

Land-use intensity affects the potential for apparent competition within and between habitats

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Funding information

Svenska Forskningsrådet Formas, Grant/Award Number: 2016-01168; Swedish Research Council, Grant/Award Number: 2016-04580

Handling Editor: Eoin O'Gorman

Abstract

1. Arthropod communities dwelling in adjacent habitats are able to impact one another via shared natural enemies. In agricultural landscapes, drastic differences in resource availability between crop and non-crop habitats cause variation in insect herbivore densities over short distances, potentially driving inter-habitat effects. Moreover, the composition of the landscape in which the habitats are embedded likely affects realised attack rates from natural enemies via impacts on local arthropod community structure.
2. Here, we examine indirect effects between herbivore species within and between habitat types by calculating the potential for apparent competition between multiple populations. Firstly, we aim to determine how disparities in resource availability impact the strength of the potential for apparent competition occurring between habitats, secondly to examine the impact of landscape composition upon these effects, and finally to couch these observations in reality by investigating the link between the potential for apparent competition and realised attack rates.
3. We used DNA metabarcoding to characterise host–parasitoid interactions within two habitat types (with divergent nutrient inputs) at 11 locations with variable landscape composition within an agroecosystem context. We then used these interaction networks to estimate the potential for apparent competition between each host pair and to compare expected versus realised attack rates across the system.
4. Shared natural enemies were found to structure host herbivore communities within and across habitat boundaries. The size of this effect was related to the resource availability of habitats, such that the habitat with high nutrient input exerted a stronger effect. The overall potential for apparent competition declined with increasing land-use intensity in the surrounding landscape and exhibited a discernible impact on realised attack rates upon herbivore species.
5. Thus, our results suggest that increasing the proportion of perennial habitat in agroecosystems could increase the prevalence of indirect effects such as apparent competition among insect herbivore communities, potentially leading to

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enhanced population regulation via increased attack rates from natural enemies like parasitoid wasps.

KEYWORDS

apparent competition, ecological networks, host–parasitoid, indirect effects, landscape composition, metabarcoding

1 | INTRODUCTION

The relative abundance of coexisting species and the interactions in which they partake affects how ecological communities function and respond to environmental change (Balvanera et al., 2005; Grimm et al., 2013; Thierry et al., 2019). While much effort has been invested into exploring the effects of direct links between predators and prey (Abrams, 2000), much less is known about the role of indirect effects as mediated by shared natural enemies (Holt, 1977; Holt & Lawton, 1993; Morris & Lewis, 2002; Müller et al., 1999; Tack et al., 2011). Of particular interest is the role indirect effects play in structuring of herbivorous arthropod communities (Holt & Lawton, 1993; Morris et al., 2005; van Veen et al., 2006), which comprise the main pests in both agricultural and forestry settings. By mapping the intricate network of interactions within communities, we can trace interaction pathways between organisms and estimate the magnitude of indirect effects. This information could then be used to better understand the factors controlling population fluctuations.

Apparent competition has been proposed as an important indirect effect structuring the abundance dynamics within communities (Bonsall & Hassell, 1997; Holt, 1977; Morris et al., 2004, 2005). It occurs when two prey species are connected by a shared predator, so that an increase in the abundance of one prey species suppresses the abundance of the other via an increased attack rate from their shared enemy (Holt, 1977). While apparent competition has been experimentally demonstrated in some ecosystems (Bonsall & Hassell, 1997; Morris et al., 2004; Muller & Godfray, 1997) the strength and sign of its impact has been questioned by other studies (Abrams et al., 1998; Kaartinen & Roslin, 2013; Tack et al., 2011). One setting where apparent competition is likely to be of high importance is within agricultural landscapes. As resource availability varies drastically between agricultural and semi-natural habitats, we can expect significant disparities in insect herbivore density over short distances (Tscharntke et al., 2005; Wetzal et al., 2016), thereby generating the potential for indirect interactions between habitats. In this context, if the natural enemies of herbivorous hosts are able to travel between different parts of the landscape, there is potential for herbivore communities within different habitats to impact one another. Impacts are hypothesised to travel from areas of high resource availability to areas with relatively low resource availability (Hilderbrand et al., 1999; Polis & Hurd, 1996; Sanzone et al., 2003). Indeed, apparent competition has been found to propagate across habitat boundaries in managed forests, leading to predictable changes in attack rates upon arthropod pests (Frost et al., 2016). How we manage our landscapes could therefore dictate both the composition and interactions of insect communities within cropping systems, with

impacts upon species abundances and levels of predation or parasitism (Birkhofer et al., 2008; Harmon & Andow, 2004).

In the present study, we test for imprints of apparent competition in the food webs of agricultural crops in a landscape setting. To understand the extent to which herbivore species could indirectly affect one another's abundance via shared parasitoids, we estimate the potential for apparent competition derived from host–parasitoid networks. To evaluate spatial effects, we do this both within and between two adjacent agricultural habitats with divergent resource availability. Further, we investigate how the density of intensively managed crops within the landscape influences these connections. Finally, we examine whether local parasitoid attack rates can be predicted from the averaged potential for apparent competition between each host pair in each habitat (derived from the regional metaweb), plus local host abundance. Should this prove the case, we infer that the potential for apparent competition might be a useful metric for understanding parasitism rates within this system and could therefore be impacting host abundances.

The habitats in question are oilseed rape, an intensively managed annual crop of economic importance (Frank et al., 2010), and ley, a low-intensity, perennial mixed grass-legume forage crop, usually kept for 2–4 years in a rotation. Both of these habitat types are common within our study region and, importantly, present contrasting levels of nutrient input and therefore resource availability. Given that oilseed has a much higher productivity, we expected to see a stronger effect of apparent competition acting from herbivorous host communities within oilseed upon those within ley. We also hypothesise that the percentage of annual crops in the surrounding landscape impacts this relationship via a modification of dispersal rates and demographic factors of local and regional arthropod populations (Thomas & Kunin, 1999). Finally, if apparent competition has a discernible impact on parasitoid attack rates, we expect that predictive models incorporating the potential for this indirect effect to explain more variance in overall attack rates than models which do not.

2 | MATERIALS AND METHODS

2.1 | Site selection and layout

All sampling was conducted in Skåne in the south of Sweden over a 10-day period between May and June 2017 (Figure S1a). Each of 11 sites comprised two adjacent fields: one containing winter oilseed rape, and one containing ley (Figure S1b). To characterise land-use intensity, we used the percentage of annual crops, since

this measure is correlated with both pesticide and chemical fertiliser inputs, and crop yield outputs per hectare (Brookfield, 1972; Lambin et al., 2000). Further, this metric has previously been used to demonstrate land-use intensification within the same geographic region (Persson et al., 2010). Landscape composition was calculated based on a digitised map layer of land use (Terrängkartan, Lantmäteriet, 2018) using ArcMap software, version 10.3.1 (ESRI, USA), from which we measured the percentage of annual crops within a 1-km buffer zone surrounding each site (measured from the centroid between the two fields). Both herbivory and parasitism are affected by landscape composition at this spatial scale in oilseed rape systems (Martin et al., 2019; Thies et al., 2003). Sites were selected such that the land-use intensity varied in a gradient between 1% to 38% within the buffer zone. The proportion of forest, urban areas and water bodies were standardised to below 8% in all locations (Table S1).

