The matrix alters the role of path redundancy on patch colonization rates

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Abstract. Landscape connectivity is central to many problems in ecology and conservation. Recently, the role of path redundancies on movement of organisms has been emphasized for understanding connectivity, because increasing the number of potential paths (i.e., redundancy) is predicted to increase movement rates, which can alter predictions for foraging theory and population dynamics. Nonetheless, experiments that test for the effects of path redundancies on connectivity remain scarce. We tested for the role of path redundancies on the movements of a habitat specialist, *Chelinidea vittiger*, using experimental arenas that altered path redundancy by varying the amount and configuration of stepping stones across a gradient of matrix resistance. We found that stepping-stone redundancies increased colonization rates to target patches, but the effects differed depending on the configuration of redundancy and the structure of the matrix. In addition, matrix effects were better explained through the use of effective distance measures that incorporate redundancy in the matrix than those that ignore redundancy. Our results provide experimental evidence that measures that ignore redundancies may be inadequate for capturing functional connectivity, illustrate the ways in which redundancies alter colonization rates, and emphasize how habitat configuration and matrix structure can interact to guide movement of individuals across landscapes.

Key words: Chelinidea vittiger; *circuit theory; corridor; landscape configuration; landscape connectivity; least-cost paths; matrix effects;* Opuntia humifusa; *patch isolation; resistance distance; stepping stone.*

INTRODUCTION

Landscape connectivity, or the degree to which the landscape influences movement of organisms among resource patches (Taylor et al. 1993), is a fundamental concept in ecology, evolution, and conservation. Connectivity can alter the behavior of individuals (Schtick-zelle et al. 2007), influence (meta) population dynamics (Fletcher et al. 2011), structure communities (Astrom and Part 2013), and alter evolutionary processes (McRae and Beier 2007).

There is increasing recognition that redundancies in connectivity may be important for interpreting the effects of ongoing environmental change (McRae et al. 2008). In this context, redundancy refers to situations where multiple paths occur between locations. Quantifying redundancy can improve predictions of connectivity (McRae and Beier 2007, Moore et al. 2011). In addition, spatial ecology theory suggests that redundancy can alter movement rates of individuals, which can increase foraging efficiency (Nonaka and Holme 2007) and reduce local extinctions via increased colonization rates and rescue effects (Holt 1992). While accumulating

evidence suggests that redundancies matter for connectivity, isolating the effects of redundancies on movement rates remains challenging.

