RESEARCH ARTICLE

Large-scale experimental landscapes reveal distinctive effects of patch shape and connectivity on arthropod communities

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Abstract The size, shape, and isolation of habitat patches can affect organism behavior and population dynamics, but little is known about the relative role of shape and connectivity in affecting ecological communities at large spatial scales. Using six sampling sessions from July 2001 until August 2002, we collected 33,685 arthropods throughout seven 12-ha experimental landscapes consisting of clear-cut patches surrounded by a matrix of mature pine forest. Patches were explicitly designed to manipulate connectivity (via habitat corridors) independently of area and edge effects. We found that patch shape, rather than connectivity, affected ground-dwelling arthropod richness and beta diversity (i.e. turnover of genera among patches). Arthropod communities contained fewer genera and exhibited less turnover in high-edge connected and high-edge unconnected patches relative to low-edge unconnected patches of similar area. Connectivity, rather than patch shape, affected the evenness of ground-dwelling arthropod communities; regardless of patch shape, high-edge connected patches had lower evenness than low- or high-edge unconnected patches. Among the most abundant arthropod orders, increased richness in low-edge unconnected patches was largely due to increased richness of Coleoptera, whereas Hymenoptera played an important role in the lower evenness in connected patches and patterns of turnover. These findings suggest that anthropogenic habitat alteration can have distinct effects on ground-dwelling arthropod communities that arise due to changes in shape and connectivity. Moreover, this work suggests that corridors, which are common conservation tools that change both patch shape and connectivity, can have multiple effects on arthropod communities via different mechanisms, and each effect may alter components of community structure.

Keywords Arthropods · Coleoptera · Corridor · Diversity · Evenness · Fragmentation · Hymenoptera · Orthoptera · Patch shape

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Introduction

The size, shape, and degree of isolation (i.e. connectivity) of habitat patches can have important effects on the local abundance of organisms (Dunning et al. 1992; Taylor et al. 1993; Collinge and Palmer 2002), interactions among species (Fagan et al. 1999), and the structure and composition of ecological communities (Turner 1989; Forman 1995). Understanding the role of patch shape and connectivity on ecological communities is important because anthropogenic habitat destruction and alteration change the size, shape and connectivity of patches in the landscape (Forman 1995; Dobson et al. 1997; Vitousek et al. 1997; Fischer and Lindenmayer 2007). Although habitat fragmentation has documented effects on communities (Harrison and Bruna 1999; Fahrig 2003; Fischer and Lindenmayer 2007), studies that independently manipulate shape and connectivity are rarely conducted at large scales (Harrison and Bruna 1999; Debinski and Holt 2000; Steffan-Dewenter and Tscharntke 2002; Öckinger and Smith 2008; Haddad et al. 2011). The lack of large-scale studies is particularly noteworthy because patch size, patch shape, and connectivity are of explicit concern for conservation strategies based on corridors (Haddad et al. 2003; Hilty et al. 2006), and for the design of conservation reserves (Janzen 1983).

In this paper, we present a landscape-level experiment that independently manipulates patch shape and connectivity of patches of similar size. Specifically, we examine the richness, evenness (i.e. relative equity in species abundance in a community), and turnover of genera in space (i.e. beta diversity) of ground-dwelling arthropod communities. Although connectivity may be important in arthropod communities (Gilbert et al. 1998; Gonzalez et al. 1998), many studies are conducted at relatively small spatial scales (reviewed in Steffan-Dewenter and Tscharntke 2002). Insight from a few large-scale studies suggests that the effect of connectivity depends on the size of the patches being connected, temporal variation in abiotic conditions, and the species of interest (Collinge 2000; Öckinger and Smith 2008). These differing outcomes of corridor experiments, coupled with the documented effects of shape on arthropod communities (Grez and Prado 2000; Collinge and Palmer 2002) and the significant effects of fragmentation on arthropod communities (e.g., Davies and Margules 1998; Didham et al. 1998; Golden and Crist 2000; Davies et al.

2001; Hunter 2002; Steffan-Dewenter and Tscharntke 2002; Ewers and Didham 2008), highlight the importance of dissecting the potential interactions between patch shape and connectivity in affecting arthropod communities.

Shape and connectivity may each have different effects on richness, evenness, and beta diversity. Patch shape determines the relative relationship between patch perimeter and area, and is thus expected to mediate the degree to which edge effects alter within-patch processes (Fagan et al. 1999; Ries et al. 2004; Fletcher et al. 2007). Fletcher et al. (2007) note that edges act via two mechanisms: changing abiotic and biotic flows, and by providing organisms with access to different resources. Abiotic flows consist of changes in temperature, moisture, and other environmental characteristics associated with edges (Chen et al. 1999). Biotic flows include the movement or dispersal of species across habitat edges, potentially giving rise to "spillover" across habitat boundaries (e.g., Brudvig et al. 2009). Biotic flows may also occur due to foraging movement. For instance, species richness may also be increased in high-edge patches if organisms are able to gain access to important resources by exploiting edge habitats (Dunning et al. 1992; Fletcher et al. 2007). Patch shape can affect immigration because the amount of patch edge may determine the effective area available to intercept organisms moving through the matrix, i.e. drift-fence effects (Forman 1995; Haddad and Baum 1999; Fried et al. 2005). Patch shape may similarly affect emigration by providing a greater amount of area for patch-dwelling organisms to enter matrix habitat (Grez and Prado 2000; Collinge and Palmer 2002).

