PRIMARY RESEARCH ARTICLE

From endogenous to exogenous pattern formation: Invasive plant species changes the spatial distribution of a native ant

Kevin Li[1]* | Yifan He[2]* iD | Susanna K. Campbell[3] | A. Shawn Colborn[3] | Eliot L. Jackson[2] | Austin Martin[2] | Ivan V. Monagan Jr.[3] | Theresa Wei Ying Ong[3] | Ivette Perfecto[2]

[1]Department of Civil, Construction, and Environmental Engineering, North Carolina State University, Raleigh, NC, USA

[2]School of Natural Resources and Environment, University of Michigan, Ann Arbor, MI, USA

[3]Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, USA

Correspondence
Ivette Perfecto, School of Natural Resources and Environment, University of Michigan, Ann Arbor, MI, USA.
Email: perfecto@umich.edu

Abstract

Invasive species are a significant threat to global biodiversity, but our understanding of how invasive species impact native communities across space and time remains limited. Based on observations in an old field in Southeast Michigan spanning 35 years, our study documents significant impacts of habitat change, likely driven by the invasion of the shrub, *Elaeagnus umbellata*, on the nest distribution patterns and population demographics of a native ant species, *Formica obscuripes*. Landcover change in aerial photographs indicates that *E. umbellata* expanded aggressively, transforming a large proportion of the original open field into dense shrubland. By comparing the ant's landcover preferences before and after the invasion, we demonstrate that this species experienced a significant unfavorable change in its foraging areas. We also find that shrub landcover significantly moderates aggression between nests, suggesting nests are more related where there is more *E. umbellata*. This may represent a shift in reproductive strategy from queen flights, reported in the past, to asexual nest budding. Our results suggest that *E. umbellata* may affect the spatial distribution of *F. obscuripes* by shifting the drivers of nest pattern formation from an endogenous process (queen flights), which led to a uniform pattern, to a process that is both endogenous (nest budding) and exogenous (loss of preferred habitat), resulting in a significantly different clustered pattern. The number and sizes of *F. obscuripes* nests in our study site are projected to decrease in the next 40 years, although further study of this population's colony structures is needed to understand the extent of this decrease. *Elaeagnus umbellata* is a common invasive shrub, and similar impacts on native species might occur in its invasive range, or in areas with similar shrub invasions.

KEYWORDS
autumn olive, *Elaeagnus umbellata*, *Formica obscuripes*, invasive species, landcover change, pattern formation, spatial distribution, thatching ant

*These authors are co-first authors.

1 | INTRODUCTION

While the impacts of invasive species are often strong and widespread, their particulars are context-dependent, relating to the functional ecology of non-native species and the structure, evolutionary experience, and diversity of native communities (Pyšek et al., 2012; Ricciardi, Hoopes, Marchetti, & Lockwood, 2013; Schirmel, Bundschuh, Entling, Kowarik, & Buchholz, 2016; Vilà et al., 2011). There exists no universal measure or theory of invasive impact (Ricciardi et al., 2013). Furthermore, the impact of invasive species on the spatial distribution of native species is often overlooked for research. Although many studies focus on the distribution of invasive species through phenomenological and mechanistic modeling (Gallien, Münkemüller, Albert, Boulangeat, & Thuiller, 2010), the subsequent impact on the spatial ecology of the native species is not as well understood.

Within the field of spatial ecology, species distribution patterns can be primarily thought of in terms of two pattern-forming processes (Fortin & Dale, 2005): exogenous processes that reflect an external ecological or environmental forcing (Belsky, 1986; Boaler & Hodge, 1962; Hook & Burke, 2000), and endogenous processes that result from dynamic interactions intrinsic to a system of ecological relationships (van de Koppel et al., 2008; Petrovskii & Malchow, 2001; Vandermeer, Perfecto, & Philpott, 2010). The Turing mechanism (Turing, 1952) is fundamental to the understanding of many endogenously formed patterns in nature and is cited among many natural systems as an underlying mechanism driving the formation of nonrandom patterns in space (Couteron & Lejeune, 2001; Rietkerk & van de Koppel, 2008; Vandermeer, Perfecto, & Philpott, 2008). Using diffusion equations, Turing demonstrated that complex spatial patterns could form in an otherwise homogenous environment, through the interaction of "activator" and "repressor" components and their rates of diffusion in space. In ecology, activation is commonly the propagation of a species in space, with repression occurring when a natural enemy (or inhibitory condition, e.g., resource depletion) increases as a result, preventing continuous expansion.

The spatial ecology of ant colonies has been extensively studied, documenting a wide range of patterns. Competition is thought to be the major mechanism driving uniform distribution of populations in space (Deslippe & Savolainen, 1995; Levings & Franks, 1982; Ryti & Case, 1986; Wiernasz & Cole, 1995). Although uniform spatial arrangements are common, aggregations (Henderson & Jeanne, 1992; Rissing, Johnson, & Pollock, 1986; Vandermeer et al., 2008) and random distributions also occur (Herbers, 1985; Soares & Schoereder, 2001; Weseloh, 1994). The Turing mechanism provides an appropriate lens for understanding many of these patterns. Vandermeer et al. (2008) demonstrated that ant nest budding by *Azteca sericeasur* (previously identified as *Azteca instabilis*) acted as the activator in the system, while natural enemy exploitation of dense colony clusters acted as the repressor, resulting in a clustered distribution. Uniform nest distributions may also form through a Turing-like mechanism, in a fashion similar to the propagation–inhibition

interactions that drive regular patterns in semiarid vegetation (Couteron & Lejeune, 2001).

The western thatching ant, *Formica obscuripes*, is native to much of temperate western North America (Weber, 1935) and was fairly common in open fields of the E. S. George Reserve (ESGR) in Michigan when intensive studies were conducted on this species (Talbot, 1959, 1972). The reproductive biology of *F. obscuripes* allows for the possibility of nest distribution patterns to be uniform or clustered. Uniform nest distributions may arise through new nest dispersal via mating flights, which Talbot (1972) observed in the ESGR. Following mating flights, inseminated queens typically engage in temporary social parasitism, whereby the nest of another ant species is forced to adopt the *F. obscuripes* queen and tend her until her own offspring take over the host nest (Stockan & Robinson, 2016; Weber, 1935). This mode of dispersal promotes uniform pattern formation because flights allow founding queens to travel farther from the original nest, where intraspecies competition is lower. Furthermore, *F. obscuripes* may tend to exclude other ant species in its proximity, so potential host nests may be more easily found farther away (Stockan & Robinson, 2016).

Nest budding, the alternate mode of dispersal for *F. obscuripes*, may promote clustered nest distributions. The colony structure of *F. obscuripes* is polygynous, in that colonies contain multiple queens (McIver, Torgersen, & Cimon, 1997). As such, *F. obscuripes* can engage in nest budding, whereby one or more queens disperse on foot with a group of workers from the "parent" nest to establish a new "daughter" nest (Muckermann, 1902; Stockan & Robinson, 2016). This results in multinest (polydomous) colonies whose workers may pass freely between associated nests (O'Neill, 1988) and can lead to a large "supercolony" nest complex (McIver et al., 1997). The distribution of such nest complexes has been found to be clustered, which is likely due to the cooperation and lack of competition between related nests. In such cases, the scale of aggregation is thought to reflect the migration distance between parent and daughter nests (McIver et al., 1997).

Since Talbot's original observations, one nesting area in the ESGR has undergone dramatic vegetative succession from an open field to a shrub-dominated field, dominated in particular by the invasive shrub *Elaeagnus umbellata*, or autumn olive (Severtsen, 2005). This shrub is native to China, Japan, and Korea and was introduced to the United States in 1830 as an ornamental and wildlife habitat plant (Black, Fordham, & Perkins-Veazie, 2005). It is considered invasive within North America, having spread across much of the Eastern United States and as far west as the Pacific Northwest and Hawaii, as well as to Ontario, Canada (EDDMapS, 2016; Munger, 2003). It is not yet invasive elsewhere outside its native range, although careful monitoring is advised in Europe (CABI, 2016). *Elaeagnus umbellata* was first collected in Michigan in 1939 (Reznicek, Voss, & Walters, 2011) and first appeared in the ESGR in the early 1980s, where it is now abundant in open grasslands, along roads, and in forest edges (Brym, Lake, Allen, & Ostling, 2011).