Our knowledge of the effects of redundancy remains limited for at least three reasons. First, redundancies can be driven primarily by the number of potential paths (e.g., habitat amount) or by the configuration of such paths. This distinction may be important because dispersal across landscapes occurs in three phases, emigration, transfer, and immigration or settlement (Baguette et al. 2013), which occur at different locations and different scales. Second, redundancies can occur in both habitat linkages (e.g., corridors, stepping stones) and in the surrounding landscape (i.e., the matrix). For example, variation in corridor width (Andreassen et al. 1996) may be viewed as altering the number of possible movement paths through changes in habitat amount. More recently, redundancies have been emphasized in matrix structure through the use of circuit theory, which, in comparison to least-cost paths that ignore redundancy, can better explain gene flow across landscapes (McRae and Beier 2007, Moore et al. 2011, but see Schwartz et al. 2009). Because experiments suggest that the matrix can play a mediating role on the effects of habitat linkages (Baum et al. 2004, Astrom and Part 2013), similar effects could arise in redundancies of habitat linkages and matrix paths (i.e., habitat
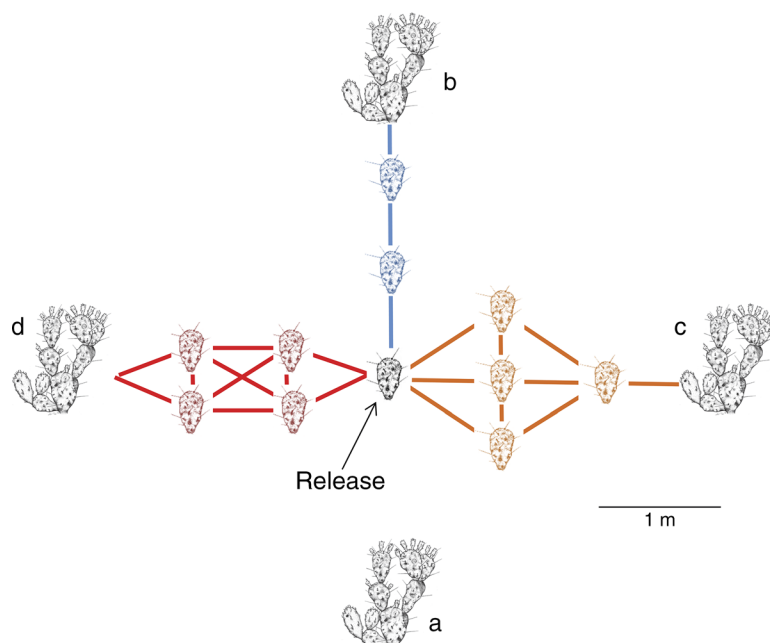
Fig. 1. Experimental design showing one arena (block) where we released cactus bugs. Each arena included one release patch and four target patches, one in each cardinal direction. Between each target patch and the release patch, the presence and configuration of stepping stones differed. Treatments included target patches: (a) unconnected by stepping stones, (b) connected by single stepping-stone configuration (blue cacti and path), (c) connected by funnel stepping-stone configuration (orange cacti and paths), and (d) connected by parallel stepping-stone configuration (red cacti and paths). Based on resistance distances that incorporate path redundancy, the rank connectivity of target patches is d > c ≫ b ≫ a.

linkage × matrix redundancy interactions). Nonetheless, such effects of redundancy have not been considered. Third, experiments designed to isolate the effects of redundancy are notably rare, with the only relevant experiments focusing on corridor width (Andreassen et al. 1996). Yet it is unclear if investigations on corridor width extend to redundancies that may occur from multiple corridors or other types of multiple linkages.

Here, we experimentally test for the role of redundancies on the short-term movement rates of an insect, the cactus bug (*Chelinidea vittiger*), that specializes on prickly pear cactus (*Opuntia* spp). We test for effects of redundancy from habitat linkages (i.e., stepping stones) and the matrix to influence patch colonization rates, and whether the amount or the configuration of path redundancy may have differential impacts on movement. By manipulating habitat linkages, we addressed whether the number of paths simply increases patch colonization rates or whether the configuration of paths is critical, where redundancy can occur near emigration or transfer locations. Furthermore, our study design explicitly allowed the ability to experimentally test the utility of two increasingly used landscape connectivity paradigms that differ in their consideration of redundancy in connectivity assessments (least-cost modeling and circuit theory) on colonization rates of species.

METHODS

Study area and focal species

We conducted a mark–recapture study at the Ordway-Swisher Biological Station (29.4° N, 82.0° W) in central Florida, USA. In this area, *C. vittiger* uses *Opuntia humifusa* primarily occurring in relatively open, grass-dominated, old field and sandhill habitats that contain limited canopy cover. These two habitat types have different amounts of ground cover (R. J. Fletcher, *personal observation*) surrounding *O. humifusa*, with sandhill habitats dominated by wiregrass (*Aristida stricta*) and old fields dominated by bare soil and broomsedge (*Andropogon virginicus*), thus providing a potentially different matrix structure for *C. vittiger*.

In the study area, female cactus bugs generally begin producing and depositing eggs on or near *Opuntia* in early March and continue egg laying through September, with two to three generations per year. Adults are winged, but rarely fly; instead, adult cactus bugs typically walk between cactus patches through an unsuitable matrix (Schooley and Wiens 2004). Movements of adults are thus relatively localized and can be easily measured. In addition, previous studies found that the structure of the matrix, described as vegetation height, influenced movement and population dynamics in this species (Schooley and Wiens 2004, 2005).

