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Habitat configuration matters when evaluating habitat-area effects on host–parasitoid interactions

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Abstract. Higher trophic levels tend to be more sensitive to habitat fragmentation than lower trophic levels, which is why parasitism rates should decline in fragmented landscapes. Habitat loss and fragmentation (the subdivision of habitat) are typically interrelated processes, and thus, their effects are confounded in most studies. To address this, we quantified parasitism rates in pea aphids (*Acyrthosiphon pisum)* within an experimental model landscape system, in which we independently controlled the amount vs. the fragmentation of habitat (red clover, *Trifolium pratense*) within individual landscape plots (16 × 16 m). Aphid densities were generally unaffected by landscape pattern, except at the local scale for interior habitat cells within fragmented landscapes, which had significantly lower aphid densities than all other cell types. Aphid parasitism rates averaged about 40% and were significantly—albeit weakly—correlated with aphid density. Habitat amount had the greatest overall effect on parasitism rates, but fragmentation effects were evident in a shift in parasitism at intermediate habitat levels: Parasitism rates were higher in fragmented landscapes with <50% habitat, but higher in clumped landscapes with >50% habitat. Edge effects alone did not explain this shift in parasitism rates. Parasitism rates were uniformly high within edge habitat and fragmented landscapes, and thus, the shift in parasitism at intermediate habitat levels was driven by increasing parasitism rates within interior cells and clumped landscapes at higher habitat amounts. Habitat configuration is thus important for evaluating habitat-area effects on species interactions, as habitat amount only affected parasitism rates within less-fragmented landscapes in this system.

Key words: aphids; biological control; edge effects; experimental model systems; habitat amount; habitat fragmentation; insects; landscape ecology; parasitoids.

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INTRODUCTION

Habitat loss and fragmentation are expected to have greater effects on species at higher trophic levels than at lower ones. In the case of host–parasitoid interactions, parasitoids are typically more sensitive to habitat loss and fragmentation than their herbivorous hosts because they are more specialized in their resource requirements and occur at lower densities than their hosts (Holt et al. 1999, Kruess and Tscharntke 2000, Tscharntke et al. 2002, Tscharntke and Brandl 2004, van Nouhuys 2005). A loss of habitat is also potentially a loss of hosts for parasitoids, especially if hosts become more patchily distributed as a consequence of habitat loss and/or fragmentation, making it difficult for parasitoids to find them. For example, the distribution of pea aphids (*Acyrthosiphon pisum*), which are a frequent target of biological control efforts in agricultural landscapes, became markedly fragmented and more dispersed when habitat (red clover, *Trifolium pratense*) comprised <20% of the area within experimental landscapes (With et al. 2002). Habitat loss

and fragmentation may also interfere directly with the movements and search behavior of parasitoids, thereby disrupting their ability to locate and/or aggregate in response to host populations (Roland and Taylor 1997, Cronin 2004, van Nouhuys 2005). As a result, parasitism rates tend to be lower in small, isolated habitat patches (Kruess and Tscharntke 1994, 2000, Olson and Andow 2008). Alternatively, parasitism rates have sometimes been observed to be higher in habitat fragments than in more continuous habitat distributions (Roth et al. 2006). Some parasitoid species are habitat specialists and may be edge-sensitive, such that they avoid crossing habitat edges. In that case, parasitoids essentially become stuck within habitat fragments, where their resulting pattern of concentrated search may lead to increased parasitism rates, especially if their hosts also exhibit edge avoidance and become more aggregated within fragments (Cronin 2009). The potential for these sorts of divergent responses to habitat loss and fragmentation underscores the difficulty of predicting how spatial structure will influence host–parasitoid interactions, which has implications for the development of effective pest management or biological control strategies in fragmented landscapes (Tscharntke et al. 2005).