Based on predictions from island biogeography (MacArthur and Wilson 1967), increased connectivity is expected to increase richness by increasing rates of colonization from suitable patches. Evenness may also be increased in more connected patches because increased input of species should reduce the likelihood that a few species will become numerically dominant. However, these two predictions assume that the classical competition-colonization tradeoff is not in operation (Amarasekare et al. 2004). In systems where increased connectivity allows superior competitors to colonize patches where inferior competitors would otherwise persist, richness and evenness would be expected to exhibit a negative relationship with connectivity (although this relationship could be

unimodal or nonlinear if there are thresholds in connectivity required for the persistence of inferior competitors). Because well-connected communities are expected to exchange greater numbers of migrants, they should also be more similar in their composition. As such, increased connectivity should reduce species turnover (i.e. beta diversity).

We used large-scale experimental landscapes to examine whether ground-dwelling arthropod communities are affected by patch shape, patch connectivity, or both. The seven experimental landscapes (Fig. 1) used three patch types of similar area that differed in shape and connectivity: (1) high-edge connected patches; (2) high-edge unconnected "winged" patches with similar amounts of edge as connected patches but no connections; and (3) low-edge unconnected "rectangular" patches. Comparison among these different patch types provides insight into the relative importance of shape and connectivity. When patch shape is most important, low-edge unconnected rectangular patches will differ from high-edge unconnected patches, and we expect greater richness and increased turnover in high-edge patches because of immigration into these patches from forest- and edge-dwelling taxa. When connectivity is most important, connected patches will differ from high-edge unconnected winged patches (Damschen et al. 2008) but the nature of this difference depends upon whether a competition-colonization tradeoff is important. If the tradeoff is operating, we predict that connected patches would have lower richness and evenness. If a competition-colonization tradeoff is not in operation, we predict that connected patches would have greater richness and greater evenness. In both cases, we expect connectivity to reduce species turnover. When both connectivity and shape are important, high-edge connected, high-edge winged, and low-edge rectangular patch types will all differ from each other.

Methods

Experimental landscapes

We conducted the study in seven replicated experimental blocks within the Savannah River Site, a National Environmental Research Park near Aiken, South Carolina (Fig. 1). Each block consisted of five patches within a mature matrix of loblolly (*Pinus taeda*) and longleaf (*P. palustris*) pine forest. Patches were clear-cut and burned in winter 1999–2000, and consisted of open habitat dominated by herbaceous plant species characteristic of early successional habitats (Damschen et al. 2006). Three types of patches (high-edge connected patches, high-edge unconnected winged patches, and low-edge unconnected rectangular patches) were created within each experimental block (Fig. 1). Each block contained two high-edge connected patches and either two low-edge unconnected rectangular patches and one high-edge unconnected winged patch or one low-edge unconnected rectangular patch and two high-edge unconnected winged patches. The central portion of all patch types was 100 m × 100 m. High-edge winged patches also had linear extensions 25 m wide and 75 m long (Fig. 1). High-edge connected patches were
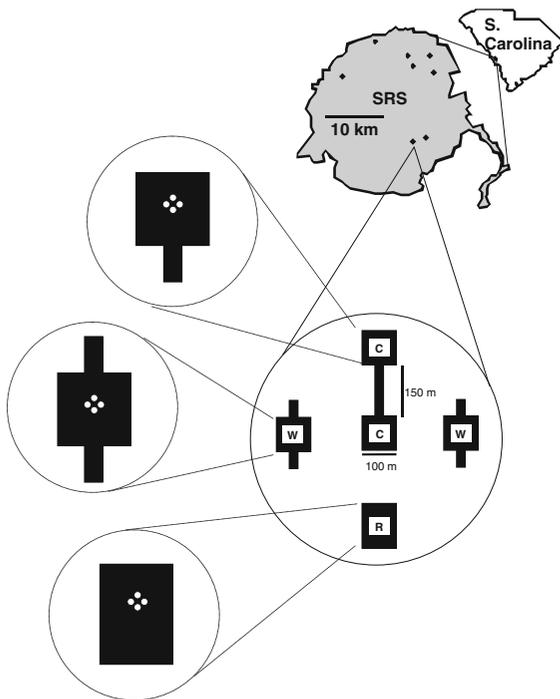
Fig. 1 Layout of the experimental design at the Savannah River Site, South Carolina. Seven experimental landscapes (*blocks*) were created within mature pine forest. Each *block* consisted of high-edge connected (*C*) and unconnected patches that were either high-edge unconnected winged (*W*) patches or low-edge unconnected rectangular (*R*) patches. Within each patch, there were four pitfall traps placed equally along an 8 × 8-m² (see text for details). The *block* depicted is aligned for clarity; orientation of actual blocks with regard to compass direction was random

connected by a corridor 25 m wide and 150 m long. Low-edge rectangular patches were 100 m wide and 138 m long. High-edged winged and low-edge rectangular patches had the same area (1.38 ha), whereas connected patches had slightly less area than unconnected patches because they shared a corridor (central patch area plus half of the corridor = 1.19 ha). Although all patch types were of similar size, the amount of edge and core habitat was different among patch types because corridors and wings added long, linear elements to connected and winged patches, respectively. Thus the area/perimeter ratio differed among patches: high-edge connected (22.62), high-edge winged (19.64), and low-edge rectangular (28.95).

