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RESEARCH ARTICLE

# An experimental test of the habitat amount hypothesis reveals little effect of habitat area but transient or indirect effects of fragmentation on local species richness

**Kimberly A. With** · **Alison R. Payne**

## Abstract

*Context* The habitat amount hypothesis (HAH) posits that local species richness is driven more by the amount of habitat in the surrounding landscape than by local patch size or habitat configuration. Habitat amount and configuration influence patch attributes, however, making it difficult to isolate these relative effects on local richness.

*Objectives* We tested the HAH in an experimental system in which the amount (10–80%) and configuration (clumped vs. fragmented) of habitat (red clover) were adjusted independently within individual 'landscapes' (256-m$^2$ plots).

*Methods* We used generalized linear models and model-selection criteria to evaluate how arthropod richness at two local scales (1 m$^2$ and 4 m$^2$) varied as a function of the amount or fragmentation of habitat and of the size or shape of the local patch.

*Results* Local richness was largely independent of the amount or configuration of habitat, as well as patch size or shape. Local richness was best modeled as a constant for all surveys but the first, in which fragmentation alone best explained variation in species richness, followed by patch shape (which is an indirect effect of fragmentation). Habitat amount had an overwhelmingly positive effect on arthropod richness at the landscape scale, however.

*Conclusions* The HAH was not supported in this experimental system: local richness was generally unaffected by the amount of habitat in the surrounding landscape, whereas habitat configuration was sometimes important. Given that habitat amount affected landscape-wide richness, it may be that the HAH only applies at the 'landscape scale', at least in this system.

**Keywords** Arthropods · Experimental landscape ecology · Habitat fragmentation · Habitat loss · Species-area relationship · Species diversity

K. A. With (✉)
Laboratory for Landscape and Conservation Ecology, Division of Biology, Kansas State University, 116 Ackert Hall, Manhattan, KS 66506, USA
e-mail: kwith@ksu.edu

A. R. Payne
Manhattan High School, Manhattan, KS 66505, USA

A. R. Payne
Environmental Studies Program, University of Kansas, Lawrence, KS 66045, USA

## Introduction

The habitat amount hypothesis (HAH) posits that species richness at a local scale, such as within a sampling site, is largely determined by the amount of

habitat in the surrounding landscape rather than by the size or isolation of the habitat patch in which that site is located (Fahrig 2013). As such, the HAH implies that habitat fragmentation—the configuration of patches—is ultimately unimportant for understanding or predicting species diversity; the size and arrangement of patches matter only to the extent that they influence the amount of habitat in the local landscape. Since its publication, the HAH has generated a great deal of debate over the relative importance of habitat amount versus fragmentation on species richness (e.g., Hanski 2015; Haddad et al. 2017).

Much of this debate stems from the inevitable confounding that exists between habitat amount and configuration across scales. The amount and configuration of habitat at the landscape scale also influence the size, shape, and distribution of patches; in other words, attributes of patches are not wholly independent of landscape properties such as total habitat amount and degree of fragmentation (Didham et al. 2012; With 2016). As a result, patch-area and isolation effects may only matter at certain habitat amounts, such as when habitat is limiting and patchily distributed (Hanski 2015). Teasing apart the relative effects of patch-scale versus landscape-scale effects on diversity is therefore a challenge, especially since habitat-area effects tend to dominate fragmentation effects when considered at a landscape scale (Fahrig 2003, 2017), whereas patch-size and isolation effects are inevitably important when considered at a patch scale in patchy (i.e., fragmented) landscapes (Fletcher et al. 2018; Haddad et al. 2017). A patch-based focus is also reflected in the design of most fragmentation experiments (Debinski and Holt 2000; Haddad et al. 2017), which manipulate the size and relative isolation of patches to create fragmented landscape patterns (i.e., a bottom-up approach; sensu With and Pavuk 2011), thereby reinforcing the apparent importance of these patch-scale effects on species diversity.

An alternative approach involves creating landscape patterns that vary in the overall amount and fragmentation of habitat at the landscape or whole-plot scale, which then results in different patch-size distributions and patch configurations (a top-down approach; sensu With and Pavuk 2011). In this paper, we take advantage of one such experimental model landscape system to test the HAH. Our experimental model system consists of a replicated series of plots ('landscapes') in which the amount and fragmentation

of habitat (red clover, *Trifolium pratense*) were independently adjusted at the whole-plot ('landscape') scale to produce a range of habitat amounts (10–80% habitat) and extremes of fragmentation ('clumped' vs. 'fragmented'; Fig. 1). Note that we are adopting a definition of 'landscape' as a collection of patches that is defined at a scale relevant to the organisms of interest (Wiens and Milne 1989). Our experimental landscape system was specifically designed to test how the amount and fragmentation of habitat at the 'landscape' (whole-plot) scale influence the species diversity of terrestrial arthropods (With and Pavuk 2011, 2012), and has previously been used to examine how fragmentation influences species-area relationships at the patch versus landscape scales (With 2016). Here, we use this experimental system to test several predictions that follow from the HAH.