From an ecological and biocontrol standpoint, it matters whether it is the sheer loss of habitat or the fragmentation of that habitat that is primarily responsible for disrupting host–parasitoid interactions. Habitat fragmentation implies both a loss of habitat and a change in the spatial configuration of habitat. Because habitat fragmentation typically occurs as a result of habitat loss, however, the effects of habitat loss and fragmentation are confounded in most fragmentation studies (Fahrig 2003, Ewers and Didham 2006). For example, many of the supposed effects of habitat fragmentation, such as a reduction in patch size and increased patch isolation, may result from habitat loss alone (Fahrig 2003). Although habitat loss and fragmentation have patch-scale consequences, these are landscape-wide disturbances whose effects should ideally be studied at the scale of the entire landscape (McGarigal and Cushman 2002). Despite this, most fragmentation research is focused on the properties of individual patches rather than properties of the landscape (e.g., patch size is the variable of interest rather than the total amount of habitat in the landscape; Fahrig 2003, 2013). Fragmentation research has been (and continues to be) influenced principally by the theory of island biogeography (MacArthur and Wilson 1967) and metapopulation theory (Levins 1969, 1970, Hanski and Gilpin 1991), in which the diversity and distribution of species are assumed to reflect colonization–extinction dynamics that in turn are assumed to be related to patch area and isolation (Hanski 1994, With 2004). This is particularly evident in the design of manipulative fragmentation experiments, in which the size and relative isolation of habitat patches are varied so as to investigate fragmentation effects (Debinski and Holt 2000, Haddad et al. 2015). While such studies have been instrumental in testing the mechanisms that underlie ecological responses to habitat loss and fragmentation, responses assayed at the patch scale cannot always be scaled-up to the landscape scale (i.e., to a particular configuration of patches) to predict the ecological consequences of landscape change (With 2016).

An alternative experimental approach is to construct landscape patterns from the top-down by altering the amount and configuration of habitat at the scale of the entire landscape, rather than from the bottom-up by adjusting individual patch properties, such as patch size and isolation, to create fragmented landscape patterns. The advantage of a top-down approach is that the total amount of habitat can be adjusted independently of the fragmentation of habitat, thereby allowing one to tease apart the relative effects of habitat amount from fragmentation per se (sensu Fahrig 2003). In addition, the resultant landscape patterns still have different patch properties, in terms of the number and size of patches or amount of edge habitat, which can aid in determining the extent to which local patch-scale effects are ultimately responsible for species' responses to habitat loss and fragmentation at the landscape scale.

In this study, we have adopted a top-down, landscape approach to investigate the independent and interactive effects of habitat amount and fragmentation on host–parasitism interactions in an experimental model landscape system. To our knowledge, this is the first such field study to investigate experimentally the relative effects of habitat amount vs. fragmentation on

parasitism rates via the independent control of each at the scale of individual landscapes. Although landscapes have traditionally been viewed as areas encompassing a broad spatial extent (i.e., defined at a km-wide scale), landscapes may be defined more generally as a spatially heterogeneous area that is scaled relative to the organism or process in question (Wiens 1989, Turner et al. 2001). From that standpoint, a landscape can be defined and studied at any scale, as the focus then lies in understanding the effect of spatial pattern on ecological process (Turner 1989, 2005). This expanded definition of landscapes is reflected in the use of experimental model landscapes for investigating the effect of spatial patterns—including habitat fragmentation—on a variety of ecological processes (e.g., Wiens and Milne 1989, With et al. 1999, Ims 2005, With and Pavuk 2011, 2012, Haddad et al. 2015).

Parasitoids and their hosts are expected to be influenced by spatial pattern across a wide range of spatiotemporal scales, from those encompassing individual movement and foraging behaviors, to the scales bounding population dynamics and metapopulation processes, all the way up to broad-scale effects on metacommunity dynamics. For example, the aphid parasitoid, *Aphidius ervi*, usually moves only a few centimeters (<11 cm) while actively searching for hosts, though they are capable of moving farther distances (>1 m) during foraging bouts (Olson et al. 2000); a related parasitoid species (*A. colemani*) was found to move up to 16 m within a day of release, although again, most moved only 1–2 m in that time frame (Langhof et al. 2005). At these finer scales bounding individual movements, the density and distribution of hosts relative to the density and distribution of host plants may influence parasitoid foraging success, and thus, parasitism rates. At the population or metapopulation level, aphid parasitism rates within small experimental arrays (2 × 32 m) were influenced more by the amount of host habitat than the scale of fragmentation, defined in that study as the distance between habitat patches, which varied between 2 and 8 m (Banks and Gagic 2016). Parasitism rates were initially highest in arrays having low amounts of habitat (25% cover), presumably because aphid populations were more aggregated within the relatively small patches of these arrays and were therefore more easily found by parasitoids (i.e., the distance between patches did not appear to interfere with parasitoid movements but may have hindered aphid dispersal among patches, at least initially; Banks and Gagic 2016). Finally, at broader scales encompassing metacommunity dynamics, parasitism rates were most correlated with landscape structure (the amount of non-crop habitat) at a scale of 1.5–2.0 km (Thies et al. 2003). At this scale, the availability of perennial (non-crop) habitats in the surrounding landscape may provide overwintering refugia and alternate resources capable of supporting a more abundant and diverse community of parasitoids that in turn contribute to higher rates of parasitism (Thies et al. 2003).