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Experimental design

We built 10 experimental arenas for experiments on path redundancy and patch colonization rates (Fig. 1). Arenas were stratified by habitat type (old field vs. sandhill; $n = 5$ arenas for each type) to capture a gradient in matrix structure, with sandhill habitats having greater vegetation height (38.8 ± 0.56 cm; mean $\pm$ SD) and density (3.2 ± 0.38; description of index provided in last paragraph of this section) than old fields (22.0 ± 0.97 cm and 1.7 ± 0.41, respectively). Arenas were built by translocating cacti from nearby areas and removing all other *O. humifusa* in and nearby the arena. Arenas were >50 m apart. Experimental releases began one week after each arena was built.

Each arena included one release patch, four target patches, and 10 stepping-stone patches (Fig. 1). Target patches were placed 2.25 m from release patches to reflect typical movement distances of adult cactus bugs for the time scale considered in this experiment (one week); a mark–recapture study found that, over 2–3 week time intervals, the median distance moved by adults was 4.5 m (Fletcher et al. 2011), or approximately 1.5–2.25 m per week. We focused on stepping stones rather than habitat corridors, because the growth form and patchiness of *Opuntia* create many opportunities for stepping stones, but not for contiguous corridors. Each release patch comprised two cactus pads (cladodes). This size was used to provide some cover for the bugs released, while being low quality (in terms of size), to promote movements of bugs. The target patches each had six cactus cladodes, which was a common patch size in the area. The stepping stones were one cladode each, based on data showing that cacti of this size are sometimes used (Fletcher et al. 2011), but no egg production, nymphs, or site fidelity of bugs have been observed on patches of this size (R. J. Fletcher, *unpublished data*). Stepping stones were 0.4–0.75 m apart; these distances were used based on a recent experiment on perceptual abilities of *C. vittiger* in this area, which showed that the perceptual range was >1 m but <2 m (Fletcher et al. 2013a). Thus, the stepping stones were within the immediate perceptual range of individuals, whereas the target patches were outside of the perceptual range. Note that based on behavioral observations of *C. vittiger*, Schooley and Wiens (2004) found that cactus pads >0.25 m apart are considered separate patches, such that all stepping stones and patches considered here can be considered distinct from the perspective of *C. vittiger* movement behavior.

Stepping stone treatments were randomized in each arena and were configured to represent different amounts of structural connectivity and path redundancy between the release and the target patches. One target patch included no stepping stones (hereafter called unconnected) to compare with the other three that included stepping stones (Fig. 1a). A second target patch was connected to the release patch by two stepping stones spaced 0.75 m apart, but had no path redundancy (hereafter called single; Fig. 1b). The remaining two target patches were connected to the release patch by four stepping stones each, which were configured in different ways to reflect variation in path redundancy. These configurations were inspired by McRae et al. (2008), who illustrated different amounts of path redundancy between two patches using circuit theory (see their Figs. 5–7). One target patch was connected by a parallel configuration consisting of two parallel paths of stepping stones, essentially doubling the path in the single treatment and providing path redundancy throughout the transfer area of the arena (Fig. 1d). We note that comparisons of single to parallel treatments identify redundancy effects arising primarily from habitat amount. The final target patch was connected by a funnel configuration consisting of initially three stepping stones, spaced 0.4 m apart and 0.75 m from the release patch, followed by another single stepping stone 0.75 away from the target patch (Fig. 1c). This configuration causes greater path redundancy near the release patch, thereby emphasizing the potential effect of redundancy on the emigration phase. Comparisons between funnel and parallel configurations identify redundancy effects based on path configuration beyond that of habitat amount. When ignoring matrix structure, these target patches were the same Euclidean distance and least-cost distance from the release patch (2.25 m) but had considerably different resistance distances based on circuit theory, using 1/distance as a weight in the connectivity matrix (unconnected was 2.25 m; single was 0.74 m; funnel was 0.44 m; parallel was 0.42 m).