According to the HAH, species richness within a local sample site should both (1) increase with the amount of habitat in the surrounding landscape, and (2) be independent of the size of the patch in which the sample site is located (Fahrig 2013). Both conditions must be true to be consistent with the HAH. Put another way, we may reject the HAH if we find that local species richness (within a sample site) does not increase with habitat amount in the surrounding landscape or that local richness is influenced more by the local patch size (i.e., the patch in which the sample site is located). Patch size tends to be correlated with habitat amount and thus their relative effects on species richness are usually evaluated statistically, albeit they can be teased apart experimentally by varying the local patch size in different landscape contexts (e.g., Seibold et al. 2017). In the case of our experiment, we are adjusting the amount and fragmentation of habitat at the 'landscape' scale, which then has an indirect effect on patch size (patches are smaller in fragmented landscapes than in clumped landscapes, especially when habitat is limiting; With 2016).

The above predictions of the HAH can be extended to include the effect of habitat fragmentation. To be consistent with the HAH, local species richness should be independent of the degree of fragmentation in the surrounding landscape. That is, local richness should not be influenced by the configuration of habitat, including the distribution of habitat within the local patch. For a given habitat amount, fragmentation not only reduces patch size, but also increases the amount
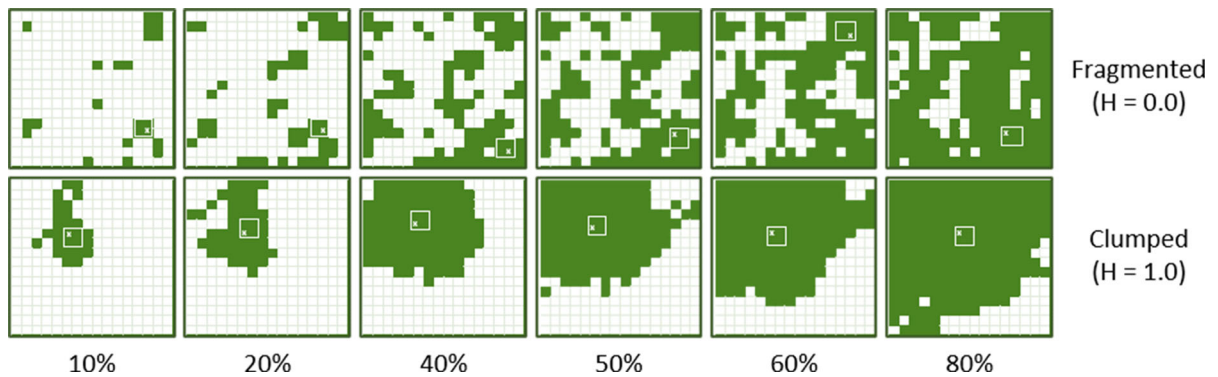
**Fig. 1** Experimental model landscapes. A replicated series of landscape plots (16 m × 16 m) was created in the field by seeding red clover in a fractal-generated pattern to produce landscapes across a range of habitat amounts at two extremes of habitat configuration (clumped vs. fragmented). The 12 landscapes shown here represent one of three replicates, totaling 36 plots, each of which was separated by 16 m on all sides (not shown). The white "x" and square marks the approximate location at which arthropod richness was assayed at a local scale (1-m$^2$ clover cell and within a 4-m$^2$ block of clover cells, respectively) within these particular plots

of edge relative to the area of those patches (i.e., an increased perimeter-to-area ratio, PAR). Patch shape (as indexed by the PAR) is thus an indirect effect of fragmentation; patches of the same size will have proportionately more edge (a higher PAR) in fragmented than in clumped landscapes (With 2016). Thus, we posit that to be consistent with the HAH, local richness should be independent of patch shape (PAR). Note that we do not consider patch isolation (e.g., distance to nearest patch) here because this measure does not vary in a consistent way with habitat amount and fragmentation. For example, patches in a landscape with 20% habitat are farther apart when habitat is clumped than when it is fragmented (i.e., 'gaps' between patches are larger in clumped than in fragmented landscapes; With and King 1999). In sum, we can reject the HAH if any one of the following conditions is true: (1) local species richness is independent of habitat amount, (2) local species richness is dependent on patch size, (3) local species richness is influenced by habitat fragmentation, or (4) local species richness is influenced by patch shape.

## Methods

### Experimental model landscape system (EMLS)

Our EMLS was established on a 4-ha site at the Ecology Research Station of Bowling Green State University, which is located within the predominantly agricultural landscape of Northwest Ohio (USA). Agricultural systems are ideal for experimental landscape studies because they are relatively simple (e.g., monocultures) and are thus easy to construct and maintain (McGarigal and Cushman 2002). We used red clover to create our EMLS because it is a common cover crop in the Midwestern United States, and thus clover seed was readily available, relatively inexpensive, easy to sow, and required no artificial irrigation to establish or maintain. Further, red clover is a perennial, meaning annual seeding of the landscape plots was not necessary, and is known to attract pollinators and other beneficial insects (i.e., predators and parasitoids of crop pests), thereby increasing its value as insect habitat.

