

# Habitat area trumps fragmentation effects on arthropods in an experimental landscape system

Kimberly A. With · Daniel M. Pavuk

Received: 11 February 2011 / Accepted: 21 June 2011 / Published online: 7 July 2011  
© Springer Science+Business Media B.V. 2011

**Abstract** The effects of habitat area and fragmentation are confounded in many studies. Since a reduction in habitat area alone reduces patch size and increases patch isolation, many studies reporting fragmentation effects may really be documenting habitat-area effects. We designed an experimental landscape system in the field, founded on fractal neutral landscape models, to study arthropod community responses to clover habitat in which we adjusted the level of fragmentation independently of habitat area. Overall, habitat area had a greater and more consistent effect on morphospecies richness than fragmentation. Morphospecies richness doubled between 10 and 80% habitat, with the greatest increase occurring up to 40% habitat. Fragmentation had a more subtle and transient effect, exhibiting an interaction at intermediate levels of habitat only at the start of the study or in the early-season (June) survey. In these early surveys, morphospecies richness was

higher in clumped 40–50% landscapes but higher in fragmented landscapes at 60–80% habitat. Rare or uncommon species are expected to be most sensitive to fragmentation effects, and we found a significant interaction with fragmentation at intermediate levels of habitat for these types of morphospecies in early surveys. Although the effects of fragmentation are expected to amplify at higher trophic levels, all trophic levels exhibited a significant fragmentation effect at intermediate levels of habitat in these early surveys. Predators/parasitoids were more sensitive to habitat area than herbivores, however. Thus, our results confirm that habitat area is more important than fragmentation for predicting arthropod community responses, at least in this agricultural system.

**Keywords** Agroecosystems · Edge effects · Insects · Patch size · Patch isolation · Scaling effects · Species–area relationship · Trophic responses

---

**Electronic supplementary material** The online version of this article (doi:[10.1007/s10980-011-9627-x](https://doi.org/10.1007/s10980-011-9627-x)) contains supplementary material, which is available to authorized users.

---

K. A. With (✉)  
Division of Biology, Kansas State University, Manhattan,  
KS 66506, USA  
e-mail: [kwith@ksu.edu](mailto:kwith@ksu.edu)

D. M. Pavuk  
Department of Biological Sciences, Bowling Green State  
University, Bowling Green, OH 43403, USA

## Introduction

Studies on the effects of habitat fragmentation have been an active area of research in ecology for two decades now. As Fahrig (2003) has pointed out, however, many of these studies do not distinguish between habitat loss and the effects of fragmentation per se. Habitat fragmentation refers to the degree to which habitat is subdivided on the landscape (i.e., the pattern of habitat on the landscape). Because habitat

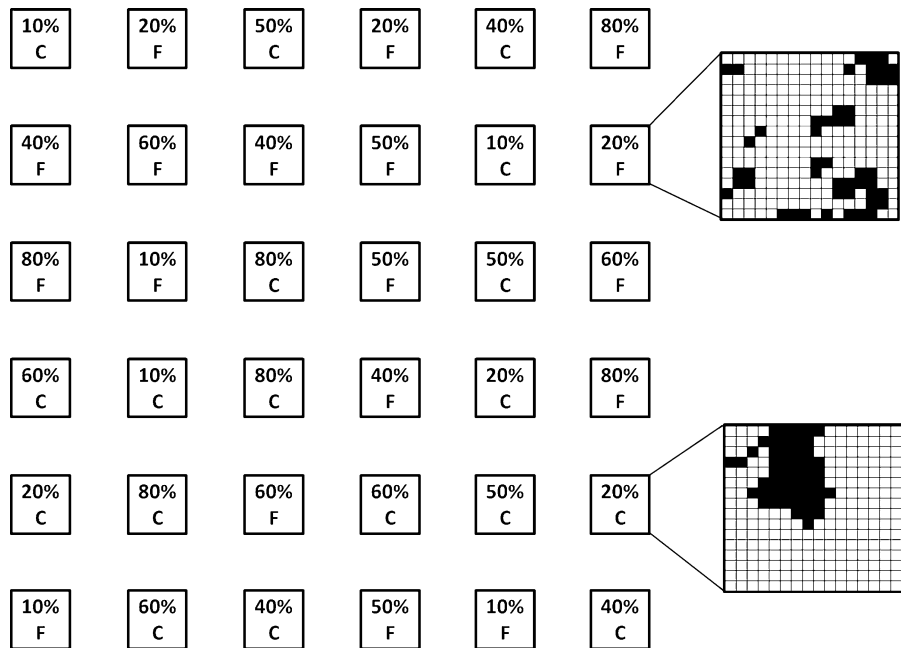
fragmentation usually occurs as a result of habitat loss, however, the effects of habitat loss and fragmentation are likely to be confounded unless care is taken to control for habitat area. In most of the studies surveyed, many of the effects attributed to fragmentation were really an effect of habitat area (Fahrig 2003). Further, many of these fragmentation studies were patch-based rather than landscape-based, such that it was the attributes of the individual habitat patches (patch size or isolation) rather than the overall landscape (percent habitat cover or degree of fragmentation) that were the object of study (see also McGarigal and Cushman 2002). Although some inferences about the effects of habitat loss and fragmentation can be made from patch-based studies, these effects are more properly studied at the landscape scale, especially if landscape context (such as the overall amount of habitat on the landscape) has an overriding effect on ecological responses within patches (Tschardt et al. 2002; Fahrig 2003; Collinge 2009).

Traditionally, the design of fragmentation studies has been heavily influenced by island biogeography and metapopulation theory, in which patch area and isolation are assumed to govern species' responses to the loss and fragmentation of habitat: small isolated patches are expected to have fewer species (owing to greater extinction rates and lower rates of recolonization) than large patches or small patches that are not isolated. Subsequently, most studies seek to identify or create patches of various sizes and degrees of isolation to test these effects on species richness or some other ecological response (e.g., Kruess and Tschardt 1994; Golden and Crist 1999; Collinge 2000; Haynes and Crist 2009). However, because of the inevitable trade-offs between patch size, inter-patch distances and replication in most studies, only a limited number of patch configurations can ultimately be explored (Debinski and Holt 2000). Further, although both habitat loss and fragmentation may reduce habitat patch area, it is unclear that fragmentation necessarily increases patch isolation. In fact, habitat fragmentation could decrease isolation if the pattern of fragmentation results in smaller gaps between remaining patches that facilitate dispersal across the landscape (Fahrig 2003). Thus, patch isolation is more a measure of the amount of habitat on the landscape than an index of fragmentation (Bender et al. 2003).

One alternative to the patch-based approach to the study of fragmentation effects is to consider the overall structure or connectivity of the landscape, rather than of individual patches. Neutral landscape models, developed in the field of landscape ecology, offer a simple way of generating complex landscape patterns across a range of habitat abundance and fragmentation (Gardner et al. 1987; With 1997). By tuning two parameters, it is possible to create complex landscape patterns that vary in both the amount ( $p$ ) and spatial autocorrelation ( $H$ ) of habitat using fractal algorithms. Patch structure (the distribution of patch sizes and distances among patches) thus emerges depending upon the specific combination of landscape parameters ( $p$  and  $H$ , With and King 1999a; Fig. 1). This then gives us the opportunity to tease apart the relative effects of habitat amount ( $p$ ) from fragmentation ( $H$ ) on ecological responses to landscape structure. Further, the structural connectivity of the landscape (whether habitat spans the landscape) is predicted to become disrupted at a critical level of habitat ( $p_c$ ) that is dependent on the pattern of habitat fragmentation ( $H$ ). Thresholds in landscape structure may presage other ecological thresholds, such as in dispersal, colonization or extinction (With and King 1999a, b). Given that the number of species on a landscape represents a tradeoff between species' colonization abilities and extinction rates, a disruption in landscape structure or connectivity may well affect species diversity and community composition.

