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

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31

32 ABSTRACT

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

53

54 INTRODUCTION

55 While the impacts of invasive species are often strong and widespread, their particulars
56 are context-dependent, relating to the functional ecology of non-native species and the structure,
57 evolutionary experience, and diversity of native communities (Vilà *et al.*, 2011; Pyšek *et al.*,
58 2012; Ricciardi *et al.*, 2013; Schirmel *et al.*, 2016). There exists no universal measure or theory
59 of invasive impact (Ricciardi *et al.*, 2013). Furthermore, the impact of invasive species on the
60 spatial distribution of native species is often overlooked for research. Although many studies

61 focus on the distribution of invasive species through phenomenological and mechanistic
62 modeling (Gallien *et al.*, 2010), the subsequent impact on the spatial ecology of the native
63 species is not as well understood.

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

78 The spatial ecology of ant colonies has been extensively studied, documenting a wide
79 range of patterns. Competition is thought to be the major mechanism driving uniform distribution
80 of populations in space (Levings & Franks, 1982; Ryti & Case, 1986; Deslippe & Savolainen,
81 1995; Wiernasz & Cole, 1995). Although uniform spatial arrangements are common,
82 aggregations (Rissing *et al.*, 1986; Henderson & Jeanne, 1992; Vandermeer *et al.*, 2008) and
83 random distributions also occur (Herbers, 1985; Weseloh, 1994; Soares & Schoereder, 2001).
84 The Turing mechanism provides an appropriate lens for understanding many of these patterns.
85 Vandermeer *et al.* (2008) demonstrated that ant nest budding by *Azteca sericeasur* (previously
86 identified as *Azteca instabilis*) acted as the activator in the system, while natural enemy
87 exploitation of dense colony clusters acted as the repressor, resulting in a clustered distribution.
88 Uniform nest distributions may also form through a Turing-like mechanism, in a fashion similar
89 to the propagation-inhibition interactions that drive regular patterns in semi-arid vegetation
90 (Couteron & Lejeune, 2001).

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

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

115 Since Talbot’s original observations, one nesting area in the ESGR has undergone
116 dramatic vegetative succession from an open field to a shrub-dominated field, dominated in
117 particular by the invasive shrub *Elaeagnus umbellata*, or autumn olive (Severtsen, 2005). This
118 shrub is native to China, Japan, and Korea, and was introduced to the United States in 1830 as an
119 ornamental and wildlife habitat plant (Black *et al.*, 2005). It is considered invasive within North
120 America, having spread across much of the Eastern US and as far west as the Pacific Northwest
121 and Hawai’i, as well as to Ontario, Canada (Munger, 2003; EDDMapS, 2016). It is not yet

122 invasive elsewhere outside its native range, although careful monitoring is advised in Europe
123 (CABI, 2016). *Elaeagnus umbellata* was first collected in Michigan in 1939 (Reznicek *et al.*,
124 2011) and first appeared in the ESGR in the early 1980s, where it is now abundant in open
125 grasslands, along roads, and in forest edges (Brym *et al.*, 2011).

126 Like many invasive shrubs, *E. umbellata* has attractive fruits and is readily bird-dispersed
127 (Lafleur *et al.*, 2007). Furthermore, it can grow as compact thickets that limit light beneath its
128 canopy and produces secondary chemicals that inhibit native species seed germination and
129 growth (Orr *et al.*, 2005; Brantley & Young, 2009). It also exhibits a relationship with nitrogen
130 fixing bacteria that alters soil chemistry (Baer *et al.*, 2006), which can affect the surrounding
131 plant composition.

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

147

148 MATERIALS AND METHODS

149 *Study Site*

150 We conducted our study on a population of *F. obscuripes* in the Edwin S. George
151 Reserve (ESGR), a 525-hectare preserve located in Livingston County, Michigan managed by
152 the University of Michigan. This population was studied by Mary Talbot beginning in 1953

153 (Talbot, 1956). In 1980, Talbot created a map of the ant nest distribution in the ESGR, which we
154 use in our analysis (Talbot, 1980). Thus we have the capability to study long term effects of the
155 introduction and invasion of *E. umbellata*, which was first observed in the ESGR in the early
156 1980s (Brym *et al.*, 2011).