Habitat distributions for our EMLS were first computer-generated using a fractal algorithm (midpoint displacement) in which the amount and spatial autocorrelation (H) of habitat were adjusted to create landscape patterns across a range of habitat amounts (10–80%) at two extremes of habitat configuration (fragmented: H = 0.0; clumped: H = 1.0; i.e., fractal

neutral landscape models, With 1997; Fig. 1). These habitat distributions were then re-created in the field by seeding red clover according to the specified landscape pattern that had been randomly assigned to each plot (16 m × 16 m = 256 m$^2$). Our EMLS comprised 36 plots ('landscapes'), representing three replicates of 12 landscape types defined by habitat amount (six levels: 10, 20, 40, 50, 60, and 80%) and degree of fragmentation (two levels: clumped vs. fragmented; see Fig. 1 in With et al. 2002 and With and Pavuk 2011 for an aerial view and detailed schematic, respectively, of the EMLS). This experimental design is thus similar to that proposed by Fahrig (2013) for testing the HAH (see Fig. 11 of Fahrig 2013). In our EMLS, plots were separated from neighboring plots on all sides by at least 16 m of bare ground (i.e., plots were separated by a distance equivalent to the dimensions of an individual plot), and this intervening area was plowed periodically to keep it weed-free. Inside plots, we hand-weeded clover areas and applied herbicide to the bare-ground matrix to maintain these distinct habitat distributions throughout the 3-year duration of the study (1997–1999).

Arthropod surveys

Arthropods are good subjects for experimental landscape studies because they are relatively small (e.g., 4–50 mm) and are thus likely to be influenced by the amount and fragmentation of habitat at scales commensurate to that of our EMLS (e.g., With and Pavuk 2011, 2012). Although the size of our experimental plots (256 m$^2$) matches or exceeds the areal dimensions of many other fragmentation experiments featuring insects (e.g., Collinge 2000; Haynes and Crist 2009), it obviously cannot capture the full range of response scales by all species to all scales of landscape structure. Nevertheless, aggregate measures such as species richness always represent the collective response of species that are responding in individual ways and at different scales to the distribution of habitat or other resources within the landscape. Thus, it doesn't matter for our purposes here whether individual patch selection and foraging dynamics or colonization-extinction dynamics resulting from population and community processes are ultimately responsible for the presence of species within a given patch. Although we might expect that species with

limited vagility will be most affected by the scale of fragmentation in our experimental landscapes, even more-mobile species might avoid smaller patches while foraging or ovipositing because of their perceived lower quality or resource abundance (With et al. 2002; With and Pavuk 2019).

Following establishment of the EMLS in May 1997, the plots were visually surveyed for arthropods six times during the three years of study (1997: 2 surveys; 1998: 3 surveys; 1999: 1 survey). Surveys entailed recording all arthropods found within a 1-min observation period in each clover cell (1 m$^2$). Visual surveys had the advantage of permitting a comprehensive survey of the entire system at multiple time periods. Each survey covered more than 3,960 clover cells (∼ 66 h of sampling), and generally took 2–3 weeks to complete. A total of 23,760 individual cell-surveys were completed over the six time periods. Non-clover cells were not surveyed because the bare-ground matrix was inhospitable to arthropods in this system. It was not possible to identify every arthropod to the species level given that arthropods were not collected during these surveys. We thus assayed the number of taxonomically distinct units ("morphospecies") that we could identify, consistent with how some previous studies have documented arthropod responses to habitat amount and fragmentation (e.g., Bolger et al. 2000). A total of 129 morphospecies were ultimately recorded in this EMLS, averaging 65 morphospecies/survey and 19 morphospecies/plot (With & Pavuk 2011).

From these survey data, we were then able to abstract morphospecies richness ("species richness" or simply "richness" hereafter) at a local site within each plot as well as for the entire plot. For local-scale richness, we initially defined the local sample site as a single, 1-m$^2$ clover cell located in the approximate center of the largest habitat patch within each plot (Fig. 1); species richness at this scale was simply the number of morphospecies in that clover cell ($S_1$). Patches were defined as a group of clover cells that shared an edge or corner; patches were thus separated by at least 1 m of bare ground. We targeted the largest patch because this contained most of the habitat and thus most of the species found in the plot (With 2016). It was not always possible to define an exact center if patches were irregularly shaped (Fig. 1); in that case, we arbitrarily selected a cell from one of the larger areas of the patch located away from a bare-ground

edge to minimize potential edge effects on morphospecies richness (With and Pavuk 2012; Fig. 1). If it was not possible to avoid an edge, we selected a clover cell having the fewest bare-ground edges amongst those available.

We also adopted a second sample-site scale, which we defined as a $2 \times 2$ group of clover cells (a 4-m$^2$ area) centered within the largest patch of each plot. Species richness at this scale was thus the number of unique morphospecies found across all four clover cells ($S_4$), including the contributions from $S_1$ (i.e., the 'central' clover cell was one of the four clover cells assayed at this scale; Fig. 1). Beyond this, it would have been difficult to define a much larger sample-site area without exceeding the largest patch size for some plots (e.g., 10% fragmented landscapes). Finally, we assayed morphospecies richness at the landscape or whole-plot scale ($S_L$) for comparison with the two scales of local richness.

