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THE MATRIX ENHANCES THE EFFECTIVENESS OF CORRIDORS AND STEPPING STONES

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Abstract. Conservation strategies often call for the utilization of corridors and/or stepping stones to promote dispersal among fragmented populations. However, the extent to which these strategies increase connectivity for an organism may depend not only on the corridors and stepping stones themselves, but also on the composition of the surrounding matrix. Using an herbivore–host-plant system consisting of the planthopper *Prokelisia crocea* and its sole host plant, prairie cordgrass (*Spartina pectinata*), we show that the effectiveness of corridors and stepping stones for promoting planthopper dispersal among patches depended strongly on the intervening matrix habitat. In a low-resistance matrix (one that facilitates high rates of interpatch dispersal), both stepping stones and corridors promoted high connectivity, increasing the number of colonists by threefold relative to patches separated by matrix habitat only. The effectiveness of stepping stones and corridors was significantly lower in a high-resistance matrix (one that promotes low rates of interpatch dispersal), with stepping stones failing to improve connectivity for the planthoppers relative to controls. Thus, we conclude that the matrix is an integral component of landscapes and should be considered together with corridors and stepping stones in strategies designed to increase dispersal among fragmented populations.

Key words: colonization; connectivity; conservation; corridors; dispersal; edge effects; habitat fragmentation; matrix; movement; Prokelisia; Spartina; *stepping stones.*

Introduction

Habitat fragmentation, degradation, and loss pose the most significant threats to the structure and persistence of animal populations and communities (Wilcox and Murphy 1985, Saunders et al. 1991, Debinski and Holt 2000, Fahrig 2003). Isolated patches of native habitat often support small populations that receive little or no immigration, increasing the probability of extinction (Brown and Kodric-Brown 1977, Pimm et al. 1988, Fahrig and Merriam 1994). Corridors and stepping stones have been proposed as strategies to increase connectivity (the extent to which the landscape promotes or impedes the movement of an organism between habitat patches [Taylor et al. 1993, Tischendorf and Fahrig 2000]) for fragmented populations (Wilson and Willis 1975, Simberloff et al. 1992, Schultz 1998, Haddad 2000). Corridors—linear strips of habitat connecting otherwise isolated patches—are perhaps the most popular strategy (Simberloff et al. 1992, Rosenberg et al. 1997, Haddad et al. 2003).

Many studies have provided support for the role of corridors in increasing connectivity, demonstrating that corridors can increase population sizes (Fahrig and Merriam 1985, Dunning et al. 1995, Haddad and Baum 1999), movement among patches (Rosenberg et al. 1997, Beier and Noss 1998, Gonzalez et al. 1998, Haddad 1999, Tewksbury et al. 2002, Haddad et al. 2003), and gene flow (Aars and Ims 1999, Hale et al. 2001, Mech and Hallet 2001). Stepping stones—a series of small patches connecting otherwise isolated patches—have received less attention, but may be more suitable for promoting movement between patches when contiguous habitat can not be obtained or when stepping stones are more representative of the natural configuration of the landscape (Gilpin 1980, Simberloff et al. 1992, Schultz 1998, Haddad 2000, Fischer and Lindenmayer 2002, Murphy and Lovett-Doust 2004).

Although theoretical and empirical evidence supports the role of corridors and stepping stones in conservation efforts (Beier and Noss 1998, Tewksbury et al. 2002, Haddad et al. 2003, Hudgens and Haddad 2003), the extent to which these strategies increase connectivity between suitable habitat patches may depend significantly on the composition of the intervening matrix (Simberloff et al. 1992, Rosenberg et al. 1997). Besides moving through corridors and stepping stones, organisms also disperse through the matrix, even if the matrix habitat is unsuitable for survival and reproduction (Wiens 1997, Roland et al. 2000, Ricketts 2001, Cronin 2003*a*, Haynes and Cronin 2003). Moreover, the composition of the matrix can significantly affect the interpatch movement rates of herbivores (Roland et al. 2000, Ricketts 2001, Haynes and Cronin 2003), and these changes in movement rates can, in theory, affect population dynamics and persistence (e.g., Vandermeer and Carvajal 2001, Cronin and Haynes 2004).