157 Our study site was a 24.5 ha section of old field located in the central part of the ESGR
158 (84.014807° W, 42.458722° N, Fig. 1). The fields of the ESGR were cleared for farmland by
159 1870 and cultivated until around 1900; afterwards, they served as pasture until the property was
160 converted to a reserve in the late 1920s (Evans & Dahl, 1955). When we conducted follow-up
161 ant nest censuses in 2013 and 2015, the site was in various stages of invasion by woody shrubs,
162 dominated by *E. umbellata*, and secondary forest. A remote-sensing study in 2005 found that,
163 within a 95 ha area of the ESGR that includes our study site, *E. umbellata* stands covered a total
164 of 13 ha, while the prior landcover type, grasses and forbes, covered only 6 ha (Severtsen, 2005).
165 The southern half of the study site was dominated by secondary forest and reflected a more
166 advanced stage of succession than the northern portion, which still consisted mainly of shrubs
167 and remnant old field. These sites were surrounded by secondary oak-hickory forest that was
168 also encroaching onto the field. Major species found in the remnant old field in addition to *E.*
169 *umbellata* included the native species *Schizachrium scoparium* (Michx.) Nash, *Monarda*
170 *fistulosa*, and *Rubus* spp., as well as the introduced species *Achillea millefolium* and *Hypericum*
171 *perforatum* (Greiling & Kichanan, 2002).

172 173 *Population Survey*

174 In October 2013, we geo-located *F. obscuripes* nests in the northern portion of the study
175 area, using a GPS (Trimble GeoXH) to mark locations while also noting nest diameter. In
176 October 2015, we conducted follow-up nest surveys, noting changes in diameter and nest activity,
177 as well as locations of new nests. We continued to use Trimble GeoXH, as well as a smartphone
178 GPS application (Trimble Outdoors Navigator) to mark nest locations. We expanded the 2013
179 survey area to include the southern portion of our field site in order to cover more of Talbot's
180 1980 survey area. We digitized ant nest locations from scanned and georeferenced copies of
181 Talbot's paper maps (Talbot, 1980) using the "heads-up" digitizing method (Bolstad, 2012).

182 183 *Ant nest aggression trials*

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

194 We performed a multiple linear regression with aggression score as the dependent
195 variable and geographic separation distance and proportion shrub landcover between nest pairs
196 as candidate independent variables. The interaction between separation distance and proportion
197 shrub landcover was also considered, in order to determine whether shrub landcover moderated
198 the effect of separation distance on aggression. We calculated proportion shrub landcover from a
199 20m-wide transect spanning nest pairs, based on the 2008 landcover map (see “Landcover
200 change and *E. umbellata* expansion” methods). We utilized R (R Core Team, 2013) to perform a
201 multiple linear regression and other statistical analyses.

202

203 *Ant nest spatial patterns*

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

214

215 *Estimating landcover change and E. umbellata expansion*

216 We used overall shrub expansion as a proxy for *E. umbellata* expansion, based on
217 observations that *E. umbellata* comprised the majority of shrub cover in this area (Severtsen,
218 2005). We quantified *E. umbellata* expansion from 1980 to 2015 by assessing landcover change
219 through historical aerial photographs of the study site. We use the term “landcover” throughout
220 this text to specifically refer to the results of our aerial photo digitization process, which
221 categorized the dominant vegetation of the study site into three classes: field, shrub, or forest.
222 Our landcover estimates were based on historical aerial photographs taken in 1975 and 2008, as
223 these years were publicly available on the USGS Earthexplorer database and the closest to the
224 ant census dates. The 1975 image was a digitized 1:36,000 scale film photograph, and the 2008
225 image was a 0.3m resolution digital image. We classified landcover by using heads-up digitizing
226 (Bolstad, 2012) to outline distinct polygons of contiguous landcover that were distinguishable by
227 size, texture, shadow, and color at a 1:1,500 scale. Although other landcover types outside our
228 three classes did exist, such as dirt roads and some small structures, these were negligible in
229 comparison to the dominant landcovers. Polygons were converted to a contiguous 1m resolution
230 raster grid for landcover preference analysis.

231

232 *Ant nest landcover preference*

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

240 To address the unique issues of working with compositional data (Aitchison, 1986), we
241 converted percent composition to log ratios between two landcover types, i.e. $\ln(x_{U1}/x_{U2})$,
242 where x_{U1} represents the percent that was landcover 1, as compared to landcover 2, x_{U2}
243 (Aebischer *et al.*, 1993). This framework represents landcover preference on a relative scale, so
244 that preference for building nests in landcover 1 is in terms of how often the ants use that
245 landcover as compared to landcover 2. This ratio was then compared to the ratio calculated using

246 the average landcover composition of the study area, which represent the landcover composition
247 of randomly distributed nests. The average random landcover composition was calculated from
248 the mean of 1000 random point placements in the landscape with the same point intensity
249 (Poisson distribution mean) as the actual data.

