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Landscape corridors can increase invasion by an exotic species and reduce diversity of native species

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Abstract. Landscape corridors are commonly used to mitigate negative effects of habitat fragmentation, but concerns persist that they may facilitate the spread of invasive species. In a replicated landscape experiment of open habitat, we measured effects of corridors on the invasive fire ant, *Solenopsis invicta*, and native ants. Fire ants have two social forms: polygyne, which tend to disperse poorly but establish at high densities, and monogyne, which disperse widely but establish at lower densities. In landscapes dominated by polygyne fire ants, fire ant abundance was higher and native ant diversity was lower in habitat patches connected by corridors than in unconnected patches. Conversely, in landscapes dominated by monogyne fire ants, connectivity had no influence on fire ant abundance and native ant diversity. Polygyne fire ants dominated recently created landscapes, suggesting that these corridor effects may be transient. Our results suggest that corridors can facilitate invasion and they highlight the importance of considering species' traits when assessing corridor utility.

Key words: ants; biodiversity; biological invasion; connectivity; corridor experiment; fire ant; habitat fragmentation; invasive ants; monogyne vs. polygyne ants; Savannah River Site, South Carolina, USA; Solenopsis invicta; *species richness.*

INTRODUCTION

Corridors, strips of habitat that connect otherwise isolated patches of the same habitat, are an increasingly common strategy to conserve biodiversity in fragmented landscapes. Although evidence for positive effects of corridors has been amassed from many studies (Tewksbury et al. 2002, Damschen et al. 2006, Gilbert-Norton et al. 2010), concerns remain about potential negative effects (Simberloff and Cox 1987, Weldon 2006, Wilkerson 2013; Haddad et al., *in press*). In particular, corridors may facilitate the spread of invasive species, which commonly threaten biodiversity and disrupt ecological processes (Simberloff and Cox 1987, Wilcove et al. 1998, Mack et al. 2000, Procheş et al. 2005). Ultimately, higher rates of dispersal by invasive species into connected patches could increase their spread, population densities, and ecological impacts. This potential drawback of corridors is critical to evaluate because the same principles that support corridor establishment for threatened species in habitat fragments suggest that corridors could simultaneously jeopardize entire communities through spread of invasive species.

Positive effects have been the focus of most corridor studies (Gilbert-Norton et al. 2010), whereas negative effects have received much less attention (Haddad et al., *in press*). Specifically, there is no evidence of corridors spreading invasive species (Haddad et al., *in press*). Perhaps corridors have not been found to spread invasive species because invasive species are typically

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good dispersers (Bufford and Daehler 2011) and therefore do not need corridors to spread through fragmented landscapes. Yet, invasive species are not uniformly strong dispersers and it is possible that corridors may differentially affect their spread, depending on the capacity of each species for movement. Recent work suggests that species traits and behaviors related to movement are important for predicting species responses to altered landscape configuration, including the presence of corridors (Damschen et al. 2008, Minor et al. 2009, Sullivan et al. 2011). We examine how differences in dispersal behavior of two social forms of invasive fire ants influence their use of corridors and their subsequent impacts on native ant diversity.

We focused on *Solenopsis invicta* (henceforth, fire ant) because it is one of the most noxious invasive species in the United States, its distribution is spreading globally (Ascunce et al. 2011), and it is responsible for displacement of native ants and a wide variety of other taxa (reviewed in Holway et al. 2002, Tschinkel 2006; but see King and Tschinkel 2006, 2008). Of central importance for our study, fire ants have two ecologically distinct social forms, monogyne and polygyne, defined by the number of reproductive queens per colony (Ross and Keller 1998). Monogyne colonies contain a single egg-laying queen, whereas polygyne colonies contain multiple egg-laying queens. The two social forms also differ in two ways highly relevant to conservation. First, ecological impacts of the polygyne social form are more severe than those of the monogyne form. In particular, polygyne invasions result in very high population densities (Macom and Porter 1996) that can devastate native ant communities (Porter and Savignano 1990), whereas the impact of monogyne invasions is comparatively more benign (King and Tschinkel 2006, Tschinkel 2006, LeBrun et al. 2012). Second, monogyne queens participate in mating flights at heights >100 m, dispersing up to several kilometers to establish new, spatially independent colonies (Markin et al. 1971). In contrast, polygyne queens are more limited in their dispersal abilities, typically establishing new colonies within several meters of their natal colony, often through budding (Tschinkel 1998, DeHeer et al. 1999). This fundamental difference in queen dispersal behavior suggests that the two social forms will respond differently to corridors, with the more dispersal-limited and ecologically damaging polygyne form benefiting most from the connectivity provided by corridors. Given how the two social forms differentially impact native species, the overall balance of negative and positive effects of corridors on ant communities may hinge on the difference in movement behavior of the two forms.

