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2 **Seed dispersal of an invasive shrub, Amur honeysuckle (*Lonicera maackii*), by white-tailed**
3 **deer in a fragmented agricultural-forest matrix**

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13 **Abstract**

14 Ungulates are potentially important seed dispersers for many invasive plant species. While our
15 understanding of which invasive plant species are dispersed by ungulates has improved over the
16 last decade, the factors influencing this process remain poorly understood. To address this, we
17 explored white-tailed deer (*Odocoileus virginianus*) seed consumption and dispersal of an
18 invasive shrub (*Lonicera maackii*) in fragmented agricultural-forest matrices in western Ohio. In
19 a pairwise browse preference experiment, deer browsed at similar levels on branches of *L.*
20 *maackii* with fruits removed and fruits intact (mean \pm 95% CI: 57 \pm 14% and 62 \pm 14%,
21 respectively). We found no evidence that white-tailed deer disperse *L. maackii* seeds along an
22 invasion front, but 31% of deer pellet groups collected in an invaded area contained germinable
23 *L. maackii* seeds (maximum number of germinable seeds = 30). By combining hourly movement
24 data specific to fragmented landscapes and gut retention time data, we projected that female deer
25 disperse 91% of ingested seeds further than 100m from seed sources (i.e. long-distance seed
26 dispersal), and rarely disperse seeds up to 7.9 km. We conclude that white-tailed deer can be
27 important long-distance seed dispersal vectors of *L. maackii*, and that invader abundance and/or
28 patch connectivity likely influence patterns of seed dispersal by white-tailed deer.

29 **Key Words:** deer browse, nearest neighbor, patch size, seed shadow projection

30 Seed dispersal represents the single point in many plants' life cycle where an individual can
31 move. The movement of seeds allows plants to escape density-dependent mortality near parent
32 plants (Janzen 1970), colonize new habitats (Clark et al. 1998), exchange genetic material across
33 populations (Excoffier et al. 2009), and rescue populations from local extinction in
34 metapopulation dynamics (Cain et al. 2000). Large-scale anthropogenic changes, such as
35 invasion of exotic plant species and habitat fragmentation, are altering seed dispersal of many
36 plant species, which has potentially negative consequences for conservation of plant populations
37 and communities (McConkey et al. 2012). Invasive plant species represent an ideal system to
38 study seed dispersal, especially along invasion fronts, and are of practical importance since
39 dispersal is a critical step in the invasion pathway. Dispersal patterns are inferred by describing
40 the proportion of seeds in discrete distance classes away from parent plants ("seed shadows",
41 Clark et al. 2005). An alternative approach to inferring seed shadows involves combining short-
42 scale vector movement and retention time data to project seed shadows (Murray 1988; Vellend et
43 al. 2003). In order to project a seed shadow, three things must be understood: the agents
44 responsible for dispersing seeds (dispersal vectors), the time period over which these vectors can
45 carry seeds (retention time), and vector movement patterns on the same time scale as retention
46 time. Seed shadow projections provide valuable insight into the importance of a dispersal vector
47 by providing expectations of the most frequent (mean, median, or mode) and longest (maximum)
48 dispersal distances a seed might experience.

49 Seed dispersal vectors that transport seeds over long distances, potentially connecting
50 disjunct populations of plant species, are especially important to understand. Increasingly,
51 suitable habitat is undergoing fragmentation due to anthropogenic land-use changes, as is the case
52 for forests in many parts of North America (Heilman and Strittholt 2002; Riitters et al. 2012).

53 North American ungulates, such as white-tailed deer (*Odocoileus virginianus*), disperse seeds
54 through endozoochory (ingestion and defecation of viable seeds). Since ungulates have long gut
55 retention times and potentially large daily movements, ungulate endozoochory occurs over long
56 distances, and can potentially link fragmented habitat patches (Eycott et al. 2007; Jaroszewicz et
57 al. 2013). Using seed shadow projection based on gut retention times and daily movement,
58 Vellend et al. (2003) showed that white-tailed deer can disperse *Trillium grandiflorum* seeds >
59 3km away from seed sources in deciduous forests. As generalist herbivores, white-tailed deer
60 consume a wide range of plant types during different seasons, including woody browse, forbs,
61 crops, and grasses (Hewitt 2011). White-tailed deer browsing during fruit production can result
62 in ingested seeds, and germinable seeds from dozens of native and exotic species have been
63 found in white-tailed deer fecal pellets from North American temperate broadleaf forests (Myers
64 et al. 2004; Williams and Ward 2006; Blyth et al. 2013). Since white-tailed deer abundance
65 throughout eastern North America has increased relative to pre-colonial abundances (Rooney
66 2001), it is possible that increased access to long-distance seed dispersal vectors has facilitated
67 the success of many ungulate-dispersed plant species.