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For habitat specialists moving through the matrix, corridors or stepping stones may function as drift fences or traps, drawing organisms toward connected or adjacent habitat patches (Haddad and Baum 1999, Tewksbury et al. 2002). Consequently, the efficacy of corridors and stepping stones may be significantly enhanced when embedded in a low-resistance matrix (one that promotes relatively high rates of interpatch dispersal) as compared to a high-resistance matrix (one that promotes relatively low rates of interpatch dispersal; Roland et al. 2000, Ricketts 2001, Haynes and Cronin 2003). To date, no experimental studies have been conducted to evaluate the role of matrix composition in the efficacy of corridors and stepping stones.

We evaluated the influence of the matrix on connectivity using a model herbivore–host-plant system consisting of the planthopper *Prokelisia crocea* Van Duzee (Hemiptera: Delphacidae) and its sole host plant, prairie cordgrass (*Spartina pectinata* Link [Poaceae]) (Cronin 2003*b*). The landscape context of this system consisted of discrete host plant patches (prairie cordgrass) surrounded by a heterogeneous non-host matrix varying in resistance to planthopper movement. We examined the influence of matrix resistance on the effectiveness of corridors and stepping stones for increasing interpatch dispersal. Results from this study are used to evaluate the functionality of corridors and stepping stones in different matrix types, and to identify important new directions for research in conservation biology.

MATERIALS AND METHODS

Life history

Prairie cordgrass is common in the prairies of North America (Hitchcock 1963) and grows in discrete patches ranging in size from just a few stems to over 4 ha (Cronin 2003*b*). The matrix associated with cordgrass patches consists of three basic types: mudflats of mostly bare ground, mixed native grasses (dominated by foxtail barley *Hordeum jubatum* L., western wheatgrass *Agropyron smithii* Rydb., and little bluestem *Andropogon scoparius* Michx.), and expansive monocultures of exotic smooth brome (*Bromus inermis* Leyss) (Cronin 2003*a*, Haynes and Cronin 2003).

Prokelisia crocea is the dominant herbivore of cordgrass and exhibits two distinct generations per year in North Dakota, with adult densities peaking in mid-late June and in early August (Cronin 2003*a*, *b*, *c*). Adults live at most two weeks in the field and lay eggs along the midrib of the adaxial surface of cordgrass leaves (Cronin 2003*a*, *b*, *c*). Although this species is wing dimorphic, populations are dominated by macropterous (long-winged) individuals fully capable of flight (Cronin 2003*c*). Planthopper emigration and immigration rates for cordgrass patches are on average 1.3 and 5.4 times higher, respectively, for cordgrass patches embedded in a matrix composed of brome than mudflat (Haynes and Cronin 2003, Cronin and Haynes 2004). Thus, brome functions as a low-resistance matrix for planthoppers and mudflat functions as a high-resistance matrix.

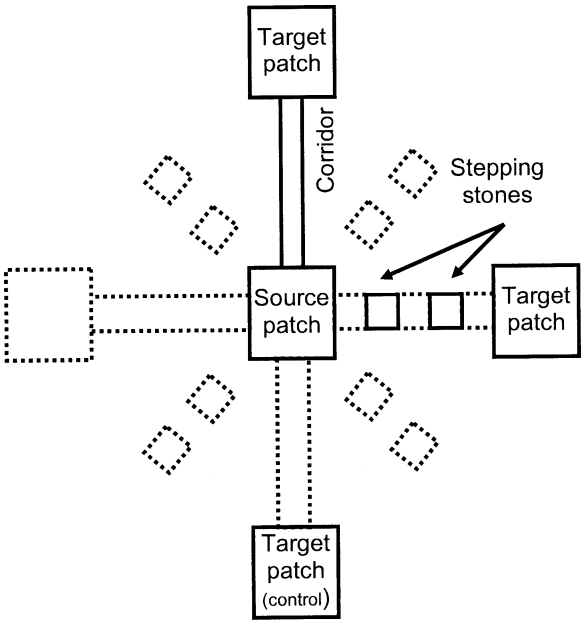

FIG. 1. Each experimental landscape consisted of a source patch (0.76 × 0.76 m) onto which marked planthoppers were released, and three vacant target patches located 2 m from the source patch and connected to the source patch by a corridor (0.12 × 2 m), two stepping stones (0.35 × 0.35 m each), or nothing (matrix-only control). Solid boxes represent planted cordgrass, and hatched boxes represent comparable areas in the matrix that were visually inspected for planthoppers.