250 Specifically, we were interested in how *F. obscuripes* preferred the field landcover class
251 to the shrub landcover class, and how its preference may have changed between 1980 and 2015
252 in context of the *E. umbellata* invasion. We tested a null hypothesis of zero difference between
253 the observed landcover log-ratio preferences and the general landcover availability using a one-
254 sample permutation test with 1000 repetitions. We performed compositional preference analysis
255 with the R package “adehabitatHS” (Calenge, 2006).

256

257 *Lefkovitch matrix population projection*

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

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

274 We estimated fecundity rates assuming that all nest stages were equally capable of
275 producing offspring, as tracking individual nest reproduction was beyond the scope of this study.
276 The fecundity, F_p , of any stage nest in 2013 is defined as the probability of producing a new nest

277 of size stage p by 2015. We found this by dividing the number of new stage- p nests in 2015 by
278 the total population in 2013. Thus, the fecundity rates for producing new stage- p nests is
279 identical across all nest stages. Since no new nests were beyond size stage 2, we did not calculate
280 fecundity rates for $p > 2$.

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

285

286 RESULTS

287 *Population survey and historical data*

288 Fifty nests mapped by Talbot in 1980 fell within our study area. In 2013, we found 44
289 nests in a census of the northern part of the study area. In 2015, we found 40 nests in this
290 northern area, with 6 new nests and 10 nests abandoned. Surveying the rest of our study area in
291 2015 also identified 20 more nests in the southern part, so there was a total of 60 nests in the
292 entire area that year.

293

294 *Ant nest aggression model*

295 Aggression between ant nests increased significantly with greater separating distance
296 ($p < 0.001$), but had a significant negative interaction with greater shrub landcover in the transect
297 between the two nests ($p < 0.001$). The fitted model was:

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

298 where *distance* and *shrub* are separating distance and proportion shrub landcover, respectively.
299 The shrub landcover main term was not significant ($p = 0.11$). Distance and shrub landcover
300 variables were not collinear ($r = 0.45$). The moderating effect of shrub landcover on the positive
301 relationship between aggression and distance is demonstrated in Fig. 3, where the dotted line
302 represents the predicted relationship between separating distance and aggression in relatively low
303 proportion shrub landcover ($\text{shrub} = 0.2$), and the solid line represents the same relationship but in
304 relatively high proportion shrub landcover ($\text{shrub} = 0.4$). The proportion of shrub landcover
305 between the nests examined ranged from 0 to 0.6, with a mean of 0.3 and interquartile range of
306 0.2. When there was a lower proportion of shrubs in the transect between nest pairs, aggression

307 increased more with distance, while in areas with a higher shrub proportion, aggression tended to
308 remain low. This multiple linear regression model explained 17% of the variance, as determined
309 by adjusted R^2 .

310

311 *Ant nest spatial patterns*

312 We performed the Ripley's K analysis on the nest spatial patterns of the years for which
313 we had the most complete spatial census, 1980 ($n = 50$) and 2015 ($n = 60$). In 1980 (Fig. 4a),
314 nests were uniform at a range of radii of approximately 0-20m, meaning no nests fell within this
315 range of distances from each other. Where the observed K -value (solid line in Fig. 4) clearly
316 departs from the random envelope at inter-nest distances of approximately 15-18m, the nest
317 pattern was significantly different from the null hypothesis of a random pattern. Likewise, at
318 radii between 20 and 30m, nest patterns appeared no different from random, and at radii above
319 30m, nests were significantly more clustered than random.

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

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

330

331 *Landcover change and changes in habitat preferences of Formica obscuripes*

332 Between 1975 and 2008, the open field landcover type decreased while forest and shrub
333 landcover increased (Fig. 1). Within a 5 to 30m radius of randomly-placed points, the expected
334 percent composition of field landcover decreased from an average of more than 70% in 1975 to
335 less than 40% in 2008, a relative change of 50%; while shrub landcover increased dramatically
336 from an average of approximately 2% to nearly 20%, a relative change of more than 900%
337 (Table 1). Forest landcover made up the difference in composition, increasing from