For each arena, we released individuals at release patches on three different occasions (trials) between 1 September and November 9 2011, which is the post-breeding time period for this species. For each trial, we released 4–6 adult *C. vittiger*, with equal numbers of males and females being released, and individuals were only used once during the experiment. Each adult was sexed and marked with an individual number on the pronotum using a nontoxic, ultra-fine point permanent ink marker to enable resighting individuals for estimating inter-patch movements. A greenhouse experiment showed that this marking procedure does not influence survival rates of adults (unmarked weekly survival = 0.982; marked survival = 0.985, $P = 0.72$; R. J. Fletcher, *unpublished data*). To reduce the likelihood of immediate flight responses due to translocation to the new location, individuals were placed under litter surrounding the release patch. Arenas were censused for adults on all patches at 3 h, 1 d, 2 d, and 7 d post-release. At 7 d, all adults remaining in the arena were removed.

At the end of releases, we measured vegetation height and density in a regular sampling grid at 50-cm increments throughout each arena (81 measurements per arena) to assess variation in matrix resistance within and among arenas (Schooley and Wiens 2005). Vegetation height was described as the maximum height at each location, whereas vegetation density was measured as

TABLE 1. Comparison of generalized linear mixed models describing the proportion of movements from release patches to target patches (colonization probability).

Model	−2LL	AIC_c	ΔAIC_c
Resistance × stepping stone	234.7	256.7	0
Resistance + stepping stone	255.4	268.2	11.5
Stepping stone	258.2	268.8	12.1
Least cost × stepping stone	248.7	268.3	12.2
Least cost + stepping stone	257.1	269.9	13.3
Matrix type + stepping stone	258.1	270.9	14.2
Matrix type × stepping stone	256.2	275.6	18.9
Resistance	288.5	294.7	38.1
Null	295.1	297.1	40.4
Least cost	291.6	297.8	41.2
Matrix type	292.7	298.9	42.2

Notes: Least cost refers to least-cost distance, resistance refers to commute distance (∝ resistance distance), stepping stone refers to the four treatments (unconnected, single, funnel, and parallel), and matrix type refers to old field vs. sandhill environments. Heading −2LL is a measure of deviance (−2 × log-likelihood), AIC_c stands for Akaike's information criterion corrected for small sample size, and ΔAIC_c stands for AIC_c for model i – minimum AIC_c. All models included target patch area as a nuisance covariate and arena as a random effect.

the number of 10-cm intervals in which vegetation hit a metal rod at each location (Schooley and Wiens 2005). Vegetation height and density measures were highly correlated ($r = 0.80$), so we used vegetation height throughout to be consistent with prior work (Schooley and Wiens 2005).

Analysis

For each trial, we summarized the proportion of individuals that moved to each target patch (pooled across all censuses) as a binomial response (i.e., [movements to patch i]/[number of bugs released]; hereafter colonization by individuals). We used generalized linear mixed models, with the number of movements/individuals released as the response variable, a logit link function, and arena as a random effect to accommodate repeated measures within arenas. We fit models that tested for stepping-stone configuration, matrix resistance, and stepping stone × matrix resistance as fixed effects on the probability an individual would colonize a target patch. Models were compared using model-selection criteria, Akaike's information criterion (AIC), corrected for sample size (AIC_c) by approximating marginal likelihoods using Gauss-Hermite adaptive quadrature. While we standardized the number of cladodes for each target patch ($n = 6$ cladodes), there was a weak tendency for target patch area (as measured in Schooley and Wiens 2005) to vary for each treatment ($F_{3,36} = 2.59$, $P = 0.07$) and for movement to be directed toward larger patches ($\beta = 0.014 \pm 0.009$; $F_{1,109} = 2.44$, $P = 0.12$). Consequently, we included target patch area as a nuisance covariate in all models. We initially considered sex in our models, but we found no evidence for effects of sex ($F_{1,217} = 0.06$, $P = 0.80$), sex × treatment ($F_{3,217} = 0.24$, $P = 0.87$), or sex × matrix resistance ($F_{1,217} = 0.06$, $P = 0.80$), so we removed sex from all models. We compared our global model (including stepping stone × matrix resistance) to reduced models that included matrix resistance only, stepping-

stone configuration only, and the additive effects of stepping stone and effective distance.