In the context of our experimental landscape system, we initially hypothesized that parasitism rates would be lower in fragmented landscapes than in landscapes with clumped habitat distributions and that parasitism rates would decline as a function of decreasing habitat, especially within fragmented landscapes. Our expectations were based on the assumption that parasitoid search efficiencies would be lower in fragmented landscapes and in landscapes with limited amounts of habitat, owing to the short-range foraging movements of aphid parasitoids (e.g., Olson et al. 2000), which should make them sensitive to the scale of fragmentation in this system, and given our previous finding that aphid populations were fragmented and more dispersed in landscapes comprising <20% habitat (With et al. 2002), which should make it more difficult for parasitoids to find aphid hosts. However, other research in this experimental system found that aphid and parasitoid densities were both greater within edge habitat than in the interior of habitat patches (With and Pavuk 2012). Higher aphid and parasitoid densities might very well translate into higher parasitism rates within edge habitat, and since fragmented landscapes have more edge habitat for a given habitat amount, it is possible that aphid parasitism rates might actually be higher in fragmented landscapes, and not lower as predicted above. Given that host–parasitoid interactions may be altered (e.g., increased) at habitat edges (Fagan et al. 1999, Olson and Andow 2008, Cronin 2009), such edge effects could explain the broader effects of habitat amount and/or fragmentation on parasitism

rates at the landscape scale. We therefore examined whether habitat edge influenced parasitism rates and, thus, whether edge effects can account for the observed effects of landscape structure on aphid parasitism rates in this system.

Methods

Experimental model landscape system

We established this experimental model landscape system (EMLS) in May 1997 on a 4-ha site north of the Bowling Green State University campus (Wood County, Ohio, USA). The EMLS consisted of 36 plots (landscapes), each of which was a 256-m^2 grid (16 × 16 m) in which we seeded red clover (*Trifolium pratense*) within grid cells (1 m^2) according to a specified fractal distribution (With et al. 2002, With and Pavuk 2011). The fractal landscape patterns were first computer-generated using the software RULE, in which the amount and spatial contagion of habitat are specified independently (With 1997, Gardner 1999). We generated fractal distributions at two levels of spatial contagion (specified by the Hurst Dimension, H, a measure of spatial dependence) to create landscape patterns in which habitat was either clumped (H = 1.0, high spatial dependence) or fragmented (H = 0.0, low spatial dependence) and covered 10%, 20%, 40%, 50%, 60%, or 80% of the landscape (Fig. 1). Three replicates of each landscape type (habitat × fragmentation level) were generated and subsequently reproduced in the field, with each map randomly assigned to a plot. Plots were maintained throughout the growing season by hand-weeding clover cells and applying herbicide to non-clover cells (bareground matrix) as needed. No irrigation was supplied to the clover. Plots were arrayed in a 6 × 6 configuration across the site, with neighboring plots separated by ~16 m of bare ground on all sides. The area between plots was plowed periodically throughout the growing season to keep it weed-free and to preserve the distinctiveness of the individual plots (see Fig. 1 in With et al. [2002] for an aerial view of the EMLS).

Aphid surveys and parasitism rates

Our survey of aphid parasitism was conducted in the second year following the establishment of the EMLS. The experimental plots had thus been previously colonized by arthropods, including aphids and their parasitoids, from the surrounding agricultural landscape prior to the start of this study (With and Pavuk 2011, 2012). The primary aphid species in our system was the pea aphid (*Acyrthosiphon pisum* Harris, Homoptera: Aphididae), which is parasitized by numerous species including *Aphidius* wasps (mostly *A. ervi* Haliday and *A. smithi* Sharma and Subba Rao, Hymenoptera: Braconidae). Aphids and braconids were among the most prevalent species in the EMLS, occurring in almost every plot throughout the three-year duration of the experiment (aphid mean plot occupancy = 0.89 ± 0.124 SD, range = 0.69–1.0, n = 6 surveys over