2.2 | Specimen collection

Host specimens were collected for two purposes: to obtain specimens for molecular characterisation of host-parasitoid networks, and to quantify the abundance of each host species in each habitat. For ley habitats, these two objectives were fulfilled using exactly the same sampling method, that is: an area 50 m × 16 m was sweep net sampled for 15 min on 2 separate days at each site. Catches were transferred to plastic bags and stored at 4°C until they could be visually examined for the presence of host specimens (within 12 hr of capture). Morphological identification was carried out to order level, after which each specimen was placed into an individual Eppendorf tube containing 95% ethanol before storing at -20°C until DNA extraction (within 3 months). For oilseed habitats host communities were sampled in a different way to ley habitats because of differences in vegetation structure (it is not possible to sweep net oilseed for herbivorous insects due to the density and size of the plants). To quantify the abundance of each host species, beat sampling of five oilseed plants over a 50-m transect was conducted on two separate days at each site. Again, catches were stored at 4°C until host specimens were placed into individual Eppendorf tubes containing 95% ethanol (within 12 hr of capture) before storing at -20°C. Since relatively few specimens were obtained using this approach, we used a second approach to attain enough specimens for molecular characterisation of host-parasitoid networks: The apical branch of a further 10 oilseed plants per site were collected and visually examined for any hosts. Specimens taken from these plants were then stored in the same way as other specimens, but not used for abundance estimates.

2.3 | Molecular characterisation of host-parasitoid networks

DNA was extracted from 1,690 individual larval specimens and 22 extraction negative controls using the DNeasy 96 Blood and Tissue

kit protocol (Qiagen), incubation was carried out for 4 hr as opposed to the suggested six. For each specimen, part of the mitochondrial COI gene was amplified using mCOLintF (Leray et al., 2013) and HCO2198 (Folmer et al., 1994) which had been modified to include 33/34 bases from the Illumina i5 and i7 adapter sequences respectively. Illumina library preparation was completed using a second PCR reaction that added the remaining adaptor sequences to amplicons using custom primers (see Table S2 for primer sequences and Supplementary Text 1 for PCR conditions). Amplicons from all DNA extracts were sequenced using two MiSeq 2x300bp V3 runs at the Biomedicum Functional Genomics Unit, Helsinki, Finland. Bioinformatic processing of reads involved the merging of paired ends using PEAR (Zhang et al., 2014); the removal of primers using 'Split_on_Primer.py' (github:Y-Lammers/Split_on_Primer), cleaning and filtering using PRINSEQ (Schmieder & Edwards, 2011); and dereplication, removal of singletons, operational taxonomic unit (OTU) clustering at 97% and mapping of reads against OTUs using UPARSE (Edgar, 2013). Taxonomic assignments were made using an RDP Classifier tool (Wang et al., 2007) against a COI database constructed from the NCBI taxonomy database (Porter & Hajibabaei, 2018; Sayers et al., 2019) and where two or more OTUs were assigned to the same species they were pooled into a single unit.

All non-metazoan OTUs were removed from the interaction matrix. These removed taxa comprised 32% of the total number of OTUs and included bacterial, fungal and plant taxa (Figure S2). Interactions that were only supported by a single read were removed from the matrix at this stage, as were any samples with fewer than 100 metazoan reads in total. The identity of the OTU with the greatest proportion of reads for each specimen was recorded as the host identity, and the inferred identity was cross-referenced against morphological identification of each specimen. The taxonomic identity of all other OTUs associated with each specimen was screened for parasitoids and these formed the basis of the interaction data. Two parasitoid OTUs (both identified as within the family Ichneumonidae) were discovered in the extraction negative control samples and were therefore removed from any further analysis. To avoid including hyperparasitoids in this analysis, we examined the cooccurrence of all parasitoids across samples. One parasitoid (again, an Ichneumonid species) only ever occurred when another parasitoid was present so it was removed from all further analysis. A host by parasitoid matrix was then generated showing the frequency of association between each host in each habitat and each parasitoid. This matrix was used to generate interaction networks and to calculate the potential for apparent competition.

2.4 | Potential for apparent competition

To calculate the potential for apparent competition (henceforth pAC) between each host pair within and across habitats, we adapted a version of the Müller index (Müller et al., 1999), a directional index that considers the relative number of attacks of each parasitoid on

a 'source' host and on a 'target' host to determine the pAC from the source upon the target. As such, the strength of apparent competition is governed by three main drivers: the discrepancy between host abundances, the number of shared parasitoids between the two hosts, and the frequency of attacks. Following Frost et al. (2016), we modified the index to incorporate host location (i.e. habitat) by distinguishing between hosts from different habitats and treating them as separate entities.

As such, the pAC was calculated between each host-habitat pair, that is, each host species was partitioned into individuals found in oilseed and individuals found in ley and effectively split into two separate 'host-habitat' groupings. In this way, we were able to calculate the effect of each host species upon other hosts within the same habitat and upon other hosts in the adjacent habitat (Figure S3). From here on in, the habitat containing the host producing the effect (the source host) will be referred to as the source habitat (B), and the habitat containing the host receiving the effect (the target host) will be referred to as the target habitat (A). The pAC for each host-habitat pair was calculated using the following equation:

$$d_{iAsjBs} = \sum_{k=1}^P \left[\frac{\alpha_{iAks}}{\sum_{l=1}^P \alpha_{iAls}} \frac{\alpha_{jBks}}{\sum_{m=1}^H \alpha_{mks}} \right], \quad (1)$$

where d_{iAsjBs} is the pAC from host j (the source host) in site s , habitat B on host i (the target host) in habitat A of the same site; H is the total number of host species in both habitats from all sites and m characterises all host species from 1 to H . P is the total number of parasitoid species, and k and l are all parasitoid species from 1 to P , α represents link strength (such that α_{iAks} is the number of attacks between host i and parasitoid k in habitat A at site s). As such, the first term ($\frac{\alpha_{iAks}}{\sum_{l=1}^P \alpha_{iAls}}$) essentially shows how much parasitoid k impacts host i relative to other parasitoid species within habitat A at site s , and the second term ($\frac{\alpha_{jBks}}{\sum_{m=1}^H \alpha_{mks}}$) shows how much parasitoid k impacts host j relative to other host species in either habitat at site s . Summed across all parasitoid species the equation indicates how much the population of species j in habitat B, site s is likely to impact the population of species i in habitat A, site s via shared parasitoids. Note that this equation is similar to equation 2 in Frost et al. (2016). However, while they calculated a single value for pAC between each host-habitat pair using the metaweb, we aim to analyse variability in the pAC by calculating it for each host-habitat pair at each site.