Like many invasive shrubs, *E. umbellata* has attractive fruits and is readily bird-dispersed (Lafleur, Rubega, & Elphic, 2007). Furthermore, it can grow as compact thickets that limit light beneath its canopy and

produces secondary chemicals that inhibit native species seed germination and growth (Brantley & Young, 2009; Orr, Rudgers, & Clay, 2005). It also exhibits a relationship with nitrogen-fixing bacteria that alters soil chemistry (Baer, Church, Williard, & Groninger, 2006), which can affect the surrounding plant composition.

Although the effects of invasive plants are widely documented, the impact of an invasive plant on native ant colony propagation and dispersal has not been studied in depth and may provide key insights into mechanisms that shape ant population distribution and determine invasive plant impacts. In this study, we focused on the distribution of *F. obscuripes* within an old-field site that has been heavily invaded by *E. umbellata*. We examined the spatial patterns of *F. obscuripes* before and after the invasion of *E. umbellata* from 1980 to 2015, with particular attention to how the spatial patterns of *F. obscuripes* may have been shaped as a result of its reproductive biology and the differing ecological processes between the two periods. We quantified landcover change with historical aerial photographs and compared landcover compositions around nests in 1980 and 2015 using georeferenced locations of historical and current nests to infer *F. obscuripes* habitat preference in those years. To examine potential relatedness of nests within the distribution pattern, we analyzed aggressiveness between nests by separation distance and shrub cover in a multiple linear regression model. Finally, we used nest size data from partial censuses in 2013 and 2015 to build a stage-structured population model and projected the trend of the *F. obscuripes* population over the next 40 years.

2 | MATERIALS AND METHODS

2.1 | Study site

We conducted our study on a population of *F. obscuripes* in the Edwin S. George Reserve (ESGR), a 525-hectare preserve located in Livingston County, Michigan, managed by the University of Michigan. This population was studied by Mary Talbot beginning in 1953 (Talbot, 1956). In 1980, Talbot created a map of the ant nest distribution in the ESGR, which we use in our analysis (Talbot, 1980). Thus, we have the capability to study long-term effects of the introduction and invasion of *E. umbellata*, which was first observed in the ESGR in the early 1980s (Brym et al., 2011).

Our study site was a 24.5 ha section of old field located in the central part of the ESGR (84.014807° W, 42.458722° N, Figure 1). The fields of the ESGR were cleared for farmland by 1870 and cultivated until around 1900; afterward, they served as pasture until the property was converted to a reserve in the late 1920s (Evans & Dahl, 1955). When we conducted follow-up ant nest censuses in 2013 and 2015, the site was in various stages of invasion by woody shrubs, dominated by *E. umbellata*, and secondary forest. A remote-sensing study in 2005 found that, within a 95 ha area of the ESGR that includes our study site, *E. umbellata* stands covered a total of 13 ha, while the prior landcover type, grasses, and forbes, covered only 6 ha (Severtsen, 2005). The southern half of the study site was dominated by secondary forest and reflected a more advanced stage of succession than the northern portion, which still consisted mainly of shrubs and remnant old field. These sites were surrounded by secondary oak–hickory forest that was also encroaching onto the field. Major species found in the remnant old field in addition to *E. umbellata* included the native species *Schizachrium scoparium* (Michx.) Nash, *Monarda fistulosa*, and *Rubus* spp., as well as the introduced species *Achillea millefolium* and *Hypericum perforatum* (Greiling & Kichanan, 2002).

2.2 | Population survey

In October 2013, we geo-located *F. obscuripes* nests in the northern portion of the study area, using a GPS (Trimble GeoXH) to mark locations while also noting nest diameter. In October 2015, we conducted
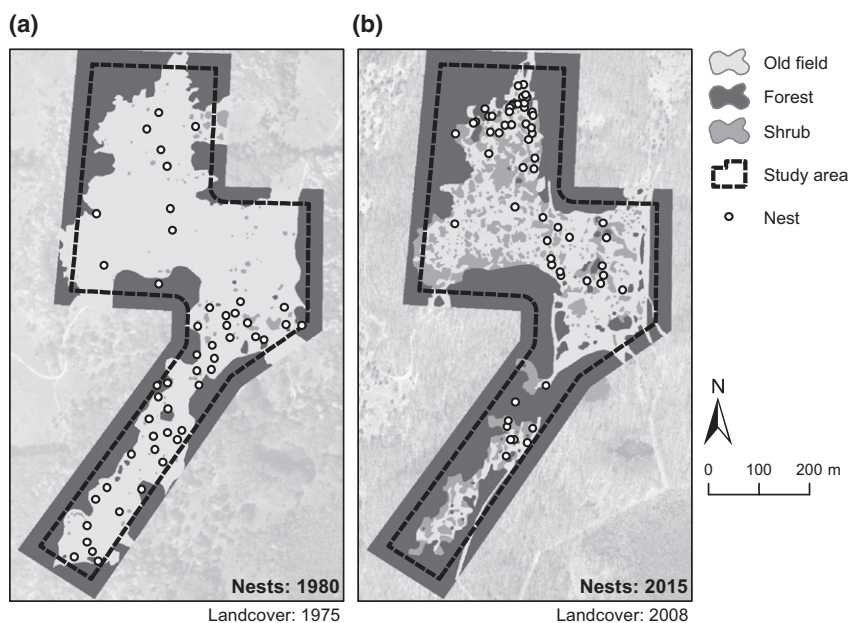
(a)   **(b)**

Old field
Forest
Shrub
Study area
○ Nest

Nests: 1980   Nests: 2015
Landcover: 1975   Landcover: 2008

N

0   100   200 m

FIGURE 1 Map of the study site with locations of nest sites of *Formica obscuripes* in the Edwin S. George Reserve, Michigan, in 1980 (a) and 2015 (b). Nest points are overlaid on digitized landcover categories for the closest dates available, 1975 and 2008. Background images are the original aerial imagery of the same years

follow-up nest surveys, noting changes in diameter and nest activity, as well as locations of new nests. We continued to use Trimble GeoXH, as well as a smartphone GPS application (Trimble Outdoors Navigator) to mark nest locations. We expanded the 2013 survey area to include the southern portion of our field site in order to cover more of Talbot's (1980) survey area. We digitized ant nest locations from scanned and georeferenced copies of Talbot's paper maps (Talbot, 1980) using the "heads-up" digitizing method (Bolstad, 2012).

2.3 | Ant nest aggression trials

In 2015, we conducted aggressive behavior assessments (Pirk, Neumann, Moritz, Pirk, & Pamilo, 2001) in on-site arenas to determine the potential relatedness of colonies of *F. obscuripes* in the northern portion of the study area. For each aggression trial, we placed two ants from different nests in a neutral arena, that is, a plastic container (Beye, Neumann, & Moritz, 1997). Two observers watched the two ants for 5 min and independently reported the level of aggression between the ants using a score based on Beye et al. (1997). The scoring scale, which we modified to better characterize *F. obscuripes* behavior, is as follows: 1—individuals ignored one another; 2—individuals antennated one another; 3—some physical contact without prolonged aggression; 4—prolonged aggression; 5—fight resulting in death of one or both ants. The two observers determined the final value by consensus.

We performed a multiple linear regression with aggression score as the dependent variable and geographic separation distance and proportion shrub landcover between nest pairs as candidate independent variables. The interaction between separation distance and proportion shrub landcover was also considered, to determine whether shrub landcover moderated the effect of separation distance on aggression. We calculated proportion shrub landcover from a 20 m-wide transect spanning nest pairs, based on the 2008 landcover map (see "Landcover change and *E. umbellata* expansion" methods). We utilized R (R Core Team, 2016) to perform a multiple linear regression and other statistical analyses.