We tested the effects of open-habitat corridors on fire ant abundance and impact through a landscape-scale randomized-block experiment (Tewksbury et al. 2002). Specifically, we tested the predictions that (1) corridors increase the population densities of polygyne fire ants, and (2) higher population densities of polygyne fire ants in connected patches negatively affect native ant diversity. The first prediction is based on expectation from theory that corridors increase population densities of species with high population growth rates and limited dispersal (such as polygyne fire ants), in short time scales (Hudgens and Haddad 2003). In our study system, there are two mechanisms by which corridors could increase population densities of fire ants. The first is that corridors promote the initial spread of fire ants, in our case from their initial and limited distribution within the matrix where our experimental patches were created. Our patches were created by harvesting plantation pine forest, where fire ants occurred at very low densities (Appendix A). In contrast, the disturbed, open patches are preferred habitat for fire ants (Stiles and Jones 1998, Tschinkel 2006). Given that the area of two patches connected by a corridor is approximately double the area of an unconnected patch, it was much more likely that connected patches would have been created in the location of an already existing polygyne colony. This would lead to higher densities in connected than unconnected patches simply because population growth and spread could start immediately after patch creation in connected patches. The second mechanism is that corridors promote a rescue effect (Brown and Kodric-Brown 1977), increasing population persistence and thus size.

Two key features of our experiment permitted an unusually direct test of corridor effects on ant distribution. First, we controlled for typically confounding effects of patch area and length of habitat edges (Didham et al. 2012) by comparing connected and unconnected patches of equal area and equivalent shape (Fig. 1; see *Methods*). Second, five of our experimental landscapes were naturally colonized by monogyne fire ants and three by polygyne fire ants, providing a unique opportunity to compare entire landscapes dominated by each social form.

METHODS

Study area

We conducted this study at the Savannah River Site, South Carolina, USA (33.20° N, 81.40° W) in eight experimental landscapes (henceforth, blocks), designed to examine effects of corridors and patch shape on movement of plants and animals (Tewksbury et al. 2002). The blocks were created in 1999–2000 ($n = 6$) and 2007 ($n = 2$). Each block contained an array of open patches of early-successional longleaf pine (*Pinus palustris*) savanna embedded in a dense plantation forest matrix of loblolly (*Pinus taeda*), slash (*Pinus elliottii*), and longleaf pine, with scattered hardwoods (Fig. 1). Longleaf pine savanna is an endangered habitat of high conservation interest (Jose et al. 2006) and high ant diversity (Lubertazzi and Tschinkel 2003). All blocks were assisted in restoration toward longleaf pine savanna and were kept open by prescribed burns every 2–3 years, removal of hardwoods, and planting of native