Arthropod sampling

Arthropods were sampled using pitfall traps, an effective method for examining the effects of habitat fragmentation on terrestrial arthropods (e.g., Davies and Margules 1998; Suarez et al. 1998; Davies et al. 2001) that has been successfully used to characterize arthropod communities in the study area (Van Pelt and Gentry 1985). Pitfalls were constructed by placing 475 ml plastic drinking cups (10 cm wide at mouth, 5 cm at base, 15 cm deep) at a depth such that the top of the cup was flush with the surface of the ground. Inside each cup, we placed plastic sample cups with approximately 40 ml of a 50% propylene glycol solution. Funnels (10 cm wide at mouth) were set flush with the ground to direct organisms into the sample cup. Specimens were identified to genus using relevant taxonomic keys (Van Pelt and Gentry 1985; Borror et al. 1989; Leonard and Bell 1999). Generic identifications were confirmed by comparisons with identified museum specimens in the Iowa State University Insect Collection, Department of Entomology, Ames, Iowa, where voucher specimens were also deposited. Use of genus was unlikely to affect the generality of our inferences because generic richness is often correlated with species-level richness in arthropod communities (Andersen 1995b; Cardoso et al. 2003). For example, the average number of ant genera was strongly correlated with the average number of ant species captured at 20 plots over 3 years ($r^2 = 0.89$, $n = 20$, $F_{1,18} = 138.91$,

$P < 0.001$; Izhaki, Levey, and Silva, unpublished data) for a pine forest ecosystem in Florida (Izhaki et al. 2003).

Each patch contained four pitfalls located near the patch center 37.5 m from the nearest edge of the patch along an 8×8-m^2 (Fig. 1). This design ensured equal spacing among pitfalls and also maintained the distance of pitfalls to the nearest patch edge for most of the pitfalls. To maintain the 37.5 m spacing from the edge for the majority of the pitfalls in the rectangular patches and also keep distances equal among pitfalls within each patch, the pitfall trap nearest the center of the rectangular patch was 50 m from the edge (as a consequence of the shape of the patch; Fig. 1). Six sampling sessions were conducted at all 160 pitfalls: three sessions in 2001 (July 31–August 3, September 3–9, and October 8–14) and in 2002 (June 7–11, July 4–8, and August 2–6), for a total of 960 pitfall samples. We combined data from all of these sampling dates because we were interested in overall differences among arthropod communities rather than seasonal shifts in arthropod abundance. The abundance of arthropods captured in pitfalls is a function of arthropod density and the likelihood that an arthropod will encounter the pitfall, which depends on arthropod activity. Throughout this paper, we use the term abundance to be synonymous with activity density.

As part of our experimental design, we created open habitats that strongly contrasted with the adjacent matrix habitat of pine forest. To determine the degree to which taxa in our experimental patches were open-habitat taxa (as opposed to matrix-inhabiting or generalist taxa), we conducted ancillary sampling using two pitfall traps 15 m from the edge of each open patch during the first sessions conducted in 2002 (Orrock, unpublished data). Taxa that were more abundant in the center of our experimental patches compared to the edge (as judged by Wilcoxon signed-rank tests) were classified as open-habitat taxa (Appendix in Supplementary material), whereas taxa that were captured more frequently near the edge of each open patch were classified as generalist taxa that are likely to reflect movement of individuals from the nearby matrix habitat; open-habitat taxa represented over 80% of the individuals captured (see "Results" section).

Statistical analyses

We examined three metrics of arthropod communities: richness, evenness, and beta diversity. Richness was measured as the number of arthropod genera. We used rarefaction (Gotelli and Colwell 2001) to estimate the richness of arthropod communities among connected, rectangular and winged patches. Rarefaction was used because the number of arthropods collected among pitfalls differed, and the number of samples was not equal among patch types due to different numbers of each patch type (14 connected patches, 11 winged patches, 10 rectangular patches; Fig. 1). We used sample-based rarefaction to estimate the number of genera present under similar sampling effort for all patches, and we present our findings as a function of the number of individuals in each sample. This approach preserved the heterogeneity in abundance inherent in the sampling data (Gotelli and Colwell 2001). To assess evenness, we used the probability of interspecific encounter (PIE; Hurlbert 1971). This measure of evenness is preferable because it is largely independent of the number of organisms in the sample (Hurlbert 1971). Moreover, PIE is readily interpretable as the probability that two individuals drawn from an assemblage in our study are from a different taxonomic group (genus in our study), such that the value of PIE varies from 0 to 1, with larger values indicating greater evenness (Hurlbert 1971). Because analyses of rarefaction and evenness were conducted separately for each patch type, we did not examine block effects (i.e. all experimental blocks contributed to each estimate of richness and evenness for each patch type).