2.4 | Ant nest spatial patterns

We compared the spatial patterns of *F. obscuripes* nests in 1980 and 2015 using the calculated Ripley's *K* statistics (Ripley, 1976) at a range of scales from 0 to 60 m. Ripley's *K* quantifies clustering as a function of the number of points within a given radius (i.e., the scale of analysis). This is compared to the expected statistic given a null hypothesis of random nest distribution. *K*-values that are greater than the expected null represent nest patterns that are more clustered than random, while *K*-values less than the null represent more uniform patterns. We compared the observed patterns to 999 simulated random patterns based on a uniform Poisson process. Given the shape and size of the study area, we limited our analyses to a maximum radius of 60 m, following recommended practices (Fortin, Dale, & ver Hoef, 2002). We performed spatial analysis and simulation using the R package "spatstat" (Baddeley & Turner, 2005).

2.5 | Estimating landcover change and *E. umbellata* expansion

We used overall shrub expansion as a proxy for *E. umbellata* expansion, based on observations that *E. umbellata* comprised the majority of shrub cover in this area (Severtsen, 2005). We quantified *E. umbellata* expansion from 1980 to 2015 by assessing landcover change through historical aerial photographs of the study site. We use the term "landcover" throughout this text to specifically refer to the results of our aerial photo digitization process, which categorized the dominant vegetation of the study site into three classes: field, shrub, or forest. Our landcover estimates were based on historical aerial photographs taken in 1975 and 2008, as these years were publicly available on the USGS EarthExplorer database and the closest to the ant census dates. The 1975 image was a digitized 1:36,000 scale film photograph, and the 2008 image was a 0.3 m resolution digital image. We classified landcover using heads-up digitizing (Bolstad, 2012) to outline distinct polygons of contiguous landcover that were distinguishable by size, texture, shadow, and color at a 1:1,500 scale. Although other landcover types outside our three classes did exist, such as dirt roads and some small structures, these were negligible in comparison with the dominant landcovers. Polygons were converted to a contiguous 1 m resolution raster grid for landcover preference analysis.

2.6 | Ant nest landcover preference

To determine whether ants showed a preference for certain landcover types within the foraging range of their nesting sites, we measured landcover compositions around nests and compared this to the general landcover availability. We quantified landcover composition as the percentage of each class of landcover within a radius around each nest, repeated for radii from 5 to 30 m, at intervals of 5 m. We compared this to the general availability of the landcover classes, which we estimated from the average landcover composition of randomly placed points in the study area.

To address the unique issues of working with compositional data (Aitchison, 1986), we converted percent composition to log ratios between two landcover types, that is, $\ln(x_{U1}/x_{U2})$, where x_{U1} represents the percent that was landcover 1, as compared to landcover 2, x_{U2} (Aebischer, Robertson, & Kenward, 1993). This framework represents landcover preference on a relative scale, so that preference for building nests in landcover 1 is in terms of how often the ants use that landcover as compared to landcover 2. This ratio was then compared to the ratio calculated using the average landcover composition of the study area, which represents the landcover composition of randomly distributed nests. The average random landcover composition was calculated from the mean of 1,000 random point placements in the landscape with the same point intensity (Poisson distribution mean) as the actual data.

Specifically, we were interested in how *F. obscuripes* preferred the field landcover class to the shrub landcover class, and how its preference may have changed between 1980 and 2015 in the context of the *E. umbellata* invasion. We tested a null hypothesis of zero

difference between the observed landcover log-ratio preferences and the general landcover availability using a one-sample permutation test with 1,000 repetitions. We performed compositional preference analysis with the R package "adehabitatHS" (Calenge, 2006).

2.7 | Lefkovitch matrix population projection

We developed a stage-structured population model (Lefkovitch, 1965) to estimate the population trend of *F. obscuripes* in the northern portion of our study area. Stage-structured population models assume populations are divided into stage classes, with independent dynamics determining the rates that individuals transition between stages. We defined the stages of the nest population based on bins of the nest size distribution, measured by the basal diameters of each nest mound. We are able to use nest size as a proxy of nest health in *Formica* species because larger nest sizes positively correlate with health indicators such as age, foraging activity and reproductive capacity (Stockan & Robinson, 2016). See Figure 2a for definitions of nest stage classes.

The model takes the form $N_{t+1} = PN_t$, where N represents a vector of the number of nests in each population stage at time t or $t + 1$. $\mathbf{P}$ represents the Lefkovitch projection matrix, which contains the transition and fecundity rates between population stages (Figure 2b). The three transition rates in the Lefkovitch matrix in Figure 2b represent the proportion of nests growing (G_{pi}) or regressing (R_{pi}) from stage i to stage p, or surviving as the same stage (S_i). As an example, among the nine nests in stage 1 in 2013, only one nest grew to stage 2 in 2015, so the growth transition rate G_{21} was 1/9.

We estimated fecundity rates assuming that all nest stages were equally capable of producing offspring, as tracking individual nest reproduction was beyond the scope of this study. The fecundity, F_p, of any stage nest in 2013 is defined as the probability of producing a new nest of size stage p by 2015. We found this by dividing the number of new stage p nests in 2015 by the total population in 2013. Thus, the fecundity rates for producing new stage p nests are identical across all nest stages. As no new nests were beyond size stage 2, we did not calculate fecundity rates for $p > 2$.

Using the R package "popbio" (Stubben & Milligan, 2007), we ran 20 iterations of the population projection to estimate the population trend for the next 40 years. We also calculated the dominant eigenvalue of the matrix, which gives the population growth rate once a stable distribution of stages has been reached (Vandermeer & Goldberg, 2013).

3 | RESULTS

3.1 | Population survey and historical data

Fifty nests mapped by Talbot in 1980 fell within our study area. In 2013, we found 44 nests in a census of the northern part of the study area. In 2015, we found 40 nests in this northern area, with six new nests and 10 nests abandoned. Surveying the rest of our study area in 2015 also identified 20 more nests in the southern part, so there was a total of 60 nests in the entire area that year.
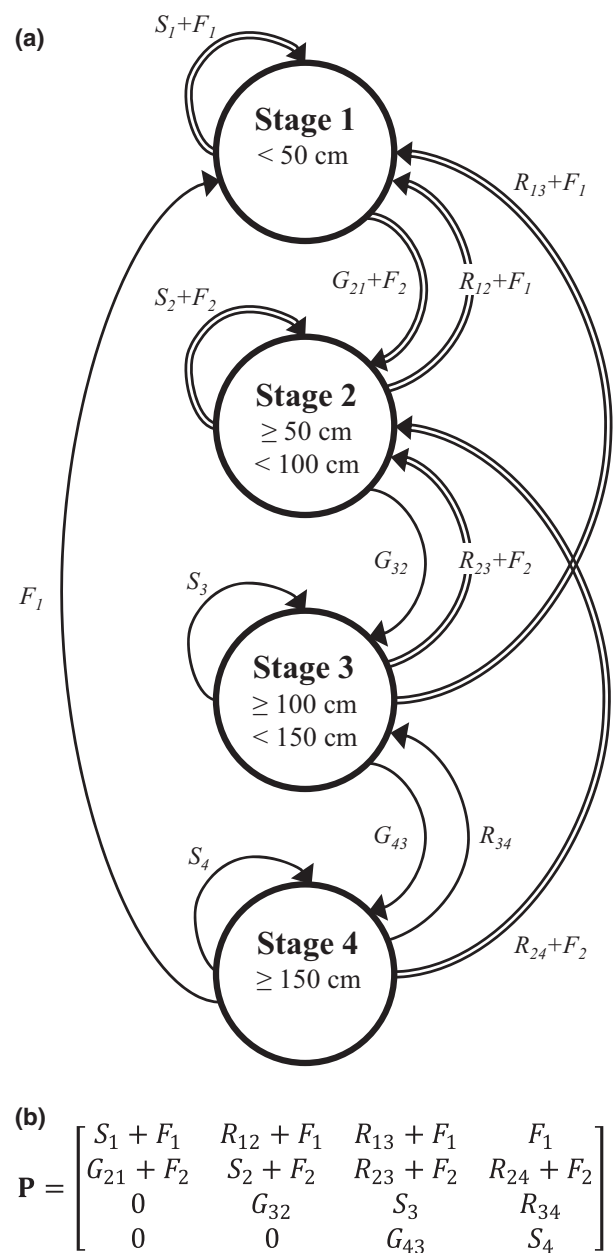