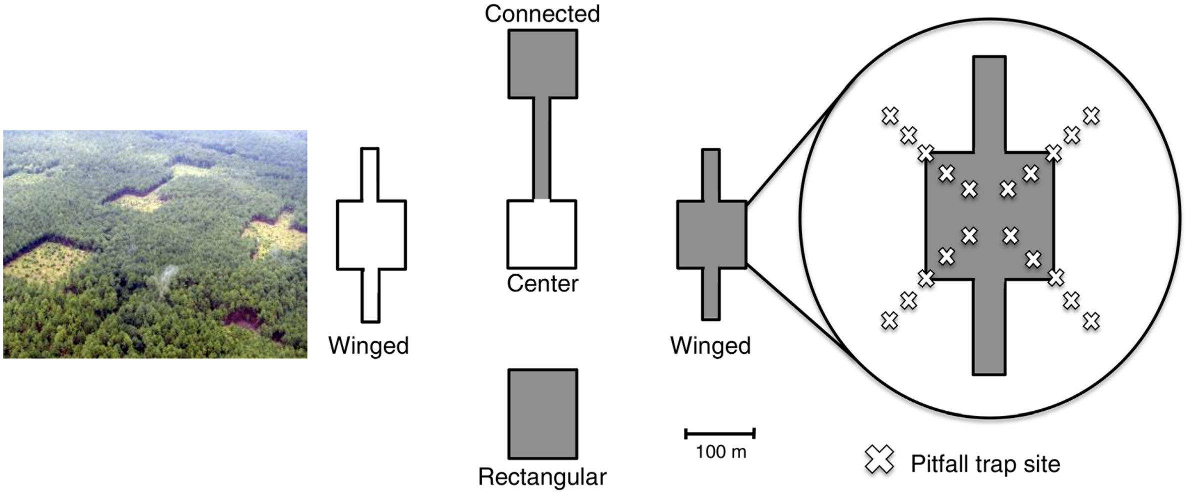

FIG. 1. Aerial photograph (credit: Ellen Damschen) and layout of one block for sampling invasive fire ants, *Solenopsis invicta*, and native ants ($n = 8$ blocks). Shaded patches (connected, winged, and rectangular) were sampled with pitfall traps. One patch is enlarged to show pitfall trap sites, which were positioned 0, 21.5, and 50 m from patch corners toward the center and 21.5 m and 50 m into the matrix.

species in an equal fashion across patch types and blocks.

Each block consists of a square, central patch (100 × 100 m) surrounded by four peripheral patches of the same habitat (Fig. 1). Each peripheral patch is 150 m from the central patch and is one of three randomly assigned patch types: "connected," "rectangular," or "winged." The connected patch is 100 × 100 m, with a 150 × 25 m corridor that connects to the center patch (1.375 ha total). Winged patches are also 100 × 100 m, but have two 75 × 25 m dead-end corridors ("wings") extending from opposite sides. Rectangular patches are 100 × 137.5 m; the additional area (100 × 37.5m) that makes these patches rectangular is equivalent to the area of the corridor of connected patches or to the wings of the winged patches. Thus, all peripheral patches have the same area. Furthermore, all patches in each block were created simultaneously from the same matrix plantations. Each block has one duplicate winged or rectangular patch (Fig. 1). In this study, we used only one, randomly selected duplicate patch from each block.

Ant sampling and identification

Within connected, rectangular, and winged patches, we sampled ants in July 2008 using pitfall traps, a standard method for measuring abundance and species composition of ground-dwelling ants (Bestelmeyer et al. 2000). We deployed 12 pitfall traps per patch. Traps were placed at 0, 21.5, and 50 m along transects that extended diagonally from the four corners of a given patch into the patch center (Fig. 1). Each trap consisted of a 15-dram (28.6 mm inner diameter) plastic vial, one-third full of 50% propylene glycol, inserted flush with the soil surface. To reduce "digging-in effects," we left traps capped for 48 h (Greenslade 1973). Once uncapped, traps were open for 48 h. Using the same methodology, we also collected ants in the pine matrix (details in Appendix A). All trapped ants were counted and identified to species, except for ants within the *Aphaenogaster rudis* species complex and the *Solenopsis* (Diplorhoptrum) *molesta* group, species of which are morphologically similar and taxonomically uncertain. Voucher specimens were deposited in the California Academy of Sciences (data *available online*).[10] As a second measure of fire ant abundance, we counted the number of active, mature fire ant nests (see details in Appendix B).

We determined the social form of fire ants using established genetic methods (Valles and Porter 2003; details in Appendix B). In all cases, one social form dominated each block. In blocks designated as monogyne blocks ($n = 5$), 99% of samples were homozygous, indicating monogyny. In blocks designated as polygyne blocks ($n = 3$), 87% of samples were heterozygous, indicating polygyny; two patches in these blocks had both social forms present. Because we could not randomly assign fire ant social form to blocks, we were concerned that factors unrelated to corridors might underlie any pattern in ant distribution that we observed among blocks. We tested two such factors that we considered especially important: land use history and block orientation; neither differed systematically between monogyne and polygne blocks (Appendix B).

Statistical analyses

To determine differences in fire ant pitfall trap incidence and number of workers in pitfall traps between polygyne and monogyne blocks, we used Mann-Whitney *U* tests. To determine effects of corridors on abundance of fire ants, we tested for an interaction between the

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[10] http://www.antweb.org

dominant fire ant social form in a given block and patch type on fire ant pitfall trap incidence, with block identity as a random effect, using a generalized linear mixed-effect model with a binomial response distribution and the Kenward-Roger approximation for hypothesis tests (Littell et al. 2006). In the main test, we restricted our analysis to the comparison of connected and winged patches; it provides the most direct test of connectivity because it simultaneously controls for edge and patch shape effects (Damschen et al. 2008). Results for analyses that include rectangular patches are provided in Appendix C. We evaluated overdispersion using the Pearson residuals generated from our analysis and found that the overdispersion parameter was close to 1.0 (±1.8), indicating an absence of overdispersion (Littell et al. 2006). For pitfall data, incidence is preferable to counts of individuals when estimating density of ants because individuals are highly aggregated in space (Gotelli et al. 2011). We employed a similar generalized linear mixed-effect model for nest counts, using a quasi-Poisson distribution to adjust for overdispersion. Results for nest data are in Appendix C.