To quantify matrix resistance, we first performed ordinary kriging using our vegetation height data to interpolate vegetation structure throughout each arena. For kriging, we considered different model variograms to explain spatial dependence of vegetation data, including circular, cubic, matern, power, spherical, and nonspatial models using the geoR package in R (Ribeiro and Diggle 2001). Once the best model was selected using AIC, we developed raster maps of vegetation heights at different resolutions, ranging from 5 to 50 cm (at 5-cm increments). Based on these different maps, we calculated least-cost paths and commute distances using the gdistance package in R (van Etten 2012). Commute distances incorporate path redundancies into calculations of cost distance and are proportional to resistance distances (McRae et al. 2008). Note that these effective distance measures only considered matrix structure (vegetation height); stepping stones were not incorporated into these measures, which allows us to better partition the effect of the matrix vs. stepping stones on movement, and prevents the need to make assumptions regarding the effective resistance of stepping stones. To assess sensitivity of results to map resolution, we initially fit global models with either least-cost or commute distances based on 5–50-cm resolutions, and chose the resolution that had the best fit to the data on the basis of AIC_c (see Appendix). With these best-fit map resolutions, we then compared models using AIC_c to assess the effects of stepping stones and matrix resistance on colonization probability into target patches, separately contrasting models based on least-cost distance to those based on commute distance or matrix type (old field vs. sandhill).

Results

We released 176 adults (88 males, 88 females) in 30 trials. Eighty-one individuals (121 resights) were ob-
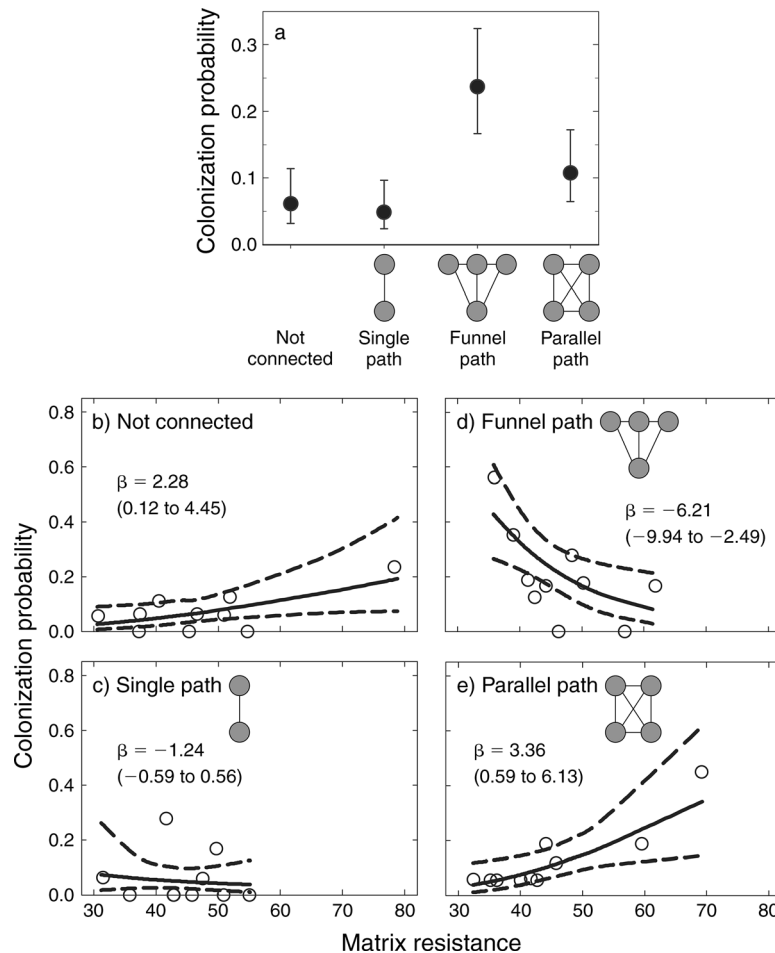
FIG. 2.　(a) Effects of stepping-stone treatments on colonization probabilities of cactus bugs. Least-square means are provided for all treatments. Vertical bars represent 95% CI. Matrix resistance effects on colonization probabilities of cactus bugs moving from release patches to target patches (b) unconnected by stepping stones, (c) connected by a single stepping-stone path, (d) connected by a funnel of stepping stones, and (e) connected by a parallel path of stepping stones (node–edge diagrams show the stepping-stone treatments). In panels (b–e), matrix resistance is quantified by commute distance (dm), which incorporates path redundancy in the matrix to calculate an effective distance between the release and target patches. Solid lines represent predictions from a binomial generalized linear mixed model, dashed lines are the 95% confidence limits for predictions, and open circles show the proportion of movements observed. The slope parameters for the matrix resistance (β) and 95% CI (values in parentheses) are also provided.