We devised an experimental model landscape system (EMLS) in the field, founded on neutral landscape models, to explore the relative effects of habitat area versus fragmentation on arthropod diversity in an agroecosystem. Experimental model systems are useful tools in ecology (Lawton 1995), and EMLSs in particular are a cornerstone of experimental landscape ecology for testing the effects of spatial pattern on ecological processes (Wiens et al. 1993; With et al. 1999, 2002). As McGarigal and Cushman (2002) pointed out, strong inferences about the relative effects of habitat area and fragmentation can only be obtained from carefully designed experiments conducted at the landscape scale. However, "landscape scale" need not imply a broad spatial extent (e.g., km-wide scale); rather, the "landscape" must be scaled to the organism or process under investigation (Wiens et al. 1993).

**Fig. 1** Design of EMLS. Red clover (*Trifolium pratense*) was planted within each plot (16 × 16 m) as a fractal distribution (*C* clumped:  $H = 1.0$ ; *F* fragmented:  $H = 0.0$ ) at different levels of habitat area (10, 20, 40, 50, 60 and 80%). Each landscape type (e.g., 10% *C*) has three replicates



Arthropods are particularly good subjects for experimental landscape studies because they are small-bodied and have short generation times, and thus might reasonably be expected to exhibit responses to habitat area and fragmentation at scales commensurate to the relatively small size and short duration of most fragmentation experiments (Debinski and Holt 2000). Agricultural systems are also ideal for the experimental study of fragmentation effects because they are relatively simple (e.g., monocultures) and are thus easy to construct and maintain (McGarigal and Cushman 2002).

We thus sought to address the following questions with our EMLS study: (1) How does habitat fragmentation, apart from habitat area, affect species richness? If fragmentation exacerbates the effects of habitat area (e.g., through edge effects, such as increased predation or competition), then species richness should be lower in fragmented landscapes, particularly in those with limited habitat where fragmentation effects are generally expected to be greatest (e.g., <30% habitat; Andr en 1994; Fahrig 1997); (2) Are different types of species differentially affected by fragmentation? Life-history traits related to dispersal, establishment, and persistence may all influence a species' vulnerability to fragmentation (Davies et al. 2000; Steffan-Dewenter and Tscharntke 2002; Ewers and Didham 2006;  ockinger et al.

2010). Rare or uncommon species, given their lower density or patch occupancy, are likely to suffer higher extinction rates and are therefore expected to be more sensitive to habitat loss and fragmentation than more common or widespread species (Davies et al. 2000; Summerville and Crist 2001). The negative effects of fragmentation may also amplify at higher trophic levels (van Nouhuys 2005), with predators and parasitoids expected to be more sensitive to habitat loss and fragmentation than herbivores (Kruess and Tscharntke 1994, 2000; Roland and Taylor 1997; Zabel and Tscharntke 1998); and, (3) How is species richness at the local scale influenced by landscape context, in terms of the overall amount or fragmentation of habitat on the landscape? If fragmented landscapes have fewer species than clumped landscapes, then local-scale richness may also be affected, perhaps comprising only the most abundant or widespread species (e.g., Golden and Crist 1999).

## Study area and methods

### Experimental model landscape system

We established our EMLS on a 4-ha site at the Bowling Green State University Ecology Research Station, located 2 km northeast of campus in

northwest Ohio, USA (41°23'44.83"N, 83°37'44.12"W). Prior to our study, this site had been used for rowcrop agriculture for many years, and thus had been plowed repeatedly and was devoid of native vegetation. Our EMLS comprised a replicated series of plots (36, 16-m × 16-m plots) that were seeded to red clover (*Trifolium pratense*) in May 1997 (Fig. 1; see also Fig. 1 in With et al. 2002). The plots ("landscapes") varied in both the total area (10, 20, 40, 50, 60 and 80% cover) and fragmentation (clumped vs. fragmented) of clover habitat. In the context of our experiment, "fragmentation" refers to the spatial contagion or arrangement of habitat, and not the process by which habitat is lost (since habitat is in fact being created in this EMLS). We selected these habitat levels because previous analysis indicated that structural connectivity was disrupted in the 40–60% range (clumped  $p_c = 0.45$ , fragmented  $p_c = 0.54$ ), but other research on dispersal and animal movement suggested that thresholds in dispersal success or movement parameters may occur at ≤20% habitat (With and King 1999a; With et al. 1999), whereas extinction thresholds may occur across a range of habitat depending on the demographic potential of the species (With and King 1999b); we therefore bracketed these habitat ranges in the design of our EMLS. Landscape patterns were first computer-generated as a fractal distribution of habitat (fragmented:  $H = 0.0$ , clumped:  $H = 1.0$ ; see With et al. 2002 for details) to produce individual landscape maps with the specified amount and degree of habitat fragmentation (6 levels of habitat × 2 levels of fragmentation = 12 landscape patterns). Three replicate maps were produced for each landscape pattern (12 landscape patterns × 3 replicates = 36 maps). These landscape patterns were then duplicated in the field by randomly assigning fractal landscape maps to plots. Each plot was laid out as a 16-m × 16-m grid (256, 1-m<sup>2</sup> cells) and was separated from neighboring plots by 16 m (Fig. 1). The scale of our EMLS thus exceeds most other experimental fragmentation studies of arthropods in grassland or agricultural systems (e.g., 169-m<sup>2</sup> plots separated by 11 m, Golden and Crist 1999; 1–100-m<sup>2</sup> plots separated by 10 m, Collinge 2000; 225-m<sup>2</sup> plots separated by 9 m, Summerville and Crist 2001). Clover seed was obtained from a commercial supplier and planted within plots according to the specified fractal pattern. Each plot was maintained throughout

the growing season (May–September) through a combination of hand-weeding (clover cells) and herbicide application (non-clover cells) as required to maintain uniform habitat and a bare soil matrix, respectively. The area between plots was also plowed periodically to keep it weed-free and reduce the potentially confounding effects of matrix heterogeneity or species "spillover" from other habitats.

#### Arthropod surveys

Arthropods colonized plots via natural dispersal and immigration from the surrounding landscape, which was dominated by rowcrop agriculture (e.g., corn, soybean, winter wheat). Plots were surveyed by one of us (DMP) one to three times per growing season, for a total of six surveys over 3 years: (1) 8–27 July 1997 (hereafter, July-Year1); (2) 25 August–27 September 1997 (August-Year1); (3) 1–14 June 1998 (June-Year2); (4) 28 June–12 July 1998 (July-Year2); (5) 31 July–19 August 1998 (August-Year2); and (6) 23 June–9 July 1999 (July-Year3). Surveys were conducted during favorable weather conditions (i.e., no precipitation, winds <32–40 kph, 10.0–32.2°C [ $\bar{x} = 24.1 \pm 3.02(\text{SD})^\circ\text{C}$ ,  $n = 6$  surveys]). Plots were surveyed by visiting each clover cell (1 m<sup>2</sup>) for ~1 min and recording the occurrence of all arthropods visible within that cell, including below the canopy. We thus standardized our survey time with respect to the spatial grain of our landscape (i.e., 1-m<sup>2</sup> cells) since this represented the finest scale of sampling (data from individual clover cells were ultimately aggregated across plots). The advantage of visual surveys was that we were able to conduct a comprehensive survey of the entire system: we censused more than 3,960 cells (i.e., every clover cell) each survey, resulting in a total of ~23,760 individual cell-censuses over the six surveys. Survey time per plot ranged from 20 min for 10% landscapes (~20 clover cells) to 3.5–4 h for 80% landscapes (~205 clover cells). Non-clover cells were not surveyed because the bareground matrix was inhospitable to arthropods in this system. Given that arthropods were not collected, it was not possible to identify every arthropod to species. We thus use the term "morphospecies" hereafter to refer to the number of taxonomically distinct units (species, genus or family) observed within cells or plots, similar to other studies that have documented arthropod

responses to fragmentation (e.g., Bolger et al. 2000). Morphospecies were additionally assigned to a trophic guild (herbivores vs. predators/parasitoids). For some morphospecies, different life stages may belong to different trophic guilds (e.g., lacewing larvae are predators but adults feed on pollen, nectar and aphid honeydew) and thus were considered different “trophic morphospecies.” Each survey was completed within a two- to three-week period to minimize possible changes in community composition across the study site during the survey period.

