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Context-dependent colonization dynamics: Regional reward contagion drives local compression in aquatic beetles

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Abstract

1. Habitat selection by colonizing organisms is an important factor in determining species abundance and community dynamics at multiple spatial scales. Many organisms select habitat patches based on intrinsic patch quality, but patches exist in complex landscapes linked by dispersal and colonization, forming metapopulations and metacommunities. Perceived patch quality can be influenced by neighbouring patches through spatial contagion, wherein perceived quality of one patch can extend beyond its borders and either increase or decrease the colonization of neighbouring patches and localities. These spatially explicit colonization dynamics can result in habitat compression, wherein more colonists occupy a patch or locality than in the absence of spatial context dependence.
2. Previous work on contagion/compression focused primarily on the role of predators in driving colonization patterns. Our goal was to determine whether resource abundance can drive multi-scale colonization dynamics of aquatic beetles through the processes of contagion and compression in naturally colonized experimental pools.
3. We established two levels (high/low quality) of within-patch resource abundances (leaf litter) using an experimental landscape of mesocosms, and assayed colonization by 35 species of aquatic beetles. Patches were arranged in localities (sets of two patches), which consisted of a combination of two patch-level resource levels in a 2×2 factorial design, allowing us to assay colonization at both locality and patch levels.
4. We demonstrate that patterns of species abundance and richness of colonizing aquatic beetles are determined by patch quality and context-dependent processes at multiple spatial scales. Localities that consisted of at least one high-quality patch were colonized at equivalent rates that were higher than localities containing only low-quality patches, displaying regional reward contagion. In localities that consisted of one high- and one low-quality patch, reward contagion produced by higher leaf litter levels resulted in greater abundance of beetles in such localities, which then compressed into the highest quality patches.
5. Our results provide further support for the critical roles of habitat selection and spatial context, particularly the quality of neighbouring habitat patches, in generating patterns of species abundances and community structure across landscapes.

KEYWORDS

colonization, community assembly, context dependence, Dytiscidae, habitat selection, Hydrophilidae, metacommunities, patch quality, reward contagion, spatial compression

1 | INTRODUCTION

Identifying the mechanisms that generate patterns of biodiversity is a central goal in ecology (Chesson, 2000), and differential rates of colonization and extinction are key components of these patterns (MacArthur & Wilson, 1967; Shurin & Allen, 2001; Wellborn, Skelly, & Werner, 1996). Habitat selection, where colonizing organisms select habitat patches (see definitions in Table 1) based on perceived quality (Figure 1), is a critical driver of patterns of species abundance and community structure within habitat patches and across landscapes (Binckley & Resetarits, 2005; Kraus & Vonesh, 2010; Resetarits & Binckley, 2009; Vonesh, Kraus, Rosenberg, & Chase, 2009). Patch quality is simply patch-specific fitness, thus patch colonization rates would be predicted to match variation in patch quality, maximizing expected fitness (Fretwell & Lucas, 1970; Morris, 2003; Pulliam & Danielson, 1991; Resetarits, 1996). Patch quality is well-established as a determinant of patch colonization, occupancy and community structure in many systems (Fretwell & Lucas, 1970; Kiflawi, Blaustein, & Mangel, 2003; Pulliam & Danielson, 1991; Resetarits & Binckley, 2013; Thompson & Pellmyr, 1991).

Many ecological processes and mechanisms generating patterns of species distributions are dependent on spatial scales beyond the level of a single habitat patch, making it necessary to link processes at multiple spatial scales across a landscape (Abteilung, 1997; Gustafson, 1998; Kareiva & Wennergren, 1995; Wiegand, Moloney, Naves, & Knauer, 1999). These processes are affected by habitat arrangement, diversity and availability, which contribute to variation in landscape structure (Andr n, 1994; Gustafson, 1998; Steffan-Dewenter, Nzenberg, Rger, Thies, & Tschartke, 2002). Traditional views of animal decision-making and habitat choice in the context of concepts such as optimal foraging and rationality theory were that each option in a landscape had a value independent of other options (Shafir, Simonson, & Tversky,

1993; Stephens & Krebs, 1986). However, animals are unlikely to independently assign fixed values to each option, as the perceived value is often dependent on other available options or prior information, resulting in context-dependent valuation (Freidin & Kacelnik, 2011; Houston, 1997; Shafir, Waite, & Smith, 2002). Context-dependent choices across multiple scales in landscapes have the potential to affect individual fitness, population dynamics and community interactions (Houston, 1997; Kareiva & Wennergren, 1995).

Thus, although perceived patch quality has traditionally been viewed as an intrinsic quality (Fretwell & Lucas, 1970; Morris, 2003), an organism's ability to accurately assess patch quality, or the actual quality itself, can be affected by spatial context; clustering of habitat patches of different quality alter colonization rates of individual patches or localities (Hughey, McCoy, Vonesh, & Warkentin, 2012; Resetarits, 2005; Resetarits & Binckley, 2009; Resetarits et al., 2005; Resetarits & Silberbush, 2016; Wesner, Billman, & Belk, 2012). This process is termed spatial contagion, which occurs when the perceived quality of a habitat patch or locality is influenced by the quality of neighbouring or constituent patches, respectively (Figure 1c and d) (Resetarits, 2005; Resetarits et al., 2005). In this context, colonization of predator-free patches that are in close proximity to predator patches is greatly reduced compared to colonization of predator-free patches distant from any predator patches (Resetarits & Binckley, 2009). Decreased colonization of predator-free patches associated with predator patches is an example of risk contagion (Figure 1c) (Resetarits, 2005), wherein proximity to predator-occupied patches presents an inherent risk if predators are able to move between patches (Brown, 1999; Lima & Dill, 1990; Pyke, 1984). While much of the work on contagion has focused on the effects of predation risk, contagion also occurs when the presence of high-quality patches increases the colonization of neighbouring patches, generating reward contagion (Figure 1d) (Hughey et al., 2012).