We define beta diversity as the turnover of genera between sampling sites. We quantified beta diversity by calculating arthropod community similarity among sites using Jaccard's index with presence-absence data, and subsequently comparing multivariate dispersion (analogous to species turnover) among sites (Anderson et al. 2006). When calculated this way, the resulting distance is interpretable as the percentage of unshared species among sampling sites (Clarke and Gorley 2006). We accommodate the multiple sampling units within a block (e.g. all blocks contained two high-edge connected patches and two replicates of one of the other patch types) by calculating the distance to centroid based upon patch type prior to these multivariate analyses (Clarke and Gorley 2006).

To evaluate whether there were compositional shifts in arthropod communities in addition to changes in beta diversity, we used permutation-based multivariate analysis of variance (PERMANOVA), with Bray–Curtis similarity on fourth-root transformed abundance data (Anderson et al. 2008) to evaluate block effects, patch type effects, and their interaction.

To complement these community-level analyses, we also conducted univariate analyses to evaluate genus-level patterns of patch occupancy and mean number of arthropods captured. To maintain reasonable sample sizes, we restricted these analyses to samples with >10 individuals. Because captures of ants can be highly heterogeneous, we also evaluated the outcome of univariate tests using log-transformed data for these taxa; we present untransformed results because these did not differ from transformed results. Due to the large number of tests conducted and associated increase in type I error rates, these analyses are used in a supporting fashion rather than as explicit hypothesis tests for each genus. To provide as full a picture of the patterns as possible, we evaluated the possibility of significant effects of experimental block as well as block × patch type interactions for univariate analyses. Because *Dorymyrmex* is an aggressive ant genus (Andersen 1995a), and was the most common member of the arthropod community (see "Results" section), we used linear regression to evaluate how the abundance of *Dorymyrmex* affected variation in the patch-level evenness of arthropod communities as quantified using William's metric of evenness (Smith and Wilson 1996).

Rarefaction and calculation of evenness were conducted using EcoSim (Gotelli and Entsminger 2000). Calculation of beta diversity, comparison of multivariate dispersion and community composition were conducted using PERMANOVA + for PRIMER (Clarke and Gorley 2006; Anderson et al. 2008). Significance values for statistical tests of beta diversity were obtained via permutation using 9,999 runs. Univariate analyses were conducted using SAS v 8.1.

Results

We captured 33,685 arthropods representing seven orders, 24 families, and 58 genera (Appendix in Supplementary material). Seven of the 10 most abundant genera were ants (percentage of total

captures in parentheses): *Dorymyrmex* spp. (38.4), *Solenopsis* spp. (27.8), *Pheidole* spp. (10.1), *Pogonomyrmex badius* (we use the full name because no other species are found at our study area; 3.8), *Formica* spp. (3.0), *Crematogaster* spp. (1.2), and *Myrmica* spp. (1.1). Along with tiger beetles (*Cicindela* spp.), grasshoppers (*Hippiscus* spp.), and crickets (*Gryllus* spp.), these genera accounted for over 90% of the individuals captured. Pooled across sessions and genera, there were no differences in the average number of arthropods captured in each patch type ($F_{2,26} = 0.89$, $P = 0.42$). Most individuals belonged to genera that had greater abundance in the open habitats created by our experimental manipulation: 27,253 of the 33,685 individuals captured (i.e., over 80%) were from genera that exhibited greater abundance near the center of the patch habitat as opposed to the area near the matrix (Appendix in Supplementary material).

Arthropod richness was significantly greater in low-edge rectangular patches compared to high-edge connected and high-edge winged patches (Fig. 2a), although this difference in richness was only apparent with larger numbers of samples. When rarefied to consist of 35 samples from each patch type, 95% confidence limits for richness in high-edge connected patches (46–52 genera) were significantly lower than the richness in low-edge rectangular patches (52–56 genera). Confidence limits from high-edge winged patches (49–53 genera) were largely consistent with high-edge connected patches, although winged patches did exhibit slight overlap with rectangular patches. These differences in richness required many samples to detect due to the large number of arthropods from particular groups, i.e. only when the richness began to reach an asymptote did differences become apparent (Fig. 2a). Evenness was significantly lower in high-edge connected patches compared to high-edge winged and low-edge rectangular patches (Fig. 2b). PERMANOVA did not detect a change in community composition due to patch type ($F_{2,14} = 1.11$, $P = 0.35$) or an interaction between patch type and experimental block ($F_{12,14} = 1.00$, $P = 0.47$), although there was a strong main effect of experimental block ($F_{6,14} = 3.42$, $P < 0.01$). The test of multivariate dispersion demonstrated that patch type had a significant effect on beta diversity ($F_{2,32} = 5.73$, $P = 0.01$). Pairwise comparisons revealed greater beta diversity among low-edge

rectangular patches compared to high-edge winged patches (Fig. 2c; $t = 2.61$, $P = 0.022$) and high-edge connected patches ($t = 2.88$, $P = 0.01$), while beta diversity was similar between high-edge winged and high-edge connected patches ($t = 0.19$, $P = 0.89$).