To determine effects of corridors on native ants at the community level, we estimated species richness and evenness, using Hurlbert's (1971) probability of interspecific encounter ("PIE") for connected, rectangular, and winged patches. We estimated these metrics with sample-based rarefaction on incidence data from pitfalls, using EcoSim v. 7.71 (Gotelli and Entsminger 2004) with 1000 iterations. We used the resulting 95% confidence intervals for each patch type to assess differences among patch types, rarified to the number of samples in the patch type with the fewest samples. We ran analyses separately for polygyne and monogyne blocks. We calculated a nonparametric estimate of asymptotic species richness, first-order jackknife (Jack1), and corresponding confidence intervals (Jack1 ± 2 SE) for each patch type using the vegan package (R package v. 2.0-2; Oksanen et al. 2013). We selected Jack1 as a richness estimator because it is appropriate for incidence data and is among the most accurate species richness estimators for intermediate-to-high sample coverage (Brose et al. 2003); evaluation of our data showed that Jack1 was highly correlated with observed species richness ($r^2 = 0.98$).

Results

We collected and identified 10 775 ants of 49 species in pitfall traps in the patches (Appendix C: Table C1). Fire ants comprised 99.8% of nonnative ants and 68% of all ants. Genetic assessment of the spatial distribution of fire ant social forms revealed that one social form dominated each block (see *Methods*). Similar to previous studies (Macom and Porter 1996, reviewed in Tschinkel 2006), social form had a strong effect on fire ant density. Pitfall traps from polygyne blocks contained more than 10 times as many individual fire ants and 1.6 times the pitfall trap incidence of fire ants as those from monogyne blocks (all $P < 0.001$). The number of fire ant nests was likewise higher in polygyne blocks (Appendix C: Fig. C1).

Corridors significantly increased the abundance of polygyne but not monogyne fire ants, as reflected by a significant interaction between the dominant social form present in a given block and patch type (with or without a corridor) on fire ant pitfall trap incidence (generalized linear mixed model; for interaction, $F_{1,12} = 7.48$, $P = 0.02$; for patch type, $F_{1,12} = 3.49$, $P = 0.09$; for block social form, $F_{1,\ 6.9}, = 5.64$, $P = 0.05$). Corridors had a positive effect on pitfall trap incidence in polygyne blocks, averaging 36% higher incidence compared to unconnected patches ($F_{1,12} = 6.67$, $P = 0.02$; Fig. 2A and Appendix C: Fig. C1). In contrast, corridors had no effect on pitfall trap incidence in monogyne blocks ($F_{1,12} = 0.91$, $P = 0.36$; Fig. 2A and Appendix C: Fig. C1).

Native ant species diversity in polygyne blocks was lower in connected patches than unconnected patches (Fig. 2B, Appendix C: Table C2, and Fig. C2). In polygyne blocks, connected patches had 23% lower species richness and 11% lower evenness than unconnected patches (Fig. 2B and Appendix C: Fig. C2, and Table C2). In monogyne blocks, however, there was no corridor effect on species richness or evenness (Fig. 2B and Appendix C: Fig. C2).

The lower species diversity in connected patches of polygyne blocks is most likely due to the higher abundance of fire ants in those patches (Fig. 2). Consistent with other studies (reviewed in Holway et al. 2002), fire ant pitfall incidence was negatively correlated with native ant species richness (Fig. 2C; overall: $r^2 = 0.65$, $P < 0.001$; from monogyne blocks: $r^2 = 0.56$, $P = 0.001$; from polygyne blocks: $r^2 = 0.70$, $P = 0.004$). Patches in which fire ants were absent from all pitfall traps had approximately six times as many native species as patches in which fire ants were present in every trap.