### Statistical analyses

We performed separate analyses for each survey because arthropods were surveyed at different times within and between years, and fragmentation effects on species richness may be transient, occurring in some surveys but not others (With and Pavuk 2011). To evaluate whether habitat amount alone best explains local species richness ($S_1$ or $S_4$), we constructed a candidate set of six generalized linear models on log-transformed data: four single-factor models (habitat amount, fragmentation, patch size, or patch shape), one with the interaction between habitat amount and fragmentation, and a constant (intercept-only) model. A model with the interaction between habitat amount and fragmentation was included because previous research in this system found that fragmentation may matter only at certain habitat amounts (With and Pavuk 2011), in which case, the regression lines of the species-area relationship intersect. For landscape-scale richness ($S_L$), we evaluated the relative likelihood of four models (habitat amount only, fragmentation only, amount x fragmentation, and intercept only) to determine whether habitat amount or fragmentation was more important when richness was assessed at the whole-plot scale.

To identify which model(s) best explained local- or landscape-scale richness, we applied model-selection procedures based on the Akaike information criterion

corrected for small sample sizes (AIC$_c$) using the *MuMIn* package (Bartoń 2020) in R (R Core Team 2019). We considered models with $\Delta$AIC$_c < 2$ to have good support and then evaluated the relative likelihood of these top-ranked models based on their summed Akaike weights ($w_i$). To be consistent with the HAH, the model with habitat amount alone should be the 'best' or highest ranked model. Even then, support for the HAH is weakened if any model other than habitat amount occurs in the top-ranked model set ($\Delta$AIC$_c < 2$), as these other models would also be considered to have good support.

### Results

Local species richness, whether assessed within 1 m$^2$ or 4 m$^2$ sample sites, was largely independent of the amount or configuration of habitat in the landscape, as well as the size or shape of the patch in which those sample sites were located (Table 1; Figs. S1 and S2, Supplementary Materials). The intercept-only model was the best model of local richness at the 1-m$^2$ scale for all but one survey (Survey 1) and was either the top-ranked model (4 surveys) or in the top-ranked model set ($\Delta$AIC$_c < 2$) for all surveys when richness was assayed at the 4-m$^2$ scale (Table 1). For Survey 1, fragmentation alone best explained variation in local richness at the 1-m$^2$ scale; this model was 2.6 $\times$ more likely than the next highest-ranked model consisting of patch shape (as indexed by the perimeter-to-area ratio, PAR). Local species richness during the first survey was greater within clumped landscapes (Fig. 2a) and in patches with lower PARs, which were mostly found in clumped landscapes (Fig. 2b). Patch shape was also the top-ranked model for two survey periods (Surveys 1 and 3) when local richness was assayed at a 4-m$^2$ scale (Table 1). Support for patch shape was weaker at this scale, however, as the intercept-only model was also among the top-ranked models in both surveys (Table 1). Nevertheless, the model with patch shape was 2.1 $\times$ more likely than the intercept-only model for Survey 1, but only about 40% more likely than the intercept-only model for Survey 3 (Table 1).

Importantly, support for the model with habitat amount alone (i.e., the HAH) was weak or non-existent. At either scale, habitat amount was in the top-ranked model set for only two of the six surveys, where

**Table 1** Top-ranked models ($\Delta AIC_c < 2$) depicting the relative influence of patch-scale (Patch size and PAR, the patch perimeter-to-area ratio) and landscape-scale (Habitat amount and Fragmentation) attributes on species richness assayed at different scales within experimental clover landscapes (cf. Fig. 1)

| Scale Survey Top-ranked models[a] | $k$ | $AIC_c$ | $\Delta AIC_c$ | $w_i$ |
|---|---|---|---|---|
| Local richness (1-m$^2$ clover cell) | | | | |
| Survey 1 | | | | |
| Fragmentation | 2 | − 31.5 | 0 | 0.477 |
| PAR | 2 | − 29.6 | 1.91 | 0.184 |
| Survey 2 | | | | |
| Intercept only | 1 | − 3.4 | 0 | 0.43 |
| Survey 3 | | | | |
| Intercept only | 1 | − 61.9 | 0 | 0.419 |
| Survey 4 | | | | |
| Intercept only | 1 | − 45.7 | 0 | 0.391 |
| Patch size | 2 | − 43.8 | 1.90 | 0.152 |
| Survey 5 | | | | |
| Intercept only | 1 | − 3.5 | 0 | 0.358 |
| PAR | 2 | − 2.3 | 1.23 | 0.194 |
| Patch size | 2 | − 2.0 | 1.56 | 0.164 |
| Habitat amount | 2 | − 1.6 | 1.96 | 0.135 |
| Survey 6 | | | | |
| Intercept only | 1 | − 48.8 | 0 | 0.291 |
| Patch size | 2 | − 48.1 | 0.61 | 0.214 |
| PAR | 2 | − 48.0 | 0.76 | 0.199 |
| Habitat amount | 2 | − 47.5 | 1.24 | 0.157 |
| Local richness (4-m$^2$ clover block) | | | | |
| Survey 1 | | | | |
| PAR | 2 | − 33.7 | 0 | 0.401 |
| Intercept only | 1 | − 32.2 | 1.50 | 0.189 |
| Survey 2 | | | | |
| Intercept only | 1 | − 33.0 | 0 | 0.223 |
| Patch size | 2 | − 33.0 | 0.04 | 0.219 |
| PAR | 2 | − 32.9 | 0.11 | 0.211 |
| Habitat amount | 2 | − 32.3 | 0.67 | 0.159 |
| Fragmentation | 2 | − 31.8 | 1.18 | 0.124 |
| Survey 3 | | | | |
| PAR | 2 | − 77.0 | 0 | 0.283 |
| Fragmentation | 2 | − 76.8 | 0.20 | 0.256 |
| Intercept only | 1 | − 76.3 | 0.69 | 0.200 |
| Survey 4 | | | | |
| Intercept only | 1 | − 77.5 | 0 | 0.408 |
| Survey 5 | | | | |
| Intercept only | 1 | − 40.9 | 0 | 0.390 |
| Patch size | 2 | − 39.3 | 1.59 | 0.176 |
| Survey 6 | | | | |