68 We investigated the potential role of white-tailed deer as a seed dispersal vector for
69 invasive shrubs in their introduced range by studying the relationship between white-tailed deer
70 and Amur honeysuckle (*Lonicera maackii* (Rupr.) Herder, Caprifoliaceae). Establishment of *L.*
71 *maackii* alters native plant population dynamics (Gould and Gorchov 2000; Gorchov and Trisel
72 2003; Miller and Gorchov 2004), community composition (Collier et al. 2002; Hartman and
73 McCarthy 2008; Christopher et al. 2014), and ecosystem functions (Arthur et al. 2012; McNeish
74 et al. 2012). Propagule pressure and movement of dispersal vectors are important for the spread
75 of this invasive shrub. *Lonicera maackii* presence in fragmented forest patches is negatively

76 correlated with both distance from the nearest town and the amount of surrounding cropland
77 (Bartuszevige et al. 2006; Gorchov et al. 2014a). Several bird species act as important seed
78 dispersal vectors by consuming the bright red fruits produced by this shrub (Ingold and Craycroft
79 1983; Bartuszevige and Gorchov 2006). White-tailed deer are also likely *L. maackii* seed
80 dispersal vectors, as 68% of the *L. maackii* seeds from the fecal pellets of captive deer fed fruit
81 of this shrub were viable (Castellano and Gorchov 2013). Also, pellets collected from free-
82 ranging white-tailed deer contained seeds of other invasive *Lonicera* species (Myers et al. 2004;
83 Williams and Ward 2006). Here, we investigate the hypothesis that white-tailed deer are
84 important seed dispersal vectors for invasive shrubs. To do this, we tested two predictions: 1)
85 free-ranging white-tailed deer consume ripe *L. maackii* fruit, and 2) free-ranging white-tailed
86 deer disperse germinable *L. maackii* seeds. Our results suggest white-tailed deer can be
87 important seed dispersal vectors of this invasive shrub, but this importance likely depends on
88 invader abundance and landscape connectivity, among other factors.

89 **Methods**

90 *Study Areas*

91 White-tailed deer foraging and seed dispersal data were collected at two sites in western
92 Ohio, reflecting areas with high and low *L. maackii* abundance. The high *L. maackii* abundance
93 (“invaded”) site was the Miami University Ecology Research Center (ERC) (39° 31’ 57” N, 84°
94 43’ 23” W), Butler County. The ERC is a 93-ha property, with interspersed patches of forest, old
95 fields, and row crops. *Lonicera maackii* was introduced to the area more than 50 years ago, and
96 is now common in forest patches throughout the county (Hutchinson and Vankat 1997). *Lonicera*
97 *maackii* is one of the most common plants at the ERC, both within forest stands and along edges
98 (Pfeiffer and Gorchov 2015).

99 The low *L. maackii* abundance (“invasion front”) site was located 50-70 km north of the
100 invaded site (40° 05’ 36” N, 84° 46’ 47” W) in Darke County (Figure 1). This site covered 23
101 km² of agricultural matrix with interspersed forest patches, agricultural fields, and residential
102 housing. Agricultural fields predominantly contained corn and soy grown as row crops. Some
103 forest patches had sparse abundance of *L. maackii* and other invasive plant species, but *L.*
104 *maackii* was not present in most forest patches. A region of isolated forest patches approximately
105 15 km southeast of this study area was initially invaded by *L. maackii* about 20 years ago
106 (Gorchov et al. 2014a). Today, established *L. maackii* populations are common in that region, as
107 well as forest patches between it and the invasion front site (PWG, personal observation),
108 defining this study area as a *L. maackii* invasion front. The discrete forest patches and low *L.*
109 *maackii* abundance made this site well-suited to determine the ability of this invasive shrub to
110 invade new areas through long-distance seed dispersal by white-tailed deer.

111 Hourly white-tailed deer movement data were collected from GPS-collared white-tailed
112 deer between 2002 and 2006 in an agricultural-forest matrix in southern Illinois (37° 42’ 24” N,
113 89° 9’ 47” W). *Lonicera maackii* is present and established throughout this study area, although
114 its abundance has not been determined. No browse preference or seed dispersal data were
115 collected from this area. More data on land use and white-tailed deer distribution in the Illinois
116 study area can be found in Storm et al. (2007).