338 approximately 26% to 44%, a 71.5% relative increase. Percent composition of each landcover
339 type did not differ significantly between radii outward from random points at the 95%
340 confidence level. In 1980, *F. obscuripes* showed a significant preference for building nests
341 in areas with a higher composition of field than other landcovers, and a significant preference for
342 shrub over forest landcover (Table 2a,b). This ranking of preference was significant for a 5 to
343 30m radius around the nests. In 2015, at shorter radii such as 5m, the ants still significantly
344 preferred field landcover (Table 2c). However, at a 30m radius, their preference for field over
345 shrub landcover was no longer significant (Table 2d), though it had been in 1980. Preference
346 values are shown for 5m and 30m in Table 2. See appendix S1 for complete values for other
347 radii. We compared the log-ratio preference for field over shrub as the radius around the nest
348 increased from 5 to 30m for 1980 and 2015 (Fig. 5). Within an immediate 5m area around nests,
349 *F. obscuripes* had a preference for field over shrub landcover that was equally strong for both
350 years. This preference decreased with increasing distance from the nest, but had a linear shape in
351 1980 and a negative exponential shape in 2015. Log-ratio preference values were significantly
352 different between the two years within a 95% confidence interval (calculated by 1000 bootstraps)
353 for radii of 10-25m, but overlapped at the closest and farthest radii (5 and 30m). In 2015,
354 preference for field over shrub was not significantly different from zero within the 25 and 30m
355 radii areas.

357 *Lefkovitch matrix population projection*

358 We developed a stage-structured population model for the subset of nests
359 surveyed in 2013 and 2015 based on the observed population dynamics of the size stage classes.
360 The initial stage population vector N_1 for 2013, with the four stages in ascending order, was (9,
361 15, 12, 8), and the subsequent N_2 for 2015 was (11, 16, 8, 5). The Lefkovitch projection matrix
362 for the model is given in Table 3. Within 20 iterations of the population projection, we observe a
363 projected decline of the *F. obscuripes* population in our study site, with a steady state growth rate
364 (i.e. dominant eigenvalue) of 0.81. Fig. 6 shows the trend of population decline for each size
365 class and the entire population over 40 years (20 iterations). Stage 2 nests are projected to remain
366 the most abundant stage, but all nest stages are projected to decrease after 2015, with larger nests
367 (stages 3 and 4) declining in a negative exponential shape. By the twentieth iteration (2053), less
368 than one nest is projected to remain in the site.

369

370 DISCUSSION

371 *Formica obscuripes* spatial distribution and *Elaeagnus umbellata*

372 Analysis of historical aerial photos suggests that, from 1975 to 2008, the study site
373 experienced a reduction in open field area along with an expansion of forest and shrubs. Based
374 on our own observations and other studies in the same area (Severtsen, 2005; Brym *et al.*, 2011,
375 2014), we know that shrub cover in our study site is dominated by *E. umbellata*, an invasive
376 plant that has a detrimental effect on the native community. This species spreads easily through
377 bird dispersal (Lafleur *et al.*, 2007), limits light penetration (Brantley & Young, 2009), and
378 produces chemicals that inhibit growth of native plants (Orr *et al.*, 2005). Given these
379 characteristics, it is not surprising that *E. umbellata* invaded the open field so aggressively, and
380 in 30 years turned large open areas into dense shrubs.

381 Our Ripley's *K* analysis suggests that the 1980 nest sites were uniformly distributed up to
382 a radius of 20m. We would expect this pattern if intraspecific competition (aggression between
383 nests) was the primary driver of nest spatial distribution (Levings & Franks, 1982; Ryti & Case,
384 1986). At distances below 20m, intraspecific competition for resources between unassociated
385 nests may serve as the repressor in a Turing-like pattern formation process (Turing, 1952;
386 Rietkerk & van de Koppel, 2008) that negatively regulates the creation of new nests (the
387 activator), which could have occurred through the mating flights observed on the site around that
388 time (Talbot, 1972). By dominating other ant species in its vicinity, *F. obscuripes* could have
389 also acted as its own repressor: dispersing social parasitic *F. obscuripes* queens must travel
390 farther to locate heterospecific host nests to take over and establish a new colony (Stockan &
391 Robinson, 2016). In either case, the clustering distribution at larger scales (>30m) may reflect the
392 dispersal limitation of the queens in mating flights.