Some species pairs exhibit a non-zero pAC, whereas other are simply disconnected from each other by not being present at the same location or because they do not share any parasitoids at all. Thus, to model the pAC, we took a dual approach. We first modelled the probability with which species pairs showed any pAC or not (1/0). Then, for the species pairs that did, we modelled the strength of apparent competition (noting that this probability is bounded >0). For both responses, we used generalised linear mixed-effects models, assuming binomially distributed errors and a logit link for the probability of finding a non-zero pAC, and truncated-Poisson errors with a log link for the strength of the non-zero distribution.

Note that this approach first tests the probability of finding some pAC before modelling how the strength of any pAC varies with landscape, it is statistically equivalent to using a hurdle model and has been used for analysing similar biological data (Chipeta et al., 2014; Hu et al., 2011).

We performed backward stepwise model selection by AIC, with source habitat, target habitat and the percentage of annual crops in the surrounding landscape as the fixed effects. Interactions between source habitat, target habitat and the percentage of annual crops were also included, and source and target host identities were included as random effects to account for the same species occurring in multiple pairs. Spatial autocorrelation was accounted for using distance-based Moran eigenvector map (dbMEM) eigenfunctions (Borcard & Legendre, 2002; Dray et al., 2006). The forward selection approach of Blanchet et al. (2008) with 9,999 permutations and an alpha of 0.05 was used to retain two eigenfunctions: MEM3 ($R^2 = 1.3 \times 10^{-3}$, $F = 14.9$, $p < 0.0001$) and MEM9 ($R^2 = 1.7 \times 10^{-3}$, $F = 14.9$, $p < 0.0001$). See Table S3 for eigenfunction values and Figure S4 for model diagnostic plots. Models were run in R v.4.0.0 (R Core Team, 2020) using RStudio v.1.2.5042 (RStudio Team, 2019) and the package GLMMTMB (Brooks et al., 2017), EMMEANS (Lenth, 2020) was used to generate slope estimates, diagnostic plots were created using DHARMA (Hartig, 2020), graphs were created using GGLOT2 (Wickham, 2016) and network graphics were created using BIPARTITE (Dormann et al., 2008).

2.5 | Parasitoid attack rates

While our inference regarding local and landscape effects on pAC concerns the expected impact of management on the *potential* for indirect effects through shared enemies (above), we can also use our observations to assess the importance of pAC for structuring herbivore populations via *realised* attack rates. To establish whether an indirect effect has a discernible impact upon attack rates, we calculated an expected attack rate in two different ways based upon equation 3 in Frost et al. (2016) and then assessed which version best aligns with realised attack rates derived from our networks.

The two approaches for generating local expected attack rate for each host OTU in each habitat and location are: (a) Utilising a direct modification of equation 3 from Frost et al. (2016) where, instead of including a measure for pAC from training datasets at time zero, we calculate pAC from the regional metaweb, and use this along with measures of herbivore abundance both locally and regionally (see Equation 2 in the current manuscript), and (b) Utilising a reduced version of Equation 2 in the current manuscript where any reference to apparent competition has been removed, this simply leaves the average number of attacks on host i within habitat A across all sites other than site s , and the local abundance of host i (Equation 3). The rationale behind this approach is to make sure that it is pAC and not any other simpler measure that lies behind the predictive power of this metric. If apparent competition does indeed impact real attack rates, then we expect predicted attack rates generated by Equation

2 (which considers pAC) to be better correlated with real attack rates than predicted attack rates generated using the Equation 3 (without pAC).

Since data for calculating these metrics were derived from metawebs (i.e. networks resulting from multiple sites), to avoid circularity, the site for which the predicted attack rate was being calculated was removed from each metaweb in an iterative 'leave-one-out' approach using the following equation:

$$pACE_{\alpha_{iAs}} = \sum_{j=1}^H \left[\frac{d_{iAjB} \times \sum_{l=1}^P \mu_{\alpha_{iAl}}}{\mu n_{jB}} n_{jBs} \right] \times \left[\frac{1}{n_{iAs}} \right], \quad (2)$$

where, H is the total number of host species in both habitats, j is the source host, p is the total number of parasitoid species, and l represents all parasitoid species from 1 to P . μ_{α} indicates an average link strength (such that, $\mu_{\alpha_{iAl}}$ would be the average number of times host i was attacked by parasitoid l in habitat A, as calculated from all sites other than s). The average number of individuals of host j in habitat B are written μn_{jB} , while n_{jBs} and n_{iAs} are the number of individuals in site s for host j , habitat B and host i , habitat A respectively. d_{iAjB} here represents the overall pAC of a host pair calculated from a metaweb generated from all sites other than s (see Supplementary Text 2 for equation). A condition was set that iA cannot equal jB so that intraspecific effects from within the same habitat were not considered.

For the second approach, this equation was modified to remove pAC and non-focal host abundances:

$$E_{\alpha_{iAs}} = \frac{\sum_{l=1}^P \mu_{\alpha_{iAl}}}{n_{iAs}}. \quad (3)$$

Here, $E_{\alpha_{iAs}}$ is the expected attack rate of host i in habitat A, site s . l represents all parasitoid species from 1 to P , μ_{α} indicates a link strength (such that, $\mu_{\alpha_{iAl}}$ would be the average number of times host i was attacked by parasitoid l in habitat A within a site, as calculated from all sites other than s), and n_{iAs} is the number of individuals of host i in habitat A, site s .

To assess the ability of expected attack rates to predict the realised attack rate, two separate linear mixed-effects models were built. The first included the expected attack rate calculated using Equation 2 (including pAC) as a main effect. In the second, this was replaced by the expected attack rate calculated using Equation 3 (without pAC). Additionally, habitat type and percentage of annual crops in the surrounding landscape were included as main effects and site and host species were included as random effects. Interactions were included between all fixed effects. For each model, backward stepwise selection based on the cAIC (Vaida & Blanchard, 2005) was used to obtain the minimum adequate models. Conditional R^2 was calculated to indicate explained variance (Nakagawa et al., 2017). All analysis was done using R, models were built using the LME4 package (Bates et al., 2015) and model testing was done using the LMERTEST package (Kuznetsova et al., 2017).

In order to understand the contribution of adjacent habitats, we used Equation 2 to calculate two separate expected attack rates

for each host in each location; one considering only within-habitat pAC (i.e. only considering the indirect effects of hosts from within the same habitat) and the other considering only between-habitat pAC (i.e. only considering the indirect effects of hosts from the adjacent habitat). The relative contribution of these two expected attack rates was then assessed using a variance partitioning approach (Borcard et al., 1992; Whittaker, 1984). Models were built as above with the LME4 package in R, the natural log of attack rates was used to meet model assumptions and backward stepwise selection based on the cAIC was used to find the most parsimonious model.