(a)

$S_1 + F_1$

Stage 1 < 50 cm

$R_{13} + F_1$

$G_{21} + F_2$ $R_{12} + F_1$

$S_2 + F_2$

Stage 2 ≥ 50 cm < 100 cm

F_1

G_{32} $R_{23} + F_2$

S_3

Stage 3 ≥ 100 cm < 150 cm

G_{43} R_{34}

S_4

Stage 4 ≥ 150 cm

$R_{24} + F_2$

(b)

$$\mathbf{P} = \begin{bmatrix} S_1 + F_1 & R_{12} + F_1 & R_{13} + F_1 & F_1 \\ G_{21} + F_2 & S_2 + F_2 & R_{23} + F_2 & R_{24} + F_2 \\ 0 & G_{32} & S_3 & R_{34} \\ 0 & 0 & G_{43} & S_4 \end{bmatrix}$$

FIGURE 2 A conceptual diagram of the stage-structured model of nest size stages (a), where terms G_{pi} and R_{pi} represent growth and regression transition rates, respectively, from stage i to p; S_i represents the probability of surviving and remaining in stage i; and fecundity rates F_1 and F_2 represent the rates that new stage 1 and stage 2 nests are produced by each stage. Each fecundity rate was assumed to be the same for all stages. Fecundity rates were added to the transition rates between appropriate stages; dynamics that were the sum of two rates are represented as double-line arrows in the diagram. These rates were used to construct the Lefkovitch projection matrix $\mathbf{P}$ (b), which was multiplied iteratively with N_t, a vector of the number of nests at each stage at time t

3.2 | Ant nest aggression model

Aggression between ant nests increased significantly with greater separating distance ($p < .001$), but had a significant negative

interaction with greater shrub landcover in the transect between the two nests ($p < .001$). The fitted model was

$$\text{aggression score} = 1.4 + 0.016 \, \text{distance} + 1.8 \, \text{shrub} - 0.037 \, \text{shrub} \times \text{distance}$$

where distance and shrub are separating distance and proportion shrub landcover, respectively. The shrub landcover main term was not significant ($p = .11$). Distance and shrub landcover variables were not collinear ($r = 0.45$). When there was a lower proportion of shrubs in the transect between nest pairs, aggression increased more with distance, while in areas with a higher shrub proportion, aggression tended to remain low. The moderating effect of shrub landcover on the positive relationship between aggression and distance is demonstrated in Figure 3, where the dotted line represents the predicted relationship between separating distance and aggression in relatively low proportion shrub landcover (shrub = 0.2), and the solid line represents the same relationship but in relatively high proportion shrub landcover (shrub = 0.4). The proportion of shrub landcover between the nests examined ranged from 0 to 0.6, with a mean of 0.3 and interquartile range of 0.2. This multiple linear regression model explained 17% of the variance, as determined by adjusted R^2.

3.3 | Ant nest spatial patterns

We performed the Ripley's K analysis on the nest spatial patterns of the years for which we had the most complete spatial census, 1980 ($n = 50$) and 2015 ($n = 60$). In 1980 (Figure 4a), nests were uniform at a range of radii of approximately 0–20 m, meaning no nests fell within this range of distances from each other. Where the observed K-value (solid line in Figure 4) clearly departs from the random envelope at internest distances of approximately 15–18 m, the nest pattern was significantly different from the null hypothesis of a
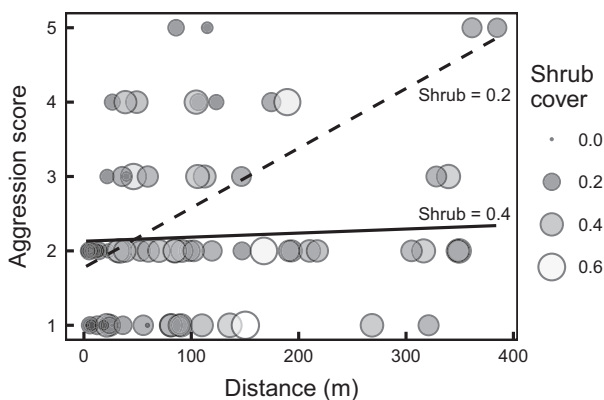

FIGURE 4 Transformed Ripley's K results for 1980 (a) and 2015 (b) nest distributions of *Formica obscuripes* in the study area. The y-axis is a transformation of the K statistic at a radius of r meters from each nest (x-axis). The transformation stabilizes variance and linearizes the plot so that the y-axis (dotted line) represents complete spatial randomness (Fortin et al., 2002). Thus, negative values are more uniform than random and positive values are more clustered than random. The solid line represents the observed K statistic for that year's nest pattern. Observed patterns were compared to 999 simulations of random patterns (gray area) and are significant when they fall outside of this random envelope

random pattern. Likewise, at radii between 20 and 30 m, nest patterns appeared no different from random, and at radii above 30 m, nests were significantly more clustered than random.

Nest patterns were much more clustered in 2015 (Figure 4b). Only at scales under 3 m did all nests have no neighbors. The K-value rose quickly with increasing radius, and above an internest distance of 5 m, the pattern was significantly clustered. At greater radii, the degree of clustering was much higher than the clustering at the same radii in 1980.

The sharp edges on the left sides of the plots, found at radii less than 18 m in Figure 4a and less than 3 m in Figure 4b, represent the lowest possible Ripley's K value ($K = 0$), where no neighboring points are found in a pattern at that radius of analysis. The 95% random envelope for these plots indicate that a value of $K = 0$ was possible within the envelope of random simulations at smaller radii, but it is notable that the observed pattern in 1980 at these smaller radii still represented the most uniform spatial distribution possible.

3.4 | Landcover change and changes in habitat preferences of *Formica obscuripes*

Between 1975 and 2008, the open field landcover type decreased while forest and shrub landcover increased (Figure 1). Within a

FIGURE 3 Nest distance and aggression score relationship between individual *Formica obscuripes* ants from different nests in 2015. The dotted line represents the predicted trend when the proportion of shrub landcover in a 20 m transect between originating nests is 0.2, and the solid line represents the trend when shrub proportion is 0.4. The proportion of shrub landcover between nests is represented by the size and shading of the circle, with larger, lighter circles corresponding to more shrubs
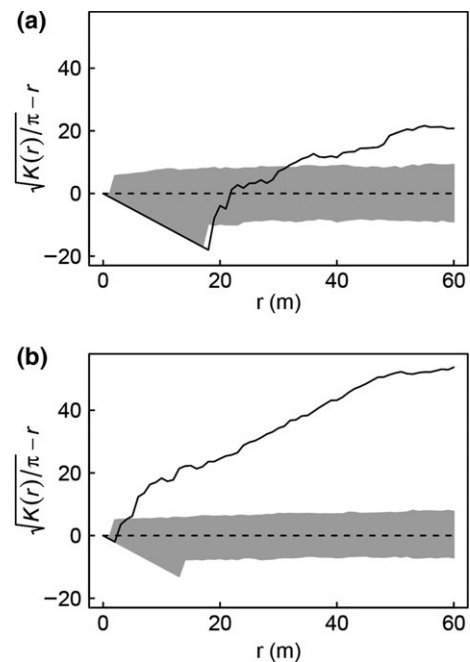
5–30 m radius of randomly placed points, the expected percent composition of field landcover decreased from an average of more than 70% in 1975 to less than 40% in 2008, a relative change of 50%; while shrub landcover increased dramatically from an average of approximately 2% to nearly 20%, a relative change of more than 900% (Table 1). Forest landcover made up the difference in composition, increasing from approximately 26% to 44%, a 71.5% relative increase. Percent composition of each landcover type did not differ significantly between radii outward from random points at the 95% confidence level. In 1980, *F. obscuripes* showed a significant preference for building nests in areas with a higher composition of field than other landcovers, and a significant preference for shrub over forest landcover (Table 2a,b). This ranking of preference was significant for a 5–30 m radius around the nests. In 2015, at shorter radii such as 5 m, the ants still significantly preferred field landcover (Table 2c). However, at a 30 m radius, their preference for field over shrub landcover was no longer significant (Table 2d), although it had been in 1980. Preference values are shown for 5 m and 30 m in Table 2. See Appendix S1 for complete values for other radii. We compared the log-ratio preference for field over shrub as the radius around the nest increased from 5 to 30 m for 1980 and 2015 (Figure 5). Within an immediate 5 m area around nests, *F. obscuripes*