117 *Browse Preference Experiment*

118 We conducted a pairwise browse preference experiment at the invaded site from October
119 2012 to January 2013, in order to monitor white-tailed deer browse on *L. maackii* stems while
120 testing for preference between shrubs with and without fruit. We only included *L. maackii*
121 growing on the forest edge for this experiment because (1) this high-light environment produces

122 a higher fruit set compared to forest interiors, ensuring that enough fruit was present on the *L.*
123 *maackii* stems to enable a perceivable treatment effect, and (2) white-tailed deer use forest edge
124 habitat extensively (Stewart et al. 2011).

125 We distinguished two age classes of stem tissue: twigs and branches. Stems produced in
126 the current year and bearing leaves were classified as twigs. Older stems, bearing multiple twigs
127 but no leaves were classified as branches. Branches generally consisted of more woody tissue
128 than twigs. On each of the 90 shrubs in this experiment, we monitored new white-tailed deer
129 browse on a single horizontal branch, including all twigs borne on the branch. In order to control
130 for factors that potentially confound white-tailed deer browse preferences (shrub age, size, or
131 reproductive status), we only observed *L. maackii* branches that were between 1 and 2m above
132 the ground, with ≥ 10 twigs (a proxy for branch size) and ≥ 10 fruits.

133 The 90 individual shrubs were divided into 45 pairs, and each pair consisted of two *L.*
134 *maackii* 5 – 10 m apart. Shrub pairs were ≥ 100 m apart, to ensure independence of browse
135 observations. In order to detect white-tailed deer browse preference between fruiting and non-
136 fruiting *L. maackii* branches, each branch within a pair was randomly assigned one of two
137 treatments: control or fruit removal. Control branches were left with fruits unaltered. Fruit
138 removal branches had all fruit on the branch manually removed, along with any fruits within 0.5
139 m of the branch, in order to create a treatment effect large enough to be perceived by white-tailed
140 deer.

141 Prior to the start of the experiment, we marked each target branch with an inconspicuous
142 white string towards the proximal end of the branch. White-tailed deer browse, which is distinct
143 from other browse (Swift and Gross 2008), was only measured distal to this point on the branch.
144 We found it appropriate to distinguish between two types of white-tailed deer browse marks in

145 this experiment: small browse marks on individual twigs (“twig browse”) and larger browse
146 marks on branches with concurrent disappearance of one or more previously existing twigs
147 (“branch browse”). The incidence of both browse types on *L. maackii* branches was recorded at
148 the beginning and end of the experiment, and the difference between the two represented the
149 amount of new white-tailed deer browse. We determined the proportion of branches in each
150 treatment that experienced new white-tailed deer browse, and used the normal approximation to
151 the binomial to develop 95% confidence intervals for each proportion.

152 We used a sign test to investigate whether deer preferred to browse on *L. maackii*
153 branches with fruits intact. A sign test determines if the proportion of trials where a specific
154 outcome occurs is significantly different from 0.5. If a *L. maackii* with fruits intact had a greater
155 amount of new white-tailed deer browse than its paired *L. maackii* with fruits removed, this was
156 considered preference for *L. maackii* with fruit. In cases where both branch and twig browse
157 were observed within shrub pair, the direction of preference was assigned based on branch
158 browse alone, since individual twigs that were browsed separately may have been missing
159 entirely after branch browse. Pairs with lost flagging (n = 3) were excluded from analysis.

160 *Seed Dispersal Observation*

161 In order to determine the extent of *L. maackii* seed dispersal by white-tailed deer, we
162 collected white-tailed deer fecal pellet groups from our study areas during the late fall and early
163 winter. Initially, we opportunistically collected white-tailed deer pellet groups at the invaded site
164 in December 2012 and January 2013. Due to the high abundance of *L. maackii* in this study area,
165 our study design made it impossible to determine the source of any seeds found within fecal
166 pellets.