3 | RESULTS

Of the 1,690 host herbivore specimens processed, 1,329 were assigned a taxonomic ID comprising 54 host herbivore OTUs. The host community was markedly different between the annual oilseed crop and the perennial ley crop both in terms of species composition and richness. Ley habitats were characterised by higher species richness than oilseed, with an average of 13.28 ($\pm SE$ 1.76) species as compared with 3.64 ($\pm SE$ 0.45) species respectively (Figure S5a,c). Communities in ley were dominated by sawflies (Tenthredinidae spp.), and by Diptera and Coleoptera in oilseed. A total of 50 parasitoid OTUs were uncovered from 339 host specimens (Figure S5b). All parasitoids were found to parasitise hosts in ley habitats and 17 parasitoid OTUs (34% of the total) were uncovered from oilseed hosts (Figure 1). Twenty-eight host species (51.9%) were found to be parasitised, and 26 parasitoids were found to be shared between multiple hosts (Figure 2).

To understand how the strength of apparent competition might vary with habitat type and landscape composition, we calculated a metric for the potential for apparent competition and then assessed whether this metric varied when comparing hosts from the same versus different habitats and how landscape composition (percentage annual crops in 1-km buffer) impacted trends. Overall, we saw different relationships between the potential for apparent competition and percentage of annual crops in the surrounding landscape depending upon the source and target habitats (Table 1). Although the trend was negative in all cases, the strength of the relationship varied such that the greatest decline occurred between habitats when the potential for apparent competition was acting from oilseed communities upon ley communities where a 10% increase in the percentage of annual crops resulted in a reduction in the probability of obtaining a non-zero potential for apparent competition by a factor of 0.32 (slope = $-0.038 \pm SE$ 9.09×10^{-3}). The weakest response was observed within ley habitats where the same increase in land-use intensity resulted in a reduction by a factor of 0.01 (slope = $-0.015 \pm SE$ 7.26×10^{-3}). In general, pAC acting from oilseed tended to exhibit the greatest response to land-use (Figure 3a). This finding is based upon the probability of finding any potential for apparent competition, that is, a value above zero.

When we examined the non-zero cases independently, we found this negative relationship between the potential for apparent

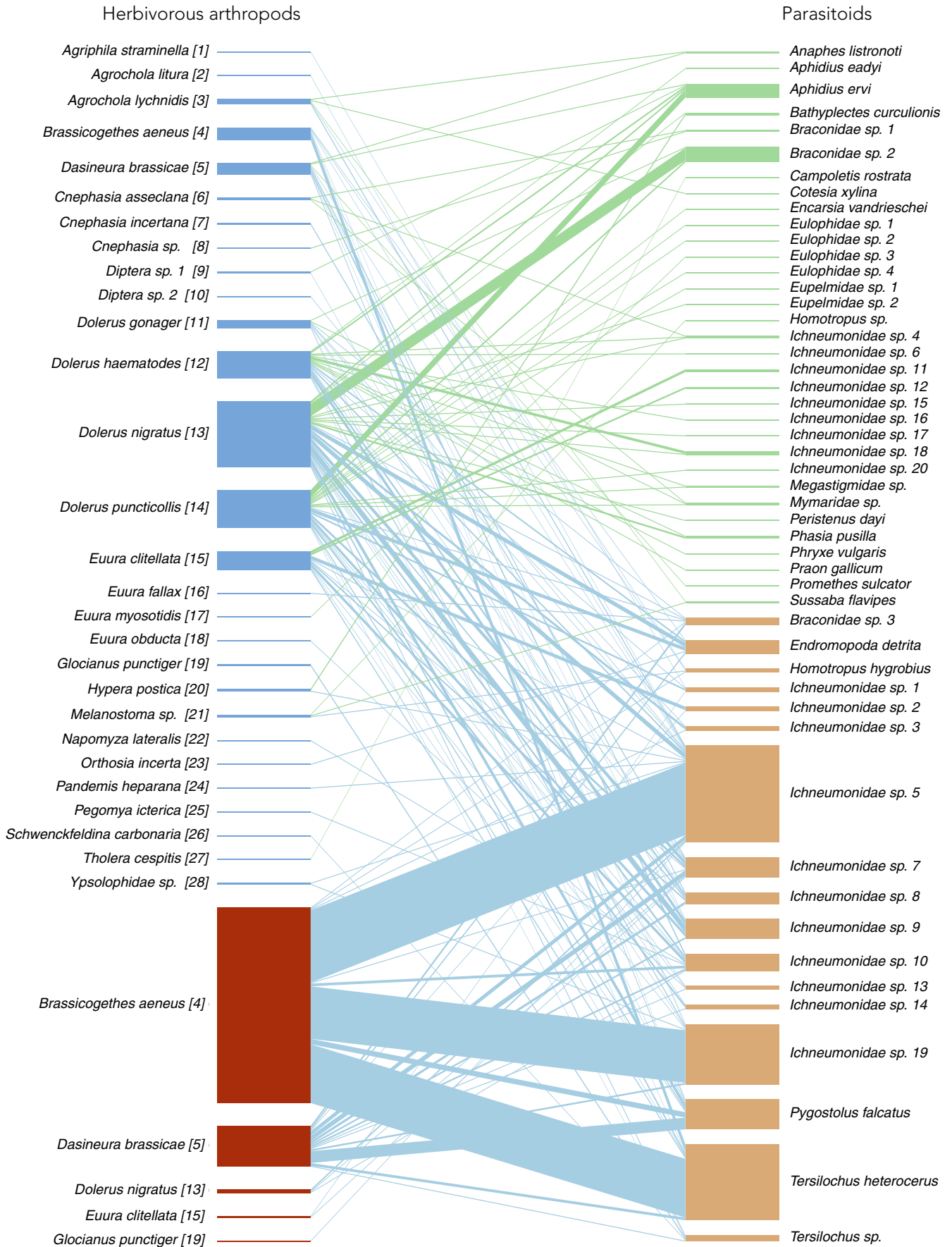


FIGURE 1 Metaweb comprising data from all locations, that is, 339 parasitism events within 1,329 host specimens. The left column represents herbivorous host species with blue bars displaying host species within ley habitats and red bars displaying host species from oilseed habitats. The right column represents parasitoid species where green bars show parasitoids only found in ley habitats and orange bars show parasitoids recovered from both ley and oilseed habitats. The width of the links between hosts and parasitoids indicate the number of parasitism events uncovered between each host–parasitoid pair