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

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

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

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

424 As a major driver of the landcover change within the old-field habitat, however, *E.*
425 *umbellata* is the proximate cause for the ants' loss of preferred habitat. *Elaeagnus umbellata* is
426 able to colonize all areas within the old field through ornithochorous dispersal (McCay *et al.*,
427 2009), which has resulted in a fragmented ant habitat and increased dispersal barriers. In contrast,
428 the forest has only encroached along field edges. The spatial distribution of the dispersal strategy
429 of *E. umbellata* suggests that this species' spread, rather than forest encroachment, is the main
430 driver of the change in spatial distribution pattern of the ant nests. Furthermore, *E. umbellata*

431 may also act as an agent of forest encroachment by fostering conditions suitable for forest
432 species in the old field. For example, *E. umbellata* has nitrogen-fixing capabilities that could
433 benefit certain native tree species (Paschke *et al.*, 1989). In addition, tree species that rely on
434 rodents for seed dispersal, such as hickory and oak, may benefit through the creation of rodent
435 habitats in newly established shrub understory (Bazzaz, 1968). However, *E. umbellata* may also
436 inhibit growth of some native species through allelopathic chemicals (Orr *et al.*, 2005). Further
437 study is needed to understand the mechanisms and pathways of succession (Connell & Slatyer,
438 1977) in this old field, i.e. whether *E. umbellata* may be facilitating succession to forest, or
439 inhibiting other species from dominating.

440

441 *Aggression and relatedness among nests after shrub invasion*

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

452 These results further support that *F. obscuripes* changed its behavior in response to
453 greater *E. umbellata* density. This could occur from either favoring nest budding as a
454 reproductive mode, or by being more tolerant of nearby unrelated colonies. Low aggression
455 across longer distances may reflect nest budding rather than habituation, as distant nests are less
456 likely to have interacted directly and become habituated. Distant but related nests may be the
457 result of multiple generations of budding that has led to a large colony of nests spanning a wide
458 area. Such networks of *F. obscuripes* colonies exhibit low inter-nest aggression and can be
459 distributed in a clustered pattern (McIver *et al.*, 1997). Clustering in polydomous ant
460 colonies can be attributed to an endogenous Turing-like mechanism (Vandermeer *et al.*,
461 2008); however, further study is needed to disentangle the relative endogenous and exogenous

462 contributions (Li *et al.*, 2016) of nest budding and habitat preference in the pattern-formation
463 process on the site.

464

465 *Change in Formica obscuripes population over time*

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

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

489 A caveat of the stage-structured population model is that these results reflect the
490 dynamics of single nests on the site but not necessarily the colonies, which effectively function
491 as the individual organism in ants (Hölldobler & Wilson, 1990). However, growth and survival
492 of single nests could still indicate trends in the health of the larger colony. Nest changes should

493 be interpreted in the context of the larger colony, which may build, use, and abandon satellite
494 nests seasonally or in response to environmental factors while maintaining a core of consistently-
495 occupied nests (Talbot, 1971; McIver *et al.*, 1997). Future studies should identify and model
496 populations of core nests or entire colonies, rather than individual nests. This project would
497 require genetic or additional aggression testing methods to understand relatedness between nests,
498 or require identifying temporary and long-term nests through observations over multiple seasons
499 and years.

500 Another factor that complicates the interpretation of the results of the population model
501 was a cold wave in 2013 and 2014, which brought below-normal temperatures to the upper
502 Midwest and Great Lakes region (Wolter *et al.*, 2015). This could have played a role in the drop
503 in the number of *F. obscuripes* nests between 2013 and 2015, which in turn skewed the nest
504 count projection towards a more extreme decline. However, *F. obscuripes* is found in sites of
505 much higher latitude, suggesting the species can tolerate colder weather (Higgins & Lindgren,
506 2012). It could be that the observed decrease in occupied nests reflects a temporary withdrawal
507 by multi-nest colonies from their satellite nests in response to extreme weather, but further work
508 is needed to investigate whether the ants at this site exhibit this behavior. However, though the
509 weather may have exacerbated the ants' projected population decline, coupled changes in spatial
510 distribution and nest preferences demonstrate the overall importance of the impact of the *E.*
511 *umbellata* invasion.

512

513 *Implications for conservation*

514 Our study provides further evidence of the impact of invasive species on natives. We
515 make a case that demonstrates the importance of invasive monitoring and control in conservation
516 and land-use management. The *Elaeagnus umbellata* invasion is widespread in North America
517 and is found worldwide (Munger, 2003; CABI, 2016; EDDMapS, 2016). *Elaeagnus umbellata*
518 shares much of its range with *F. obscuripes* and other members of mound-building wood ant
519 species (Janicki *et al.*, 2016; Stockan & Robinson, 2016). The invasive characteristics of *E.*
520 *umbellata* that result in dense, monotypic stands (Orr *et al.*, 2005) is also shared among many
521 invasive shrubs (Van Kleunen *et al.*, 2010; Vilà *et al.*, 2011). Likewise, the habitat requirements
522 and reproductive strategies of *F. obscuripes* are common to many mound-building wood ant
523 species (Stockan & Robinson, 2016). We propose that the interaction and resulting competition