167 In order to quantify the role of white-tailed deer in the spread of invasive shrubs to new
168 areas, a more rigorous approach was taken the following year. Within the invasion front site, we
169 located the closest *L. maackii* seed sources to our collection areas. Individual shrubs were
170 considered reproductive if flowers were present in spring 2013. We identified two potential seed
171 source populations, and recorded each individual's GPS coordinates. One population, located on
172 the north end of the study area, consisted of several reproducing individuals near a pine (*Pinus*
173 spp.) forest. A second population, located on the south end of the study area, consisted of two
174 large individuals growing in a hedge row in high-light conditions. We chose forest patches
175 neighboring these seed sources as collection areas, where reproducing *L. maackii* was either
176 absent or found in abundances low enough to facilitate manual removal of shrubs. Forest patches
177 were closed-canopy, secondary growth mixed deciduous forests, and ranged in size from 1.5 to 9
178 ha. Each had a history of logging, and white-tailed deer hunting was permitted throughout the
179 study area. We established 10 collection areas, seven of which had reproducing *L. maackii*
180 (range: 1 to 13) which were manually removed in June 2013. Removal of reproducing shrubs
181 ensured that any *L. maackii* seeds found in collected white-tailed deer pellets were dispersed
182 over long distances from other forest patches.

183 We collected white-tailed deer fecal pellets along transects in each collection area at the
184 invasion front site. The GPS coordinates of each corner of the collection areas were used to
185 establish two 100 m east-west transects per collection area, that were evenly spaced north-south
186 throughout the forest patch. Each transect started at the forest edge, and extended into the forest
187 interior. Every 10 m, we established a 2m x 10m subplot, centered on the transect. Transects
188 were cleared of white-tailed deer pellets during the last week in September 2013, and fresh
189 pellets were collected bi-weekly through the end of December 2013.

190 After collection, all pellets were cold stored at 5°C for six weeks before being transferred
191 intact to sterile vermiculite, where they were kept at 24°C during the day and 15°C at night in a
192 greenhouse, representing conditions favorable for *L. maackii* germination (Hidayati et al. 2000).
193 Once samples were planted, seedling emergence was recorded weekly. In order to control for the
194 unlikely event of contamination by other *Lonicera* seeds in the greenhouse, control pots,
195 containing only sterile vermiculite, were used.

196 *Seed Shadow Projection*

197 In order to develop an expected distribution of seed dispersal distances for white-tailed
198 deer endozoochory of an invasive shrub, we projected a seed shadow using existing gut retention
199 time and movement data (Murray 1988; Vellend et al. 2003). Each of these data sets is described
200 by a matrix. The matrix describing vector gut retention time provides the probability that a seed
201 is passed out of the dispersal vector's intestinal tract during a given hour. It has a single column,
202 and a number of rows (72) equal to the maximum retention time (in hours) for a seed. Forage
203 quality affects gut retention time in mammals (Warner 1981), so we used gut retention data from
204 a captive male white-tailed deer that was fed a diet of sumac (*Rhus typhina*) inflorescences
205 (Mautz and Petrides 1971). This was a more appropriate analog to white-tailed deer browse on *L.*
206 *maackii* than diets employed in other captive white-tailed deer gut retention studies (Jenks and
207 Leslie 1989; Barnes et al. 1992). It is important to note that these data could differ from the
208 retention times of free-ranging white-tailed deer, but we are not aware of any such studies. We
209 estimated the retention time (X-axis) and cumulative percent of marker defecated (Y-axis) for
210 each point in Figure 1 in Mautz and Petrides (1971). The distribution of retention times were fit
211 to a lognormal distribution (Rawsthorne et al. 2009) using the MASS package in R (Venables
212 and Ripley 2002). This lognormal distribution ($\mu = 3.38$, $\sigma = 0.35$) allowed us to calculate the

213 probability density that a seed was defecated each hour. This approach showed that 26% of
214 ingested material was egested after 24 hours, 93% was egested after 48 hours, and >99% was
215 egested within 72 hours. Hence, we projected seed dispersal by white-tailed deer over 72-hour
216 periods. We populated the retention time matrix with lognormal probability densities values for
217 hours 1-72; these values summed to 0.997 so they did not require rescaling to constitute a
218 probability distribution (which sums to 1).

219 The matrix describing a dispersal vector's hourly movement provides the probability that
220 a vector is located in a discrete displacement class away from a starting point (rows) at hourly
221 intervals (columns). We calculated Euclidean distance between each hourly position from the
222 GPS-collared white-tailed deer. The dataset included hourly position data for 26 white-tailed
223 deer between October and December, totaling over 39,000 point positions. All but one of the 26
224 white-tailed deer in the study were female, due to the original study's focus on overlap of doe
225 home ranges (Kjaer et al. 2008). Fourteen white-tailed deer were adult females, one was an adult
226 male, ten were female yearlings, and one was a female fawn. Female white-tailed deer in each
227 age class had similar hourly movement patterns (Appendix A) and consequently were pooled for
228 seed shadow projection. Details regarding study findings and capture methods from this dataset,
229 including Institutional Animal Care and Use Committee approvals, are found elsewhere
230 (Schauber et al. 2007; Storm et al. 2007; Kjaer et al. 2008; Anderson et al. 2011). We chose
231 6:00PM for the starting time of the 72-hour period, since white-tailed deer are often most active
232 at this time (Roleau et al. 2002). Hourly displacement was summarized into 100 m distances
233 classes (Vellend et al. 2003). The number of rows was the number of 100 m distance classes
234 extended to the maximum displacement covered (in this case, 7.9 km). This displacement matrix
235 thus had 79 rows and 72 columns.