TABLE 1 Mean and standard deviation of % landcover composition of field, forest, and shrub around simulated random points in the 1975 and 2008 conditions for the study site. Values represent the aggregated statistics for 1,000 simulations of random nest patterns. Percent composition was calculated for an area around each random point in a 5, 10, 15, 20, 25, and 30 m radius, but only values at a 30 m radius are reported here, as values did not differ significantly between radii at the 95% confidence level

Landcover	1975 % comp. (SD)	2008 % comp. (SD)	Relative change %
Field	72.5 (4.3)	36.4 (3.3)	−49.8
Forest	25.6 (4.4)	43.9 (4.6)	+71.5
Shrub	1.9 (0.6)	19.6 (2.2)	+931.6

TABLE 2 Log-ratio preference between different landcover types within a 5 m and 30 m radius. Positive values indicate preference for the landcover type in the row over the landcover type in the column. The reverse of these comparisons can be found by negating their preference values. Differences that were significantly nonzero are indicated with an asterisk

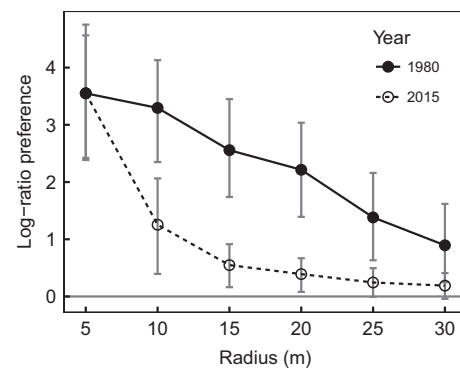|	1980			2015	
	Shrub	**Forest**		**Shrub**	**Forest**
(a) 5 m			(c) 5 m		
Field	3.55*	4.91*	Field	3.55*	7.67*
Shrub		1.35*	Shrub		4.12*
(b) 30 m			(d) 30 m		
Field	0.89*	2.74*	Field	0.19	1.93*
Shrub		1.84*	Shrub		1.74*

FIGURE 5 Log-ratio preference for field over shrub landcover in 1980 (closed circles and solid lines) and 2015 (open circles and dotted lines). Error bars represent 95% confidence intervals calculated by bootstrapping the data. The error bars of the preference values for 25 and 30 m radii overlap zero in 2015, indicating that preference at those radii were not significant

had a preference for field over shrub landcover that was equally strong for both years. This preference decreased with increasing distance from the nest, but had a linear shape in 1980 and a negative exponential shape in 2015. Log-ratio preference values were significantly different between the 2 years within a 95% confidence interval (calculated by 1,000 bootstraps) for radii of 10–25 m, but overlapped at the closest and farthest radii (5 and 30 m). In 2015, preference for field over shrub was not significantly different from zero within the 25 and 30 m radii areas.

3.5 | Lefkovitch matrix population projection

We developed a stage-structured population model for the subset of nests surveyed in 2013 and 2015 based on the observed population dynamics of the size stage classes. The initial stage population vector N_1 for 2013, with the four stages in ascending order, was (9, 15, 12, 8), and the subsequent N_2 for 2015 was (11, 16, 8, 5). The Lefkovitch projection matrix for the model is given in Table 3. Within 20 iterations of the population projection, we observe a projected decline of the *F. obscuripes* population in our study site, with a steady state growth rate (i.e., dominant eigenvalue) of 0.81. Figure 6 shows the trend of population decline for each size class and the entire population over 40 years (20 iterations). Stage 2 nests are projected to remain the most abundant stage, but all nest stages are projected to decrease after 2015, with larger nests (stages 3 and 4) declining in a negative exponential shape. By the twentieth iteration (2053), less than one nest is projected to remain in the site.

4 | DISCUSSION

4.1 | *Formica obscuripes* spatial distribution and *Elaeagnus umbellata*

Analysis of historical aerial photographs suggests that, from 1975 to 2008, the study site experienced a reduction in open-field area along

TABLE 3 Lefkovitch projection matrix for stage-structured population model. Transition rates are shown from the stages named in the columns to the stages named in the rows of the table. These positions correspond to the Lefkovitch matrix in Figure 2b. Transition rates are represented as the fraction of the total population of the stage in the column (denominator) undergoing the transition to the stage in the row (numerator) from 2013 to 2015, plus fecundity rates where applicable. Fecundity rates F_1 and F_2 represent the rates that new stage 1 and stage 2 nests were produced; they are uniform across columns because we assumed all stages were equally capable of reproducing. Their values are equal to the number of new nests in 2015 for that stage divided by the total nest population in 2013; thus $F_1 = 4/44$ and $F_2 = 2/44$

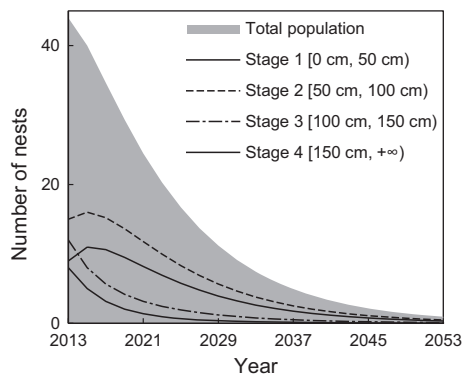|	Stage 1	Stage 2	Stage 3	Stage 4
Stage 1	$2/9 + F_1$	$3/15 + F_1$	$2/12 + F_1$	F_1
Stage 2	$1/9 + F_2$	$9/15 + F_2$	$2/12 + F_2$	$2/8 + F_2$
Stage 3		$1/15$	$5/12$	$2/8$
Stage 4			$1/12$	$4/8$

FIGURE 6 Projected change in *F. obscuripes* population at ESGS based on survey data from 2013 and 2015. Using a stage-structured population model, we project the population trend of all nests (solid gray trend) and each size stage class (lines) for 20 iterations over 40 years

with an expansion of forest and shrubs. Based on our own observations and other studies in the same area (Brym, Allen, & Ibáñez, 2014; Brym et al., 2011; Severtsen, 2005), we know that shrub cover in our study site is dominated by *E. umbellata*, an invasive plant that has a detrimental effect on the native community. This species spreads easily through bird dispersal (Lafleur et al., 2007), limits light penetration (Brantley & Young, 2009), and produces chemicals that inhibit growth of native plants (Orr et al., 2005). Given these characteristics, it is not surprising that *E. umbellata* invaded the open field so aggressively, and in 30 years turned large open areas into dense shrubs.

Our Ripley's *K* analysis suggests that the 1980 nest sites were uniformly distributed up to a radius of 20 m. We would expect this pattern if intraspecific competition (aggression between nests) was the primary driver of nest spatial distribution (Levings & Franks, 1982; Ryti & Case, 1986). At distances below 20 m, intraspecific competition for resources between unassociated nests may serve as

the repressor in a Turing-like pattern-formation process (Rietkerk & van de Koppel, 2008; Turing, 1952) that negatively regulates the creation of new nests (the activator), which could have occurred through the mating flights observed on the site around that time (Talbot, 1972). By dominating other ant species in its vicinity, *F. obscuripes* could have also acted as its own repressor: Dispersing social parasitic *F. obscuripes* queens must travel farther to locate heterospecific host nests to take over and establish a new colony (Stockan & Robinson, 2016). In either case, the clustering distribution at larger scales (>30 m) may reflect the dispersal limitation of the queens in mating flights.