Experimental landscapes

We created 20 experimental landscapes in a tallgrass prairie in northeast North Dakota, USA. Each landscape consisted of a central source patch surrounded by three vacant target patches (0.76 × 0.76 m) located 2 m away and connected to the source patch by either a corridor, two stepping stones, or nothing (matrix-only control; Fig. 1). One-half of the landscapes had a matrix composed of smooth brome and the other half had a matrix composed of experimentally created mudflat. The mudflat matrix was created by cutting brome to ground level. The movement behavior of planthoppers at the cordgrass–mudflat boundary and within the experimental mudflat matrix is indistinguishable from the behavior of these insects in naturally occurring mudflats (Cronin and Haynes 2004). The orientation of the target patches was randomly selected from the four cardinal directions. The corridor was equal in size to the two stepping stones, with both representing 41.5% of the area of a single patch. Patch area and separation distance were within the range of areas and distances encountered in the field (Cronin 2003*b*). Planthoppers, on average, move <1 m within a 24-h period (Cronin

2003*b*), so the distance separating the source patch from the target patches was nontrivial relative to the dispersal capabilities of the planthoppers. Moreover, Haynes and Cronin (2003) have demonstrated previously that an isolation distance of 2 m is sufficient to detect large effects of matrix composition on interpatch movement rates.

Five hundred adult female planthoppers were collected from nearby prairie habitat, marked with fluorescent powder (Dayglo Corporation, Cleveland, Ohio, USA), and released in the source patch of each experimental landscape (Cronin 2003*b*). We used females because they are generally mated prior to dispersal and therefore responsible for population spread (Cronin 2003*b*). The fluorescent powder used to mark the planthoppers has no measurable effects on planthopper survival or dispersal (Cronin 2003*b*). The release density was ~1.3 planthoppers per cordgrass stem, well within the range of densities observed under natural conditions (Cronin 2003*b*). For seven days following the release of marked planthoppers (spanning the majority of the dispersal period for this species; Cronin 2003*b*), the source patch, three target patches, corridor, stepping stones, and portions of the matrix habitat within each experimental landscape were thoroughly searched for planthoppers (Fig. 1). We removed marked planthoppers in the target patches each day to avoid recounting individuals and overestimating the number of successful colonists. Planthoppers located in the source patches, corridor, stepping stones, or matrix were not removed because they remained potential colonists to the target patches.

Numbers of colonists of the three target patches were nonindependent because planthoppers shared the same source patch and experimental landscape, and the colonization of one patch would preclude colonization of another patch. We used a profile ANOVA, the equivalent of a repeated-measures ANOVA, to compare the effect of matrix type on the number of planthopper colonists (Simms and Burdick 1988, Tabachnick and Fidell 2001). In this case, the repeated (nonindependent) measures consisted of the number of planthopper colonists to each of the three target patches within the same experimental landscape. Matrix type was the independent variable. The assumptions of normality and equality of variances were met by performing a square-root transformation on the number of colonists per patch. Differences in the number of planthopper colonists among the three target patches within a matrix (control, corridor-connected, and stepping-stone-connected patches) were evaluated using separate paired *t* tests. Differences between brome and mudflat in the number of planthopper colonists to each target patch, the number of planthoppers found within the matrix habitat, and the number of planthoppers found within the corridors and stepping stones were evaluated using unpaired two-sample *t* tests. Significance was evaluated using sequential Bonferroni corrections and $\alpha = 0.05$ for each group of tests.