Discussion

Our results reveal how the effect of corridors on ant communities can hinge on variation in dispersal ability and population density associated with colony social form of an invasive ant species. The different dispersal behaviors of monogyne and polygyne fire ant queens probably determined their response to corridors, and differences in colony density of the two forms in turn determined effects on native ant communities. Habitat patches connected by corridors are expected to harbor higher, not lower, species richness than unconnected patches of the same area (Gonzalez et al. 1998, Damschen et al. 2006, Gilbert-Norton et al. 2010). Yet, in blocks dominated by polygyne fire ants, we found negative net effects of corridors at the community level; species richness and evenness were both lower in connected than in unconnected patches. By increasing abundance of polygyne fire ants, patch connectivity via corridors apparently negated any potential benefit of corridors to other ant species. This finding provides a possible

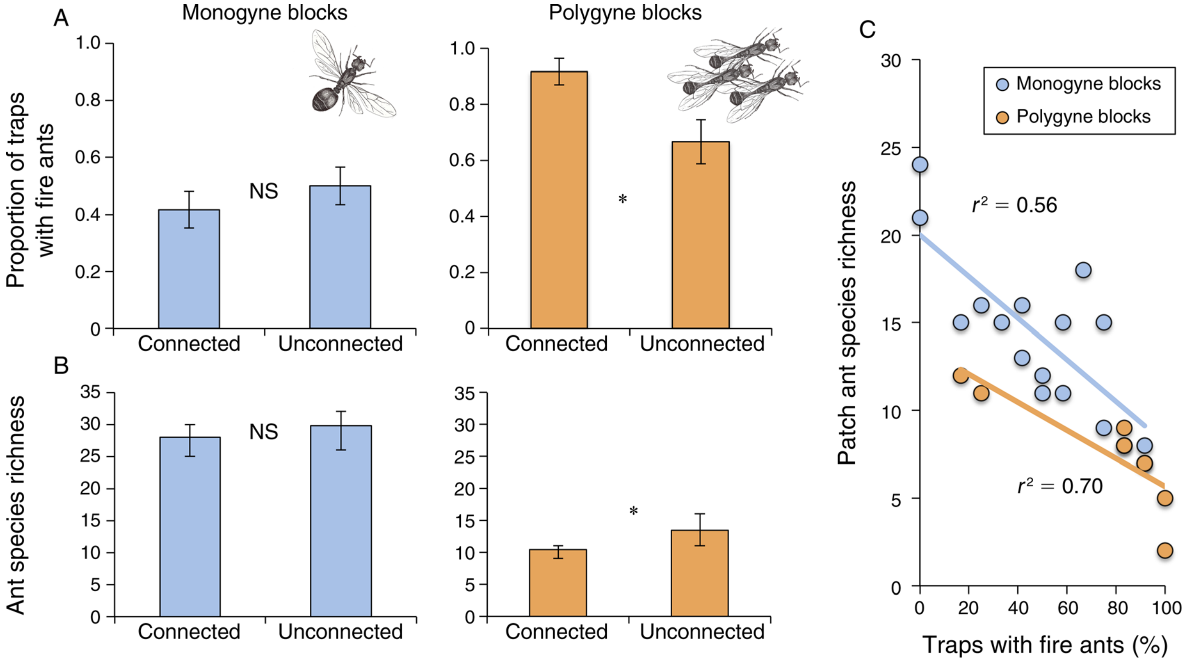

FIG. 2. (A) Effect of corridors on fire ant abundance, measured as proportion of traps with fire ants (mean ± SE) in connected and unconnected patches (unconnected patches are represented by winged patches, which are equal in area and nearly equivalent in edge : area ratio to connected patches). Fire ants have two social forms: monogyne, which disperse widely but establish at lower densities, and polygyne, which tend to disperse poorly but establish at high densities. Blue bars indicate monogyne blocks ($n = 5$) and orange bars indicate polygyne blocks ($n = 3$). (B) Effect of corridors on native ant species richness, rarefied to lowest number of samples per patch type across blocks. Error bars indicate rarefaction 95% confidence intervals. Asterisks indicate statistical significance ($P < 0.05$) for the polygene blocks (A, B). (C) Negative correlation of fire ant abundance and species richness of native ants in both monogyne and polygyne blocks. Points represent patches.

explanation for patterns from a previous study in a subset of our blocks that found lower evenness among ant genera in connected patches (Orrock et al. 2011), although that study did not provide data on ant species or social form.