served on target patches (12 unconnected, 10 single, 23 parallel, 36 funnel). Forty-six individuals (67 resights) were observed using stepping stones, highlighting that stepping stones were frequently used during movement. Overall, commute and least-cost distances from release patches to target patches were only weakly positively correlated ($r = 0.28$, $P = 0.079$). Models using commute distance generally fit the data better than least-cost distances, consistent with multiple paths in the matrix being important for colonization rates (Appendix, Table 1). Based on this sensitivity analysis to changes in grain size (Appendix), we used the best-fit grain size for both measures (45 cm for commute, 20 cm for least-cost). Note that using a consistent grain size of 45 cm (which was within 1.5 AIC$_c$ units of the best grain for least-cost

distances; Appendix) for both effective distances provided the same results.

Colonization probabilities to target patches varied by stepping-stone treatments (Fig. 2a; likelihood-ratio test: $\chi^2 = 36.1$, df = 3, $P < 0.001$), with the parallel treatment (Fig. 1d) causing ~2 times greater colonization probability than single (Fig. 1b) and unconnected (Fig. 1a) treatments, and the funnel treatment (Fig. 1c) resulting in ~2 times greater colonization probability than the parallel treatment. Yet model selection (Table 1) provided strong support that this effect was mediated by matrix resistance as described by commute distance (Fig. 2b–e; marginal pseudo R^2 for best model = 0.19; Nakagawa and Schielzeth 2013). With increasing commute distance, colonization probabilities decreased

toward patches connected through the funnel stepping stones and increased toward unconnected patches and patches connected by parallel stepping stones (Fig. 2d, e). The positive effect of the matrix for the unconnected treatment was driven entirely by one arena; removal of this arena led to no significant relationship ($\beta = 0.92$, CI $= -3.51–5.36$). In this best-fitting model, the effect of target patch area was weak ($\beta = 0.021 \pm 0.014$; $F_{1, 102} = 2.35$, $P = 0.129$). We note that the effect of stepping stones was generally greater than that of matrix resistance (Table 1), where a model that included stepping-stone treatments only had more support than a model with matrix resistance only ($\Delta AIC_c = 26.0$).

DISCUSSION

Our experiment revealed that both stepping stones and the matrix were important predictors of colonization probabilities of target patches, that path redundancy in both stepping stones and the matrix were influential, and that these redundancies interacted. These results emphasize that accounting for redundancies may be necessary for capturing functional connectivity and illustrate the ways in which redundancies alter movement and colonization rates.