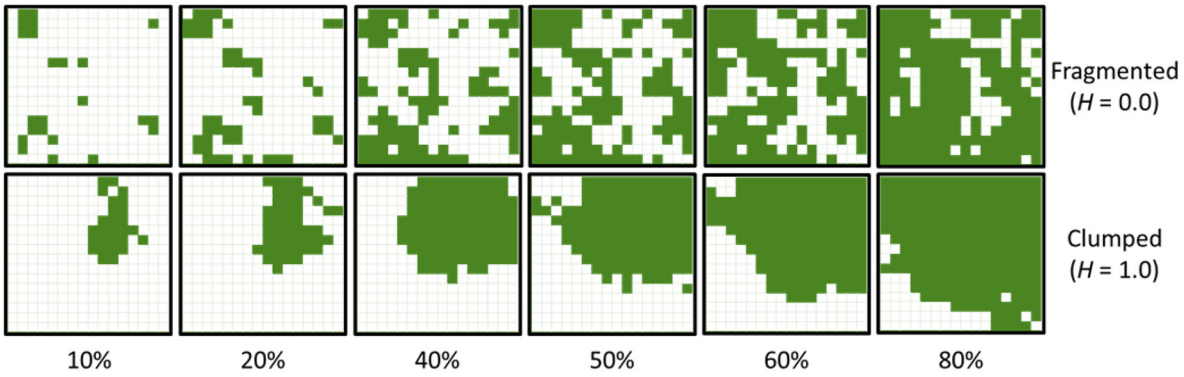

Fig. 1. An array of experimental landscapes, in which individual plots (16 × 16 m) were planted to red clover (*Trifolium pratense*) as a fractal distribution, each having a different habitat amount and level of fragmentation (clumped, H = 1.0 vs. fragmented, H = 0.0). The entire experimental landscape system consisted of three such arrays (total = 36 plots), all with different landscape patterns that had been randomly assigned to each plot.

3 yr; braconid mean plot occupancy = 0.92 ± 0.154, range = 0.61–1.0, n = 6 surveys; With and Pavuk 2011). Populations of aphid parasitoids, such as *A. ervi*, are tightly coupled to those of their pea aphid hosts, in that aphid parasitoids exhibit strong host specificity, a high reproductive potential, and a similar generation time as their hosts (Snyder and Ives 2003), making this an ideal system for comparing the effects of habitat amount and fragmentation on host–parasitoid interactions.

We assayed aphid populations and rates of parasitism by surveying 10% of the clover cells within each plot during a week-long survey in the first half of the growing season (17–20 June 1998). Clover cells were randomly selected prior to the survey, without regard to whether the cell was at the edge or interior of a clover patch. Cells were then classified afterward as either an interior cell if they were completely surrounded by other clover cells or as an edge cell if they shared at least one edge with the bareground matrix. In total, we surveyed 384 clover cells and ended up with slightly more interior cells (206 cells = 54%) than edge cells (178 cells = 46%). None of the interior cells came from the 10% or 20% fragmented landscape plots. Thus, the sampling design was unbalanced with respect to cell type but reflected the relative availability of edge vs. interior cells within these landscapes (Appendix S1: Fig. S1).

To quantify the degree of aphid parasitism, we counted the total number of aphids and aphid mummies across a sample of 10 clover stems that we arbitrarily selected from within each of the sampled cells, and then calculated parasitism rate as the proportion of parasitized aphids per cell. Parasitized aphids (mummies) have a distinctive appearance, making them easy to identify: They are large, round, and tan or whitish in color, in contrast to the light green of unparasitized aphids. Since our assessment of parasitism is based on the proportion of mummies, it is possible that we underestimated parasitism rates in the case of aphids that were only recently parasitized (i.e., within a few days of our survey). Conversely, if parasitoids are attacked by hyperparasitoids, this may increase apparent parasitism rates because of their longer development time (i.e., aphids remain mummified longer in the field). Given that our interest lies in comparing the relative rather than absolute rates of parasitism among different landscapes, these potential sources of bias should not affect the results or conclusions of our study, assuming these effects were evenly distributed among all cell types and landscape plots.

Statistical analysis

We investigated the main effects and two-way interactions between habitat amount, fragmentation, and cell type (interior vs. edge) on aphid density and aphid parasitism rates using a general linear model (GLM), with Type III sums of squares because of the unbalanced sampling design for cell type (PROC GLM, SAS Software, version 9.4; SAS Institute, Cary, North Carolina, USA). The lack of interior cells from 10% and 20% fragmented landscapes prevented us from exploring the three-way interaction between habitat amount, fragmentation, and cell type in a full-factorial design. Because of this, we also analyzed a subset of the data (i.e., landscape plots having 40–80% habitat) to explore the potential for significant three-way interactions in this domain. Prior to analysis, we performed an arcsine square-root transformation of parasitism rates given that proportions are not normally distributed (Zar 1999). We present the untransformed rates in the figures for ease of interpretation. Differences between the adjusted group means (least-square means) were evaluated during post hoc comparisons of significant effects using Tukey-Kramer tests ($P < 0.05$).