Morphospecies richness ( $S$ ) was assayed at two scales within plots: local scale ( $S_C$ ), the number of morphospecies within an individual clover cell; and landscape scale ( $S_L$ ), the total number of morphospecies observed across all clover cells within a plot. Average local-scale richness ( $\bar{S}_C$ ) was obtained for each plot as  $\bar{S}_C = (\sum_{i=1}^n S_C)/n$ , where  $n$  is the number of clover cells in a given plot (which varied from about 25 to 205, depending on habitat area). In addition, we quantified the relative richness of herbivores and predators/parasitoids, as well as the number of “widespread” morphospecies (occupying  $\geq 50\%$  plots in a given survey) versus those that were encountered less frequently (“uncommon”) at the landscape scale ( $S_L$ ).

### Statistical analysis

Because individual plots were sampled repeatedly over the course of the study, we examined the effect of habitat area and fragmentation on plot-level richness ( $S_L$ ) within a repeated measures analysis of variance (SAS PROC GLM), in which the within-subject effects of survey were tested against the between-subject effects of cover, fragmentation and their interaction. We used Mauchly's sphericity test (based on orthogonal components) to test for compound symmetry in the variance–covariance matrix. In the event that the assumption of sphericity was violated, we used the Huynh–Feldt adjusted probabilities for testing within-subject effects. Similar analyses were also performed for each trophic level (herbivores vs. predators/parasitoids) and level of occurrence (widespread vs. uncommon morphospecies), and thus we applied the Bonferroni correction and interpreted tests with  $P \leq 0.01$  ( $\alpha = 0.05/5$ ) as statistically significant. Because there was always a strong survey effect (see “Results” section), we also

conducted a series of post-hoc analyses to aid our interpretation of main results by examining habitat area and fragmentation effects for each survey individually (two-factor ANOVA) to determine whether patterns were consistent among surveys, followed by post-hoc comparisons of significant treatment effects (Tukey tests). For each survey, we also tested for non-linear trends in the relationship between morphospecies richness and habitat area through orthogonal polynomial contrasts (6 levels of habitat—1 = 5-degree polynomial), in which we retained the highest-order polynomial that was significant. A finding that a higher-order polynomial is significant (e.g., quartic or quintic) means that there is a high degree of non-linearity, with one or more inflection points (2 for quartic, 3 for quintic) in which the relationship changes direction. Because of non-linearities in the relationship (see “Results” section), we took the logs of both richness and habitat area and fit a linear regression to the transformed data to obtain the slope and examine the rate at which morphospecies increased per unit habitat area.

The broader landscape context (habitat area or degree of fragmentation) might influence richness at the local scale (cell) within plots. We therefore performed a repeated measures ANOVA on average cell morphospecies richness within plots ( $\bar{S}_C$ ), complete with sphericity test. Again, there was a strong survey effect (see “Results” section) and so we highlight the results of post-hoc tests for individual surveys. The relationship between cell richness and plot richness was further explored through partial correlation analysis, in which the effect of survey was removed to determine whether plots with high morphospecies richness also have high richness at a local scale.

## Results

We recorded more than 100 arthropod morphospecies ( $S = 129$ ) in this EMLS during our three-year study, averaging 65 morphospecies per survey (summed across all plots; Table 1). Overall, plots averaged about 19 morphospecies ( $S_L = 18.6 \pm 5.80$  SD,  $n = 216$  plot-survey-years). There were about 25–33% fewer morphospecies per plot at the beginning of the study (July-Year1:  $16.7 \pm 5.76$ ,  $n = 36$  plots) or early in the season (June-Year2:  $15.1 \pm 3.98$ ), than at the end of the

**Table 1** Number and proportion (in parentheses) of arthropod morphospecies encountered within experimental clover landscapes ( $n = 36$  plots)

| Survey       | Widespread morphospecies <sup>a</sup> | Uncommon morphospecies <sup>a</sup> | Herbivores   | Predators/parasitoids | Total <sup>b</sup> |
|--------------|---------------------------------------|-------------------------------------|--------------|-----------------------|--------------------|
| July-Year1   | 13 (0.186)                            | 54 (0.771)                          | 35 (0.500)   | 30 (0.429)            | 70                 |
| August-Year1 | 21 (0.284)                            | 51 (0.689)                          | 39 (0.527)   | 28 (0.378)            | 74                 |
| June-Year2   | 12 (0.214)                            | 43 (0.768)                          | 26 (0.464)   | 22 (0.393)            | 56                 |
| July-Year2   | 13 (0.188)                            | 55 (0.797)                          | 35 (0.507)   | 26 (0.377)            | 69                 |
| August-Year2 | 18 (0.419)                            | 25 (0.581)                          | 22 (0.511)   | 16 (0.372)            | 43                 |
| July-Year3   | 15 (0.192)                            | 63 (0.808)                          | 43 (0.551)   | 32 (0.410)            | 78                 |
| Average      | 15.3 (0.247)                          | 48.5 (0.736)                        | 33.3 (0.510) | 25.7 (0.393)          | 65                 |
| SD           | 3.50 (0.092)                          | 13.20 (0.086)                       | 7.92 (0.029) | 5.85 (0.022)          | 13.08              |

The total number of morphospecies encountered in a given survey (total) is divided into species groups (widespread vs. uncommon; herbivores vs. predators/parasitoids), both of which may contain fewer species than the total

<sup>a</sup> Widespread morphospecies are those occupying  $\geq 50\%$  plots in a given survey; uncommon morphospecies occupied  $< 50\%$  plots in that survey

<sup>b</sup> Total morphospecies richness includes nectarivores and morphospecies that do not feed as adults (e.g., Ephemeroptera), and thus exceeds total sum of herbivores and predators/parasitoids

study (July-Year3:  $21.4 \pm 6.02$ ) or later in the season (August-Year1:  $22.7 \pm 5.52$ ). Herbivores made up half of the arthropod community in this system, with predators/parasitoids comprising 40% (Table 1). Among surveys, 12–21 morphospecies ( $15.3 \pm 3.50$ ,  $n = 6$  surveys) were widespread in occurrence ( $\geq 50\%$  plots in a given survey), which represents 25% of all morphospecies found in our EMLS (Table 1). Potato leafhoppers (*Empoasca fabae*), pea aphids (*Acyrtosiphon pisum*), tarnished plant bugs (*Lygus lineolaris*), spittlebugs (Cercopidae), and grasshoppers (Acrididae) were some of the most frequently encountered herbivores; braconid wasps (Braconidae), spiders (Araneae), damsel bugs (*Nabis* spp.), spotted lady beetles (*Coleomegilla maculata*) and Asian lady beetles (*Harmonia axyridis*) were among the most common parasitoids/predators found within our clover plots (Supplemental Table 1).

