equally likely to be captured in the interception traps (Irwin et al., 2000). Therefore, only those species with directional flight that cannot avoid the trap have been included in this analysis. However for 15 of the taxa that were captured in the traps we found no significant ecotone effect (Table 1). For those species that did not respond to ecotone we conclude that the ecotone did not represent a significant barrier to movement as compared to crop/crop interfaces. These species, such as *Nysius vinitor* (Rutherglen bug) and *Micromus* sp. are known to use resources in multiple habitat-types in these landscapes and will therefore not necessarily show strong movement patterns in relation to NV patches. For those taxa that showed a significant ecotone effect, we found a range of movement responses to ecotone. Previous studies have shown that species response to ecotone can be idiosyncratic (Perovic and Gurr, 2012). Here we found that *Microgastrinae* parasitoids moved more commonly across the crop/crop interface than across the ecotone. In contrast, *Aphidiinae* parasitoids moved more often from NV into crops than between crops.

The analysis at the functional group level indicated that predators preferentially moved out of NV early in the season, whereas at the taxon level only few predator species showed significant responses to ecotone (Table 1; but see *Melangyna* for an exception). We further explored the influence of *Melangyna* on the predator functional group by removing this taxon and re-running the models, however, this did not alter the outcome. This suggests that the functional group result may be caused by the cumulative movement patterns of many predatory taxa and not necessarily a single dominant taxon.

#### 4.4. Regional differences

Considering the large differences between the two regions in terms of cropping strategies, landscape features, weather conditions and pest management strategies, it is notable that we found consistent patterns in insect movement patterns from NV across these regions. Once we standardised for differences in crop development (using AGDD) there were few taxa that showed a significant interaction between ecotone and region (Table 1; but see *Aphidiinae* spp. for an exception). There were, however, regional differences in the number of individuals moving, regardless of ecotone. For example, *Micromus* sp. showed no ecotone effect, but was significantly more abundant in the samples in NSW than in QLD.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at <http://dx.doi.org/10.1016/j.agee.2014.11.012>.

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