236 The matrix describing hourly movement was multiplied by the matrix describing gut
237 retention time to project a seed shadow, described by a single column matrix with 79 rows (one
238 for each 100 m distance from the origin, Eqn. 1). Each element in this matrix describes the
239 probability that a *L. maackii* seed is dispersed into the discrete displacement class.

240 *Landscape configuration*

241 We compared the landscape configurations of our three study areas to assess the
242 applicability of the Illinois deer movement data to the Ohio landscapes where seed dispersal data
243 were collected. In the case of the invaded area, where the collection area was small (<0.5 km),
244 we collected landscape statistics in a 2 km buffer around the collection area. This represents an
245 area large enough to properly describe the home range of white-tailed deer in an agricultural-
246 forest matrix (Quinn et al. 2013). Land use in the study areas were classified as either forest
247 patch or non-forest patch. Specifically, we compared forest patch area-weighted shape index,
248 nearest neighbor, and patch area coefficient-of-variation, as well as road density in each study
249 area, due to their influence on white-tailed deer movement (Ng et al. 2008; Walter et al. 2009).

250 **Results**

251 *Browse Preference*

252 We observed new white-tailed deer browse on the majority of *L. maackii* branches.
253 Specifically, $62 \pm 14\%$ of *L. maackii* branches with fruits intact and $57 \pm 14\%$ of branches with
254 fruits removed were browsed (95% confidence intervals). White-tailed deer browsed more on
255 the fruiting branch in 55% of pairs, browsed more on the branch with fruits removed in 31% of
256 pairs, browsed equally on both branches in 9% of pairs, and browsed on neither branch in 5% of
257 pairs (Figure 2). Overall, there was no significant browse preference for branches with fruit over
258 branches without fruit (number of trials = 42, $P = 0.64$).

259 *Seed Dispersal Observation*

260 From the 29 white-tailed deer pellet groups we collected from the invaded site in
261 December 2012 and January 2013, *L. maackii* seedlings emerged from 9 pellet groups (31%),
262 with an average of 2.5 ± 6.7 germinable seeds per collected pellet group (maximum = 30). The
263 following year, we collected a total of 53 white-tailed deer pellet groups from the invasion front
264 site between October and December 2013 and no *L. maackii* seedlings emerged (Table 1).

265 *Seed Shadow Projection*

266 The maximum displacement of a white-tailed deer within a 72-hour movement period
267 was 7.9 km. A strikingly high proportion of seeds (91%) were projected to disperse >100m away
268 from the seed source. The mode and median (50% cumulative probability) of our seed shadow
269 projection showed that white-tailed deer are most likely to disperse seeds approximately 300 m
270 from a seed source in fragmented landscapes. Seven percent of seeds were projected to disperse
271 >1 km, and in extreme cases (0.3%) seeds were projected to disperse >7 km away from seed
272 sources (Figure 3).

273 *Landscape configuration*

274 Forest patches were typically closest together in the invaded area (mean nearest neighbor
275 = 55.3 ± 36.2 m), while forest patches in the invasion front had the most regular shapes (mean
276 shape index = 2.55 ± 0.67) and the least variation in size (forest patch coefficient of variation =
277 180.7). Road density varied little among study areas (range 1.22 to 1.43 km km⁻², Table 2).

278 **Discussion**

279 In this study, we tested the importance of white-tailed deer as seed dispersal vectors of
280 invasive shrubs. We found that white-tailed deer in an invaded area frequently browsed on *L.*
281 *maackii* while fruits were ripe, providing an opportunity for seed ingestion and subsequent seed

282 dispersal. We also found evidence of white-tailed deer dispersing *L. maackii* seeds in a heavily
283 invaded area, but not along an invasion front, despite the presence of nearby seed sources. A
284 projected seed shadow, which used habitat-specific movement data, suggests that white-tailed
285 deer disperse *L. maackii* seeds over long distances in a landscape of forest fragments in an
286 agricultural matrix.