524 we demonstrate in this paper can be found in locations where similar species of invasive shrubs
525 are changing the habitat of wood ant species. Beyond the inherent conservation importance of *F.*
526 *obscuripes* and other wood ants, this species group also has the potential, when found in
527 sufficient numbers, to provide an important ecosystem service through biological control of
528 herbivore pests (McIver *et al.*, 1997; Stockan & Robinson, 2016). By examining the spatial
529 patterns and relationships of *F. obscuripes* nests in relation to *E. umbellata* invasion, we
530 identified significant pathways of impact by shrub invasions on an important species of ant.
531 Further study is needed to clarify the mechanisms of impact, the geographical extent of these
532 effects, and if similar effects are found in other invaded ecosystems.

533

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538

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707 SUPPORTING INFORMATION CAPTIONS

708 **S1:** Log-ratio preference for land cover at 5, 10, 15, 20, 25, and 30m. Positive values indicate

709 preference for the land cover type in the row over the land cover type in the column. The reverse

710 of these comparisons can be found by negating their preference values. Differences that were
711 significantly non-zero are indicated with an asterisk.

712

713

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715

716 TABLES

717

718 **Table 1:** Mean and standard deviation of % landcover composition of field, forest, and shrub
719 around simulated random points in the 1975 and 2008 conditions for the study site. Values
720 represent the aggregated statistics for 1000 simulations of random nest patterns. Percent
721 composition was calculated for an area around each random point in a 5, 10, 15, 20, 25, and 30m
722 radius, but only values at a 30m radius are reported here, as values did not differ significantly
723 between radii at the 95% confidence level.

| | 1975 | 2008 | <i>relative change</i> |
|------------------|-----------------------|-----------------------|-------------------------------|
| <i>landcover</i> | <i>% comp. (s.d.)</i> | <i>% comp. (s.d.)</i> | <i>%</i> |
| <i>field</i> | 72.5 (4.3) | 36.4 (3.3) | -49.8 |
| <i>forest</i> | 25.6 (4.4) | 43.9 (4.6) | +71.5 |
| <i>shrub</i> | 1.9 (0.6) | 19.6 (2.2) | +931.6 |

724

725

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

| 1980 | | | 2015 | | |
|---------------|--------------|---------------|---------------|--------------|---------------|
| a) 5m | | | c) 5m | | |
| | <i>shrub</i> | <i>forest</i> | | <i>shrub</i> | <i>forest</i> |
| <i>field</i> | 3.55* | 4.91* | <i>field</i> | 3.55* | 7.67* |
| <i>shrub</i> | | 1.35* | <i>shrub</i> | | 4.12* |
| b) 30m | | | d) 30m | | |
| | <i>shrub</i> | <i>forest</i> | | <i>shrub</i> | <i>forest</i> |
| <i>field</i> | 0.89* | 2.74* | <i>field</i> | 0.19 | 1.93* |
| <i>shrub</i> | | 1.84* | <i>shrub</i> | | 1.74* |

730

731

732 **Table 3:** Lefkovitch projection matrix for stage-structured population model. Transition rates are
733 shown from the stages named in the columns to the stages named in the rows of the table. These
734 positions correspond to the Lefkovitch matrix in Fig. 2b. Transition rates are represented as the
735 fraction of the total population of the stage in the column (denominator) undergoing the
736 transition to the stage in the row (numerator) from 2013 to 2015, plus fecundity rates where
737 applicable. Fecundity rates F_1 and F_2 represent the rates that new stage 1 and stage 2 nests were
738 produced; they are uniform across columns because we assumed all stages were equally capable
739 of reproducing. Their values are equal to the number of new nests in 2015 for that stage divided
740 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 |

741

742

743

744 FIGURE CAPTIONS

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

749
750 **Figure 2:** A conceptual diagram of the stage-structured model of nest size stages (a), where
751 terms G_{pi} and R_{pi} represent growth and regression transition rates, respectively, from stage i to p ;
752 S_i represents the probability of surviving and remaining in stage i ; and fecundity rates F_1 and F_2
753 represent the rates that new stage 1 and 2 nests are produced by each stage. Each fecundity rate
754 was assumed to be the same for all stages. Fecundity rates were added to the transition rates
755 between appropriate stages; dynamics that were the sum of two rates are represented as double-
756 line arrows in the diagram. These rates were used to construct the Lefkovich projection matrix \mathbf{P}
757 (b), which was multiplied iteratively with N_t , a vector of the number of nests at each stage at
758 time t .