On the other hand, the nest distribution in 2015 was clustered at most radii. This change in nest distribution may indicate a change in the nest pattern-formation process. This change may be driven by the prolific invasion of *E. umbellata*, which decreased the open areas that *F. obscuripes* prefers for nests (Beattie & Culver, 1977). As *E. umbellata* began to overtake the open field, nests became constrained to small patches of remnant open areas. Our analysis of ant nesting preference between field and shrub cover types supports this proposed mechanism of spatial pattern formation.

In 1980, *F. obscuripes* demonstrated a significant preference for open field over shrub, out to distances of 30 m from the nest; however, this range decreased to 20 m by 2015. With the exception of the area immediately around its nest, the strength and shape of *F. obscuripes* preference for field over shrub changed from an approximately linear decrease in 1980 to a negative exponential-like curve in 2015. This suggests that *F. obscuripes* has had to compromise on the quality of its foraging area at greater distances from its nest to tolerate less favorable habitats outside of its immediate vicinity since the invasion of *E. umbellata*.

By overtaking open space, *E. umbellata* may have become the driver of *F. obscuripes* nest spatial pattern, overshadowing intraspecific competition. Whether this effect directly leads to the extirpation of *F. obscuripes* is a matter of speculation. That the ant's preference for field landcover within 5 m of its nest remained consistent throughout the years of study could suggest that *F. obscuripes* is intolerant to changes in habitat composition within this short distance to the nest. Alternately, this radius may simply reflect an ongoing series of compromises in preferred habitat that will continue to shrink as *E. umbellata* expands. Further study is needed to understand what might happen once all preferred habitat is eliminated.

As an open areas specialist (Talbot, 1972; Weber, 1935), *F. obscuripes* may prefer a plant community typical of prairie and old-field habitat. Our data also support that *F. obscuripes* may avoid forest in favor of shrub and field. We know this based on observed tolerance for significantly increased shrub, but not forest, in the larger radii around its nests (Table 2). An increase in forest landcover could pose an even greater threat to *F. obscuripes* in the long term. However, because *E. umbellata* was distributed throughout the remnant old fields that are the ant's preferred habitat, while the forest was mainly limited to the edges of the field and our study site, it is not clear whether our results truly represent the strength of the ants' preference against forest or reflect our sampling bias.

As a major driver of the landcover change within the old-field habitat, however, *E. umbellata* is the proximate cause for the ants' loss of preferred habitat. *Elaeagnus umbellata* is able to colonize all areas within the old field through ornithochorous dispersal (McCay, McCay, & Czajka, 2009), which has resulted in a fragmented ant habitat and increased dispersal barriers. In contrast, the forest has only encroached along field edges. The spatial distribution of the dispersal strategy of *E. umbellata* suggests that this species' spread, rather than forest encroachment, is the main driver of the change in spatial distribution pattern of the ant nests. Furthermore, *E. umbellata* may also act as an agent of forest encroachment by fostering conditions suitable for forest species in the old field. For example, *E. umbellata* has nitrogen-fixing capabilities that could benefit certain native tree species (Paschke, Dawson, & David, 1989). In addition, tree species that rely on rodents for seed dispersal, such as hickory and oak, may benefit through the creation of rodent habitats in newly established shrub understory (Bazzaz, 1968). However, *E. umbellata* may also inhibit growth of some native species through allelopathic chemicals (Orr et al., 2005). Further study is needed to understand the mechanisms and pathways of succession (Connell & Slatyer, 1977) in this old field, that is, whether *E. umbellata* may be facilitating succession to forest, or inhibiting other species from dominating.

4.2 | Aggression and relatedness among nests after shrub invasion

The aggression between nests of *Formica* species has been shown to correlate with genetic relatedness (Beye et al., 1997) and with distance in combination with relatedness (Pirk et al., 2001). Positive correlation between aggression and distance among nests may indicate that budding is a prevalent mode of nest formation, as less-aggressive nests may be more closely related (Pirk et al., 2001). Our multiple linear regression results reflect this relationship, although the positive relationship between nest aggression and distance was moderated when there was a higher proportion of shrub cover between nests. Thus, under denser shrub conditions, *F. obscuripes* nests exhibited less aggression toward each other. This can be explained by greater relatedness among these nests or perhaps greater habituation, in cases where nests interact directly (Langen, Tripet, & Nonacs, 2000).

These results further support that *F. obscuripes* changed its behavior in response to greater *E. umbellata* density. This could occur from either favoring nest budding as a reproductive mode, or by being more tolerant of nearby unrelated colonies. Low aggression across longer distances may reflect nest budding rather than habituation, as distant nests are less likely to have interacted directly and become habituated. Distant but related nests may be the result of multiple generations of budding that has led to a large colony of nests spanning a wide area. Such networks of *F. obscuripes* colonies exhibit low internest aggression and can be distributed in a clustered pattern (McIver et al., 1997). Clustering in polydomous ant colonies can be attributed to an endogenous Turing-like mechanism (Vandermeer et al., 2008); however, further study is needed to disentangle the relative endogenous and exogenous contributions (Li, Vandermeer, & Perfecto, 2016) of nest budding and habitat preference in the pattern-formation process on the site.

4.3 | Change in *Formica obscuripes* population over time

The change in nest pattern between 1980 and 2015 from uniform to clustered, combined with observations of reproductive flights in the past (Talbot, 1972) and evidence of prevalent nest budding in 2015, suggests that this population of *F. obscuripes* has undergone a shift in its dominant reproductive strategy. This change is explained by the environmental changes imposed by the invasion of *E. umbellata*. Talbot (1972) observed that reproductive swarms of *F. obscuripes* were located centrally among the participating nests in the field and that the flying reproductive alates stayed relatively close to the ground. Dense, brushy stands of *E. umbellata* may prevent such congregations by obstructing alate flights and complicating navigation to a centralized swarming site. Furthermore, inseminated queens may have more difficulty locating a host nest to parasitize within a shrub-dominated landscape. As *F. obscuripes* can suspend outbreeding when long-distance dispersal is not profitable (Hölldobler & Wilson, 1990; McIver et al., 1997), budding may have been more beneficial when *E. umbellata* became denser. However, nest budding as an adaptive strategy is not without consequence: Higher population density from clustering could also increase nest vulnerability to exploitation by natural enemy attack (Philpott, Perfecto, Vandermeer, & Uno, 2009; Vandermeer et al., 2010).

Because nest budding is a form of asexual reproduction, the daughter and parent of budding nests are considered to be part of the same colony (McIver et al., 1997). Populations containing budding nests therefore complicate our estimations of population size. Although 50 nests were found in 1980 and 60 were found in 2015, due to the prevalent probable reproductive strategies at the time, it is likely that many of the 50 nests in 1980 were individual colonies, while many of the 60 nests in 2015 were members of a larger colony. A better understanding of the population size could be achieved through genetic analysis or exhaustive pairwise aggression experiments, but this is outside the scope of this study.

A caveat of the stage-structured population model is that these results reflect the dynamics of single nests on the site but not necessarily the colonies, which effectively function as the individual organism in ants (Hölldobler & Wilson, 1990). However, growth and survival of single nests could still indicate trends in the health of the larger colony. Nest changes should be interpreted in the context of the larger colony, which may build, use, and abandon satellite nests seasonally or in response to environmental factors while maintaining a core of consistently occupied nests (McIver et al., 1997; Talbot, 1971). Future studies should identify and model populations of core nests or entire colonies, rather than individual nests. This project would require genetic or additional aggression testing methods to

understand relatedness between nests or require identifying temporary and long-term nests through observations over multiple seasons and years.