**Table 1** continued

| Scale Survey Top-ranked models[a] | $k$ | $AIC_c$ | $\Delta AIC_c$ | $w_i$ |
|---|---|---|---|---|
| Intercept only | 1 | − 67.5 | 0 | 0.284 |
| Habitat amount | 2 | − 67.0 | 0.50 | 0.222 |
| Patch size | 2 | − 66.5 | 0.96 | 0.176 |
| PAR | 2 | − 66.4 | 1.05 | 0.168 |
| Landscape richness (256-m² plot)[b] | | | | |
| Survey 1 | | | | |
| Habitat amount | 2 | − 63.3 | 0 | 0.746 |
| Habitat amount × fragmentation | 3 | − 61.1 | 2.16 | 0.254 |
| Survey 2 | | | | |
| Habitat amount | 2 | − 80.1 | 0 | 0.768 |
| Habitat amount × fragmentation | 3 | − 77.7 | 2.39 | 0.232 |
| Survey 3 | | | | |
| Habitat amount | 2 | − 61.1 | 0 | 0.708 |
| Habitat amount × fragmentation | 3 | − 59.3 | 1.78 | 0.291 |
| Survey 4 | | | | |
| Habitat amount | 2 | − 72.5 | 0 | 0.753 |
| Habitat amount × fragmentation | 3 | − 70.2 | 2.23 | 0.247 |
| Survey 5 | | | | |
| Habitat amount | 2 | − 86.3 | 0 | 0.708 |
| Habitat amount × fragmentation | 3 | − 84.5 | 1.77 | 0.292 |
| Survey 6 | | | | |
| Habitat amount | 2 | − 75.0 | 0 | 0.759 |
| Habitat amount × fragmentation | 3 | − 72.7 | 2.29 | 0.241 |

[a]Patch size, habitat amount, and species richness were all log-transformed in the generalized linear models being evaluated here

[b]The top-ranked models for landscape richness are presented here as $\Delta AIC_c < 3$ because there was a large discrepancy in the $\Delta AIC_c$ scores between the two top-ranked models and the rest of the models in the candidate set (i.e., these two models received all of the support)

it was outranked by other competing models, including the intercept-only model. In addition, models with patch attributes (patch size and/or shape) generally received more support than those with landscape attributes (habitat amount and fragmentation), which also runs counter to the predictions of the HAH. Still, we reiterate that the intercept-only model was either the best model or in the top-ranked model set for all but one survey, and so could be considered the most parsimonious model for local richness at either scale. Thus, the HAH is not supported when assayed at a local scale.

At the landscape scale, habitat amount alone best explained species richness when assayed at the scale of the entire plot ($S_L$; Table 1; Fig. 3). Habitat amount was the top-ranked model in all surveys and was 2.4–3.3 × more likely than the next-highest ranked model, which included the interactive effects of
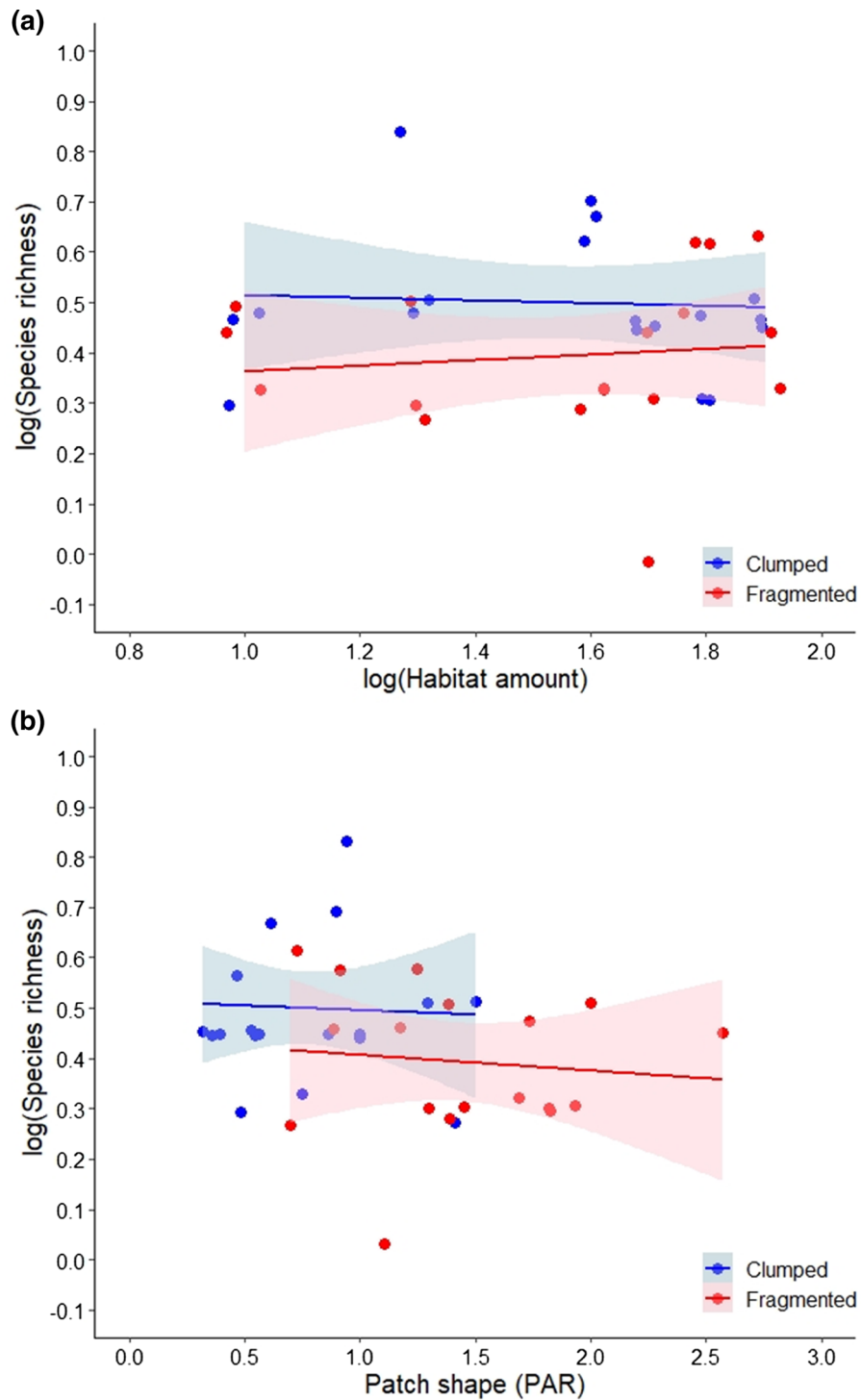
**(a)**