Results

Parasitism rates were significantly correlated with aphid density, albeit weakly (Fig. 2). When considered over the entire habitat range (10–80%), aphid density was not affected by the amount or fragmentation of habitat at the landscape-plot scale and was only marginally affected by cell type at the local scale (all $P \geq 0.05$; Table 1). There was a significant interaction between fragmentation and cell type, however, as aphid densities were lowest within interior habitat cells of fragmented landscapes (Table 1, Fig. 3).

When considered over just the 40–80% habitat range, all three main effects had a significant effect on aphid density (Appendix S1: Table S1).

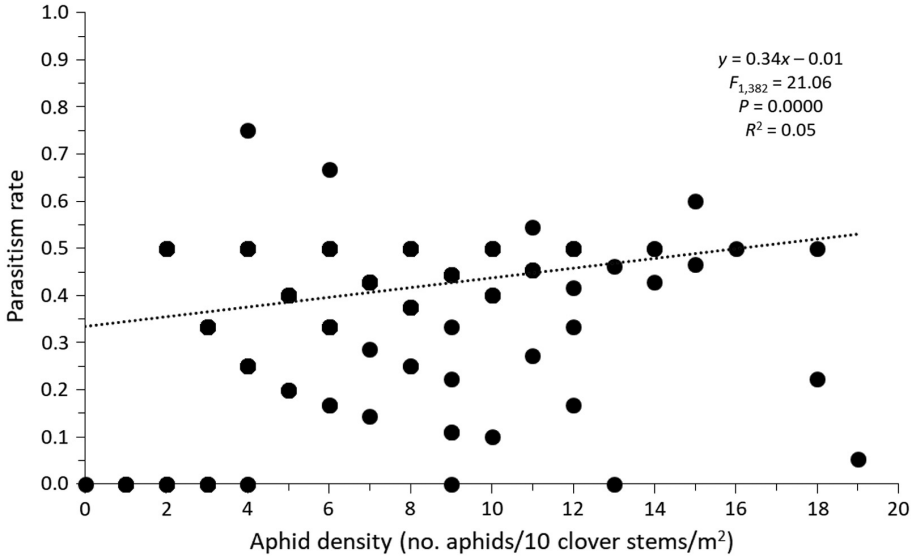

Fig. 2. Parasitism rate as a function of aphid density (no. aphids·10 clover stems^{-1}·m^{-2}) within individual clover cells (1 m^2, n = 384) that were randomly selected within each plot of the experimental landscape system (cf. Fig. 1).

Table 1. Summary of landscape effects on total aphid density and aphid parasitism rates (arcsine square-root transformed data) within experimental landscape plots with different amounts of habitat (red clover, *Trifolium pratense*) arrayed as either a clumped or fragmented distribution (cf. Fig. 1).

Source of variation	DF	MS	*F*	*P*
Aphid density†				
Habitat amount	5	17.58	2.01	0.077
Habitat fragmentation	1	15.26	1.74	0.188
Cell type	1	33.70	3.85	0.051
Amount × Fragmentation	5	9.73	1.11	0.354
Amount × Cell type	5	15.42	1.76	0.120
Fragmentation × Cell type	1	39.10	4.46	0.035
Aphid parasitism rates‡				
Habitat amount	5	0.103	2.91	0.014
Habitat fragmentation	1	0.012	0.33	0.567
Cell type	1	0.129	3.64	0.057
Amount × Fragmentation	5	0.111	3.11	0.009
Amount × Cell type	5	0.094	2.65	0.023
Fragmentation × Cell type	1	0.051	1.43	0.232

Note: Clover cells were also characterized by their relative location within a landscape plot (cell type = habitat interior vs. edge).

† Model R^2 = 0.09, $F_{18,\ 365}$ = 2.12, P = 0.005; GLM, Type III sums of squares.

‡ Model R^2 = 0.13, $F_{18,\ 365}$ = 3.00, P < 0.0001; GLM, Type III sums of squares.