TABLE 1 Definitions of key terms

| Term | Definition |
|-------------|---|
| Patch | A single habitat or patch in habitat selection literature (Fretwell & Lucas, 1970; Leibold et al., 2004; Rosenzweig, 1981). Processes that occur within a patch occur at the patch scale. In our experiment, patch is equivalent to a single pool, which contains one habitat type |
| Locality | A geographical area containing multiple patches; a nested subset of all the patches in a larger region (Leibold et al., 2004). Nearest neighbour distances are smaller among patches within a locality than among patches at the scale of the region. Processes that occur within localities occur at the local scale. In our experiment a locality consists of two patches |
| Region | Equivalent of an experimental array (Leibold et al., 2004). Contains multiple localities with greater spatial separation than among individual patches within a locality. Processes that occur within regions (among localities) occur at the regional scale. One region consists of six localities in our experiment; equivalent to block |
| Landscape | An area that is spatially heterogeneous in at least one factor of interest (Forman, 1995; Turner, Gardner, & O'Neill, 2001). In our experiment, we consider the landscape to be our entire study site, encompassing all regions, the terrestrial matrix and surrounding habitats. Processes and patterns that occur among regions occur at the landscape scale (i.e. block effects) |
| Contagion | The effect of characteristics of nearby patches on the perceived quality of a given focal patch or the entire locality—this can be either negative (risk contagion) or positive (reward contagion) (Resetarits, Binckley, & Chalcraft, 2005) |
| Compression | An increase in the colonization rate of preferred patches/localities resulting from a reduction in the availability of preferred patches/localities through either changes in actual quality or perceived quality (Resetarits et al., 2005; Resetarits & Silberbush, 2016) |

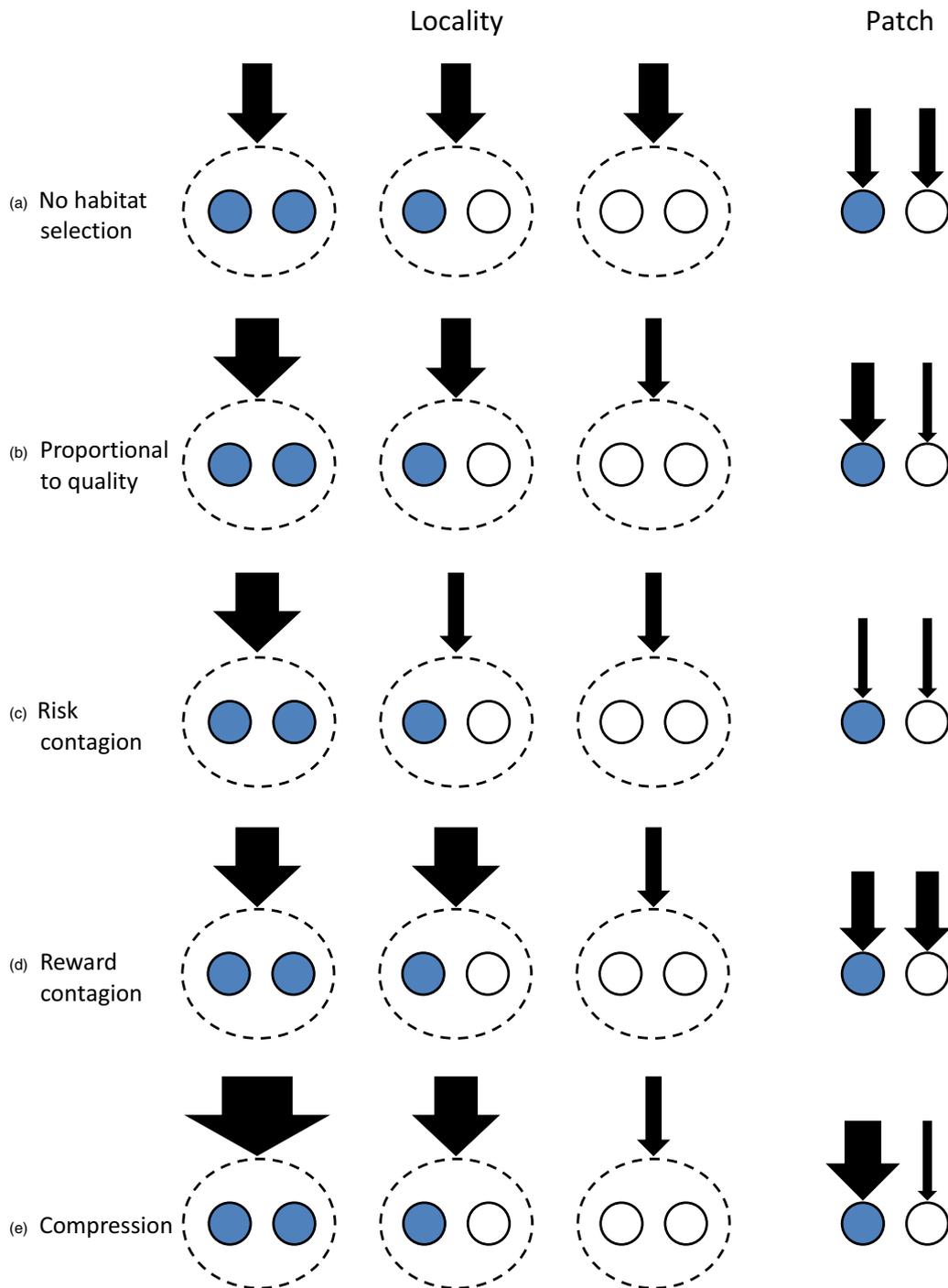


FIGURE 1 Five potential colonization scenarios at the locality and patch levels. Thickness of the arrows corresponds to the number of individuals colonizing a locality/patch (thicker arrows = more individuals). Blue circles represent a high-quality patch, and white circles represent a low-quality patch. The two patches within the dashed circles represent one locality. (a) No habitat selection or context dependence where colonization is equivalent among all sites regardless of quality. (b) Colonization that is proportional to the overall quality of each locality and patch. (c) Risk contagion wherein low-quality patches decrease the colonization of adjacent high-quality patches and/or of the entire locality. (d) Reward contagion wherein high-quality patches increase the colonization of adjacent low-quality patches and/or of the entire locality. (e) Compression, wherein more individuals colonize high-quality localities and patches than would be expected if colonization was in proportion to their overall quality. Patch-level diagrams are not continuations of the locality-level diagrams, rather a representation of the same processes occurring at both scales. Each of these processes can occur independently at the patch or locality levels, or concurrently with one process occurring at the locality level and another at the patch level. We present only heterogeneous patch-level scenarios (within a mixed locality) because homogenous patch types would be expected to have equivalent colonization in all scenarios