**(b)**



**Fig. 2** Both **a** habitat fragmentation and **b** patch shape (as indexed by the perimeter-to-area ratio, PAR) were significant predictors of local arthropod richness at the 1-m$^2$ scale ($S_1$) within experimental clover landscapes (cf. Fig. 1) at the start of the study (Survey 1)
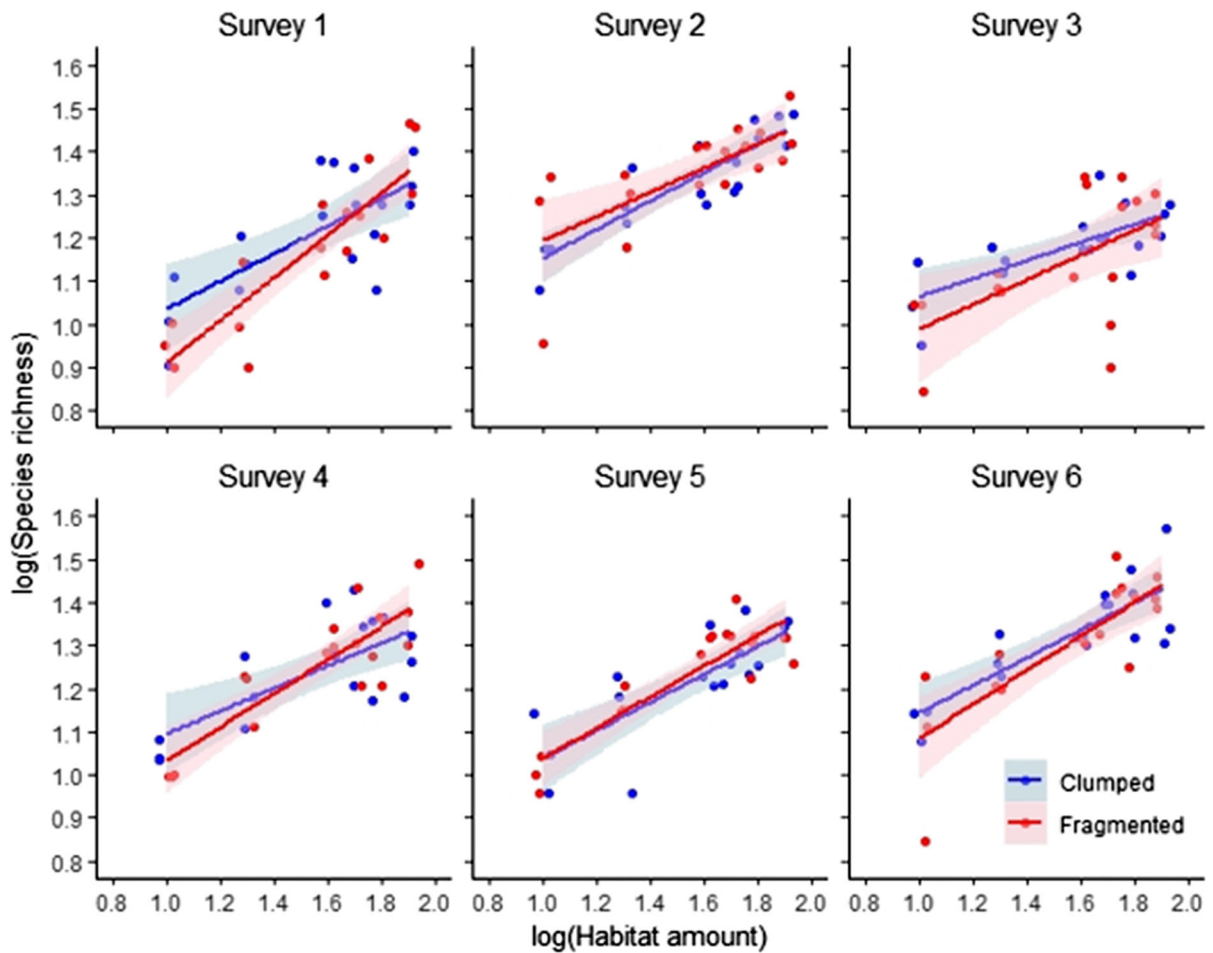
**Fig. 3** Habitat amount was the most important predictor of arthropod richness at the landscape or whole-plot scale ($S_L$) within experimental clover landscapes (cf. Fig. 1), and was 3x more likely than the next highest-ranked model consisting of the interaction between habitat amount and fragmentation (Table 1)