Aphid densities were greater in clumped than fragmented landscapes (clumped: 6.4 ± 2.99 [SD] aphids, n = 171 cells; fragmented: 5.8 ± 3.13 [SD] aphids, n = 171 cells) and greater within edge than interior clover cells (edge: 6.4 ± 3.39 [SD] aphids, n = 150 cells; interior: 5.8 ± 2.78 [SD] aphids, n = 192 cells). Although the two-way interaction with fragmentation was not significant, there was a significant interaction between habitat amount and cell type, with aphid densities remaining fairly constant across habitat levels for interior cells but exhibiting a more variable response for edge cells (Appendix S1: Fig. S2). Aphid densities were significantly greater in edge than interior cells in landscapes with either 50% or 80% habitat but were marginally lower in edge than interior cells in 60% landscapes, accounting for the significant interaction. There was no significant three-way interaction between habitat amount, fragmentation, and cell type.

Aphid parasitism rates within clover cells averaged 40% (0.40 ± 0.136 SD, range = 0.00–0.75, n = 384 clover cells). Of the main effects, only habitat amount significantly affected parasitism rates (Table 1). The greatest difference in parasitism rates occurred between 20% and 50% habitat, where the rate of parasitism increased from 35% to 42% (Fig. 4A).

Although neither fragmentation nor cell type had a significant effect on aphid parasitism rates by themselves, each exhibited a significant

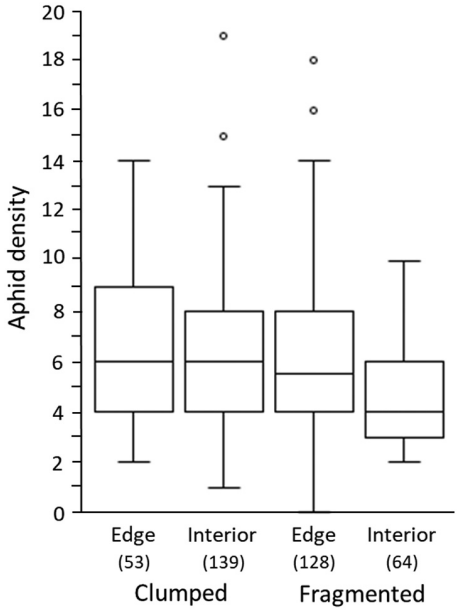

Fig. 3. Comparison of aphid density (no. aphids·10 clover stems^{-1}·m^{-2}) within edge and interior habitat cells in landscape plots having either a clumped (H = 1.0) or fragmented (H = 0.0) distribution of red clover (*Trifolium pratense*). Numbers in parentheses are the sample sizes (number of clover cells sampled) for each category. Boxes encompass the first through third quartiles of the data, the midline is the median value, and the length of the whiskers captures the local minimum and maximum values. Points beyond the box-and-whiskers are outliers, defined as data values that lie 1.5 times beyond the interquartile range (i.e., the length of the box).

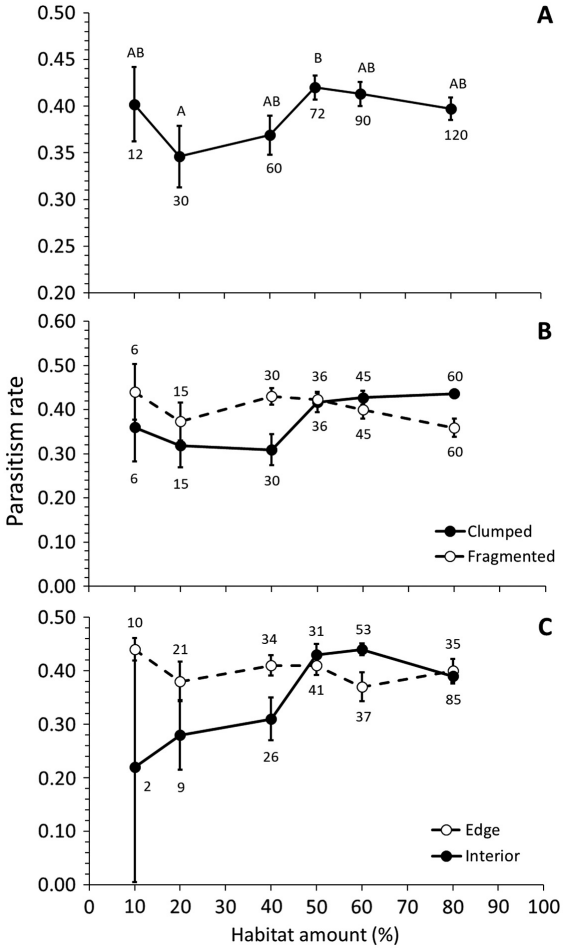

Fig. 4. Aphid parasitism rates ($\bar{x} \pm 1$ SE) as a function of habitat amount (red clover, *Trifolium pratense*) in an experimental landscape system for (A) all plots combined, (B) clumped vs. fragmented plots, and (C) edge vs. interior habitat cells. Means in (A) with the same letter are not significantly different ($P \geq 0.05$; Tukey-Kramer test). Numerals above or below symbols are the number of clover cells sampled across all plots at that level of habitat.