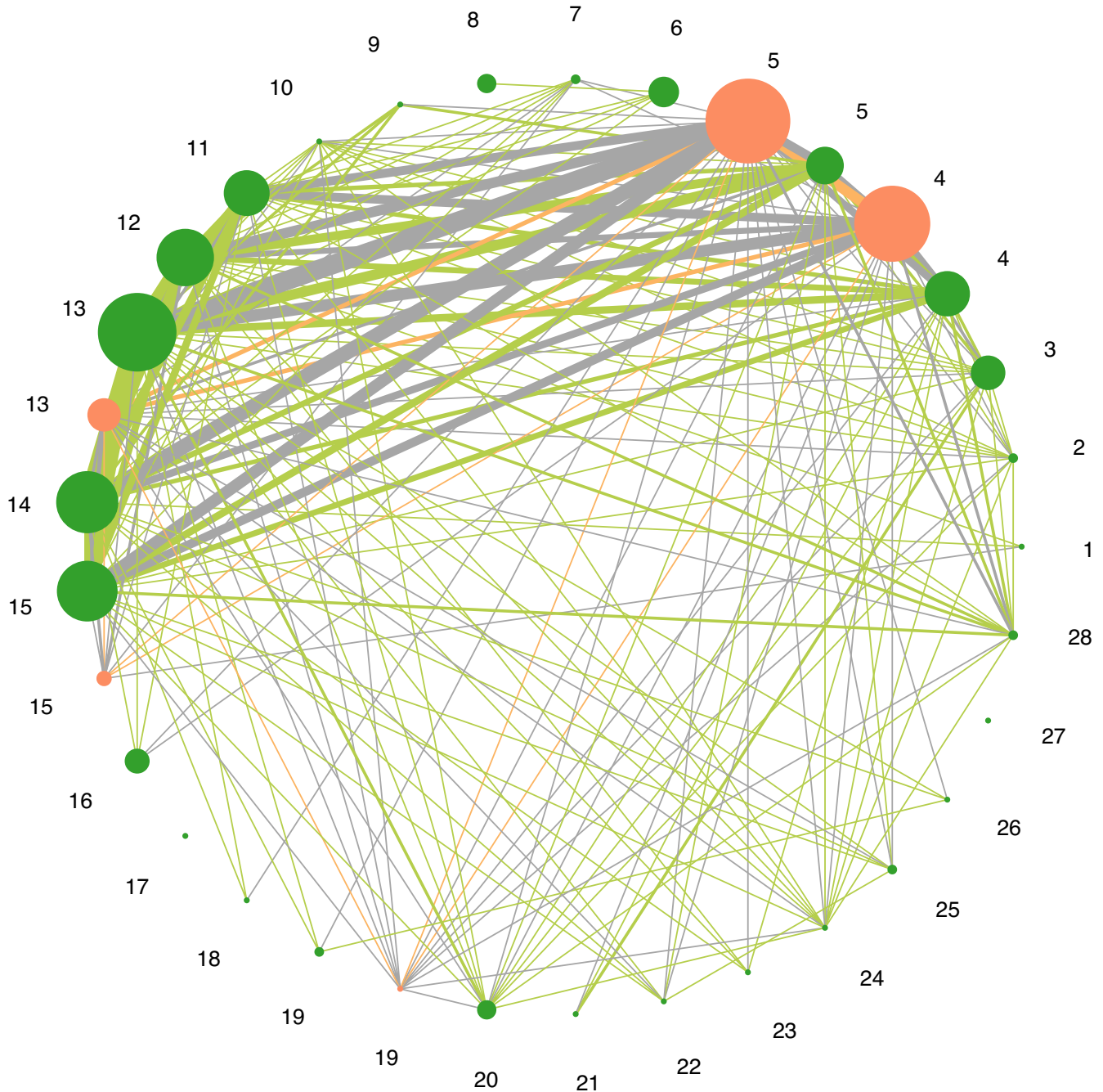


FIGURE 2 Data from 339 parasitism events within 1,329 herbivore specimens collected from all 22 sampling locations. Figure shows a circularised network showing the links between herbivore hosts based upon the number of parasitoid species attacking both hosts. Node label numbers represent host OTU ids and are the same as in Figure 1, the size of nodes show the log abundance of each host, and node colour represent the habitat from which the host was found where yellow indicates oilseed and green represents ley. Light green links indicate that both hosts are found within ley habitats, red links indicate that both hosts are found within oilseed habitats and green lines indicate that hosts are from different habitats. Line thickness indicates the number of parasitoids shared by each host pair

competition and percentage of annual crops persisted when pAC was acting from oilseed communities, either upon ley communities or upon themselves. The size of this correlation was more

modest, with a 10% increase in the percentage of annual crops reducing the potential for apparent competition by a factor of 0.02 (slope = $0.007 \pm SE 0.002$) But, the relationship was positive when

TABLE 1 Coefficient estimates for a mixed effects logistic regression modelling the probability of finding any potential for apparent competition (i.e. a non-zero value). Residual degrees of freedom = 11,605. Here, the estimates for the continuous variables (MEM9, MEM3 and % annual crops) represent the estimated amount by which the log odds of the pAC (i.e. the log of the of probability that the potential for apparent competition is not zero) would change if that continuous variable were one unit higher. For interactions, this is for OSR, relative to ley for both source and habitat. The estimates for categorical variables represent the change in the mean log odds of the pAC from ley to OSR. Significant predictors in bold

Independent predictors	Estimate ($\pm SE$)	Z-value	p-value
Spatial eigenfunction 1 (MEM9)	-1.02 (0.09)	-11.96	$<2.00 \times 10^{-16}$
Spatial eigenfunction 2 (MEM3)	0.93 (0.13)	7.42	1.17×10^{-13}
% Annual crops (%An)	-0.02 (0.01)	-2.07	0.04
Target Habitat (OSR)	0.64 (0.44)	1.43	0.15
Source habitat (OSR)	0.89 (0.43)	2.07	0.04
Target habitat (OSR):%An	-0.02 (0.01)	-1.73	0.08
Source habitat (OSR):%An	-0.02 (0.01)	-2.44	0.02
Source habitat (OSR): Target habitat (OSR):%An	0.02 (0.01)	2.17	0.03