Common arthropod orders differ in their response to shape and connectivity

The three most common orders in our study, Hymenoptera, Coleoptera, and Orthoptera, accounted for 77% of the genera captured and 96% of the individuals captured. There were no differences in the average abundance of any of these three orders among patch types ($F_{2,26} < 2.13$, $P > 0.13$). Richness did not differ among patch types type for Hymenoptera or Orthoptera (Fig. 3), but patterns of richness for Coleoptera mirrored those of the overall arthropod community: there were more Coleoptera genera in low-edge rectangular patches compared to high-edge winged and high-edge connected patches (Fig. 3). Similar to the overall community, evenness of Hymenoptera was greatest in high-edge winged and low-edge rectangular patches (Fig. 3). Evenness of Coleoptera was greater in low-edge rectangular patches compared to high-edge connected and high-edge winged patches (Fig. 3), while Orthoptera communities exhibited a trend of lower evenness in high-edge winged patches compared to low-edge rectangular patches, with intermediate evenness in high-edge connected patches (Fig. 3). Patch type affected beta diversity of Hymenoptera ($F_{2,32} = 4.13$, $P = 0.03$). Communities in low-edge rectangular patches exhibited greater turnover than communities in high-edge connected patches ($t = 2.92$, $P < 0.01$), with a similar trend compared to high-edge winged patches ($t = 1.73$, $P = 0.12$). Patch type did not affect turnover of Coleoptera ($F_{2,32} = 1.13$, $P = 0.39$) or Orthoptera ($F_{2,32} = 1.02$, $P = 0.39$).

Univariate analyses provided insight into the genera contributing to the multivariate patterns we observed. Of the 6 patches where *Melanotus* spp. were captured and the 8 patches where *Epicauta* spp. were found, none of these were high-edge connected patches (χ^2 test with P values obtained via 2,000 randomization replicates, both $P < 0.02$). *Sphenophorus* spp. were more frequently found in high-edge connected patches compared to low-edge rectangular and high-edge winged patches ($P < 0.01$). *Pogonomyrmex badius*

was found in all high-edge connected and winged patches, but was not found in 3 of the 10 low-edge rectangular patches ($P < 0.02$). Similarly, *Alydus* spp. were found in all patches with the exception of two of the low-edge rectangular patches, although this trend was only marginally significant ($P = 0.08$). Average abundance of several genera also differed as a function of patch type. *Sphenophorus* spp. abundance (patch type main effect, $F_{2,14} = 6.16$, $P = 0.01$) was greater in high-edge connected patches compared to winged and low-edge rectangular patches (linear contrast, $F_{1,14} = 12.03$, $P < 0.01$). *Pogonomyrmex badius* abundance differed according to patch type ($F_{2,14} = 9.35$, $P < 0.01$), being greater in low-edge rectangular compared to high-edge connected and winged patches (linear contrast, $F_{1,14} = 16.96$, $P < 0.01$), but the strength of the patch type effect was dependent upon experimental block (patch type × block interaction, $F_{12,14} = 12.41$, $P < 0.001$). Abundance of *Agonum* spp. (patch type main effect, $F_{2,14} = 4.72$, $P < 0.03$) was greater in low-edge rectangular compared to high-edge connected and winged patches (linear contrast, $F_{1,14} = 9.02$, $P = 0.01$). Abundance of *Canthon* spp. (patch type main effect, $F_{2,14} = 7.59$, $P < 0.01$) was greatest in high-edge unconnected winged patches (linear contrast, $F_{1,14} = 14.88$, $P < 0.01$). Similarly, abundance of *Cicindela* spp. exhibited a trend (patch type main effect, $F_{2,14} = 3.17$, $P = 0.07$) of being greater in high-edge unconnected winged patches (linear contrast, $F_{1,14} = 2.23$, $P = 0.07$).

We found some evidence to suggest that corridors lead to increases in the activity density of *Dormyrmex* spp. (binomial generalized linear model, $F_{2,31.7} = 2.65$, $P = 0.09$): the proportion of ant community comprised of *Dorymyrmex* was larger in high-edge connected patches (0.50 ± 0.06) compared to low-edge rectangular (0.31 ± 0.06) and high-edge winged (0.37 ± 0.06) patches. *Dorymyrmex* abundance was negatively related to patch-level evenness ($r^2 = 0.28$, $F_{1,33} = 12.79$, $P < 0.01$).