287 *Browse Preference*

288 White-tailed deer frequently browsed on *L. maackii* in the invaded study area in the late
289 fall and early winter, as new browse marks were observed on most branches. This pattern may be
290 explained by *L. maackii* phenology, since this invasive shrub is frost-tolerant and retains its
291 foliage into late fall unlike other common food sources in this region (Wilfong et al. 2009;
292 Johnston et al. 2012). Dichromatic color vision in white-tailed deer may explain the lack of
293 browse preference for fruiting *L. maackii* branches observed in this study. Many seed dispersal
294 vectors, including many bird species, respond to chromatic signals (Schaefer 2006), such as the
295 bright red colors found in *L. maackii* fruits. Accordingly, at least 12 species of birds in
296 southwestern Ohio consume *L. maackii* fruits (Ingold and Craycroft 1983; Bartuszevige and
297 Gorchoff 2006). However, many mammalian herbivores, including white-tailed deer, have only
298 two ocular cones, restricting the ability of these species to see colors in the red end of the visible
299 spectrum (Ditchkoff 2011). While *L. maackii* fruits do not attract white-tailed deer in the same
300 way they attract avian frugivores, our work shows that white-tailed deer do consume ripe fruits
301 while browsing *L. maackii* during late fall to early winter, providing an opportunity for white-
302 tailed deer to disperse seeds of this invasive shrub.

303 White-tailed deer browse has been implicated as a major driver of population decline in
304 some native plant species (Rooney and Waller 2003), but it often facilitates both invasive herbs

305 and invasive shrubs (Eschtruth and Battles 2009; Knight et al. 2009). We present evidence that
306 white-tailed deer browse can be widespread throughout a population of reproducing *L. maackii*
307 (approximately 60% of observed shrubs had at least some woody tissue consumed). Our work,
308 focused on the implication of white-tailed deer browse for seed dispersal, was not designed to
309 assess the possible negative impacts of browse on population dynamics of invasive shrubs.
310 However, other research shows that white-tailed deer browse can reduce recruitment of invasive
311 shrubs. Near our invaded site, cover of *L. maackii* at heights from 0.5 to 1.5 m was significantly
312 higher after four years of deer exclosure than in paired deer access plots (J. Peebles-Spencer and
313 D. Gorchov, unpubl. data). Both recruitment of *L. maackii* and the combined diameter growth
314 rate of four species of invasive shrubs (*L. maackii*, *Rosa multiflora*, *Berberis thunbergii*,
315 *Ligustrum vulgare*) were higher in deer exclosures than ambient-density controls in Indiana
316 (Shelton et al. 2014). The importance of deer browse on both invasive plant recruitment and seed
317 dispersal is likely context-dependent, determined in part by the overall palatability of the plant
318 community (Bee et al. 2011). It is not surprising that the invaded study area, which is dominated
319 by unpalatable invasive shrubs, white-tailed deer browse on *L. maackii* is extensive.

320 *Seed Dispersal*

321 Seed dispersal of invasive *L. maackii* seeds by white-tailed deer was relatively common
322 in the invaded study area (31% of pellet groups contained germinable *L. maackii* seeds). Our
323 seed shadow projection indicated that white-tailed deer-dispersed seeds were likely traveling
324 hundreds of meters, although our study design was unable to confirm this. This suggests that
325 seed dispersal by white-tailed deer has potential importance for population dynamics and genetic
326 structure in areas of high *L. maackii* abundance. *Lonicera maackii* populations in southwestern
327 Ohio exhibit high levels of genetic diversity that suggest frequent long-distance seed dispersal

328 among populations (Barriball et al. in press). Our results suggest that this genetic variation may
329 partly be maintained through long-distance seed dispersal by white-tailed deer. Additionally,
330 seed dispersal by white-tailed deer could rescue populations of *L. maackii* from eradication
331 efforts by land managers, since long-distance seed dispersal has been shown to prevent local
332 extinctions of populations undergoing metapopulation dynamics (Cain et al. 2000).