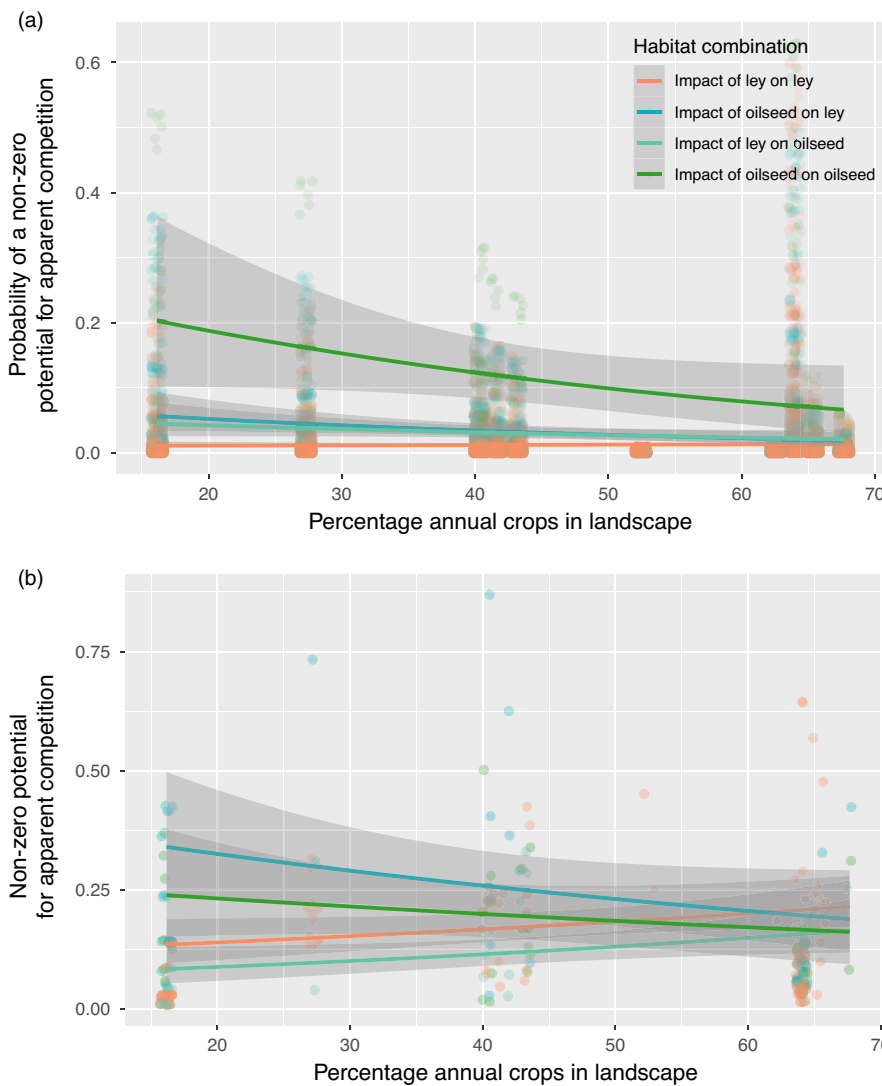


FIGURE 3 (a) Probability of achieving a non-zero potential for apparent competition against the percentage of annual crops in the surrounding landscape. Points show model predicted probability of a non-zero value. Lines show model fit for each source and target habitat combination. (b) Non-zero potential for apparent competition between host pairs plotted against the percentage of annual crops in the surrounding landscape. Lines represent the model fit for each source habitat. Grey shading shows the standard error

ley was the source habitat both when acting upon ley or upon oilseed communities. Here, the relationship was slightly stronger with a 10% increase in the percentage of annual crops increasing the potential for apparent competition by a factor of 1.10 (slope = $0.010 \pm SE$ 0.003; Table 2; Figure 3b).

To examine whether apparent competition had a discernible impact upon the parasitism of arthropod herbivores in this system, we predicted attack rates for each herbivore species at each location with and without considering the pAC. We then assessed how well the expected attack rates explained the realised attack rate by building separate models. The most parsimonious model incorporating pAC retained the expected attack rate, habitat type and the percentage of annual crops within the landscape as fixed effects (Table 3). In this model, the expected attack rate (generated using pAC, see Equation 2) was positively correlated with realised attack rate that is, the actual proportion of parasitised specimens per host species per site, per habitat (Figure 4a), uniquely explaining 9.7% of its variation. However, the expected attack rate generated without using pAC (from Equation 3) was removed during model selection, leaving only habitat type and the percentage of annual crops within the landscape as fixed effects. When added back into the model, this non-pAC expected attack rate is non-significant (Table 4) and

explains only 1.6% of the variation in realised attack rate (Figure 4b). Taken together, the difference in the variance explained by the two expected attack rates suggest that apparent competition does have a modest but discernible effect upon real levels of parasitism in the field. In all models, the percentage of annual crops in the landscape was also found to be positively correlated with the realised attack rate (Figure 4c). We further employed variance partitioning to understand the relative contribution of within and between habitat apparent competition on realised attack rates (see Supplementary Text 3 for a discussion) and found that while the majority of variance explained by these two predictors was shared (26.1%), 7.7% was uniquely explained by predicted attack rates calculated using only between-habitat potential for apparent competition. This indicates that apparent competition acting between habitats exerts a stronger influence than that acting within each habitat independently (Figure 4d).

4 | DISCUSSION

Our findings demonstrate that the potential for apparent competition is reflected by realised parasitoid attack rates upon herbivorous

TABLE 2 Coefficient estimates for a generalised linear regression with truncated-Poisson errors and a log link modelling the potential for apparent competition where only cases above zero are included. Residual degrees of freedom = 209. Here, the estimates for the continuous variables (MEM9, MEM3 and % annual crops), when exponentiated, are multiplicative terms used to calculate the predicted pAC when the given continuous variable increases by one. For categorical variables, these are stated for OSR relative to ley. Significant predictors in bold

Independent predictors	Estimate ($\pm SE$)	Z-value	p-value
Spatial eigenfunction 1 (MEM9)	0.28 (0.02)	13.95	$<2.00 \times 10^{-16}$
Spatial eigenfunction 2 (MEM3)	-0.26 (0.03)	-8.52	$<2.00 \times 10^{-16}$
% Annual crops (%An)	-1.87×10^{-4} (0.01)	-0.07	0.95
Source habitat (OSR)	0.25 (0.15)	1.65	0.10
Target habitat (OSR)	-1.20 (0.22)	-5.39	7.01×10^{-8}
Source habitat (OSR): Target habitat (OSR)	0.88 (0.26)	3.36	7.93×10^{-4}
Source habitat (OSR): %An	-0.01 (0.00)	-2.65	7.95×10^{-3}
Target habitat (OSR): %An	0.02 (0.00)	4.98	6.45×10^{-7}
Source habitat (OSR):Target habitat (OSR): %An	-0.02 (0.01)	-3.38	7.22×10^{-4}

TABLE 3 Coefficient estimates for the fixed effects of a linear mixed effects regression modelling the realised attack rate against the expected attack rate calculated using potential for apparent competition (pAC). Number of observations = 33. t tests use Satterthwaite's method, implemented using "LMERTEST" package in R. Significant predictors in bold

Independent predictors	Estimate ($\pm SE$)	df	t value	p-value
Fixed effects				
Intercept	-0.17 (0.09)	25.06	-1.78	0.09
pAC expected attack rate	6.74 (1.47)	13.71	4.58	4.50×10^{-4}
Habitat (OSR)	0.09 (0.07)	15.46	1.34	0.20
% Annual crops	0.65 (0.16)	21.06	4.16	4.40×10^{-4}
Interactions				
pAC expected attack rate: % Annual crops	-9.58 (2.31)	13.84	-4.14	1.01×10^{-3}
Habitat (OSR): % Annual crops	-0.48 (0.13)	15.76	-3.63	2.28×10^{-3}