#### Effect of landscape structure on arthropod richness

Morphospecies richness at the plot level ( $S_L$ ) was only affected by habitat area (Table 2). In general, plots with 80% cover had 2× more morphospecies than plots with 10% cover, amounting to a difference of about 12 morphospecies (10%:  $11.6 \pm 3.22$ ,  $n = 36$  plot-survey-years; 80%:  $23.1 \pm 5.34$ ,  $n = 36$  plot-survey-years; Fig. 2). Morphospecies richness scaled as  $z = 0.33$  with an increase in habitat area

(fitted double-log plot;  $S = cA^Z = 0.75A^{0.33}$ ,  $R^2 = 0.982$ ).

Morphospecies richness differed among surveys (Table 2). Habitat area still had the greatest influence on plot-level richness in all surveys ( $P \leq 0.001$ ), although a weak-to-moderate interaction between habitat area and fragmentation was observed in the first surveys of both the first and second years (July-Year1:  $F_{5,24} = 2.51$ ,  $P = 0.058$ ; June-Year2:  $F_{5,24} = 4.26$ ,  $P = 0.007$ ; Fig. 3). In these surveys, morphospecies richness was higher in the clumped landscape plots at 40–50% habitat, but became greater in the fragmented plots at 60% habitat (total, Fig. 3). These early surveys also averaged 5–7 fewer morphospecies than surveys conducted either later in the season (August-Year1) or later in the study (July-Year3; compare horizontal lines in Supplemental Fig. 1). The complexity of the morphospecies–area relationship was evident in the higher-order polynomial that best described these trends (quartic or quintic, Table 3). In general, the morphospecies–area relationship was a non-linear one; only the relationship for August-Year1 was linear.

#### Trophic responses to landscape structure

Herbivore morphospecies richness was affected by the amount of habitat cover, although there was a significant survey by cover interaction (Table 2; Supplemental Fig. 2). Among surveys, there was a

**Table 2** Repeated measures analysis of variance of habitat area and fragmentation effects on morphospecies richness in experimental clover landscapes. Survey is the within-subjects, repeated measures variable

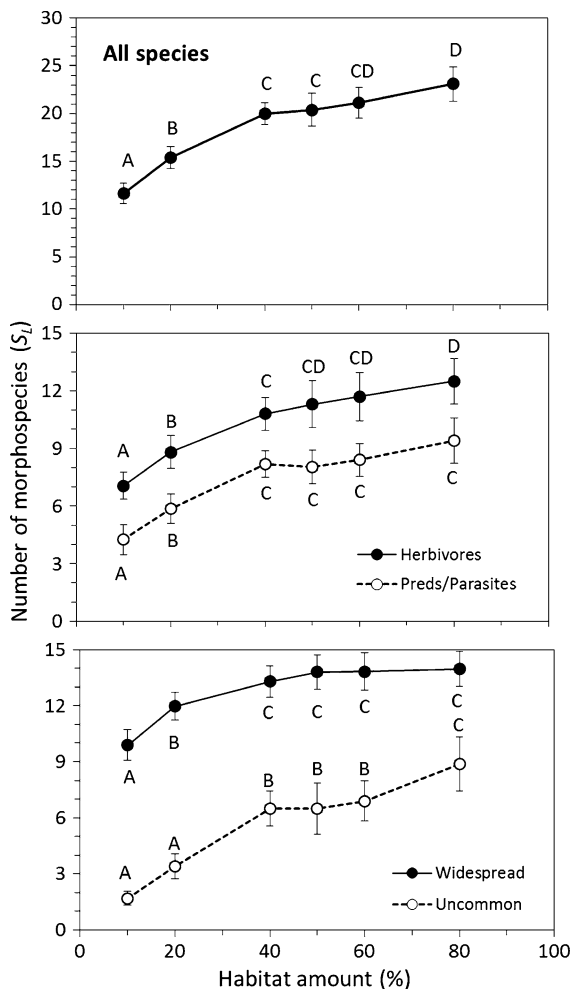
| Source of variation                              | DF  | MS     | F      | P       |
|--|-----|--------|--------|---------|
| <b>Morphospecies richness (<math>S_L</math>)</b> |     |        |        |         |
| Habitat area                                     | 5   | 655.69 | 78.20  | <0.0001 |
| Fragmentation                                    | 1   | 0.02   | 0.00   | 0.963   |
| Habitat area × fragmentation                     | 5   | 6.73   | 0.80   | 0.559   |
| Error  | 24  | 8.38   |        |         |
| Survey   | 5   | 302.68 | 25.99  | <0.0001 |
| Survey × habitat area                            | 25  | 14.51  | 1.25   | 0.215   |
| Survey × fragmentation                           | 5   | 4.32   | 0.37   | 0.868   |
| Survey × habitat area × fragmentation            | 25  | 16.67  | 1.43   | 0.104   |
| Error (survey)                                   | 120 | 11.65  |        |         |
| <b>Herbivores</b>                                |     |        |        |         |
| Habitat area                                     | 5   | 150.06 | 47.04  | <0.0001 |
| Fragmentation                                    | 1   | 0.56   | 0.18   | 0.679   |
| Habitat area × fragmentation                     | 5   | 1.97   | 0.62   | 0.687   |
| Error  | 24  | 3.19   |        |         |
| Survey   | 5   | 242.75 | 68.60  | <0.0001 |
| Survey × habitat area                            | 25  | 7.12   | 2.01   | 0.007   |
| Survey × fragmentation                           | 5   | 3.10   | 0.88   | 0.498   |
| Survey × habitat area × fragmentation            | 25  | 4.38   | 1.24   | 0.220   |
| Error (survey)                                   | 120 | 3.53   |        |         |
| <b>Predators/parasitoids*</b>                    |     |        |        |         |
| Habitat area                                     | 5   | 132.05 | 52.34  | <0.0001 |
| Fragmentation                                    | 1   | 0.12   | 0.05   | 0.832   |
| Habitat area × fragmentation                     | 5   | 2.09   | 0.83   | 0.541   |
| Error  | 24  | 2.52   |        |         |
| Survey   | 5   | 75.3   | 13.06  | <0.0001 |
| Survey × habitat area                            | 25  | 5.24   | 0.91   | 0.594   |
| Survey × fragmentation                           | 5   | 1.80   | 0.31   | 0.904   |
| Survey × habitat area × fragmentation            | 25  | 6.70   | 1.16   | 0.289   |
| Error (survey)                                   | 120 | 5.77   |        |         |
| <b>Widespread morphospecies</b>                  |     |        |        |         |
| Habitat area                                     | 5   | 92.86  | 37.99  | <0.0001 |
| Fragmentation                                    | 1   | 0.04   | 0.02   | 0.897   |
| Habitat area × fragmentation                     | 5   | 1.52   | 0.62   | 0.685   |
| Error  | 24  | 2.44   |        |         |
| Survey   | 5   | 206.29 | 108.26 | <0.0001 |