333 Despite collecting 53 white-tailed deer pellet groups at the invasion front site (a greater
334 sampling effort than collection at the invaded area), no germinable *L. maackii* seeds were found.
335 Germinable seeds from 13 plant species were contained within pellets (Guiden, unpublished
336 data), indicating that our handling of pellets was not responsible for the lack of viable *L. maackii*
337 seeds. Collection areas at the invasion front site ranged from approximately 500 m to 2100 m
338 from the closest seed source. According to our seed shadow projection, 43% of *L. maackii* seeds
339 consumed by white-tailed deer should have been dispersed over these distances. We conclude
340 that seed dispersal by white-tailed deer is uncommon along an invasion front and not primarily
341 responsible for the spread of this invasive shrub. Our finding that white-tailed deer are
342 conditional seed dispersal vectors for *L. maackii* has implications for management of invasive
343 plants and white-tailed deer. White-tailed deer dispersal of seeds is most important in areas
344 where *L. maackii* is established. Although we did not detect seed dispersal by white-tailed deer at
345 the invasion front, it is possible that in different contexts (e.g. more continuous forest habitat,
346 more abundant seed sources) white-tailed deer could introduce *L. maackii* seeds to uninvaded
347 habitat, and this potential should not be neglected.

348 There are two non-mutually exclusive explanations for the observed discrepancies in seed
349 dispersal patterns between sites. The first involves white-tailed deer browse preference. White-
350 tailed deer consumption and dispersal of *L. maackii* seeds (and perhaps seeds of other invasive

351 species) is likely dependent on the relative abundance of the invasive plant. Where it establishes,
352 *L. maackii* is associated with declines in forest herb, seedling, and sapling layers (Hartman and
353 McCarthy 2008), which can constitute important elements of white-tailed deer diets (Vangilder
354 et al. 1982; Johnson et al. 1995). As the abundance of preferred food sources declines, large
355 herbivores should increase consumption of less preferred plant species (van Beest et al. 2010),
356 such as *L. maackii*. Differences in white-tailed deer densities could achieve the same effect: a
357 higher density of consumers could result in decreased availability of preferred food sources, and
358 hence more consumption of less preferred *L. maackii*. Pellet count surveys suggest that white-
359 tailed deer abundance was lower at the invasion front (Guiden 2014) than the invaded study are
360 (Crist, unpublished data), but different analyses were used to reach these conclusions, making
361 direct comparisons speculative. If this invasive shrub continues to spread within the invasion
362 front, or white-tailed deer densities increased dramatically, we would expect increased *L.*
363 *maackii* consumption and seed dispersal.

364 Alternatively, idiosyncrasies in landscape configuration, such as patch connectivity,
365 shape, and size can affect white-tailed deer movement (Walter et al. 2009, Williams et al. 2011).
366 Forest patches in the invaded area were more connected (lower mean distance between nearest
367 neighboring forest patch), while forest patches in the invasion front were more condensed (less
368 perimeter per area) and more variable in size (larger coefficient of variation). All else being
369 equal, we expect fewer long movements by white-tailed deer at the invasion front in our study,
370 and therefore less seed dispersal between disjunct forest patches. This highlights the need to
371 account for differences in landscape configuration when comparing patterns of seed dispersal in
372 different areas.

373 Our seed shadow projection builds upon the understanding of seed dispersal by white-
374 tailed deer described in Vellend et al. (2003)'s seed shadow projection of *T.grandiflorum* by only
375 using movement data collected in a fragmented landscape at the time of *L. maackii* fruit ripening.
376 The mode of projected dispersal distances were similar (300m), but our seed shadow projection
377 shows a much greater maximum dispersal distance (7.9 km vs. 3.9 km; Vellend et al. 2003). This
378 suggests that seasonality and landscape configuration, factors known to influence white-tailed
379 deer movement, could consequently alter the long-distance seed dispersal capacity of white-
380 tailed deer. To explore how seed dispersal by male deer might differ from that projected for
381 females, we used the movement data from the single male white-tailed deer in our movement
382 data set, and the same gut retention data, to project a seed shadow. The mean seed dispersal
383 distance for the male white-tailed deer (900m, Guiden unpublished data) was approximately
384 three times further than the projected median seed dispersal distance for female white-tailed deer
385 (300m), which is consistent with existing knowledge of white-tailed deer behavior (Nixon et al.
386 1991, Walter et al. 2009). This could suggest that when seed dispersal vectors have strong sexual
387 dimorphism, including many ungulate species, the contributions of each sex to seed dispersal
388 merits consideration.

389 While the ecological consequences of white-tailed deer herbivory have been well studied
390 over the past several decades (reviewed by Côté et al. 2004), less is known about the causes and
391 consequences of native and invasive plant seed dispersal by white-tailed deer. Reports of exotic
392 species seed dispersal by white-tailed deer are becoming increasingly common in the literature
393 (Vellend 2002; Myers et al. 2004; Williams and Ward 2006), highlighting the complex
394 interactions between white-tailed deer and plant communities. Since North American white-
395 tailed deer abundances have increased dramatically since pre-colonial times (Rooney 2001),

396 understanding how seed dispersal by white-tailed deer has contributed to the spread of invasive
397 plants will be an important aspect to consider when planning eradication and control of these
398 plant species. Our study demonstrates the need to shift efforts beyond compiling lists of plant
399 species that are dispersed by white-tailed deer to a more mechanistic understanding of how
400 ecological context impacts seed dispersal by white-tailed deer.