759
760 **Figure 3:** Nest distance and aggression score relationship between individual *Formica*
761 *obscuripes* ants from different nests in 2015. The dotted line represents the predicted trend when
762 the proportion of shrub landcover in a 20m transect between originating nests is 0.2, and the
763 solid line represents the trend when shrub proportion is 0.4. The proportion of shrub landcover
764 between nests is represented by the size and shading of the circle, with larger, lighter circles
765 corresponding to more shrubs.

766
767 **Figure 4:** Transformed Ripley's K results for 1980 (a) and 2015 (b) nest distributions of
768 *Formica obscuripes* in the study area. The y-axis is a transformation of the K statistic at a radius
769 of r meters from each nest (x-axis). The transformation stabilizes variance and linearizes the plot
770 so that the y-axis (dotted line) represents complete spatial randomness (Fortin *et al.*, 2002). Thus,
771 negative values are more uniform than random and positive values are more clustered than
772 random. The solid line represents the observed K statistic for that year's nest pattern. Observed
773 patterns were compared to 999 simulations of random patterns (grey area) and are significant
774 when they fall outside of this random envelope.

775

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

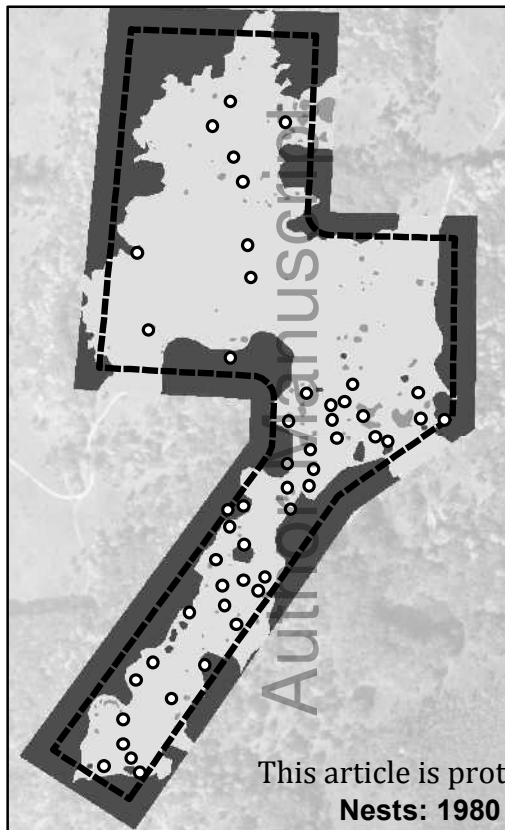
780

781 **Figure 6:** Projected change of *F. obscuripes* population at ESGS based on survey data from
782 2013 and 2015. Using a stage-structured population model, we project the population trend of all
783 nests (solid grey trend) and each size stage class (lines) for 20 iterations over 40 years.

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(a)