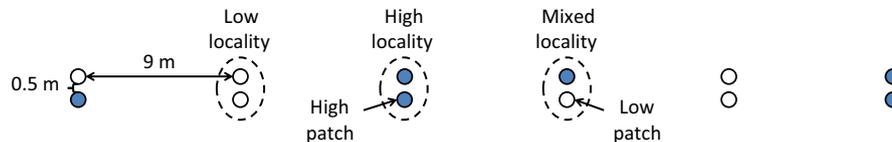


FIGURE 2 Schematic of one region (block). White circles indicate low-quality pools with 0.25-kg leaf litter; blue circles indicate high-quality pools with 1-kg leaf litter. Each individual pool was considered one patch. Two pools separated by 0.5 m constituted a locality. Localities were separated by 9 m. Each block consisted of 12 pools (patches) in six localities (two replicates of each locality-level treatment) arranged in a line. The exact linear order of localities varied by block, but each locality was always adjacent to only one locality of each of the other two locality types. Figure is drawn approximately to scale

As an explicitly spatial process, contagion can affect colonization dynamics at multiple spatial scales, from individual patches to localities or across landscapes, resulting in context-dependent colonization rates (Hughey et al., 2012; Resetarits, 2005; Resetarits & Binckley, 2009; Resetarits & Silberbush, 2016). The movement of colonizers away from low-quality habitats or those in proximity to low-quality habitats can result in increased colonization of high-quality habitats, compressing more individuals into high-quality habitats than they would support if colonization were proportional to quality (Figure 1b and e). The original metacommunity paradigms excluded spatially explicit processes (Leibold et al., 2004); however, processes that increase or decrease the colonization rate of one patch of necessity affect the colonization rate of other patches, linking those communities. Thus, the habitat matching perspective was proposed as an additional, spatially explicit, view of metacommunities (Resetarits & Silberbush, 2016), which links communities across space and is akin to species sorting at the immigration phase (Leibold et al., 2004). Habitat matching would be expected to interact with post-immigration species sorting and mass effects, further influencing metacommunity dynamics. Determining the effects of these complex context-dependent spatial processes is critical for understanding how metacommunities function (Logue, Mouquet, Peter, & Hillebrand, 2011; Resetarits et al., 2005; Wilson, 1992).

A fundamental component of patch quality that contributes to metacommunity dynamics is resource availability, as it affects species abundances, diversity, and species interactions within habitat patches and across metacommunities (Cadotte, Fortner, & Fukami, 2006; Fukami & Morin, 2003; Huston & DeAngelis, 1994; Marcarelli, Baxter, Mineau, & Hall, 2011; Polis, Anderson, & Holt, 1997). In many aquatic systems, inputs of terrestrial leaf litter provide nutrients that drive ecosystem productivity, supporting higher abundances of primary producers and consumers than autochthonous resources can produce alone (Anderson & Sedell, 1979; Minshall, 1967; Stoler & Relyea, 2013). Determining the spatial dynamics of how resource availability affects colonization decisions in individual patches, and how resource levels within one patch interact with those of neighbouring patches, are important to understanding community assembly and patterns of species abundance and richness.

Aquatic beetles are an excellent system in which to study habitat selection and community dynamics, as they readily colonize experimental mesocosms, exhibit selective habitat preferences in the

context of both risk and reward, and form highly diverse assemblages of species that vary widely in their size, morphology, life history and trophic position (Batzer & Palik, 2007; Binckley & Resetarits, 2005; Fairchild, Faulds, & Matta, 2000; Merritt, Cummins, & Berg, 2008; Resetarits, 2001; Resetarits & Pintar, 2016). Dispersing/colonizing aquatic beetles have multiple sensory capabilities they use when locating and assessing habitat patches, although these capabilities are poorly understood (Bilton, 2014). Experimental work shows that these abilities enable beetles to assess habitat availability and quality across a range of scales from landscapes of >100 m to habitat patches separated by less than a metre (Bilton, 2014; Bilton, Freeland, & Okamura, 2001; Pintar & Resetarits, 2017a; Resetarits & Binckley, 2009).

Greater inputs of leaf litter support higher primary and secondary productivity, including periphyton and zooplankton, which are primary food sources for both omnivorous and predaceous aquatic beetles, respectively (Leibold, 1999; Merritt et al., 2008; Williams, 2005). While many aquatic beetle taxa do not directly consume leaf litter, they do exhibit preferences when selecting habitats based on leaf litter quality or other patch characteristics that vary with leaf litter (Pintar & Resetarits, 2017a). We manipulated resource levels (leaf litter) at the patch scale and formed localities from combinations of patches (Figure 2) that varied in quality to examine the effects of resource availability on colonization dynamics of aquatic beetles in a landscape context.

We tested three competing hypotheses at both the locality and patch levels, along with the null hypothesis of no habitat selection (Figure 1a). Our first hypothesis was that no spatial processes influenced colonization, with colonization proportional to overall patch/locality quality (Figure 1b). We also hypothesized that in spatially context-dependent scenarios, reward contagion (Figure 1d) could result if high-quality patches increased the colonization of adjacent lower quality patches or of mixed localities. Lastly, compression (Figure 1e) of high-quality patches/localities could occur if beetles disproportionately colonized the highest quality patches/localities. Each of these four hypotheses can occur independently at either the patch or locality scales, but processes at one scale can certainly influence colonization processes at the other scale. Risk contagion (Figure 1c) was excluded as an alternative as our low-quality patches presented no strong risk to colonizers, such as that of predation.