**Table 2** continued

| Source of variation  | DF  | MS     | F     | P       |
|--|-----|--------|-------|---------|
| Survey × habitat area  | 25  | 3.65   | 1.91  | 0.011   |
| Survey × fragmentation                                       | 5   | 1.93   | 1.01  | 0.413   |
| Survey × habitat area × fragmentation                        | 25  | 2.12   | 1.11  | 0.343   |
| Error (survey)   | 120 | 1.91   |       |         |
| <b>Uncommon morphospecies</b>                                |     |        |       |         |
| Habitat area   | 5   | 250.54 | 76.76 | <0.0001 |
| Fragmentation  | 1   | 0.17   | 0.05  | 0.823   |
| Habitat area × fragmentation                                 | 5   | 11.69  | 3.58  | 0.015   |
| Error  | 24  | 3.26   |       |         |
| Survey   | 5   | 91.46  | 11.26 | <0.0001 |
| Survey × habitat area  | 25  | 10.15  | 1.25  | 0.213   |
| Survey × fragmentation                                       | 5   | 1.26   | 0.15  | 0.978   |
| Survey × habitat area × fragmentation                        | 25  | 10.38  | 1.28  | 0.192   |
| Error (survey)   | 120 | 8.13   |       |         |
| <b>Cell morphospecies richness (<math>\bar{S}_C</math>)*</b> |     |        |       |         |
| Habitat area   | 5   | 0.13   | 0.40  | 0.843   |
| Fragmentation  | 1   | 0.03   | 0.10  | 0.750   |
| Habitat area × fragmentation                                 | 5   | 0.69   | 2.22  | 0.086   |
| Error  | 24  | 0.31   |       |         |
| Survey   | 5   | 50.57  | 90.37 | <0.0001 |
| Survey × habitat area  | 25  | 0.25   | 0.44  | 0.977   |
| Survey × fragmentation                                       | 5   | 0.39   | 0.70  | 0.587   |
| Survey × habitat area × fragmentation                        | 25  | 0.65   | 1.17  | 0.301   |
| Error (survey)   | 120 | 0.56   |       |         |

\* Huynh–Feldt adjusted probabilities used in these within-subjects tests

significant cover by fragmentation effect at the start of the study (July-Year1:  $F_{5,24} = 2.81$ ,  $P = 0.039$ ); herbivore richness was higher in clumped landscapes, except in 60% landscapes where richness was greater in fragmented landscapes (Herbivores, Fig. 3). Overall, herbivore richness was almost twice as high (1.8×) in 80% plots as in 10% plots, resulting in a gain of more than five morphospecies in the former (Fig. 2). Herbivore richness scaled as  $z = 0.27$  with an increase in habitat area ( $S = 1.34A^{0.27}$ ,  $R^2 = 0.994$ ). Herbivore richness generally exhibited a non-linear relationship with habitat area, however (67% of surveys; Table 3).



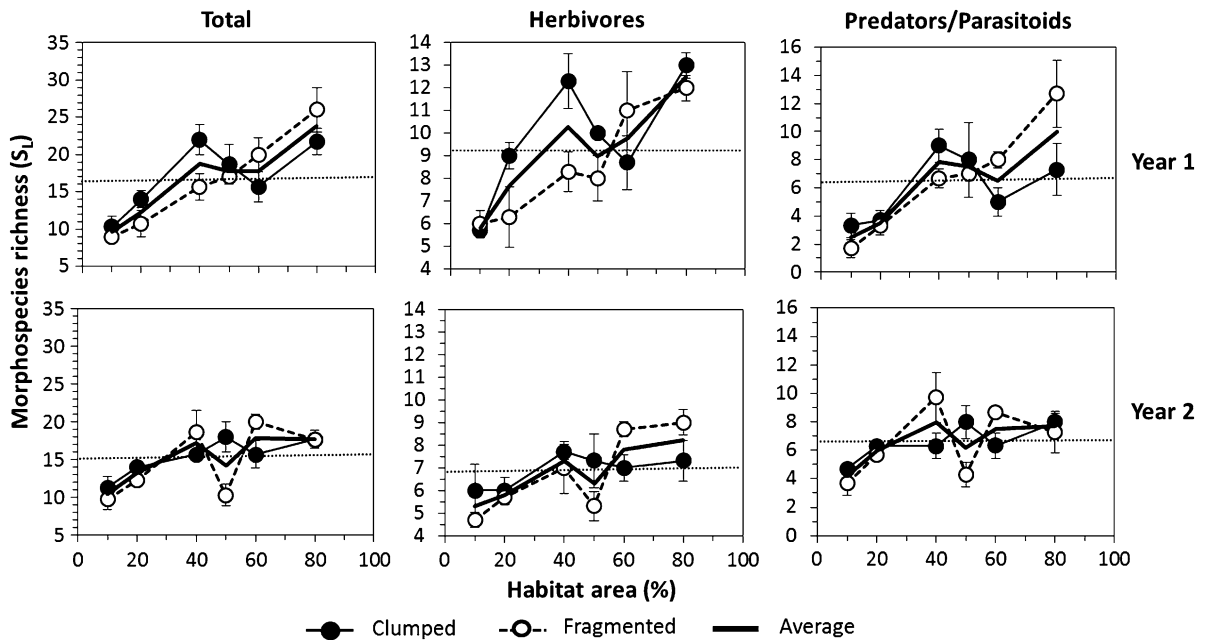
**Fig. 2** Effect of habitat area (% red clover) on arthropod morphospecies richness (mean  $\pm$  2 SE) within experimental landscape plots ( $S_L$ ) for (top) all morphospecies combined, (center) different trophic groups (herbivores vs. predators/parasitoids), and (bottom) different levels of occurrence (widespread vs. uncommon morphospecies; widespread:  $\geq 50\%$  plot occupancy in a given survey). In each group, means ( $n = 36$  plot-surveys) with the same letter are not significantly different ( $P > 0.05$ , Tukey test)

For predators/parasitoids, habitat area also had a significant effect on richness, although again there were differences among surveys (Table 2). Habitat cover had a significant effect on predator/parasitoid richness in five of six surveys (there were no significant effects of cover or fragmentation on predator/parasitoid richness in August-Year1; Supplemental Fig. 3). There was a significant cover by fragmentation interaction for the first survey (July-Year1:  $F_{5,24} = 8.91$ ,  $P < 0.001$ ) and for the first

survey in the second year of the study (June-Year2:  $F_{5,24} = 3.66$ ,  $P = 0.013$ ). In the first survey, predator/parasitoid richness was initially greater in clumped landscapes before switching to higher richness in 60 and 80% fragmented landscapes; predator richness was nearly  $2\times$  ( $1.7\times$ ) greater in 80% fragmented than clumped landscapes (predators/parasitoids; Fig. 3). The relationship was more complex in the first survey of the second year (June-Year2), with higher predator/parasitoid richness in 40 and 60% fragmented landscapes, but lower richness in 50% fragmented landscapes, than in clumped landscapes (Fig. 3). Overall, plots with 80% habitat tended to have  $2.2\times$  more predators/parasitoids than 10% plots, resulting in a gain of about five morphospecies in the former (Fig. 2). Predator/parasitoid richness thus scaled as  $z = 0.37$  as a function of habitat area ( $S = 0.63A^{0.37}$ ,  $R^2 = 0.980$ ); predator richness by itself scaled as  $z = 0.41$  with habitat area ( $S = 0.31A^{0.41}$ ,  $R^2 = 0.972$ ). The above treatment effects remained unchanged when only predators were analyzed (i.e., when parasitoids were omitted from analysis). In general, predators/parasitoids exhibited non-linear morphospecies–area relationships in half of the surveys (Table 3).