habitat amount and fragmentation (Table 1). Importantly, models with fragmentation alone or just the intercept received no support at this scale.

## Discussion

As originally presented, the HAH predicts that local richness should increase with the amount of habitat in the surrounding landscape, with no additional effects due to habitat configuration or the size of the patch in which the sample site is located (Fahrig 2013). In testing the HAH, we therefore considered four conditions pertaining to the expected effects of habitat amount, patch size, fragmentation, or patch shape on local arthropod richness. We found that local richness (assessed at either the 1-m$^2$ or 4-m$^2$ scales) in our experimental model landscape system was largely independent of the amount of habitat in the surrounding landscape (Condition 1 was rejected), but also tended to be independent of the local patch size (consistent with Condition 2). Although the latter finding is consistent with the HAH, both Conditions 1 and 2 must be met to accept the HAH. In addition, the spatial configuration of habitat in the surrounding landscape or of the patch itself (as assayed by the PAR) was more important than habitat amount for evaluating local richness in some surveys (Conditions 3 and 4 were rejected in these cases). This was especially evident in the first survey, when fragmentation alone best explained local-scale richness at the 1-m$^2$ scale because richness was greater within

clumped than fragmented landscapes. Apart from this first survey, the constant (intercept-only) model was either the best model or in the top-ranked model set ($\Delta AIC_c < 2$) for all other surveys and therefore can be considered the most parsimonious model of local richness. The HAH is thus not supported in this experimental system.

The issue of scale is central to testing the HAH, especially in terms of defining the size of the local landscape in which the amount of habitat is being quantified (see also Saura 2021). Fahrig (2013) suggested that the size of the local landscape could be estimated via multi-scale analysis to identify where the relationship between local richness and habitat amount is greatest (i.e., the "scale of effect"). Although this might seem to bias testing in favor of accepting the HAH, it could also be argued that scaling mismatches would increase the likelihood of rejecting the HAH when it is in fact true. Given the experimental nature of our study, we necessarily defined the size of the local landscape at the outset and created habitat distributions within that fixed spatial extent (256 m²). That this spatial scale is appropriate for investigating habitat-area effects on arthropod richness is evidenced by our finding here of a significant effect of habitat amount on landscape-wide richness (see also With and Pavuk 2011), as well as by a previous study that found a significant relationship between patch size and patch-scale richness (With 2016). Further, our sample sites (a single clover cell or a 2 × 2 block of clover cells) were located within the largest patch of each landscape. Given that the largest patch contains most of the habitat present in the local landscape (With 2016) and our analysis here additionally considered the effect of patch size on local richness, other scales of analysis (e.g., an 8 × 8 block or 16 × 16 block around sample sites) would be unlikely to yield different results, in terms of maximizing the scale of effect on local richness. So, although we did not explicitly adopt a multi-scale analysis to identify the maximum scale of effect, we do not believe that our inability to find a relationship between local richness and either patch size or habitat amount represents a scaling mismatch in this case.

Instead, our finding that local richness was largely independent of habitat amount or patch size likely reflects species-area limits on arthropod diversity, particularly at the finest habitat scale in this system (i.e., a 1-m² clover cell). A previous analysis of a

**Table 2** Local arthropod richness assayed at two scales (1 m² and 4 m²) within 36 experimental landscapes that varied in the amount and configuration of clover habitat (cf. Figure 1)

|  | 1-m² clover cell | 4-m² clover block |
|---|---|---|
| Survey 1 | 3.0 (1.11)[A] | 5.3 (1.76)[A] |
|  | 1–7 species | 3–10 species |
| Survey 2 | 3.1 (1.59)[A] | 6.6 (1.93)[B] |
|  | 1–7 species | 2–10 species |
| Survey 3 | 4.4 (0.91)[B] | 6.6 (1.29)[B] |
|  | 2–6 species | 5–10 species |
| Survey 4 | 5.4 (1.44)[C] | 8.2 (1.38)[C] |
|  | 3–8 species | 5–11 species |
| Survey 5 | 3.1 (1.41)[A] | 6.4 (1.78)[B] |
|  | 1–6 species | 3–10 species |
| Survey 6 | 5.1 (1.37)[B,C] | 7.9 (1.58)[C] |
|  | 3–8 species | 5–12 species |