2 | MATERIALS AND METHODS

We conducted a mesocosm field experiment in a naturally colonized experimental landscape at the University of Mississippi Field Station (UMFS). Each pool (plastic wading pools: 1 m diameter, 0.2 m deep, 110 L, $N = 48$) constituted a single habitat patch, and were arranged in pairs, forming localities (Table 1; Figure 2). Mesocosms were established in fields at UMFS on 20 May 2014 and filled with water from nearby ponds, filtered through 1.13-mm screen. We added dry hardwood leaf litter (primarily *Quercus* spp.) to form a resource base and set the patch-level treatment differences. Patch-level resource abundances were either 1-kg leaf litter (High) or 0.25-kg leaf litter (Low), representing a range of leaf litter abundances commonly seen in small, ephemeral pools. Although we only manipulated leaf litter abundance, it served as a nutrient base in our pools that spurred primary and secondary productivity, including likely supporting larger amounts of periphyton, zooplankton and larval stages of other insects that are all food sources for adult beetles (Culler, Ohba, & Crumrine, 2014; Leibold, 1999; Merritt et al., 2008).

Pools were established in four regions (spatial blocks) separated by >40 m, with two blocks in each of two fields. Each region consisted of 12 pools arranged in a linear arrangement of six localities, with two pools at each locality (Figure 2). Localities were separated by 9 m, and patches within each locality were separated by 0.5 m (edge-to-edge). The locality-level separation of 9 m is the maximum we could achieve given space limitations, but within the scale that habitat selection has been observed by colonization aquatic beetles (Resetarits & Binckley, 2013). Localities consisted of either two Low patches (Low locality), two High patches (High locality), or one Low patch and one High patch (Mixed locality). Spatial arrangement of patches and localities were systematically arranged to vary the position of locality-level treatments within each region such that each locality did not border another locality of the same treatment and each locality type occurred at the end of a region at least twice. Each locality-level treatment (Low, Mixed and High) had eight replicates ($N = 8$). The four patch-level treatments consisted of a combination of resource levels in each patch (Low and High) and locality-level treatment (Low, Mixed and High). These four patch-level treatments were: Low patch in Low locality (Low/Low, $N = 16$), Low patch in Mixed locality (Low/Mixed, $N = 8$), High patch in Mixed locality (High/Mixed, $N = 8$) and High patch in High locality (High/High, $N = 16$).

Pools were covered with window screening (1.3 mm², 1.13 mm opening) that was initially kept above the water surface to prevent colonization while allowing for the development of zooplankton and periphyton communities within the pools. We opened pools to colonizing insects on 10 June by depressing the screens below the water surface, which allowed colonizing insects to enter the pools while maintaining separation from the leaf litter. We collected all colonizing adult insects without replacement weekly until 8 July, after which the experiment was terminated. A diverse assemblage of aquatic beetles has been recorded at UMFS (115 species), 94 of which have been collected from our mesocosms (Pintar & Resetarits, 2017c). We preserved all beetles in ethanol and identified them to species, with the exception of the genus *Paracymus*, which were identified to genus.

2.1 | Data analysis

Abundances of colonizing beetles were summed across the duration of the experiment for each patch, and the two patches within each locality were summed for locality-level analyses. We conducted three analyses on our data: (1) a primary 2×2 factorial ANOVA on patch-level responses, (2) locality-level ANOVAs and (3) ANOVAs on colonization differences between patches in the same locality. In analyses 1 and 2, we conducted separate ANOVAs on each of our response variables: beetle abundance (of all beetles), beetle species richness (rarefied), and abundances of Dytiscidae, Hydrophilidae and species with total abundances greater than 75 individuals. Because one species (*Copelatus glypticus*, Dytiscidae) accounted for 70.6% of all beetles and 82.4% of dytiscids collected, we also analysed the abundances of all beetles and Dytiscidae with this species excluded.

Our primary analysis (1) consisted of a 2×2 ANOVA on block, the effects of Focal patch (Low and High), Adjacent patch (Low and High) and their interaction. For analyses with interactions with $p < .10$, we followed with a Fisher's Protected LSD ($\alpha = 0.05$) on the full design. For Locality-level effects (2), we analysed how colonization varied using ANOVA with locality-level treatment (Low, Mixed and High) and block as factors. In our final analysis (3), we compared colonization differences between pools in the same locality by taking the absolute value of the difference in total beetle colonization and species richness between these two pools. We then analysed the differences in beetle abundance and species richness (not rarefied) with two separate ANOVAs that included locality-level treatment and block as factors. All of our analyses consisted of separate ANOVAs with type III SS with $\alpha = 0.05$, and block was rolled into the error term when $p > .25$. Treatment means in analyses 2 and 3 were compared using Fisher's Protected LSD only when the main effect of Treatment had $p < .10$, using $\alpha = 0.05$ for individual LSD comparisons. All analyses, except rarefied species richness, used square root transformed count data ($\sqrt{X + 0.5}$) and were conducted in R v. 3.3.2 (R Core Team 2016) and SAS v. 9.3 (SAS Institute, Cary, NC, USA).

3 | RESULTS

Our experiment was colonized by 3,181 beetles from 35 species in three families, including four species with abundances >75 (Table 2). Pools were also colonized by limited numbers of hemipterans ($N = 73$, 6 genera), but all were below our analysis threshold. In (1) our 2×2 patch-level analysis, we observed significant or marginal interactions between Focal and Adjacent patches and significant main effect in all analyses except species richness, which only had a significant effect of Focal patch. Analyses of the four abundant species had a significant interaction and main effect of Focal patch, with a marginal effect of Adjacent patch (Table 3). We (2, 3) observed significant effects of treatment in all analyses at both the locality and patch levels (Table 3; Figures 3 and 4). There were significant block effects in all analyses except for those of species richness and *Enochrus ochraceus*. Rarefied species richness was significantly affected by the quality of the Focal