Another factor that complicates the interpretation of the results of the population model was a cold wave in 2013 and 2014, which brought below-normal temperatures to the upper Midwest and Great Lakes region (Wolter et al., 2015). This could have played a role in the drop in the number of *F. obscuripes* nests between 2013 and 2015, which in turn skewed the nest count projection toward a more extreme decline. However, *F. obscuripes* is found in sites of much higher latitude, suggesting the species can tolerate colder weather (Higgins & Lindgren, 2012). It could be that the observed decrease in occupied nests reflects a temporary withdrawal by multinest colonies from their satellite nests in response to extreme weather, but further work is needed to investigate whether the ants at this site exhibit this behavior. However, although the weather may have exacerbated the ants' projected population decline, coupled changes in spatial distribution and nest preferences demonstrate the overall importance of the impact of the *E. umbellata* invasion.

4.4 | Implications for conservation

Our study provides further evidence of the impact of invasive species on natives. We make a case that demonstrates the importance of invasive monitoring and control in conservation and land-use management. The *Elaeagnus umbellata* invasion is widespread in North America and is found worldwide (CABI, 2016; EDDMapS, 2016; Munger, 2003). *Elaeagnus umbellata* shares much of its range with *F. obscuripes* and other members of mound-building wood ant species (Janicki, Narula, Ziegler, Guénard, & Economo, 2016; Stockan & Robinson, 2016). The invasive characteristics of *E. umbellata* that result in dense, monotypic stands (Orr et al., 2005) are also shared among many invasive shrubs (Van Kleunen, Weber, & Fischer, 2010; Vilà et al., 2011). Likewise, the habitat requirements and reproductive strategies of *F. obscuripes* are common to many mound-building wood ant species (Stockan & Robinson, 2016). We propose that the interaction and resulting competition we demonstrate in this paper can be found in locations where similar species of invasive shrubs are changing the habitat of wood ant species. Beyond the inherent conservation importance of *F. obscuripes* and other wood ants, this species group also has the potential, when found in sufficient numbers, to provide an important ecosystem service through biological control of herbivore pests (McIver et al., 1997; Stockan & Robinson, 2016). By examining the spatial patterns and relationships of *F. obscuripes* nests in relation to *E. umbellata* invasion, we identified significant pathways of impact by shrub invasions on an important species of ant. Further study is needed to clarify the mechanisms of impact, the geographic extent of these effects, and if similar effects are found in other invaded ecosystems.

REFERENCES

Aebischer, N. J., Robertson, P. A., & Kenward, R. E. (1993). Compositional analysis of habitat use from animal radio-tracking data. *Ecology*, 74, 1313–1325.

Aitchison, J. (1986). *The statistical analysis of compositional data*. London: Chapman and Hall ; New York, xv, 416 p.

Baddeley, A., & Turner, R. (2005). spatstat: An R package for analyzing spatial point patterns. *Journal of Statistical Software*, 12, 1–42.

Baer, S. G., Church, J. M., Williard, K. W. J., & Groninger, J. W. (2006). Changes in intrasystem N cycling from N2-fixing shrub encroachment in grassland: Multiple positive feedbacks. *Agriculture, Ecosystems and Environment*, 115, 174–182.

Bazzaz, F. A. (1968). Succession on abandoned fields in the Shawnee Hills, Southern Illinois. *Ecology*, 49, 924–936.

Beattie, A. J., & Culver, D. C. (1977). Effects of the mound nests of the ant, *Formica obscuripes*, on the surrounding vegetation. *American Midland Naturalist*, 97(2), 390–399.

Belsky, A. J. (1986). Population and community processes in a mosaic grassland in the Serengeti, Tanzania. *Journal of Ecology*, 74, 841–856.

Beye, M., Neumann, P., & Moritz, R. F. A. (1997). Nestmate recognition and the genetic gestalt in the mound-building ant *Formica polyctena*. *Insectes Sociaux*, 44, 49–58.

Black, B. L., Fordham, I. M., & Perkins-Veazie, P. (2005). Autumnberry (*Elaeagnus umbellata*): A potential cash crop. *Journal of the American Pomological Society*, 59, 125–134.

Boaler, S. B., & Hodge, C. A. H. (1962). Vegetation stripes in somaliland. *Journal of Ecology*, 50, 465–474.

Bolstad, P. (2012). *GIS fundamentals: A first text on geographic information systems*. White Bear Lake, MN: Eider Press, x, 674 p.

Brantley, S. T., & Young, D. R. (2009). Contribution of sunflecks is minimal in expanding shrub thickets compared to temperate forest. *Ecology*, 90, 1021–1029.

Brym, Z. T., Allen, D., & Ibáñez, I. (2014). Community control on growth and survival of an exotic shrub. *Biological Invasions*, 16, 2529–2541.

Brym, Z. T., Lake, J. K., Allen, D., & Ostling, A. (2011). Plant functional traits suggest novel ecological strategy for an invasive shrub in an understorey woody plant community. *Journal of Applied Ecology*, 48, 1098–1106.

CABI (2016). *Elaeagnus umbellata* (autumn olive). *Invasive Species Compendium*.

Calenge, C. (2006). The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197, 516–519.

Connell, J. H., & Slatyer, R. O. (1977). Mechanisms of succession in natural communities and their role in community stability and organisation. *The American Naturalist*, 111, 1119–1144.

Couteron, P., & Lejeune, O. (2001). Periodic spotted patterns in semi-arid vegetation explained by a propagation-inhibition model. *Journal of Ecology*, 89, 616–628.

Deslippe, R. J., & Savolainen, R. (1995). Mechanisms of competition in a guild of Formicine ants. *Oikos*, 72, 67–73.

EDDMapS (2016). *Early detection & distribution mapping system*. Tifton, GA: The University of Georgia – Center for Invasive Species and Ecosystem Health. https://www.eddmaps.org. (accessed 17 October 2016).

Evans, F. C., & Dahl, E. (1955). The vegetational structure of an abandoned field in southeastern Michigan and its relation to environmental factors. *Ecology*, 36, 685–706.

Fortin, M.-J., & Dale, M. R. T. (2005). *Spatial analysis: A guide for ecologists*. Cambridge, UK; New York: Cambridge University Press, xiii, 365 p.

Fortin, M.-J., Dale, M. R. T., & ver Hoef, J. (2002). *Spatial analysis in ecology*, A. H. El-Shaarawi & W. W. Piegorsch (Eds.), Vol. 4 (pp. 2051–2058). Chichester; New York: John Wiley & Sons Ltd.

Gallien, L., Münkemüller, T., Albert, C. H., Boulangeat, I., & Thuiller, W. (2010). Predicting potential distributions of invasive species: Where to go from here? *Diversity and Distributions*, 16, 331–342.

Greiling, D. A., & Kichanan, N. (2002). Old-field seedling responses to insecticide, seed addition, and competition. *Plant Ecology*, 159, 175–183.

Henderson, G., & Jeanne, R. L. (1992). Population biology and foraging ecology of prairie ants in southern Wisconsin (Hymenoptera: Formicidae). *Journal of the Kansas Entomological Society*, 65(1), 16–29.

Herbers, J. M. (1985). Seasonal structuring of a north temperature ant community. *Insectes Sociaux*, 32, 224–240.

Higgins, R. J., & Lindgren, B. S. (2012). An evaluation of methods for sampling ants (Hymenoptera: Formicidae) in British Columbia, Canada. *The Canadian Entomologist*, 144, 491–507.

Hölldobler, B., & Wilson, E. (1990). *The ants*. Cambridge, MA: Belknap Press. pp. 1–1530.

Hook, P. B., & Burke, I. C. (2000). Biogeochemistry in a shortgrass landscape: Control by topography, soil texture, and microclimate. *Ecology*, 81, 2686–2703.

Janicki, J., Narula, N., Ziegler, M., Guénard, B., & Economo, E. P. (2016). Visualizing and interacting with large-volume biodiversity data using client-server web-mapping applications: The design and implementation of antmaps.org. *Ecological Informatics*, 32, 185–193.

van de Koppel, J., Gascoigne, J. C., Theraulaz, G., Rietkerk, M., Mooij, W. M., & Herman, P. M. J. (2008). Experimental evidence for spatial self-organization and its emergent effects in mussel bed ecosystems. *Science*, 322, 739–742.