#### Landscape effects on widespread versus uncommon morphospecies

Despite the fact that uncommon morphospecies outnumbered widespread morphospecies 3:1 in this EMLS (Table 1), plots averaged twice as many widespread morphospecies ( $12.8 \pm 3.01$ ) as uncommon morphospecies ( $5.7 \pm 3.94$ ,  $n = 216$  plot-survey-years). For widespread morphospecies, there was a significant survey (within-subjects effects:  $F_{5,120} = 108.26$ ,  $P < 0.0001$ ) and survey by cover interaction ( $F_{25,120} = 1.91$ ,  $P = 0.01$ ; Supplemental Fig. 4). Habitat area had a significant effect on the richness of widespread morphospecies (Table 2), with a third fewer morphospecies in 10% than 80% plots (a difference of four morphospecies, Fig. 2). Widespread morphospecies scaled as  $z = 0.17$  with an increase in habitat area ( $S = 1.94A^{0.17}$ ,  $R^2 = 0.937$ ), although the relationship reached an asymptote at 40% with 13–14 morphospecies (Fig. 2). Thus, the morphospecies–area relationship was non-linear in all surveys (quadratic or cubic; Table 3).



**Fig. 3** Interaction between habitat area and fragmentation for arthropod morphospecies (mean  $\pm$  SE) within experimental clover plots ( $S_L$ ) for “early” surveys at the beginning of the

study (Year1-July) and early in the season (Year2-June). Horizontal line in each panel is the average morphospecies richness for that survey

For uncommon morphospecies, survey also had a significant effect, and there were significant habitat area and habitat area by fragmentation effects (Table 2). There were 5.4 $\times$  more uncommon morphospecies in 80% than 10% plots, resulting in a difference of about seven morphospecies (Fig. 2). Both the first (July-Year1) and early-season (June-Year2) surveys exhibited significant interactions between habitat area and fragmentation (July-Year1:  $F_{5,24} = 3.32$ ,  $P = 0.02$ ; June-Year2:  $F_{5,24} = 5.03$ ,  $P = 0.003$ ). Uncommon morphospecies exhibited greater richness in the clumped landscape plots at 40-50% habitat, but became greater in the fragmented plots at 60% habitat (Supplemental Fig. 5). Uncommon morphospecies scaled as  $z = 0.79$  with increasing habitat area ( $S = -1.21A^{0.79}$ ,  $R^2 = 0.970$ ), although the morphospecies–area relationship was non-linear in two-thirds of surveys (Table 3).

#### Relationship between local- and landscape-scale richness

Average local richness ( $\bar{S}_C$ ) was unaffected by landscape context, such as the amount or fragmentation of habitat within the plot (Table 2). Other than

at the start of the experiment (July-Year1),  $\bar{S}_C$  was significantly greater in July (mid-season) surveys than all other surveys (July-Year2:  $5.5 \pm 0.47$ ,  $n = 36$  plots; July-Year3:  $5.1 \pm 0.42$ ,  $n = 36$ ; July-Year1<sup>A</sup> = August-Year1<sup>A</sup> = August-Year2<sup>A</sup> < June-Year2<sup>B</sup> < July-Year3<sup>C</sup> = July-Year2<sup>C</sup>; Tukey test). Local richness was 2 $\times$  higher in these mid-season surveys than the lowest level encountered at the start of the study (July-Year1:  $2.7 \pm 0.68$ ,  $n = 36$ ). Overall, clover cells averaged four morphospecies ( $\bar{S}_C = 4.0 \pm 1.29$ ,  $n = 216$  plot-survey-years) regardless of habitat area or level of fragmentation. There was no correlation between local and landscape richness (Pearson partial correlation coefficient = 0.09,  $P = 0.188$ ,  $n = 216$ ; Supplemental Fig. 6). Thus, plots with higher morphospecies richness did not have a greater local richness than plots with fewer morphospecies.

#### Discussion

Habitat area had a far greater—and more consistent—effect than fragmentation on arthropod morphospecies richness within these clover landscapes.

**Table 3** Significant trend that best described the relationship between morphospecies richness and habitat area in experimental clover landscapes by survey, based on an analysis of all orthogonal polynomial contrasts ( $n = 5$ )

| Survey                           | Trend     | $F_{1,24}$ | $P$     |
|----------------------------------|-----------|------------|---------|
| Morphospecies richness ( $S_L$ ) |           |            |         |
| Year 1                           |           |            |         |
| July                             | Quartic   | 5.28       | 0.031   |
| August                           | Linear    | 52.68      | <0.0001 |
| Year 2                           |           |            |         |
| June                             | Quintic   | 8.01       | 0.009   |
| July                             | Quadratic | 9.50       | 0.005   |
| August                           | Quadratic | 13.41      | 0.001   |
| Year 3                           |           |            |         |
| July                             | Quadratic | 4.68       | 0.041   |
| Herbivores                       |           |            |         |
| Year 1                           |           |            |         |
| July                             | Cubic     | 6.76       | 0.016   |
| August                           | Linear    | 72.50      | <0.0001 |
| Year 2                           |           |            |         |
| June                             | Quintic   | 4.14       | 0.053   |
| July                             | Quadratic | 7.34       | 0.012   |
| August                           | Quadratic | 8.74       | 0.007   |
| Year 3                           |           |            |         |
| July                             | Linear    | 23.43      | <0.0001 |
| Predators/parasitoids            |           |            |         |
| Year 1                           |           |            |         |
| July                             | Quadratic | 6.93       | 0.015   |
| August                           | Linear    | 6.79       | 0.016   |
| Year 2                           |           |            |         |
| June                             | Quintic   | 4.55       | 0.043   |
| July                             | Linear    | 16.22      | 0.0005  |
| August                           | Quadratic | 18.48      | 0.0002  |
| Year 3                           |           |            |         |
| July                             | Linear    | 26.39      | <0.0001 |
| Widespread morphospecies         |           |            |         |
| Year 1                           |           |            |         |
| July                             | Cubic     | 5.09       | 0.033   |
| August                           | Quadratic | 7.00       | 0.014   |
| Year 2                           |           |            |         |
| June                             | Quadratic | 5.26       | 0.031   |
| July                             | Quadratic | 15.09      | 0.0007  |
| August                           | Quadratic | 13.47      | 0.0012  |
| Year 3                           |           |            |         |
| July                             | Quadratic | 5.09       | 0.033   |
| Uncommon morphospecies           |           |            |         |
| Year 1                           |           |            |         |

**Table 3** continued

| Survey | Trend     | $F_{1,24}$ | $P$     |
|--------|-----------|------------|---------|
| July   | Quartic   | 4.24       | 0.051   |
| August | Linear    | 27.86      | <0.0001 |
| Year 2 |           |            |         |
| June   | Quintic   | 7.70       | 0.011   |
| July   | Quadratic | 4.62       | 0.042   |
| August | Quartic   | 4.70       | 0.040   |
| Year 3 |           |            |         |
| July   | Linear    | 33.40      | <0.0001 |

Our study thus adds to the growing body of evidence that it is the overall amount of habitat on the landscape rather than how that habitat is arrayed that is ultimately most important for understanding community responses to landscape pattern (Fahrig 2003). Overall, morphospecies richness in 80% plots (205-m<sup>2</sup> total habitat area) was double that found in 10% plots (26-m<sup>2</sup> total habitat area). This gain in morphospecies richness was not a linear function of increasing habitat area, however. Morphospecies richness increased by 72% from 10 to 40% habitat, but only by about 16% (15.7%) between 40 and 80% habitat (Fig. 2). Given that our experimental landscapes were clover monocultures in fixed-sized plots, an increase in richness with habitat area obviously cannot be explained by an increase in habitat diversity, which is one of the explanations usually given for the species–area relationship (e.g., Holt et al. 1999). The fact that morphospecies richness at the local level ( $\bar{S}_C$ ) was unaffected by the amount of habitat within the plot ( $(\bar{S}_C) \sim 4.0$  morphospecies; Supplemental Fig. 6), however, suggests that plots with more habitat cells are effectively “sampling” the regional source pool to a greater degree than plots with less habitat area, and thus tend to accumulate more morphospecies at the plot level. Thus, this is essentially equivalent to a rarefaction analysis, in which we have standardized samples by some minimum area (1 m<sup>2</sup>) rather than number of individuals, since we only have presence-absence data available.