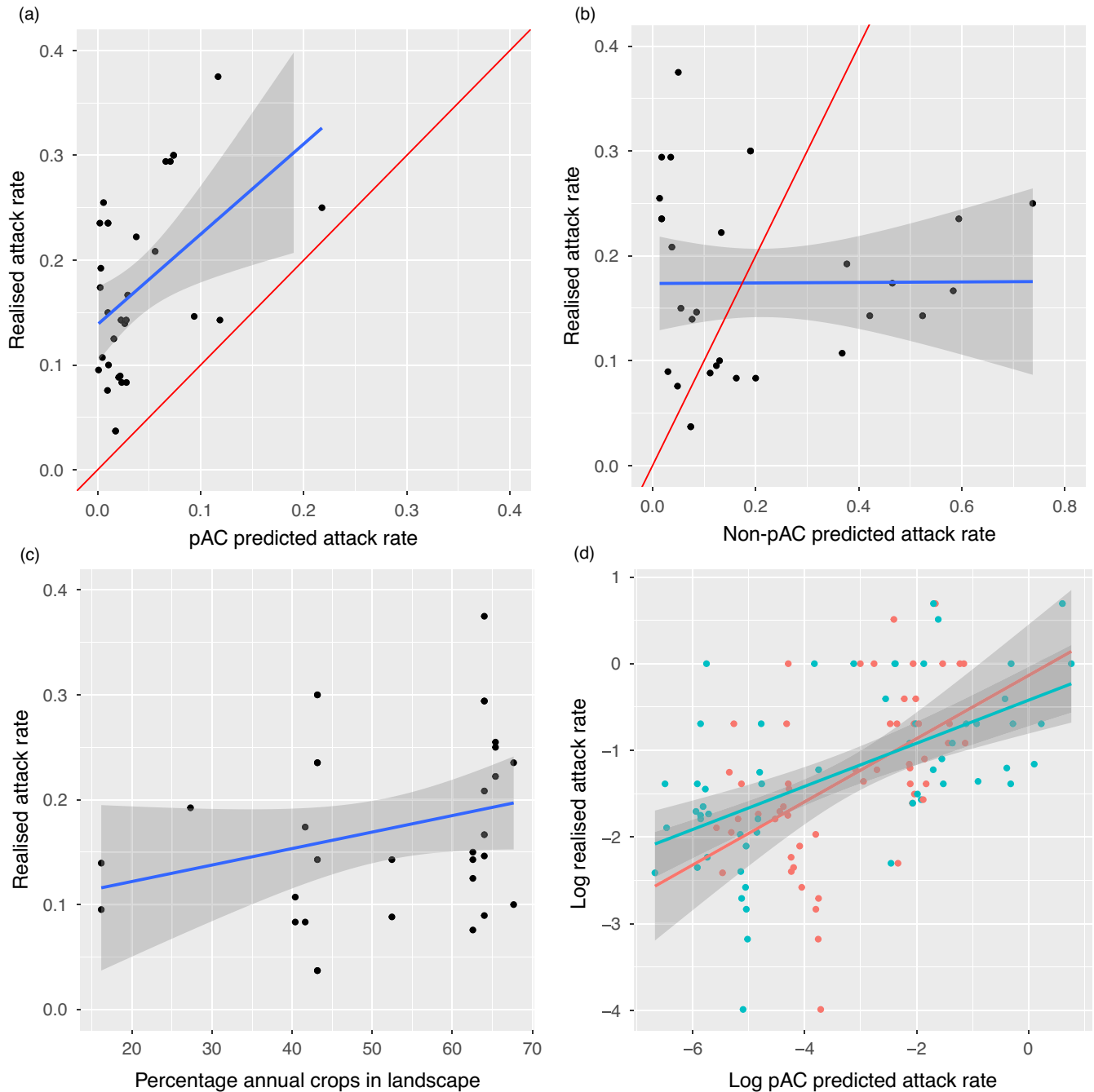


FIGURE 4 Realised attack rates plotted against predicted attack rates calculated (a) with and (b) without using the potential for apparent competition, red line indicates $y = x$ correlation for comparison (c) Realised attack rates plotted against the percentage of annual crops within the landscape (d) the natural log of realised attack rates against the natural log of predicted attack rates where blue points are predicted using the potential for apparent competition between hosts from different habitats only and red points are predicted using the potential for apparent competition between hosts within the same habitat only

arthropod hosts, and that increasing the proportion of annual crops in the surrounding landscape reduces overall potential for apparent competition at the community level within both oilseed and ley habitats. Thus, these results support the notion that landscape scale management impacts invertebrate communities at the local level, and contribute to a growing realisation that the consideration of species interactions as being isolated and spatially explicit limits our understanding of the processes governing ecological communities

(Guichard, 2017). Instead, networks of networks combined into a single 'metaweb' can provide a powerful tool for understanding landscape level deterministic processes (Saravia et al., 2019).

If spatially structured indirect effects are widespread, then the composition of landscapes is expected to influence local variation in the occurrence and strength of apparent competition (Fabian et al., 2013; Jonsson et al., 2015; Martin et al., 2019; Rusch et al., 2016). In the context of agroecosystems, the distribution of

TABLE 4 Coefficient estimates for the fixed effects of a linear mixed effects regression modelling the realised attack rate against the expected attack rate calculated without using potential for apparent competition (pAC). Number of observations = 33. *t* tests use Satterthwaite's method, implemented using 'LMERTEST' package in R. Significant predictors in bold

Independent predictors	Estimate (\pm SE)	df	<i>t</i> value	<i>p</i> -value
Fixed effects				
Intercept	-0.01 (0.09)	27.92	-0.13	0.90
Null expected attack rate	0.04 (0.04)	25.01	0.94	0.36
Habitat (OSR)	0.05 (0.09)	23.69	0.57	0.58
% Annual crops	0.43 (0.15)	25.18	2.78	1.01×10^{-2}
Interactions				
Habitat(OSR): % Annual crops	-0.40 (0.17)	24.72	-2.37	2.62×10^{-2}

natural and semi-natural habitats has often been highlighted as a crucial basis for effective ecosystem functioning (Duelli & Obrist, 2010; Söderström et al., 2001). The placement of less intensively managed crops next to heavily managed ones is thought to enhance biocontrol, and ultimately to increase crop yield via the bolstering of natural enemy communities (Amaral et al., 2013; Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Thies & Tscharntke, 1999; Wyss, 1995). Our findings suggest that such landscape-level impacts may derive both from direct and indirect community processes. The last half-century has seen a profusion of studies examining how populations and communities in the habitats surrounding cropland affect populations, communities and ecosystem services within cropland. In particular, the effect of subsidies (spill-over) of arthropods from surrounding habitats into crop habitats has received much attention (Ferrante et al., 2017; Opatovsky et al., 2010; Rand & Louda, 2006; Woodcock et al., 2016). Only relatively recently have we come to realise that these effects go both ways, and begun to look at effects of crops on adjacent habitats (Holzschuh et al., 2016; Montero-Castaño et al., 2016). Our current results show that indirect effects occur both within and between adjacent habitats in agroecosystems, and that increasing agricultural intensification at the landscape level can impact the strength of these connections depending upon the habitat in question.

As predicted, host communities within oilseed rape habitats exert a stronger influence in terms of apparent competition than those within ley habitats overall, likely due to higher herbivore abundances in oilseed rape. The negative trends detected between overall apparent competition and the proportion of annual crops in the surrounding landscape are ultimately driven by a greater proportion of zeros at sites with high agricultural intensification (i.e. a high percentage of annual crops). However, the mechanisms behind this finding are likely dependent upon multiple factors. A zero potential for apparent competition is found when either one or both of the host herbivores is not present, or when they share no parasitoids.