interaction with habitat amount (Table 1). Parasitism rates were higher in fragmented than in clumped landscapes when habitat comprised <50% of the landscape (although this difference was significant only at 40% habitat) but were higher in clumped than in fragmented landscapes when habitat amount was >50% (significantly so at 80% habitat; Fig. 4B). Parasitism rates increased with increasing habitat within clumped landscapes but remained fairly constant in fragmented landscapes. Thus, habitat amount exerted its greatest effect on parasitism rates primarily within clumped landscapes.

A similar shift in parasitism rates at intermediate habitat levels also occurred between cell types. Parasitism rates were initially higher in edge than in interior cells when habitat comprised <50% of the landscape (albeit this was significant only at 40% habitat) but were significantly higher in interior cells than in edge cells at 60% habitat (Fig. 4C). Although parasitism rates remained uniformly high within edge cells, parasitism rates within interior cells increased with increasing habitat. Thus, habitat amount exerted an effect on parasitism rates primarily within interior cells.

When considered over just the 40–80% range, the main effect of habitat amount on parasitism rates was no longer significant, but its interaction with fragmentation and cell type was still important in explaining the shift in parasitism rates, which is unsurprising given that this shift occurred at 50% habitat (Appendix S1: Table S1; Fig. 4B, C). As with aphid density, there was no significant three-way interaction between habitat amount, fragmentation, and cell type in this habitat domain.

Discussion

Although habitat loss and fragmentation are both assumed to affect the occurrence and distribution of species, unraveling their relative contributions is complicated by the inevitable confounding that occurs between these related components of landscape change. While habitat loss can occur in the absence of fragmentation, habitat fragmentation almost always entails a loss of habitat. Partitioning out the effects due to habitat amount vs. fragmentation has thus been a challenge in practice, especially as fragmentation is often characterized by patch-based metrics (patch size and isolation) that may not be independent of total habitat amount in the surrounding landscape (Fahrig 2003, 2013, Ewers and Didham 2006). By controlling the amount and fragmentation of habitat independently at a landscape-plot scale within our experimental system, we can more easily tease apart the relative effects of these two factors on species and their interactions. In the context of the present study, we can thus assert that habitat amount rather than fragmentation (the configuration of habitat) had the greatest overall effect on aphid parasitism rates, with the greatest increase in parasitism rates (from 0.35 to 0.42) occurring between 20% and 50% habitat.

This does not mean that habitat fragmentation had no effect on aphid parasitism rates, however. Fragmentation exhibited a significant interaction with habitat amount: Parasitism rates were higher in fragmented landscapes with <50% habitat but higher in clumped landscapes with >50% habitat. Although fragmentation is assessed here at a landscape-plot scale, fragmentation effects may also operate indirectly through local-scale edge effects (With and Pavuk 2012). The degree to which edges are important in explaining ecological responses to habitat fragmentation depends on the strength of the ecological response, the type of habitat edge (high-contrast or hard edges tend to elicit stronger ecological responses), and the relative amount of edge habitat in a landscape (Ries et al. 2004). Fragmented landscapes have proportionately more edge than clumped landscapes at all habitat levels, but the greatest difference between landscape types in our samples occurred between 20% and 50% habitat (Appendix S1: Fig. S1A). Edges are clearly high contrast in our experimental landscapes given the bareground matrix, and thus, we might reasonably expect a strong edge response.

Although we did not study parasitoid foraging behavior and so cannot evaluate their edge response directly, we can at least make some inferences based on the distributions of aphids and parasitoids relative to observed rates of parasitism. A previous survey found that densities of aphids and *Aphidius* parasitic wasps were both greater within edge than interior habitat cells of these clover landscapes, despite edge cells having lower overall richness and total insect abundance (With and Pavuk 2012). In the current study, we once again found that total aphid densities were significantly greater within edge than interior cells, at least in fragmented landscapes (Fig. 3). Thus, if parasitoids spend more time foraging within edge cells, whether because they are attracted to areas of high aphid density or because they exhibit edge sensitivity (Roth et al. 2006, Cronin 2009), we might expect to see higher rates of parasitism within edge than interior cells in landscapes that had a greater proportion of edge habitat, such as fragmented landscapes with 20–50% habitat (Appendix S1: Fig. S1A). Our results are thus consistent with this expectation.