TABLE 2 Species and abundances for colonizing beetles

| Dytiscidae | 2,726 | Hydrophilidae | 419 |
|--------------------------------|-----------|--------------------------------|-----|
| <i>Acilius fraternus</i> | 1 | <i>Berosus aculeatus</i> | 1 |
| <i>Celina angustata</i> | 3 | <i>Berosus striatus</i> | 3 |
| <i>Celina hubbelli</i> | 4 | <i>Cymbiodyta chamberlaini</i> | 8 |
| <i>Copelatus chevrolati</i> | 21 | <i>Cymbiodyta vindicata</i> | 28 |
| <i>Copelatus glyphicus</i> | 2,246 | <i>Enochrus consors</i> | 1 |
| <i>Desmopachria convexa</i> | 3 | <i>Enochrus hamiltoni</i> | 4 |
| <i>Hydaticus bimarginatus</i> | 11 | <i>Enochrus ochraceus</i> | 102 |
| <i>Hydroporus rufilabris</i> | 1 | <i>Enochrus perplexus</i> | 13 |
| <i>Ilybius biguttulus</i> | 1 | <i>Enochrus sayi</i> | 1 |
| <i>Ilybius gagates</i> | 1 | <i>Berosus infuscatus</i> | 54 |
| <i>Laccophilus fasciatus</i> | 347 | <i>Helochares maculicollis</i> | 9 |
| <i>Laccophilus proximus</i> | 54 | <i>Hydrochara soror</i> | 5 |
| <i>Mediorhantus calidus</i> | 13 | <i>Paracymus</i> | 59 |
| <i>Neobidessus pullus</i> | 2 | <i>Hydrochara spangleri</i> | 1 |
| <i>Thermonectus basillaris</i> | 9 | <i>Tropisternus blatchleyi</i> | 6 |
| <i>Uvarus granarius</i> | 5 | <i>Tropisternus collaris</i> | 43 |
| <i>Uvarus lacustris</i> | 4 | <i>Tropisternus lateralis</i> | 81 |
| Halplidae | 36 | | |
| <i>Peltodytes muticus</i> | 36 | | |

patch but not the Adjacent patch (Table 3) and was equally high in High and Mixed localities (Figure 3c and d).

At the locality level, abundances of all beetles, species richness, families and individual species were all largely consistent: colonization was not significantly different between High and Mixed localities, but these two locality types each had significantly greater colonization

than Low localities (Figures 3, 4, and S1). Except for species richness, in all analyses at the patch-level colonization of High patches in Mixed localities (High/Mixed) was significantly greater than all other patch types, including High patches in High localities (High/High) (Figures 3 and 4). Colonization of Low/Mixed patches did not differ significantly from Low/Low patches, but was significantly lower than High/High patches in most analyses (not in *C. glyphicus* or *T. lateralis*; Figure 4b and i). Analyses of all Dytiscidae, Hydrophilidae, and beetle abundance and dytiscid abundance that excluded *C. glyphicus* had the same results and patterns as the analyses that included *C. glyphicus* (Table 1, Figure S1), so we present only figures for abundances of all beetles (Figure 3). In comparisons of colonization differences between adjacent pools, differences in colonization were significantly greater in Mixed localities than in Low or High localities, which did not differ from each other, for both total beetle abundance ($F_{2,21} = 14.12$, $p = .0001$) and species richness ($F_{2,21} = 4.11$, $p = .0311$) (Figure S2).

4 | DISCUSSION

By connecting species interactions across multiple spatial scales, metacommunity ecology has greatly contributed to understanding the mechanisms that generate species distributions and maintain biodiversity (Chesson, 2000; Grainger & Gilbert, 2016; Leibold et al., 2004). In this context, the direct, non-lethal effects of habitat selection can play as strong or stronger role in creating species distributions than direct, lethal effects (Resetarits & Silberbush, 2016; Vonesh et al., 2009). Here we expand the role of habitat selection and our understanding of spatial processes creating linkages across multiple spatial scales, documenting the effects of local habitat compression generated by regional reward contagion (Table 1; Figure 1).

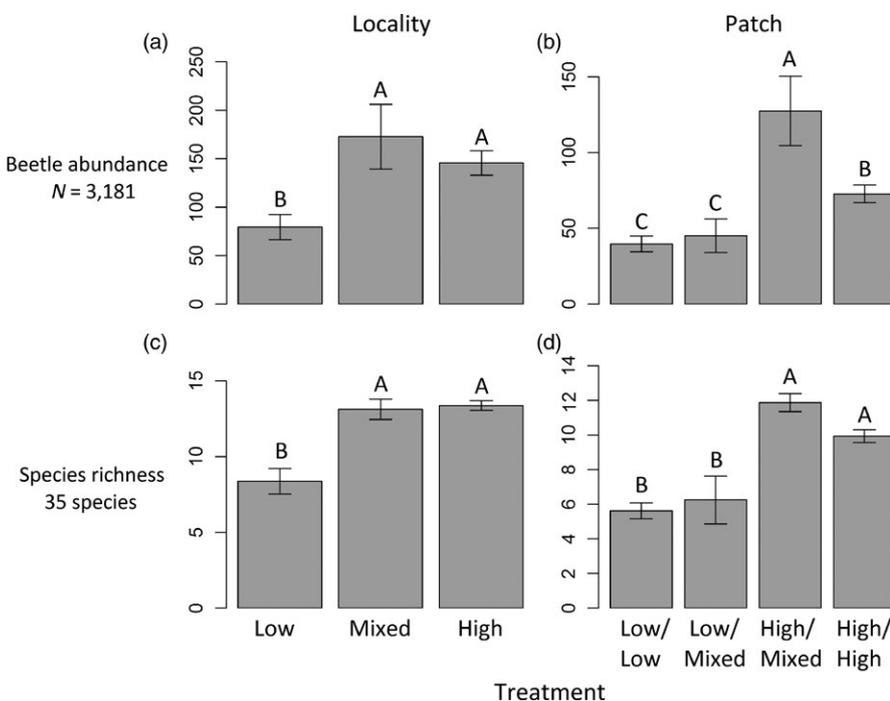


FIGURE 3 Abundances per locality (left) and per patch (right) for all beetles (a, b) and species richness (c, d) (means \pm SE). Patches consisted of either Low (0.25 kg) or High (1 kg) abundances of leaf litter. Locality-level treatments consisted of two Low patches (Low locality), two High patches (High locality), or one Low and one High patch (Mixed locality). Treatments on patch figures consisted of patch-level treatment/locality-level treatment