Our results support the prediction that corridors promote spread of polygyne fire ants, increasing their densities in connected patches. Previous studies have also concluded that corridors increase population densities (Haddad and Baum 1999, Collinge 2000, Baum et al. 2004, Gilbert-Norton et al. 2010). In our study, fire ants occurred at low densities in the matrix habitat before patch creation (Appendix A; see also Tschinkel 2006). Because fire ants thrive in open and disturbed habitats (Stiles and Jones 1998, Tschinkel 2006), their populations increased in all patches upon creation. This increase was pronounced for polygyne fire ants in connected patches. We suggest two interrelated reasons. First, polygyne fire ants benefited from connectivity more than monogyne fire ants because they are more dispersal limited. Second, the high growth rate potential of polygyne colonies and the relatively short time scale of our study are conditions that favor large population size in connected patches (Hudgens and Haddad 2003).

The spread of polygyne fire ants via corridors may be a transient phenomenon. Indeed, two of the three polygyne blocks were created more recently (although patches within each block were created at the same time) than the monogyne blocks and only those two blocks showed higher fire ant abundance in connected patches. Other studies in our system have found that that time mediates community dynamics (Damschen et al. 2008, Damschen and Brudvig 2012). However, the low number of newly created blocks in our study prevents us from teasing apart effects of patch age, social form, and corridors on fire ant abundance. In spite of potential transience, the ecological impacts of fire ant invasion on native ant communities can be dramatic during the initial phase of invasion. Porter and Savignano (1990) documented that during the initial phase of invasion, polygyne fire ants caused extreme declines in native ants. Morrison (2002) resampled the same sites as Porter and Savignano (1990) 12 years later and found that fire ant abundances had declined and native ants had partially recovered. This pattern may be common in invasions (Strayer et al. 2006, Dostál et al. 2013). Future work will be needed to assess the potentially transient nature of the role of corridors on invasions and the specific roles that corridors play in the long-term abundances of both invasive and native species.

Our interpretation of why connected patches in polygyne blocks had higher densities of fire ants than unconnected patches in the same blocks is tempered by the caveat that we did not observe the establishment or spread of fire ants between patches. Although we tested and rejected alternative hypotheses (corridor orientation and land use history) that might account for the distribution of polygyne fire ants (Appendix B), the only unambiguous way to show that polygyne fire ants benefit from corridors would be to eliminate all fire ants from all patches, reintroduce the polygyne social form into the center patch of each block, and monitor their spread. Ethical considerations and logistical constraints prevented us from doing so.

Despite the detrimental effects of corridors presented here, the weight of empirical evidence still favors beneficial effects of corridors in conservation (Haddad et al. 2011). Many more studies have shown beneficial rather than detrimental effects of corridors on dispersal and diversity (Gilbert-Norton et al. 2010). In situations where corridors are likely to facilitate dispersal of invasive species, efforts should be made to mitigate their impacts, for example, by reducing the abundance or impact of the invasive species or by taking steps to reduce its spread.

Considering that concerns about corridors facilitating the spread of invasive species were raised almost 30 years ago (Simberloff and Cox 1987), it is perhaps surprising that empirical examples of the phenomenon have not been reported previously (Haddad et al., *in press*). This may be because invasive species often have high dispersal capabilities (Bufford and Daehler 2011), as is the case with the monogyne form of fire ants. Given that species with strong movement capacities are typically not dispersal limited, corridors are unlikely to facilitate their spread; indeed, landscape connectivity appears generally more important for native than for invasive species (Damschen et al. 2006, Minor et al. 2009). Some invasive species, however, have inherently poor dispersal abilities but spread well through accidental human transport (Mack and Lonsdale 2001; e.g., polygyne fire ants [Tschinkel 2006, King et al. 2009] and Argentine ants [*Linepithema humile*; Suarez et al. 2001]). In such cases with invasive species that are dispersal limited (but successful by other measures), corridors are likely to facilitate spread and could result in a net negative impact on native species. More studies on species with various dispersal abilities and with different habitats and types of corridors would provide further guidance on when corridors are most likely to spread invasive species across conservation lands.

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SUPPLEMENTAL MATERIAL

Appendix A

Pine matrix sampling and patch–matrix comparisons (*Ecological Archives* E095-179-A1).

Appendix B

Information on nest counts, social form determination, land use, and block orientation (*Ecological Archives* E095-179-A2).

Appendix C

Rectangular patch and nest results, rarefaction curves, species list, and diversity measures (*Ecological Archives* E095-179-A3).