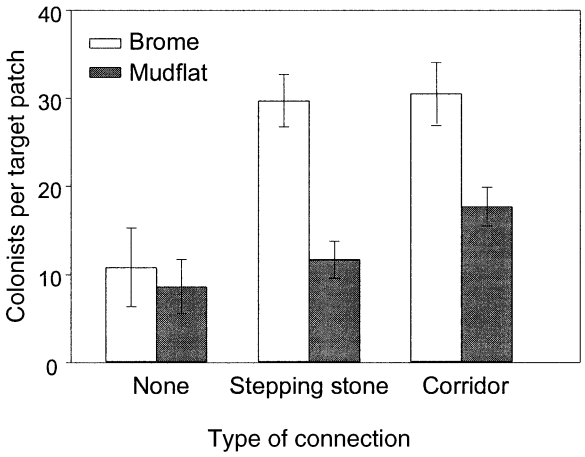

FIG. 2. Total number of planthopper colonists (mean ± 1 SE) in the target patches over a 7-d period.

RESULTS

The efficacy of corridors and stepping stones strongly depended upon matrix composition (Fig. 2; $F_{1,18} = 11.94$, $P = 0.003$). Significantly more planthoppers colonized patches connected by stepping stones ($t = 3.92$, df = 18, $P = 0.001$) and corridors ($t = 2.75$, df = 18, $P = 0.013$) in the brome than the mudflat, but no significant difference between matrix types was observed for the control patches (target patches separated from the source patch by matrix habitat only; $t = 0.98$, df = 18, $P = 0.339$). Because there was a marginally significant matrix-connector interaction term ($F_{2,36} = 2.94$, $P = 0.066$), tests for differences between corridors and stepping stones were performed subsequently within a matrix. In a high-resistance matrix (mudflat), stepping stones failed to improve colonization relative to controls ($t = 1.40$, df = 9, $P = 0.197$), but corridors increased colonization by 106% relative to controls ($t = 3.18$, df = 9, $P = 0.011$). In the low-resistance matrix (brome), corridors and stepping stones increased interpatch dispersal by 182% and 175%, respectively, compared to control patches (Fig. 2; corridors: $t = 9.29$, df = 9, $P < 0.001$; stepping stones: $t = 3.99$, df = 9, $P = 0.003$). Within each matrix, corridors and stepping stones promoted similar levels of planthopper connectivity among patches (Fig. 2; brome: $t = 0.23$, df = 9, $P = 0.823$; mudflat: $t = 2.62$, df = 9, $P = 0.028$, a nonsignificant result based on a sequential Bonferroni correction).

In our experimental landscapes, we recorded 463% more marked planthoppers within the brome matrix than the mudflat matrix ($t = 5.09$, df = 18, $P < 0.001$). The number of planthoppers detected within the corridors and stepping stones did not differ between brome and mudflat (corridors: $t = 0.80$, df = 18, $P = 0.436$; stepping stones: $t = 2.36$, df = 18, $P = 0.030$, a non-

significant result based on a sequential Bonferroni correction).

Discussion

The effectiveness of corridors and stepping stones depended on the surrounding matrix habitat, with higher connectivity for planthoppers in brome compared to mudflat. In brome, corridors and stepping stones increased colonization by threefold over controls (i.e., matrix habitat only). However, in mudflat, only the corridors increased colonization (by twofold) relative to controls.

The matrix not only influences planthopper movement behavior, but also the permeability of corridors, stepping stones, and patches. The matrix may cause patch edges to be perceived as hard (low probability of crossing a patch edge) or soft (high probability of crossing a patch edge; Stamps et al. 1987, Ries and Debinski 2001, Schtickzelle and Baguette 2003). Planthoppers are less likely to cross cordgrass–mudflat boundaries (hard edges) than cordgrass–brome boundaries (soft edges) suggesting that patch boundaries function more as dispersal barriers for planthoppers in a high-resistance matrix (mudflat) than in a low-resistance matrix (brome; Haynes and Cronin 2003). The use of stepping stones requires an organism to cross multiple patch–matrix boundaries, while no boundaries need to be crossed when using a corridor. Thus, the failure of stepping stones in the mudflat matrix corroborates the view that stepping stones prove most useful when habitat boundaries do not function as dispersal barriers for organisms (Haddad 2000).