The effects of fragmentation on arthropod richness in this system were at best subtle and transient, in that they were evident only in “early” surveys either at the start of the study (July-Year1) or early in the season (June-Year2). Here again, the effect was

decidedly non-linear in that richness was higher in clumped 40–50% landscapes but higher in fragmented landscapes at 60–80% habitat. The reason for the crossover is unclear. Neutral landscape theory predicts a threshold in structural connectivity in the domain between 40 and 60% habitat, depending upon the specific fractal configuration (clumped:  $H = 1.0$ ,  $p_c = 0.45$ ; fragmented,  $H = 0.0$ ,  $p_c = 0.54$ ). It is therefore interesting that this is the domain where fragmentation effects occur, when they do. In some contexts, a disruption of landscape connectivity has actually been used to define when landscapes become fragmented (e.g., With 1997). Clumped landscapes should therefore maintain connectivity at lower levels of habitat abundance, and thus might support higher richness below this threshold relative to more fragmented landscapes. This would not explain why morphospecies richness is greater in fragmented landscapes above the threshold, however.

Rather than overall connectivity, morphospecies responses to fragmentation might be affected by some other aspect of landscape structure, such as the amount or complexity of patch edges (e.g., Ewers and Didham 2007). The amount of edge exhibits a parabolic distribution with increasing habitat cover, peaking at intermediate habitat densities, and fragmented fractal landscapes certainly have more edge than clumped fractal landscapes (With and King 1999a). Some species may benefit from intermediate levels of habitat loss and fragmentation because of greater resource diversity or more favorable microclimates along habitat edges (Crist and Ahern 1999). This sort of response might increase morphospecies richness at intermediate habitat levels, particularly in fragmented landscapes (i.e., another manifestation of the intermediate disturbance hypothesis). However, habitat edges negatively affect patch quality for other species, resulting in lower survival or reproduction if predation or parasitism is greater along edges, especially in small patches or patches with high edge contrast (e.g., Kruess and Tscharntke 1994; Thies and Tscharntke 1999; Cronin 2003). Although the patch-size distribution in fragmented fractal landscapes is shifted toward smaller patches at low habitat levels, patch sizes are pretty equivalent between fragmented and clumped fractal landscapes at higher habitat abundances (i.e., above the connectivity threshold; With and King 1999a). Fragmented fractal landscapes may thus afford suitably large patches beyond

the connectivity threshold, but nevertheless have more edge habitat and thus greater microhabitat diversity that can support more morphospecies than clumped landscapes at this level. Changes in landscape structure—either in terms of structural connectivity, amount of edge or both—might thus be responsible for altering the effect of habitat fragmentation on morphospecies richness at intermediate habitat densities.

Higher trophic levels are expected to be most sensitive to the effects of habitat fragmentation (Tscharntke et al. 2002; van Nouhuys 2005). For example, parasitism rates are often lower in fragmented landscapes (Roland and Taylor 1997; van Nouhuys 2005). To the extent that patch isolation is related to habitat fragmentation (and it may not be, see Fahrig 2003), then parasitoids are affected more by isolation than their herbivorous hosts (Kruess and Tscharntke 1994, 2000). For example, small (1.2 m<sup>2</sup>) isolated clover patches (separated 500 m from the nearest meadow) had 2–6× fewer species of parasitoids and 19–60% lower rates of parasitism than clover patches within meadows (Kruess and Tscharntke 1994). Recall that in our study, fragmentation effects were evident only in “early” surveys and manifest as a crossover effect in which morphospecies richness was alternately higher in clumped landscapes up to about 40–50% habitat, and then in fragmented landscapes beyond 50–60% habitat. Although predators/parasitoids exhibited this sort of crossover effect at the start of the survey (July-Year1), and early in the season (June-Year2), herbivores also exhibited a crossover in the relative importance of fragmentation on diversity (Fig. 3). Thus, our findings do not provide unequivocal support for the idea that higher trophic levels (predators/parasitoids) are necessarily more sensitive to habitat fragmentation than lower trophic levels (herbivores).

Predators/parasitoids in our EMLS were more sensitive to habitat area than herbivores, however, in that predators/parasitoids had a steeper species–area relationship ( $z = 0.37$  vs. 0.27, respectively; Fig. 2). Most of the gain in predator/parasitoid morphospecies occurred between 10 and 40%: morphospecies richness increased by 89% across this range, compared to only a 17% increase in morphospecies richness between 40 and 80% habitat. For herbivores, the increase between 10 and 40% habitat was 53%, compared to only a 16% gain in morphospecies

between 40 and 80% habitat. The size of clover patches has previously been shown to affect herbivore densities and levels of herbivory, especially by the potato leafhopper *Empoasca fabae* (Haynes and Crist 2009). This is a ubiquitous herbivore in our EMLS as well, which was found in almost every cell of every plot, thus swamping any habitat area or fragmentation effect for this species at the landscape scale (Supplemental Table 1).

Given that morphospecies richness increased throughout the season and over the course of the study (Fig. 3), it is possible that fragmentation effects were simply being swamped, especially by widespread and common morphospecies like the potato leafhopper. In our EMLS, widespread morphospecies showed only a strong effect of habitat area, not fragmentation (Fig. 2). Because of their widespread distribution, these morphospecies will likely drive community responses to landscape structure, especially in terms of the relative importance of habitat area versus fragmentation (Haynes and Crist 2009). Rare or less-widespread morphospecies might therefore be expected to show a greater sensitivity to habitat area and fragmentation (e.g., Golden and Crist 1999; Kruess and Tscharrntke 2000; Summerville and Crist 2001). Widespread morphospecies in our EMLS exhibited a significant effect of habitat area, but only up to about 40% habitat, at which point richness leveled off to an average 13–14 morphospecies per plot. Overall, the richness of widespread morphospecies increased 41% between 10 and 80%, with half of that increase (21%) occurring between 10 and 20%. Morphospecies that were less frequently encountered showed the most rapid accumulation of morphospecies with increasing habitat area: a fivefold increase between 10 and 80%, with the number of morphospecies doubling between 10 and 20% and again between 20 and 40%. These morphospecies were also influenced by fragmentation, at least in some surveys (the “early” surveys), showing crossover effects at around 40–50% habitat and 60% (Supplemental Fig. 5). Because uncommon or rare species tend to occur at low density or occupancy and have greater spatial variability, they are expected to have higher extinction rates (Kruess and Tscharrntke 2000), and thus if fragmentation effects are ultimately driven by the extinction or absence of these rare or uncommon species, then it would be difficult to detect such effects when more-common or widespread

morphospecies are also included in the analysis (Golden and Crist 1999).