Discussion

Using replicated large-scale experimental landscapes, our work demonstrates that ground-dwelling arthropod communities were affected by patch shape and connectivity. Importantly, we show that shape and
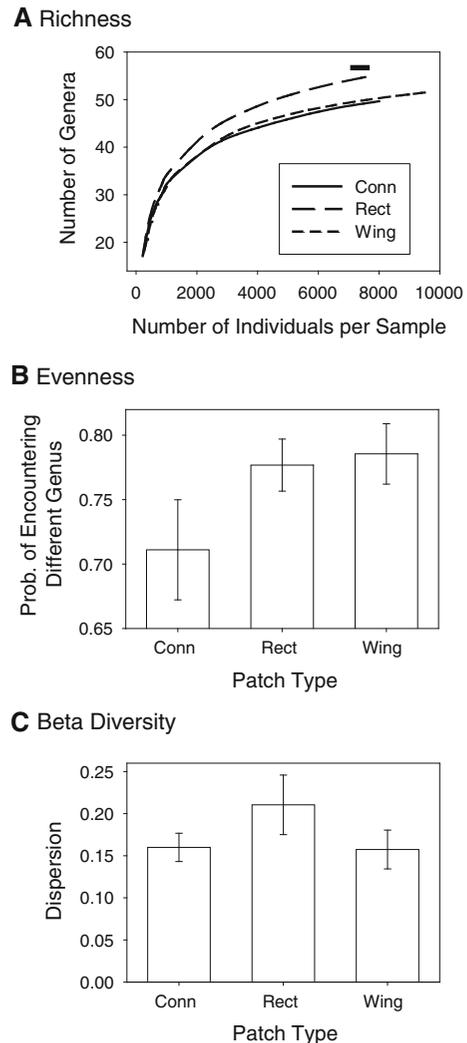
Fig. 2 a Mean richness of arthropod communities as determined using rarefaction to estimate the richness of genera and abundance of individuals in 35 samples taken from each patch type. Due to differences in the number of patch types, the number of samples differed, with 56 samples in high-edge connected patches (Conn), 40 samples in low-edge unconnected rectangular patches (Rect), and 44 samples in high-edge unconnected winged patches (Wing). Although not illustrated for clarity, confidence limits for Wing and Conn exhibit considerable overlap through the entire range of samples. The *horizontal bar* indicates where there is no overlap between Rect patches compared to Conn and Wing patches. **b** Evenness as a function of patch type, measured as the probability that two individuals drawn from a sample will be from the same genus. *Bars* represent 95% confidence limits determined by 5,000 permutations of the original data. **c** Beta diversity as indicated by mean multivariate dispersion by patch type. *Bars* indicate 95% confidence limits
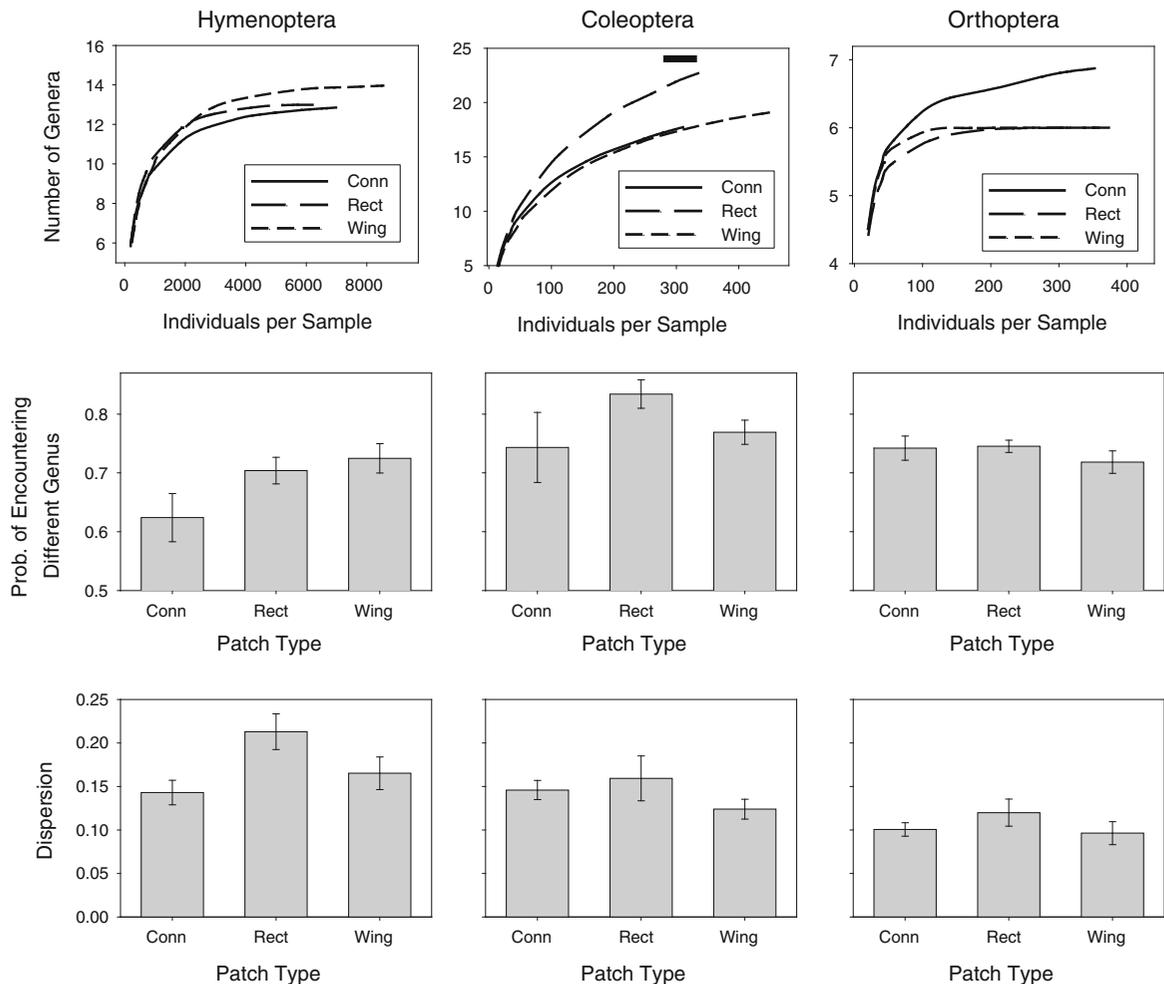
Fig. 3 Mean richness, evenness, and beta diversity of the three most common arthropod orders collected within the experimental landscapes (see text and Fig. 2 for additional information on "Methods" section). Arthropods were sampled using pitfall traps in three different patch types: high-edge connected patches (Conn), low-edge unconnected rectangular patches (Rect, and high-edge unconnected winged patches (Wing). For clarity, confidence limits are not illustrated for rarefaction results; when differences exist among patch types, these are denoted by a *horizontal bar*. Note that the scale of the *y*-axis for richness panels differs for each order due to large differences in numbers of genera. *Error bars* for evenness and beta diversity represent 95% confidence limits