Path redundancies can alter movement rates through at least two mechanisms. First, movement can be passive (e.g., diffusion), in which case redundancy increases random flow through landscapes (McRae et al. 2008). Second, redundancies can potentially result in greater area of paths, such that individuals may prefer to move toward areas with greater habitat amount (Andreassen et al. 1996). Our results cannot solely be explained by the first mechanism, because circuit theory alone, which assumes random-walk movement behavior, was insufficient to explain colonization rates (i.e., a resistance-only model provided a poor fit to the data and movements among treatments were not consistent with predictions from circuit theory). Rather, we hypothesize that the synergistic effects of stepping-stone redundancy and matrix effects are related to the area and configuration of stepping stones coupled with how matrix structure (vegetation height) may influence patch detection by *C. vittiger*. We found that under low matrix resistance, cactus bugs preferentially colonized target patches that were connected through redundant stepping stones that funneled organisms away from release patches, thereby influencing their emigration direction (cf. Kuefler et al. 2010). Yet under high matrix resistance where patch detection may be more difficult, the attenuation of these stepping stones may have reduced the likelihood that individuals would reach target patches. Conversely, the array of parallel stepping stones provided a redundant path throughout the transfer area, resulting in higher colonization rates into these target patches under high matrix resistance. Consistent with this hypothesis, resightings at the distal stepping stones (near the target patch) for the parallel treatment were positively correlated with matrix resistance ($r = 0.71$, $P = 0.02$),

whereas we observed no resightings on the single distal stepping stone in the funnel treatment under high matrix resistance. In addition, correlations of matrix resistance with movements to proximal stepping stones for the funnel and parallel treatments were similar (and not statistically significant; $P > 0.22$). These results emphasize that understanding the ways in which redundancy influences emigration, search and transfer through the matrix, and immigration into new habitats will be useful for accurately predicting functional connectivity.

Perhaps surprisingly, matrix resistance as described by vegetation height showed a positive relationship with patch colonization rates for the unconnected treatment and no relationship for the single path treatment. While the pattern in the unconnected treatment was driven by one trial in one arena, three alternative hypotheses may explain these general lack of effects. First, vegetation height may have been a poor descriptor of the resistance of the matrix. However, Schooley and Wiens (2004, but see Schooley and Wiens 2005) showed strong effects of this measure on *C. vittiger* movements in Colorado, and this measure is negatively correlated with movements in a 56-patch network in the study area (Fletcher et al. 2013b). Second, dispersal is a multicausal process where vegetation could have several effects, such as impeding movement while simultaneously providing protection from predators (Baguette et al. 2013). Third, our experimental design was relative, in the sense that individuals released in arenas could move toward one of four target patches. We suggest that these results could most parsimoniously be explained by the fact that most individuals chose to move toward the redundancy treatments such that there was less power to detect effects in the other treatments.

Recently, there have been debates regarding the role of landscape composition (amount) relative to landscape configuration on biodiversity (Fahrig 2003). While much of the debate focuses on patterns of diversity (Fahrig 2003, Didham et al. 2012), our experiment provides evidence regarding the role of landscape configuration on the process of movement across landscapes. This effect is consistent with theory that emphasizes that configurations of stepping stones can alter colonization rates (while holding habitat amount constant [Gilpin 1980, Saura et al. 2014]). To better interpret the roles of landscape composition and configuration, we propose that investigations should focus more on the processes hypothesized to be differentially impacted by composition and configuration rather than patterns of biodiversity.

From a systems and network perspective, redundancy is thought to have major impacts on the persistence, stability, and resilience of systems (Albert et al. 2000, Ahern 2011). In a population context, redundancy is predicted to alter movement rates, leading to area effects and potentially greater metapopulation viability (Holt 1992, Fletcher et al. 2013b). This work provides experimental evidence that redundancy can indeed

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increase patch colonization rates and thus functional connectivity. Yet it emphasizes that not all redundancy is the same, and may have differential effects on emigration, search through the matrix, and immigration processes.

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Supplemental Material

Appendix

Identification of the best grain size (resolution) for assessing matrix resistance (*Ecological Archives* E095-126-A1).