Lafleur, N. E., Rubega, M. A., & Elphic, C. S. (2007). Invasive fruits, novel foods, and choice: An investigation of European starling and American robin frugivory. *The Wilson Journal of Ornithology*, 119, 429–438.

Langen, T. A., Tripet, F., & Nonacs, P. (2000). The red and the black: Habituation and the dear-enemy phenomenon in two desert Pheidole ants. *Behavioral Ecology and Sociobiology*, 48, 285–292.

Lefkovitch, L. P. (1965). The study of population growth in organisms grouped by stages. *Biometrics*, 21, 1–18.

Levings, S. C., & Franks, N. R. (1982). Patterns of nested dispersion in a tropical ground ant community. *Ecology*, 63, 338–344.

Li, K., Vandermeer, J. H., & Perfecto, I. (2016). Disentangling endogenous versus exogenous pattern formation in spatial ecology: A case study of the ant Azteca sericeasur in southern Mexico. *Royal Society Open Science*, 3, 160073.

McCay, T. S., McCay, D. H., & Czajka, J. L. (2009). Deposition of exotic bird-dispersed seeds into three habitats of a fragmented landscape in the northeastern United States. *Plant Ecology*, 203, 59–67.

Mclver, J. D., Torgersen, T. R., & Cimon, N. J. (1997). A supercolony of the thatch ant *Formica obscuripes* Forel (Hymenoptera, Formicidae) from the Blue Mountains of Oregon. *Northwest Science*, 71, 18–29.

Muckermann, H. (1902). The structure of the nests of some North American species of Formica. *Psyche*, 9, 355–360.

Munger, G. T. (2003). *Elaeagnus umbellata*. Fire Effects Information System, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Missoula Fire Sciences Laboratory. Retrieved from https://www.fs.fed.us/database/feis/plants/shrub/elaumb/all.html. (accessed 17 October 2016).

O'Neill, K. M. (1988). Trail patterns and movement of workers among nests in the ant *Formica obscuripes* (Hymenoptera: Formicidae). *Psyche*, 95, 1–14.

Orr, S. P., Rudgers, J. A., & Clay, K. (2005). Invasive plants can inhibit native tree seedlings: Testing potential allelopathic mechanisms. *Plant Ecology*, 181, 153–165.

Paschke, M. W., Dawson, J. O., & David, M. B. (1989). Soil nitrogen mineralization in plantations of *Juglans nigra* interplanted with actinorhizal *Elaeagnus umbellata* or *Alnus glutinosa*. *Plant and Soil*, 118, 33–42.

Petrovskii, S. V., & Malchow, H. (2001). Wave of chaos: New mechanism of pattern formation in spatio-temporal population dynamics. *Theoretical Population Biology*, 59, 157–174.

Philpott, S. M., Perfecto, I., Vandermeer, J., & Uno, S. (2009). Spatial scale and density dependence in a host parasitoid system: An arboreal ant, *Azteca instabilis*, and its *Pseudacteon* phorid parasitoid. *Environmental Entomology*, 38, 790–796.

Pirk, C. W. W., Neumann, P., Moritz, R. F. A., Pirk, C. W. W., & Pamilo, P. (2001). Intranest relatedness and nestmate recognition in the meadow ant *Formica pratensis* (R.). *Behavioral Ecology and Sociobiology*, 49, 366–374.

Pyšek, P., Jarošík, V., Hulme, P. E., Pergl, J., Hejda, M., Schaffner, U., & Vilà, M. (2012). A global assessment of invasive plant impacts on resident species, communities and ecosystems: The interaction of impact measures, invading species' traits and environment. *Global Change Biology*, 18, 1725–1737.

R Core Team (2016). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from https://www.R-project.org (accessed 31 October 2016).

Reznicek, A. A., Voss, E. G., & Walters, B. S. (2011). *Elaeagnus umbellata*.

Ricciardi, A., Hoopes, M. F., Marchetti, M. P., & Lockwood, J. L. (2013). Progress toward understanding the ecological impacts of nonnative species. *Ecological Monographs*, 83, 263–282.

Rietkerk, M., & van de Koppel, J. (2008). Regular pattern formation in real ecosystems. *Trends in Ecology & Evolution*, 23, 169–175.

Ripley, B. D. (1976). The second-order analysis of stationary point processes. *Journal of Applied Probability*, 13(2), 255–266.

Rissing, S. W., Johnson, R. A., & Pollock, G. B. (1986). Natal nest distribution and pleometrosis in the desert leaf-cutter ant, *Acromyrmex versicolor* (Pergande) (Hymenoptera: Formicidae). *Psyche*, 93, 177–186.

Ryti, R. T., & Case, T. J. (1986). Overdispersion of ant colonies: A test of hypotheses. *Oecologia*, 69, 446–453.

Schirmel, J., Bundschuh, M., Entling, M. H., Kowarik, I., & Buchholz, S. (2016). Impacts of invasive plants on resident animals across ecosystems, taxa, and feeding types: A global assessment. *Global Change Biology*, 22, 594–603.

Severtsen, E. M. (2005). *Monitoring an exotic species invasion using high resolution remote sensing*. Master's thesis, University of Michigan, Ann Arbor, MI, 1–76 pp.

Soares, S. M., & Schoereder, J. H. (2001). Ant-nest distribution in a remnant of tropical rainforest in southeastern Brazil. *Insectes Sociaux*, 48, 280–286.

Stockan, J. A., & Robinson, E. J. H. (2016). *Wood ant ecology and conservation*. Cambridge, UK: Cambridge University Press.

Stubben, C., & Milligan, B. (2007). Estimating and analyzing demographic models using the popbio package in R. *Journal of Statistical Software*, 22, 1–23.

Talbot, M. (1956). Flight activities of the ant *Dolichoderus (Hypoclinea) mariae* Forel. *Psyche*, 63, 134–139.

Talbot, M. (1959). Flight activities of two species of ants of the genus Formica. *American Midland Naturalist*, 61, 124–132.

Talbot, M. (1971). Flights of the ant *Formica dakotensis* Emery. *Psyche*, 78, 169–179.

Talbot, M. (1972). Flights and swarms of the ant *Formica obscuripes* Forel. *Journal of the Kansas Entomological Society*, 45(2), 254–258.

Talbot, M. (1980). Distribution of *Formica obscuripes* in 1980.

Turing, A. M. (1952). The chemical basis of morphogenesis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 237, 37–72.

Van Kleunen, M., Weber, E., & Fischer, M. (2010). A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters*, 13, 235–245.

Vandermeer, J. H., & Goldberg, D. E. (2013). *Population ecology: First principles*. Princeton, NJ: Princeton University Press.

Vandermeer, J., Perfecto, I., & Philpott, S. M. (2008). Clusters of ant colonies and robust criticality in a tropical agroecosystem. *Nature*, *451*, 457–459.

Vandermeer, J., Perfecto, I., & Philpott, S. (2010). Ecological complexity and pest control in organic coffee production: Uncovering an autonomous ecosystem service. *BioScience*, *60*, 527–537.

Vilà, M., Espinar, J. L., Hejda, M., Hulme, P. E., Jarošík, V., Maron, J. L., … Pyšek, P. (2011). Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, *14*, 702–708.

Weber, N. A. (1935). The biology of the thatching ant, *Formica rufa obscuripes* Forel, in North Dakota. *Ecological Monographs*, *5*, 165–206.

Weseloh, R. M. (1994). Spatial distribution of the ants *Formica subsericea*, *F. neogagates*, and *Aphaenogaster fulva* (Hymenoptera: Formicidae) in Connecticut. *Environmental Entomology*, *23*, 1165–1170.

Wiernasz, D. C., & Cole, B. J. (1995). Spatial distribution of *Pogonomyrmex occidentalis*: Recruitment, mortality and overdispersion. *Journal of Animal Ecology*, *64*, 519–527.

Wolter, K., Hoerling, M., Eischeid, J. K., van Oldenborgh, G. J., Quan, X.-W., Walsh, J. E., … Dole, R. M. (2015). How unusual was the cold winter of 2013/14 in the upper Midwest? *Bulletin of the American Meteorological Society*, *96*, S10–S14.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.