connectivity differ in the community components they affected: patch shape affected the richness and beta diversity of arthropod communities, with low-edge patches characterized by increased richness and turnover of species, whereas connectivity reduced the evenness of arthropod communities. Community-level patterns were driven by order-specific responses with the numerically dominant Hymenoptera contributing to the pattern of reduced evenness in connected patches and increased turnover in low-edge unconnected patches, and Coleoptera contributing to increased richness in low-edge unconnected patches.

These trends became most evident once larger samples of the arthropod community were taken, which illustrates that understanding the effects of shape and connectivity are likely to require substantial sampling efforts.

Unique effects of patch shape on arthropod communities

Our findings provide large-scale, experimental confirmation of the influence of patch shape in affecting arthropod communities. Two potential mechanisms

could create these shape-mediated effects. First, the increased amount of core habitat in low-edge unconnected patches (i.e. areas not under the abiotic effect of edge) may provide habitat for thermophilic genera. Arthropod abundance and distribution are influenced by many factors, including air and soil temperature, humidity, and soil composition (Porter and Tschinkel 1987; Holldobler and Wilson 1990; Stiles and Jones 1998; Kaspari et al. 2000; Retana and Cerdá 2000), and edges often exhibit different moisture and temperature regimes (Chen et al. 1999; Ries et al. 2004; Fletcher et al. 2007). For example, because of greater area away from the shading effects of the patch edge, we expect that low-edge rectangular patches will have more area that receives full sunlight throughout the day relative to high-edge connected and high-edge winged patches. Second, the increased core area in low-edge patches would also be free of the biotic effects of the edge in the form of increased immigration of edge- and matrix-dwelling taxa (i.e. shape-mediated mass effects). For example, greatly increased immigration of forest-dwelling arthropods via the large amount of edge in connected and winged patches could serve to reduce local richness even if edge- and matrix-dwelling species are poor competitors, i.e. effects of edge taxa that are maintained by mass effects (Leibold et al. 2004). These abiotic and biotic mechanisms may both contribute to the pattern that we observed, as both would be expected to increase richness and also increase evenness. Both of these hypotheses make identical predictions in the form of turnover, as increased numbers of thermophilic genera and decreased genera from matrix habitats would both be expected to increase turnover among low-edge habitats, which we observed for all arthropods combined (Fig. 2).

We found that patch shape affected Coleoptera richness (Fig. 3), as richness was greatest in rectangular patches with lower relative amounts of edge habitat and greater relative amounts of core habitat. Unlike the trend observed for other arthropods (i.e. greatest evenness in unconnected patches regardless of shape), evenness of Coleoptera was also greatest in low-edge rectangular patches (Fig. 3). These patterns suggest that patch shape may have a strong effect on Coleoptera, consistent with the finding that Coleoptera often contain edge-averse species (Didham et al. 1998) and habitat edges can have strong effects on beetle communities (Davies et al. 2001; Ewers and Didham

2008). The importance of patch shape in affecting beetle richness in southeastern landscapes also affirms the findings of Yaccobi et al. (2007) that patch shape was important for affecting richness of Carabidae. Our results provide some support for the hypothesis that core area increases area available for some Coleopteran taxa, as *Agonum* spp. were more abundant in low-edge rectangular patches. Our finding that evenness is greatest in low-edge unconnected rectangular patches may reflect the relatively lower abundance of several common Coleoptera genera in rectangular patches. For example, *Sphenophorus* spp. were more abundant in high-edge connected patches, and *Canthon* spp. and *Cicindela* spp. were more abundant in high-edge unconnected winged patches. The notion that high-edge patches provide quality habitat for potentially dominant edge- and matrix-dwelling taxa is supported by the finding that the single most abundant Coleopteran genus, *Cicindela*, was more common near the patch edge (Appendix in Supplementary material).