The mean, standard deviation, and range in the number of species found at each scale is presented for each survey. Within a scale, survey means that were significantly different have different letter superscripts (Tukey test, $p < 0.05$)

single survey from this same experimental system found no effect of patch size or habitat amount on species richness when assayed at the scale of a 1-m² clover cell, which averaged about 3 species/clover cell in that survey (With 2016). In our expanded analysis here, we similarly find that local richness averaged about 3–5 species/clover cell across the six surveys (Table 2), which suggests there may be a limit to the number of species that are found within a given-sized area (e.g., an individual clover cell). There was still a good deal of variability in the number of species encountered within and among individual clover cells, however (range 1–8 species/clover cell, Table 2; see also With and Pavuk 2012, With 2016).

Our finding that this finest scale of local richness was largely independent of habitat amount or patch size is not in itself incompatible with the HAH. The HAH is founded on the assumption that richness within equal-sized quadrats is the same, on average, irrespective of the total size of the area (i.e., the size of the patch or amount of habitat in the local landscape) containing those quadrats (see dashed line in Fig. 3 of Fahrig 2013); it is thus the total richness across quadrats that increases as these are aggregated to form larger sample areas (e.g., a local sample site or study

plot), giving rise to the sample-area effect that underlies the HAH. Our experimental landscape patterns were generated as a collection of equal-sized clover cells, and at the scale of the individual clover cell, we likewise found that species richness was generally the same regardless of patch size or the amount of habitat within the landscape. Given that these arthropod communities appear to form via a process of random assembly, beta diversity between cells is relatively high (clover cells have only about 40% of their species in common; With and Pavuk 2012), and thus larger sample areas should have greater total richness, in line with the expectations of the HAH. However, we still found that neither habitat amount nor patch size had a significant effect on local richness when we expanded our sample area to a 4-m$^2$ block of clover cells. In other words, the HAH was not supported despite a quadrupling of the size of the area sampled (from 1 to 4 m$^2$), which nearly doubled the number of species encountered (an average 1.75-fold increase; Table 2), and thus demonstrated the sort of sample-area effect that purportedly underlies the HAH (Fahrig 2013).

This raises another scaling issue: we may also need to consider the dimensions of the area sampled within patches (the size of the local sample site) in addition to the size of the local landscape when evaluating or testing the HAH. The dimensions of our local sample site were ultimately constrained by the size of the smallest largest patch within these experimental landscapes, which was found within 10% fragmented landscapes. Although other sampling designs could have been adopted (e.g., linear arrays, randomly selected cells), we opted for a block of contiguous cells for consistency. Based on a previous analysis of species-area relationships in this experimental system, we know that patch size has a significant effect on richness when assayed at the patch scale and that total habitat amount has a significant effect on landscape-scale richness (With 2016). Recall, too, that our expanded analysis here also found a significant effect of habitat amount on richness at the landscape-plot scale. In other words, habitat amount *is* important for predicting species richness in this system, but only when richness is assayed at the patch or landscape scale, and not at a local sample-site scale. However, if we must sample an area equivalent to the size of our habitat patches or landscapes to find this sort of relationship between habitat amount and richness, we

can again conclude that the HAH is not supported within this experimental system.

## Conclusions

Using an experimental model landscape system that was specifically designed to tease apart the relative effects of habitat fragmentation from habitat amount on species richness, we tested several predictions of the HAH and conclude that local richness was largely unaffected by the amount of habitat in the local landscape or by the size of the patch in which the sample site was located. In addition, we occasionally found that habitat fragmentation had direct or indirect (via patch shape) effects on local richness, counter to the predictions of the HAH. Still, these fragmentation effects on local richness were transient, occurring only at the beginning of the experiment, such that an intercept-only model proved to be the most parsimonious model of local richness overall.

Our inability to find an effect of habitat amount on local richness should not be viewed as an indictment of the HAH per se. As Fahrig (2015) pointed out, the HAH is "just a hypothesis" that is meant to be tested, and as such, cannot be proved but only supported or falsified. As the number of studies that purport to test the HAH grows, we can anticipate a wide range of findings that reflect the varied responses of different species to habitat distributions within different landscape contexts (see, for example, the meta-analysis by Martin 2018 and the synthesis by Watling et al. 2020). That habitat amount is important for explaining or predicting species richness is a given: the species-area relationship is considered one of the few laws of ecology (Lawton 1999; Lomolino 2000). However, there are scales where the species-area relationship does not apply, such as at finer spatial scales (i.e., the 'small-island effect', Lomolino and Weiser 2001; Triantis et al. 2006; With 2016), just as there are examples where habitat fragmentation clearly matters, at least at some scales or over some range of habitat amounts (e.g., Hanski 2015; Haddad et al. 2017; Herse et al. 2020). The interesting question is thus not whether habitat amount is more important for species richness, but when and at what scales does the spatial configuration of habitat matter?

**Data availability** Will be made available upon reasonable request.

**Code availability** Will be made available upon reasonable request.

**Declarations**

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