Although our plot dimensions were larger than many other experimental fragmentation studies that have studied arthropods in agricultural or grassland habitats, our plots no doubt represented foraging patches for many morphospecies in this agricultural system, rather than discrete landscapes in which they completed their entire life-cycle. For example, individual ladybird beetles were observed to fly among plots while foraging for pea aphids (With et al. 2002). The scale of habitat fragmentation can always be expected to have a differential effect on species, however. Rare or less-widespread species with limited vagility are sensitive to patch isolation even at the scales studied here (e.g., Golden and Crist 1999), whereas more-mobile species that have no difficulty colonizing plots might nevertheless avoid smaller patches because of their perceived low resource abundance or quality (Summerville and Crist 2001). Even at more traditionally defined landscape scales (km-wide), broad-scale population processes such as local extinction and patch colonization may ultimately manifest through the collective response of individual patch-selection and foraging dynamics (Golden and Crist 1999; van Nouhuys 2005). It is precisely because of these sorts of species-specific responses to patch structure, where different types of responses occur simultaneously across a range of scales, which make fragmentation effects so difficult to isolate experimentally (McGarigal and Cushman 2002). Further, over short time-scales (e.g., among surveys within a season or over a few years), responses by individual species can generate idiosyncratic patterns, in which the effect of fragmentation may well be transient (Greze et al. 2004). Highly mobile species in particular, whose individual or population-level responses may encompass a spatial domain much larger than a single landscape or plot, likely contribute to such transient dynamics (Debinski and Holt 2000). Finally, some species are themselves “transient” or early-successional species, thus adding an additional idiosyncratic component to the community’s response to landscape structure.

In conclusion, community responses to habitat area and fragmentation will always represent the collective response of species that are responding in individual ways and at different scales to landscape pattern. The important distinction is to what extent

habitat area, as opposed to fragmentation per se, is ultimately responsible for community patterns, while recognizing that only certain types of species are likely to respond to the scale of fragmentation of the system, and even then, fragmentation effects may be subtle and transient. Although controlling for the confounding effects of habitat area and fragmentation can be difficult in empirical studies, especially those conducted at traditionally defined landscape scales, the use of appropriately scaled experimental landscapes provide a convenient means of testing the relative effects of habitat area and fragmentation on species' responses, especially for groups such as arthropods that operate at relatively fine spatial scales. Because fragmentation is a landscape-scale phenomenon, however, such studies should ideally focus on landscape-based attributes (i.e., the total amount and overall fragmentation of habitat on the landscape) rather than on patch-based properties (i.e., patch area and isolation) that may or may not relate to fragmentation per se.

**Acknowledgments** This research was supported by a grant from the National Science Foundation (DEB-9610159). We appreciate the assistance of the dozen or so undergraduates who helped to establish and maintain this experimental system. We thank L. Murray for statistical advice, J. R. Nechols and two anonymous reviewers for their comments on the manuscript.

## References

- Andrén H (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71:355–366
- Bender DJ, Tischendorf L, Fahrig L (2003) Evaluation of patch isolation metrics for predicting animal movement in binary landscapes. *Landscape Ecol* 18:17–39
- Bolger DT, Suarez AV, Crooks KR, Morrison SA, Case TJ (2000) Arthropods in urban habitat fragments in southern California: area, age and edge effects. *Ecol Appl* 10:1230–1248
- Collinge SK (2000) Effects of grassland fragmentation on insect species loss, colonization, and movement patterns. *Ecology* 81:2211–2226
- Collinge SK (2009) *Ecology of fragmented landscapes*. Johns Hopkins University Press, Baltimore
- Crist TO, Ahern RG (1999) Effects of habitat patch size and temperature on the distribution and abundance of ground beetles (Coleoptera: Carabidae) in an old field. *Environ Entomol* 28:681–689
- Cronin JT (2003) Patch structure, oviposition behavior, and the distribution of parasitism risk. *Ecol Monogr* 73:283–300
- Davies K, Margules C, Lawrence JF (2000) Which traits of species predict population declines in experimental forest fragments? *Ecology* 81:1450–1461
- Debinski DM, Holt RD (2000) A survey and overview of habitat fragmentation experiments. *Conserv Biol* 14:342–355
- Ewers RM, Didham RK (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biol Rev* 81:117–142
- Ewers RM, Didham RK (2007) The effect of fragment shape and species' sensitivity to habitat edges on animal population size. *Conserv Biol* 21:926–936
- Fahrig L (1997) Relative effects of habitat loss and fragmentation on population extinction. *J Wildl Manag* 61:603–610
- Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Annu Rev Ecol Syst* 34:487–515
- Gardner RH, Milne BT, Turner MG, O'Neill RV (1987) Neutral models for the analysis of broad-scale landscape pattern. *Landscape Ecol* 1:19–28
- Golden DM, Crist TO (1999) Experimental effects of habitat fragmentation on old-field canopy insects: community, guild and species responses. *Oecologia* 118:371–380
- Grez A, Zaviezo T, Tischendorf L, Fahrig L (2004) A transient, positive effect of habitat fragmentation on insect population densities. *Oecologia* 141:444–451
- Haynes KJ, Crist TO (2009) Insect herbivory in an experimental agroecosystem: the relative importance of habitat area, fragmentation, and the matrix. *Oikos* 118:1477–1486
- Holt RD, Lawton JH, Polis GA, Martinez ND (1999) Trophic rank and the species–area relationship. *Ecology* 80:1495–1504
- Kruess A, Tscharntke T (1994) Habitat fragmentation, species loss and biological control. *Science* 264:1581–1584
- Kruess A, Tscharntke T (2000) Species richness and parasitism in a fragmented landscape: experiments and field studies with insects on *Vicia sepium*. *Oecologia* 122:129–137
- Lawton JH (1995) Ecological experiments with model systems. *Science* 269:328–331
- McGarigal K, Cushman SA (2002) Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecol Appl* 12:335–345
- Öckinger E, Schweiger O, Crist TO, Debinski DM, Krauss J, Kuussaari M, Petersen JD, Pöyry J, Settele J, Summerville KS, Bommarco R (2010) Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. *Ecol Lett* 13:969–979
- Roland J, Taylor PD (1997) Insect parasitoid species respond to forest structure at different scales. *Nature* 386:710–713
- Steffan-Dewenter I, Tscharntke T (2002) Insect communities and biotic interactions on fragmented calcareous grasslands—a mini review. *Biol Conserv* 104:275–284
- Summerville KS, Crist TO (2001) Effects of experimental habitat fragmentation on patch use by butterflies and skippers (Lepidoptera). *Ecology* 82:1360–1370
- Thies C, Tscharntke T (1999) Landscape structure and biological control in agroecosystems. *Science* 285:893–895
- Tscharntke T, Steffan-Dewenter I, Kruess A, Thies C (2002) Characteristics of insect populations on habitat fragments: a mini-review. *Ecol Res* 17:229–239
- Van Nouhuys S (2005) Effects of habitat fragmentation at different trophic levels in insect communities. *Ann Zool Fennici* 42:433–447

- Wiens JA, Stenseth NC, Van Horne B, Ims RA (1993) Ecological mechanisms and landscape ecology. *Oikos* 66: 369–380
- With KA (1997) The application of neutral landscape models in conservation biology. *Conserv Biol* 11:1069–1080
- With KA, King AW (1999a) Dispersal success in fractal landscapes: a consequence of lacunarity thresholds. *Landscape Ecol* 14:73–82
- With KA, King AW (1999b) Extinction thresholds in fractal landscapes. *Conserv Biol* 13:314–326
- With KA, Cadaret SJ, Davis C (1999) Movement responses to patch structure in experimental fractal landscapes. *Ecology* 80:1340–1353
- With KA, Pavuk DM, Worchuck JL, Oates RK, Fisher JL (2002) Threshold effects of landscape structure on biological control in agroecosystems. *Ecol Appl* 12:52–65
- Zabel J, Tschardt T (1998) Does fragmentation of *Urtica* habitats affect phytophagous and predatory insects differentially? *Oecologia* 116:419–425