TABLE 3 ANOVA results for locality and patch-level analyses (Figure 3)

| | Locality | | | | | Patch | | | |
|--|----------|----|-------|--------|-----------|--------|----|--------|--------|
| | SS | df | F | p | | SS | df | F | p |
| All beetles | | | | | | | | | |
| Block | 68.77 | 3 | 6.27 | .0042 | Block | 72.05 | 3 | 10.40 | <.0001 |
| Treatment | 73.14 | 2 | 10.00 | .0012 | Focal | 129.16 | 1 | 55.94 | <.0001 |
| Residuals | 65.82 | 18 | | | Adjacent | 14.11 | 1 | 6.11 | .0177 |
| | | | | | Focal:Adj | 20.81 | 1 | 9.01 | .0045 |
| | | | | | Residuals | 94.67 | 41 | | |
| All beetles without <i>Copelatus glypticus</i> | | | | | | | | | |
| Block | 20.46 | 3 | 5.90 | .0055 | Block | 21.60 | 3 | 9.15 | <.0001 |
| Treatment | 43.66 | 2 | 18.89 | <.0001 | Focal | 74.41 | 1 | 94.61 | <.0001 |
| Residuals | 20.80 | 18 | | | Adjacent | 6.68 | 1 | 8.49 | .0058 |
| | | | | | Focal:Adj | 8.13 | 1 | 10.33 | .0025 |
| | | | | | Residuals | 32.25 | 41 | | |
| Dytiscidae | | | | | | | | | |
| Block | 68.26 | 3 | 6.00 | .0051 | Block | 69.01 | 3 | 9.40 | <.0001 |
| Treatment | 53.95 | 2 | 6.98 | .0057 | Focal | 91.75 | 1 | 37.49 | <.0001 |
| Residuals | 68.27 | 18 | | | Adjacent | 9.50 | 1 | 3.88 | .0555 |
| | | | | | Focal:Adj | 17.01 | 1 | 6.98 | .0116 |
| | | | | | Residuals | 100.33 | 41 | | |
| Dytiscidae without <i>C. glypticus</i> | | | | | | | | | |
| Block | 25.29 | 3 | 6.94 | .0027 | Block | 22.29 | 3 | 10.11 | <.0001 |
| Treatment | 19.90 | 2 | 8.19 | .0030 | Focal | 31.13 | 1 | 42.38 | <.0001 |
| Residuals | 21.86 | 18 | | | Adjacent | 1.27 | 1 | 1.73 | .1963 |
| | | | | | Focal:Adj | 4.63 | 1 | 6.31 | .0161 |
| | | | | | Residuals | 30.12 | 41 | | |
| Hydrophilidae | | | | | | | | | |
| Block | 6.46 | 3 | 7.30 | .0021 | Block | 7.80 | 3 | 9.37 | <.0001 |
| Treatment | 22.74 | 2 | 38.50 | <.0001 | Focal | 40.73 | 1 | 146.74 | <.0001 |
| Residuals | 5.31 | 18 | | | Adjacent | 5.07 | 1 | 18.25 | .0001 |
| | | | | | Focal:Adj | 4.27 | 1 | 15.38 | .0003 |
| | | | | | Residuals | 11.38 | 41 | | |
| Species richness (rarefied) | | | | | | | | | |
| Treatment | 0.88 | 2 | 4.43 | .0248 | Focal | 0.26 | 1 | 11.65 | .0014 |
| Residuals | 2.07 | 21 | | | Adjacent | 0.01 | 1 | 0.57 | .4561 |
| | | | | | Focal:Adj | 0.00 | 1 | 0.03 | .8577 |
| | | | | | Residuals | 0.98 | 44 | | |
| <i>C. glypticus</i> | | | | | | | | | |
| Block | 50.17 | 3 | 5.05 | .0103 | Block | 50.32 | 3 | 6.85 | .0008 |
| Treatment | 35.85 | 2 | 5.41 | .0144 | Focal | 62.59 | 1 | 25.55 | <.0001 |
| Residuals | 59.59 | 18 | | | Adjacent | 7.61 | 1 | 3.11 | .0854 |
| | | | | | Focal:Adj | 12.71 | 1 | 5.19 | .0280 |
| | | | | | Residuals | 100.44 | 41 | | |
| <i>Laccophilus fasciatus</i> | | | | | | | | | |
| Block | 25.56 | 3 | 13.33 | <.0001 | Block | 22.25 | 3 | 14.46 | <.0001 |
| Treatment | 13.52 | 2 | 10.57 | .0009 | Focal | 24.32 | 1 | 47.40 | <.0001 |

(Continues)

TABLE 3 (Continued)

| | Locality | | | | | Patch | | | |
|-------------------------------|----------|----|-------|--------|-----------|-------|----|-------|--------|
| | SS | df | F | p | | SS | df | F | p |
| Residuals | 11.51 | 18 | | | Adjacent | 1.79 | 1 | 3.49 | .0690 |
| | | | | | Focal:Adj | 2.23 | 1 | 4.35 | .0434 |
| | | | | | Residuals | 21.03 | 41 | | |
| <i>Enochrus ochraceus</i> | | | | | | | | | |
| Treatment | 6.88 | 2 | 15.01 | <.0001 | Focal | 7.91 | 1 | 38.23 | <.0001 |
| Residuals | 4.81 | 21 | | | Adjacent | 0.80 | 1 | 3.89 | .0550 |
| | | | | | Focal:Adj | 2.11 | 1 | 10.18 | .0026 |
| | | | | | Residuals | 9.10 | 44 | | |
| <i>Tropisternus lateralis</i> | | | | | | | | | |
| Block | 4.47 | 3 | 4.90 | .0116 | Block | 4.07 | 3 | 7.75 | .0003 |
| Treatment | 3.94 | 2 | 6.48 | .0076 | Focal | 4.55 | 1 | 25.97 | <.0001 |
| Residuals | 5.47 | 18 | | | Adjacent | 0.50 | 1 | 2.87 | .0979 |
| | | | | | Focal:Adj | 1.16 | 1 | 6.60 | .0140 |
| | | | | | Residuals | 7.19 | 41 | | |

At the regional scale, colonizing beetles selected localities containing High patches at equivalent rates, regardless of whether those localities contained one or two High patches (Figure 3). Localities that contained two Low patches were colonized at significantly lower rates than those Mixed and High localities. If beetles selected localities based on the overall, combined quality of the two patches at each locality, we would expect colonization rates of Mixed localities to be intermediate between Low and High localities (Figure 1b). Equal colonization of Mixed and High localities indicates that presence of a single High patch overrides the presence of a Low patch, producing regional reward contagion (Figure 1d). We did not observe risk contagion at any scale, as our Low patches, while lower in quality, did not negatively impact the perceived quality of High patches (Figure 1c). Beetles were conceivably able to move between patches during the 7 days between collections, however, such secondary dispersal would form part of the colonization process, prior to beetles finally settling in a patch.