Patch shape also had a significant effect on beta diversity, which appears to be largely generated by ant communities (Fig. 3). For Hymenoptera, the effect of patch shape on beta diversity was largely due to the difference between high-edge connected and low-edge unconnected rectangular patches (Fig. 3). At least two potential mechanisms, which are not mutually exclusive, may contribute to this pattern. First, increased turnover in low-edge unconnected rectangular patches relative to high-edge connected and high-edge winged patches may be because communities in high-edge patch types are homogenized to a greater degree by the input of generalist or matrix-inhabiting genera, reducing turnover among high-edge connected and winged patches. Second, with greater core habitat available for thermophilic species in rectangular patches, chance colonization events in these patches are more likely to be successful, and local populations of core-dwelling arthropods may become locally established, leading to turnover in patterns within low-edge rectangular patches that are not observed in other high-edge connected and winged patches. Patterns in the abundance of *Pogonomyrmex badius*, one of the ten most abundant taxa in our study, are consistent with the hypothesis that patch shape can promote colonization as well as alter within-patch abundance. Although *P. badius* did not occupy all of the low-edge unconnected rectangular patches, it had a greater abundance in rectangular patches where it did occur, i.e. *P. badius*

was more successful at colonizing high-edge connected and high-edge unconnected winged patches, but was more abundant in low-edge unconnected rectangular patches once colonization occurred.

Unique effects of patch connectivity on arthropod communities

Results from our large-scale experiment provide evidence that connectivity alters the evenness of ground-dwelling arthropod communities, but not richness or beta diversity. Communities in connected patches exhibited significantly lower evenness compared to both winged and rectangular patches (Fig. 2b). These patterns were largely driven by Hymenoptera (Fig. 3). Because of their abundance (87.5% of total individuals captured, almost entirely ants), ground-dwelling Hymenoptera have an important bearing on evenness as measured by the probability of inter-genus encounter. One plausible mechanism by which connectivity changes the evenness of Hymenoptera is by promoting the colonization of species that are capable of becoming dominant members of the community after colonization. That is, connectivity reduces evenness by altering the competition-colonization tradeoff. An examination of occurrence data for the four most common ant genera (*Dorymyrmex*, *Solenopsis*, *Formica*, and *Pogonomyrmex*) suggests that there were no differences in occurrence due to patch type during the first sampling period (χ^2 test, all $P > 0.16$), as might be predicted if connectivity increased initial establishment. However, because our study occurred in late summer 2001 and summer 2002, some time after patches were created in the winter of 1999–2000, our study may have been conducted too late to capture differences in initial colonization due to connectivity. Even so, we find some evidence that corridors lead to increases in the activity density of *Dormyrmex* spp., a relatively aggressive ant genus (Andersen 1995a), and the most common member of the arthropod community (over 38% of the individuals captured). As a result, changes in the abundance of *Dorymyrmex* in connected patches may play a role in the evenness reduction we observed in connected patches, as supported by the negative relationship between evenness and *Dorymyrmex* abundance. Moreover, differences in Hymenoptera evenness became less significant when the analysis was repeated without *Dorymyrmex*, with 95%

confidence limits of 0.44–0.64, 0.56–0.67, and 0.63–0.71 for high-edge connected, low-edge unconnected rectangular patches, and high-edge unconnected winged patches, respectively.

Conclusions and future directions

Our study demonstrates that corridor-mediated changes in connectivity may be important for affecting arthropod community evenness, but that corridor-mediated changes in patch shape, independent of connectivity, can lead to changes in the richness and turnover of arthropod communities. Our work supports other findings that corridors can have community-level effects (Damschen et al. 2006, 2008), but also illustrates that the effects of corridors are likely to differ depending upon the community metric (e.g. richness, evenness) and the taxa (e.g. Coleoptera, Hymenoptera, vascular plants) under consideration. The context-dependence of corridor effects highlights the need for a mechanistic framework for predicting the response of particular taxa to corridors based upon quantifiable characteristics; quantitative correlates of dispersal ability may be one promising way to predict responses to corridors (e.g., Damschen et al. 2008). In finding a strong effect of patch shape on arthropod communities, our work also supports previous findings of strong edge effects in altering the characteristics of arthropod communities (Davies and Margules 1998; Didham et al. 1998; Davies et al. 2001; Yaccobi et al. 2007; Ewers and Didham 2008). Given the strong and taxa-specific role of patch shape and connectivity in affecting arthropod communities, future work is also needed to understand how shape, connectivity, and matrix composition affect key interactions, especially given the role of arthropods in affecting important ecological processes (e.g. pollination, seed predation) and mounting evidence that these processes can be mediated by connectivity and patch shape (Tewksbury et al. 2002; Orrock et al. 2003; Orrock and Damschen 2005), as well as by matrix composition (Haynes and Cronin 2003).

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