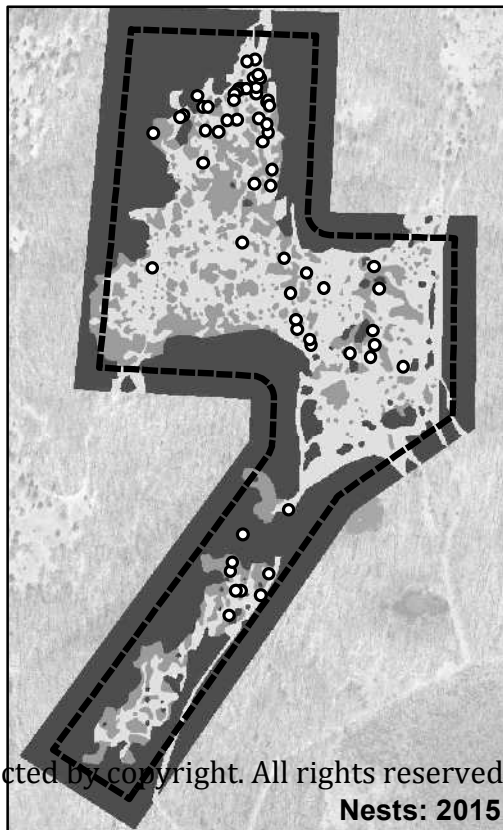
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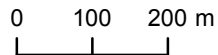
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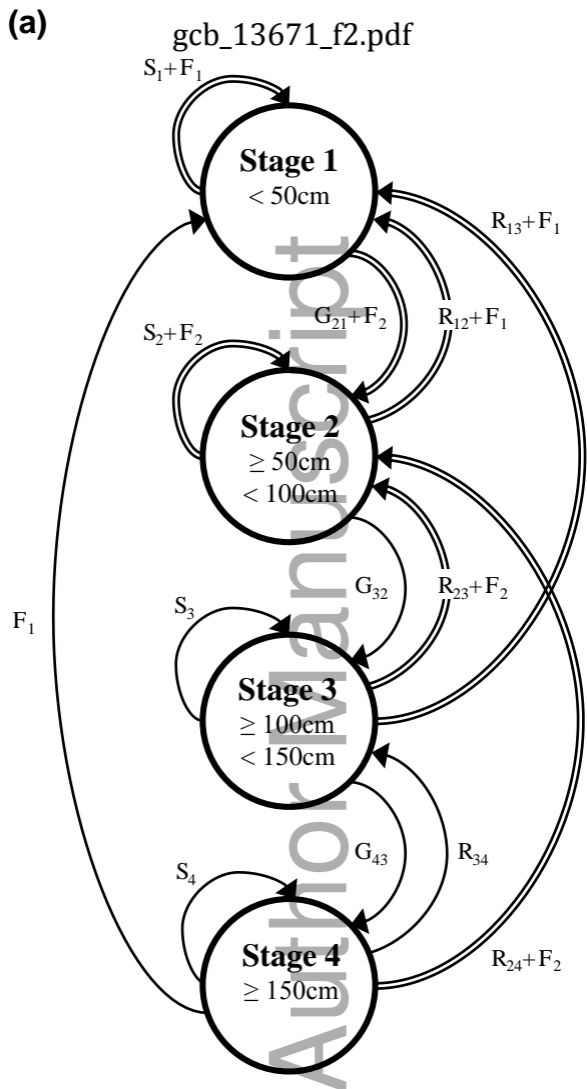
Landcover: 1975



Nests: 2015

Landcover: 2008

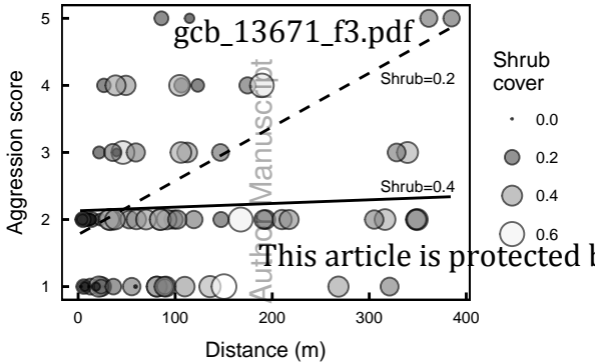


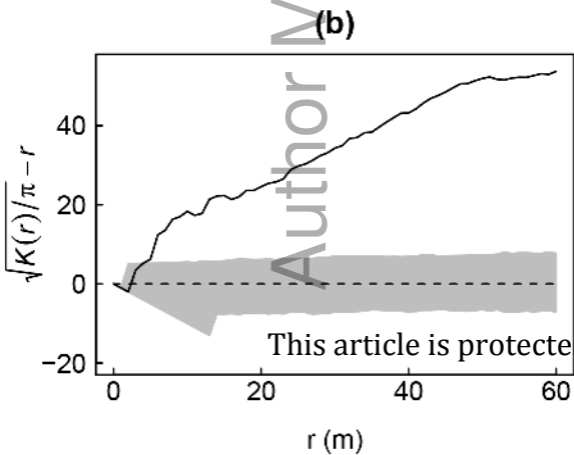
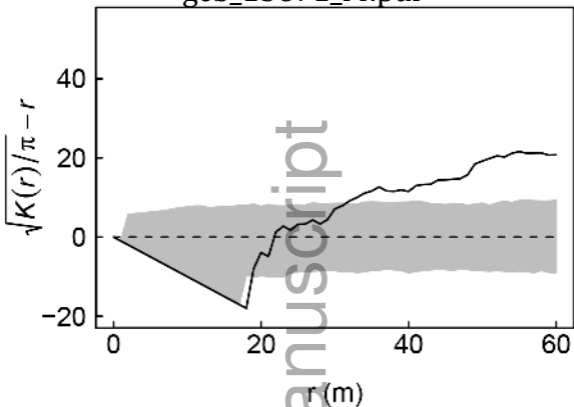


(b)

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





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Year

● 1980

○ 2015

Log-ratio preference

4

3

2

1

0

5

10

15

20

25

30

Radius (m)

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