Higher than expected colonization at the regional scale in Mixed localities did not result in reward contagion at the local scale in Low/Mixed patches. Under local reward contagion, the proximity of Low/Mixed patches to High/Mixed patches should result in greater colonization of Low/Mixed patches than Low/Low patches (Figure 1d). Low/Mixed patches were colonized at rates equivalent to Low/Low patches, and significantly lower than High/High patches in all but two analyses (Figures 3 and 4). At the local scale within Mixed localities, beetles preferentially colonized High patches over Low patches. The combined effects of regional reward contagion and preferential colonization of High patches resulted in High/Mixed patches receiving significantly more colonizing beetles than any other patch type. Beetles were compressed into High/Mixed patches resulting in significantly greater colonization than would be expected if the quality of both patches were equivalent, hence local compression (Figure 1e).

At the regional scale, beetles perceived High and Mixed localities as equivalent. This misperception at the regional scale of the true overall quality of Mixed localities resulted in the compression of beetles into High/Mixed patches at the local scale. This compression could result in density-dependent intra- or interspecific competition or density-dependent movements of individuals among patches or localities. However, lack of local reward contagion in Low/Mixed patches indicates little or no density-dependent secondary dispersal (sensu the Ideal Free Distribution; Fretwell & Lucas, 1970). If density dependence was a factor, we would have expected spillover from the patches with the most colonizers (High/Mixed) into the adjacent patches (Low/Mixed) (Shmida & Wilson, 1985). The equivalence of Low patches (and lack of local reward contagion) may be due to a limit on the number of individuals Low patches could support. Compression in High/Mixed patches suggests that colonization of High patches was not limited by patch quality, but rather by the number of beetles dispersing across the landscape, although our study occurred during peak annual dispersal of aquatic beetles at UMFS.

The responses of four abundant species, as well as the overall abundances of species in the families Dytiscidae and Hydrophilidae, were nearly identical with respect to variation in resource abundance at both the local and regional scales (Figures 3, 4, and S1). The observed patterns of regional reward contagion and local compression stress the importance of habitat selection and spatial context dependence in determining local and regional abundances of these species. Overall, we observed regional contagion with equally high numbers of species in High and Mixed localities, significantly more than were in Low localities (Figure 3c). However, we did not observe local compression for species richness, as the numbers of species in High/Mixed and High/High patches were statistically equivalent (Figure 3d). Nevertheless, the spatially explicit process of contagion produced locally and regionally different patterns of species richness,