As such, possible explanations include a reduced herbivore diversity with increasing agricultural intensification, leading to an increased number of 'absent' herbivores; a reduction in the parasitoid diversity leading to an increased number of 'absent' parasitoids; or a turnover in species composition such that host pairs have no shared parasitoids. Visual examination of these potential drivers (Figure S6a-f) highlights the difficulty in determining the mechanisms behind our results. While herbivore diversity (Shannon diversity) does appear to decline with agricultural intensification, parasitoid diversity appears to increase. However, it should be noted that, based upon Pearson correlation tests (Table S4) with Bonferroni correction, none of these trends are significant. Additionally, the relative contribution of each of these drivers, among others, are difficult to untangle. Overall, agricultural intensification is a global driver of biodiversity decline (Matson et al., 1997; Tilman et al., 2001), but its specific consequences have been shown to be difficult to predict as partly due to a poor understanding of the links between species and habitats (Peterson & Allen, 1998; Snyder et al., 2005; Tscharntke et al., 2012). The present results add important details to this issue, by adding even further complexity: Not only may links between species and habitats be hard to establish, but even more so are the associations between habitats, landscape structure and trophic link structure (Ryser et al., 2019).

When we remove the effect of species composition by focusing on non-zero values alone, the potential for apparent competition derived from oilseed herbivore communities decreases with the proportion of annual crops in the landscape. By contrast, the potential for apparent competition derived from ley communities increases. This inconsistency in response between adjacent habitats comes with an important corollary: it highlights landscape composition as a key determinant of agricultural management practices. In other words, it supports the assertion that individual fields should not be considered in isolation, but rather as part of a matrix of interconnected habitats. It also emphasises the fact that crop habitats can disproportionately influence surrounding natural and semi-natural habitats via not only direct interactions of species that 'spillover' (Rand et al., 2006), but also via the indirect effects that these species facilitate. This phenomenon has been identified as one of potential functional significance, but previously lacked empirical scrutiny (Blitzer et al., 2012).

In terms of realised attack rates on herbivores, our finding that the potential for apparent competition successfully predicts attack rates provides evidence that network reconstruction offers a strong platform for functional insight. We therefore add to a growing body of literature supporting the premise that species interactions are key to understanding the link between biodiversity and ecosystem functioning (Creamer et al., 2016; Harvey et al., 2017; Ives et al., 2005). Our results on the impact of apparent competition between herbivores in different habitats upon attack rates mirror those of Frost et al. (2016) who concluded that the apparent competition between hosts in adjacent habitats can elicit a discernible impact on herbivore populations. It should be noted that to fully demonstrate realised apparent competition it would be necessary to show an influence of pAC upon herbivore abundances. Here, as with Frost et al. (2016),

we use realised attack rates as a proxy for this response since increased attack rates are likely to impact herbivore abundances (Hassell, 2000). Where Frost et al. (2016) experimentally reduce herbivore abundance to create a disparity between adjacent habitats, we substitute time for space by using existing variation arising from differences in landscape management. Thus, our study shows how the predictions from a previous experiment convert to realised impact in an agricultural setting. That indirect effects reach between disparate habitats in both forest and agricultural ecosystems suggests that these effects are indeed pervasive structural drivers of biological communities in a variety of ecosystems.

The results of this study are based upon a single sampling event. Apparent competition can occur both between generations due to high host population densities giving rise to large numbers of parasitoids emerging from parasitised hosts (Frost et al., 2016; Muller & Godfray, 1997), and within generations due to dispersal of predators and, specifically, their aggregation in areas of high prey densities (Harmon & Andow, 2004; Holt, 1984; Holt & Kotler, 1987; Holt & Lawton, 1993). This study aims to demonstrate the effect of within-generation apparent competition in agricultural habitats, driven by the high levels of heterogeneity in host herbivore densities. The high densities of herbivorous pests often found in crop monocultures, tend to attract natural enemies (Birkhofer et al., 2008; Evans, 2018), including parasitoids. When the host range of these parasitoids extends beyond a given pest species to non-pest herbivores, increased parasitism rates could occur in these non-pest species.

Methodological limitations exist irrespective of the approach one takes. Molecular characterisation of trophic interactions is a relatively new discipline and is not exempt from such limitations and biases. Clustering of sequence DNA in to OTUs can both clump together separate species and split up single species leading to a misrepresentation of network characteristics (Clare et al., 2016). Equally, in this study we took the approach of pooling OTUs identified as same species into a single entity to avoid overrepresentation. Since this was not possible for any OTU identified above the species level, it essentially meant that OTUs derived from taxa poorly represented in reference databases may have been overrepresented in our dataset. However, this effect is not correlated with any predictor variables and is, as such, unlikely to interfere with the trends reported. As reference datasets become more complete, this type of issue will be more easily avoided. Overall, a molecular approach enables the examination of a much greater diversity of hosts and parasitoids than traditional methods (Roslin et al., 2019) and as these methods develop, they provide an increasingly useful way to rapidly survey habitats and facilitate spatial and temporal replication.

At present, the concept of including set asides, semi-natural areas, flower strips within agricultural ecosystems is widespread (Dainese et al., 2015; Duelli & Obrist, 2003; Dufлот et al., 2014; Van Buskirk & Willi, 2004). However, the mechanisms linking biological communities in adjacent habitats are not well understood. Indirect effects have largely been left out of the equation, but the techniques employed here can help us better understand their impacts. Our finding that the potential for apparent competition is reflected in a

discernible way by realised attack rates on herbivore species, combined with the discovery that increasing agricultural intensification appears to reduce overall apparent competition at the community level, has strong implications for agricultural landscape management and biological control. Specifically, we suggest that landscape composition incorporating a lower proportion of intensively managed cropland could mitigate negative impacts of these crops upon surrounding natural habitats at the local scale. Additionally, we advocate the consideration of indirect effects between pest and non-pest herbivores when trying to understand the link between biological control and insect herbivore densities.

ACKNOWLEDGEMENTS

Our thanks go to Maylis Moro, Nina Roth, Pernilla Borgström, Laura Riggi, George Orfanidis, Milda Norkutė, Carol Högfeltdt and Gerard Malsher for their assistance with fieldwork and collecting the specimens; Eero Vesterinen for discussions of lab protocols, to Tytti Vanhala for her assistance in the lab, Kate Wootton for discussions around R scripting, and to the farmers for allowing us access to their fields. Funding for this research was provided by the Swedish Research Council for Sustainable Development FORMAS (grant 2016-01168) to R.B. and T.R. and the Swedish Research Council (grant 2016-04580) to T.R. and R.B.

AUTHORS' CONTRIBUTIONS

T.R., R.B., K.E.M. and G.A. conceived the ideas and designed methodology; K.E.M. and G.A. collected the data; K.E.M. carried out laboratory work and bioinformatics; K.E.M. and T.R. analysed the data; K.E.M. and T.R. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Merged reads and an OTU by sample matrix plus sample metadata are available from the Figshare Digital Repositories: Merged reads file: <https://doi.org/10.6084/m9.figshare.12174012> (Miller, 2021a); OTU by sample matrix: <https://doi.org/10.6084/m9.figshare.12174102> (Miller, 2021b).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Miller KE, Aguilera G, Bommarco R, Roslin T. Land-use intensity affects the potential for apparent competition within and between habitats. *J Anim Ecol*. 2021;90: 1891–1905. <https://doi.org/10.1111/1365-2656.13508>