Corridors and stepping stones (brome matrix only) increased colonization relative to patches connected by matrix habitat only, indicating the planthoppers used the corridors and stepping stones. The corridors and stepping stones also functioned to increase connectivity more in brome than mudflat. Similar numbers of planthoppers were found within the corridors in both matrix types and within the stepping stones in both matrix types. Therefore, the difference in colonization between brome and mudflat must be due to the effect of matrix composition on corridor and stepping stone use. The corridors and stepping stones may have functioned as drift fences or traps, drawing insects in from the matrix and funneling them into connected or adjacent patches (Haddad and Baum 1999, Tewksbury et al. 2002). Planthoppers not only emigrate more frequently into a matrix composed of brome than mudflat, but their movement patterns also differ markedly within each matrix type (Haynes and Cronin 2003; K. J. Haynes and J. T. Cronin, *unpublished data*). Planthoppers exhibit highly directional and rapid movement through a mudflat matrix, but tend to move slower and follow more circuitous paths in a brome matrix (K. J. Haynes and J. T. Cronin, *unpublished manuscript*). These movement patterns and the presence of more planthoppers in the brome matrix should increase the probability of individuals encountering a corridor or stepping stone, enhancing the potential ''drift fence'' effect of corridors in brome. In the only explicit test of the ''drift fence'' effect, Tewksbury et al. (2002) were unable to find evidence that corridors functioned as drift fences, but their study was conducted within a matrix resistant to movement by the study organisms. We suggest that a low-resistance (dispersal-facilitating) matrix might generate or enhance the ''drift fence'' effect of corridors.

Based on our findings regarding the contribution of the matrix to connectivity, the conclusions of previously published studies on corridors and stepping stones may not apply to landscapes composed of different matrix types. In general, corridors have been proposed for landscapes where the matrix strongly contrasts with suitable, isolated patches of habitat (Haddad et al. 2003), based on the idea that corridor use increases as the resistance of the matrix to movement increases (Rosenberg et al. 1997, Hudgens and Haddad 2003). We found the opposite result—greater dispersal among patches connected by corridors and stepping stones in a low-resistance than a high-resistance matrix. Although we know the contribution of the matrix and the combined contribution of the matrix and corridors or stepping stones to patch connectivity for planthoppers, we do not know how corridors or stepping stones function alone (in isolation of the matrix) to increase connectivity. Separating these contributions would provide insight into the mechanisms underlying corridor and stepping stone functionality and the role of the matrix in increasing connectivity.

The presence of other species (i.e., competitors, predators, or mutualists) within habitat patches and the matrix also may significantly alter connectivity (e.g., Fraser et al. 1995, Melian and Bascompte 2002, Tscharntke et al. 2002, Schmitt and Holbrook 2003, Cronin et al. 2004, Denno et al. 2004). Natural enemies abundant in the matrix may force prey to move through corridors and/or stepping stones to reduce predation risk. Alternatively, if predators aggregate along corridors or in stepping stones, prey may reduce predation risk by moving through the matrix. The distribution and abundance of natural enemies, and hence their expected impact on the connectivity of their prey, will depend on how they respond to different components of the landscape, such as the matrix, corridors, and patch–matrix boundaries (see for review Denno et al. 2004). However, relatively little is known about how predators and their prey respond to landscape structure and studies of connectivity have largely ignored interspecific interactions (but see Burkey 1997, Tewksbury et al. 2002, Cronin 2003*a*, Haddad et al. 2003, Cronin and Haynes 2004, Cronin et al. 2004).

In conclusion, we demonstrate that the matrix can determine whether, and to what extent, corridors or stepping stones increase the connectivity of a landscape for an organism. The combination of a low-resistance

matrix with corridors and/or stepping stones may prove a useful strategy for increasing dispersal among patches for some fragmented populations. Future research and conservation plans must include a more holistic view of the landscape (e.g., consideration of the matrix) and interactions among species when evaluating strategies designed to increase connectivity.

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