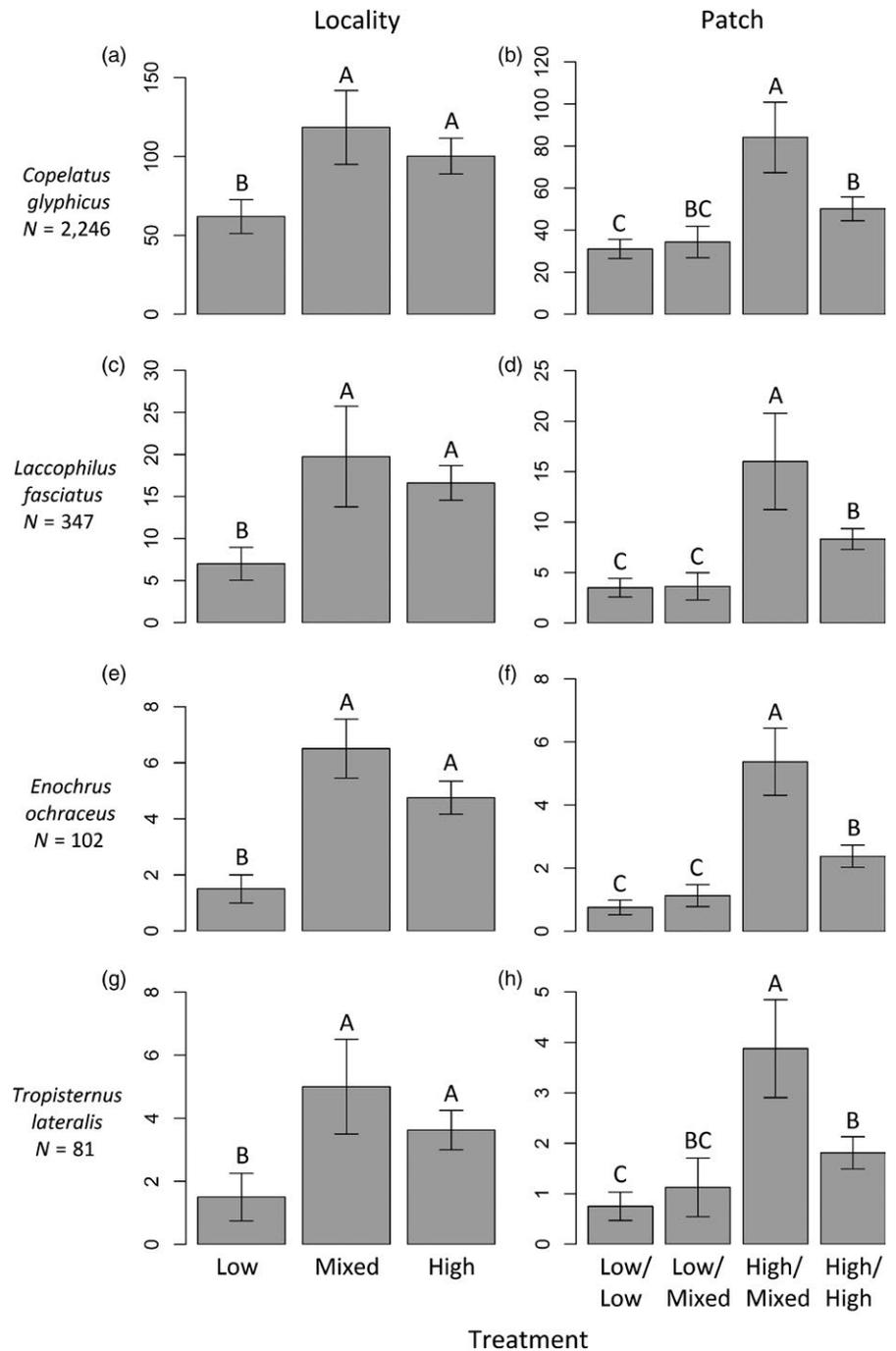


FIGURE 4 Abundances per locality (left) and per patch (right) for species with abundances >75: *Copelatus glypticus* (a, b), *Laccophilus fasciatus* (c, d), *Enochrus ochraceus* (e, f) and *Tropisternus lateralis* (g, h) (means \pm SE). Patches consisted of either Low (0.25 kg) or High (1 kg) abundances of leaf litter. Locality-level treatments consisted of two Low patches (Low locality), two High patches (High locality), or one Low and one High patch (Mixed locality). Treatments on patch figures consisted of patch-level treatment/locality-level treatment

which itself can affect metacommunity dynamics through variation in species interactions (Leibold et al., 2004; Resetarits et al., 2005; Wilson, 1992).

Aquatic beetles occupy diverse trophic positions, have diverse morphologies and life histories, and often have unique colonization responses to a variety of factors (Culler et al., 2014; Merritt et al., 2008; Pintar & Resetarits, 2017a; Resetarits & Pintar, 2016). Thus, it is noteworthy that we observed consistent responses across our four abundant species, which included both dytiscids, which have predaceous adults and larvae, and hydrophilids, which have omnivorous adults and predaceous larvae. Leaf litter acts as a nutrient base that spurs primary and secondary productivity, including organisms that beetles feed on,

such as zooplankton, periphyton and other insect larvae (Culler et al., 2014; Leibold, 1999; Merritt et al., 2008). We do not have abundance data for any other taxa, so we can only speculate as to the proximal cues used to assess patch quality in this study, and we did not notice any accumulation of larvae over the course of the experiment.

Colonization decisions of aquatic beetles are particularly critical as they select habitats for both themselves and their offspring (Bilton, 2014; Layton & Voshell, 1991). Poor colonization decisions have fitness consequences for the adults as once initial colonization is complete secondary dispersal rarely occurs (Zera & Denno, 1997). This is due to the oogenesis-flight syndrome in which individuals disperse early in their adult life, soon after pupation, before autolysing flight

muscles to provide energy for reproduction (Bilton, 1994, 2014; Hocking, 1952; Jackson, 1952; Johnson, 1969). The greater colonization High/Mixed patches means that both adults and their offspring in these systems could experience greater competition for resources than in High/High patches. This is further compounded among larvae by their propensity for cannibalism, although evidence for competition for food among adults is limited (Culler et al., 2014; Juliano & Lawton, 1990). Thus, for some species, the habitat matching perspective of metacommunity dynamics may be much more important than other perspectives, such as mass effects and species sorting, as movement from patches after colonization is unlikely and sorting at the immigration stage may preempt post-colonization sorting (Leibold et al., 2004; Resetarits & Silberbush, 2016). The diverse assemblages formed by aquatic beetles present a great opportunity for further investigation into factors generating patterns of species diversity across landscapes.

Local contagion can result from both risk and reward in a diverse set of organisms, including treefrogs, beetles, dragonflies, frogflies and mosquitoes (Hughes et al., 2012; Resetarits & Binkley, 2009, 2014; Resetarits & Silberbush, 2016; Wesner et al., 2012), and regional compression resulting from local risk contagion has recently been documented in mosquitoes (Resetarits & Silberbush, 2016). We expect contagion and compression occur at multiple spatial scales and in the context of both risk and reward, across many taxa. While our experimental landscape may have produced results more extreme than those in natural systems, experimental analyses such as these are necessary to identify processes that are difficult to detect in more variable natural systems. However, our experiment was not unrealistic, as natural pools in our system can be quite small, are commonly separated by very small distances and have large variation in the range of litter or other nutrients.

Our experiment has shown that regional reward contagion can lead to local compression, thereby expanding the realm of known scales on which these two processes operate. We would expect contagion and compression to be common across landscapes, but additional work on a variety of species at different spatial scales is necessary to determine the frequency and intensity of such effects, as well as how they may interact with other processes structuring communities.

Concepts such as the ideal free distribution and optimal foraging theory, and the extensive body of work conducted around them, have provided a considerable foundation upon which the link between habitat selection and metacommunity ecology has been constructed (Charnov, 1976; Fretwell & Lucas, 1970; Leibold et al., 2004; Lima & Dill, 1990; Morris, 2003; Pulliam & Danielson, 1991; Resetarits et al., 2005; Werner & Hall, 1974). Effects on local and regional patterns of species distribution and abundance are generated by a variety of factors and processes that interact to produce patch-specific colonization rates (Abrams, Cressman, & Krivan, 2007). While not ignored, spatial context has been an underserved component of many of the theories that unpin these broader concepts. Spatially explicit, context-dependent processes such as contagion and compression inherently affect metacommunity dynamics by shifting patterns of colonization among patches and localities. Thus, habitat selection, which is based on the ability of organisms to accurately assess patch quality at the colonization stage, and other spatially explicit processes, are critical

drivers of patterns of individual species abundances and community composition. Context-dependent colonization may break down the relationship between perceived and actual patch quality, adding further complexity to the mechanisms driving variation in patch-specific colonization rates and landscape scale patterns. Our understanding of the role of spatial dynamics and context dependence, as well the actual importance of such processes will likely only increase, particularly as habitats and landscapes altered by anthropogenic activities reveal preference/performance mismatches. Full integration of the myriad theories that form the science of ecology is incomplete and a lofty goal, but even a piece by piece melding of individual components provides a more comprehensive view of how the world works.

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AUTHORS' CONTRIBUTIONS

M.R.P. designed and conducted the experiment, identified the beetles, analysed the data and wrote the paper. W.J.R. contributed to the analysis, writing and interpretation of the data.

DATA ACCESSIBILITY

Data available from Dryad Digital Repository <https://doi.org/10.5061/dryad.55dh5> (Pintar & Resetarits, 2017b).

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SUPPORTING INFORMATION

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