Fragmentation and/or edge effects should become less important as habitat amount increases beyond 50% and the proportion of edge habitat declines (Appendix S1: Fig. S1B). Parasitism rates did not decline in this domain as expected, however. Instead, parasitism rates remained high in fragmented landscapes and within edge cells regardless of habitat amount, whereas parasitism rates in clumped landscapes and interior cells actually increased with

increasing habitat, eventually matching or exceeding rates observed within edge cells and fragmented landscapes. Given the greater prevalence of interior habitat in landscapes with >50% habitat, the sorts of edge effects discussed previously (higher aphid density and concentrated foraging by parasitoids within edge cells) no longer suffice to explain why parasitism rates remained high in fragmented landscapes with >50% habitat, nor why parasitism rates should increase with increasing habitat in clumped landscapes. In both cases, the proportion of edge habitat has declined, albeit it is still higher in fragmented than in clumped landscapes, even at 80% habitat (40% edge vs. 18% edge, respectively, of cells sampled).

Although we are unable to say definitively why parasitism rates increased with increasing habitat amount in clumped landscapes, we posit that the distribution and/or persistence of aphid populations may be enhanced past some critical patch size, especially if aphids initially colonize habitat along patch edges (as alates) and then slowly spread into the habitat interior (when apterous). In that case, a fragmented habitat distribution would promote aphid colonization, but hinder population spatial spread (With 2002). As for their natural enemies, previous research in this system found that predators and parasitoids, as a group, were more sensitive to habitat amount than herbivorous species, with 80% landscapes having twice as many predator and parasitoid species as 10% landscapes (With and Pavuk 2011). A greater number and diversity of parasitoids might well account for the observed increase in parasitism rates with increasing habitat, especially as aphid densities were also greater within clumped landscapes with abundant habitat (i.e., across the 40–80% habitat range). In addition, predators and parasitoids can actually enhance the movement and dispersal of pea aphids (e.g., by increasing the production of winged morphs; Sloggett and Weisser 2002, Irwin et al. 2007). In that case, the higher habitat connectivity of clumped landscapes, coupled with a larger and more diverse community of natural enemies, may act to promote aphid dispersal and population spread in these landscapes, leading to a more uniform distribution in clumped landscapes. In support, we note that aphid densities did not differ between edge and interior cells within clumped landscapes (Fig. 3). If the size and persistence of parasitoid populations also increase with patch size (which average larger in clumped landscapes) and/or parasitoids are simply tracking aphids (parasitism is somewhat density-dependent in this system; Fig. 2), then parasitism rates should again increase with habitat amount in clumped landscapes, especially if aphid populations are larger and more uniformly distributed within these landscapes. Again, we observed that parasitism rates increased with increasing habitat only in interior cells and only in clumped landscapes, which were dominated by interior cells at high habitat levels (i.e., 60–80% habitat; Appendix S1: Fig. S1). Thus, habitat-area effects rather than edge effects may account for increased parasitism rates in clumped landscapes, whereas edge effects predominate in fragmented landscapes regardless of habitat amount.

In conclusion, this experimental model landscape system has demonstrated a means by which the independent and interactive effects of habitat amount vs. fragmentation can be distinguished, which in this case has confirmed that habitat amount generally has a greater effect on parasitism rates in this system. Nevertheless, fragmentation effects were evident in a shift in parasitism rates at intermediate habitat levels, where parasitism rates were higher in fragmented landscapes with <50% habitat but higher in clumped landscapes with >50% habitat. Although edge effects are usually invoked to explain fragmentation effects, our results show that edge effects alone are not responsible for this shift in parasitism rates at intermediate habitat levels. Parasitism rates were uniformly high within edge cells and fragmented landscapes, such that it was only in clumped landscapes that a habitat-area effect was observed. Habitat configuration is thus important for evaluating habitat-area effects on host–parasitoid interactions, at least at this scale in this system. That the effects of habitat loss (a reduction in total habitat area) might matter more in clumped landscapes than in landscapes that are extensively fragmented (whether naturally or because of human land use) is not always explicitly considered in fragmentation studies and might well account for some of the conflicting views in the literature

regarding the relative importance of fragmentation effects on species' responses to landscape change (e.g., Fahrig 2017, Fletcher et al. 2018, Fahrig et al. 2019).

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