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410 **References**

- 411 Anderson CW, Nielsen CK, Storm DJ, Schauber EM (2011) Modeling habitat use of deer in an
412 exurban landscape. *Wildl Soc Bull* 35:235–242.
- 413 Arthur MA, Bray SR, Kuchle CR, McEwan RW (2012) The influence of the invasive shrub,
414 *Lonicera maackii*, on leaf decomposition and microbial community dynamics. *Plant Ecol*
415 213:1571–1582.
- 416 Barnes TG, Varner LW, Blankenship LH, Gallagher JF (1992) Indigestible particulate passage in
417 white-tailed deer. In: Brown RD (ed) *The Biology of Deer*. Springer-Verlag, New York pp.
418 436–442.
- 419 Barriball, K., E.J. McNutt, D.L. Gorchov, and O.J. Rocha. In press. Inferring invasion patterns of
420 *Lonicera maackii* (Rupr) Herder (Caprifoliaceae) from the genetic structure of 41
421 naturalized populations in a recently invaded area. *Biol Invasions*.
- 422 Bartuszevige AM, Gorchov DL (2006) Avian seed dispersal of an invasive shrub. *Biol Invasions*
423 8:1013–1022.
- 424 Bartuszevige AM, Gorchov DL, Raab L (2006) The relative importance of landscape and
425 community features in the invasion of an exotic shrub in a fragmented landscape.
426 *Ecography* 29:213–222.
- 427 Bee JN, Tanentzap AJ, Lee WG, Lavers RB, Mark AF, Mills JA, Coomes DA (2011). Influence
428 of foliar traits on forage selection by introduced red deer in New Zealand. *Basic Appl Ecol*
429 12:56–63.
- 430 Blyth LH, Ouborg LJ, Johnson DM, Anderson LJ (2013). The short-term germination and
431 establishment success of deer-dispersed seeds in mesic temperate forests. *J Torrey Bot Soc*
432 140:334–348.

433 Cain M, Milligan B, Strand A (2000) Long-distance seed dispersal in plant populations. *Am J*
434 *Bot* 87:1217–1227.

435 Castellano SM, Gorchov DL (2013) White-tailed deer (*Odocoileus virginianus*) disperse seeds of
436 the invasive shrub, Amur honeysuckle (*Lonicera maackii*). *Nat Areas J* 33:78–80.

437 Christopher CC, Matter SF, Cameron GN (2014) Individual and interactive effects of Amur
438 honeysuckle (*Lonicera maackii*) and white-tailed deer (*Odocoileus virginianus*) on herbs in
439 a deciduous forest in the eastern United States. *Biol Invasions* 16:2247–2261.

440 Clark J, Fastie C, Hurtt G, Jackson ST, Johnson C, King GA, Lewis M, Lynch J, Pacala S,
441 Prentice C, Schpp EW, Webb III T, Wyckoff P (1998) Reid’s paradox of rapid plant
442 migration. *Bioscience* 48:13–24.

443 Clark CJ, Poulsen JR, Bolker BM, Connor EF, Parker VT (2005) Comparative seed shadows of
444 bird-, monkey-, and wind-dispersed trees. *Ecology* 86:2684–2694.

445 Collier M, Vankat J, Hughes M (2002) Diminished plant richness and abundance below
446 *Lonicera maackii*, an invasive shrub. *Am Midl Nat* 147:60–71.

447 Côté SD, Rooney TP, Tremblay JP, Dussault C, Waller DM. (2004) Ecological impacts of deer
448 overabundance. *Annu Rev Ecol Evol Syst* 35:113–147.

449 Ditchkoff SS (2011) Anatomy and physiology. In: Hewitt DG (ed) *Biology and Management of*
450 *White-tailed Deer*. CRC Press, Boca Raton pp. 75-105.

451 Eschtruth AK, Battles JJ (2009) Acceleration of exotic plant invasion in a forested ecosystem by
452 a generalist herbivore. *Conserv Biol* 23:388–99.

453 Excoffier L, Foll M, Petit RJ (2009) Genetic consequences of range expansions. *Annu Rev Ecol*
454 *Evol Syst* 40:481–501.

455 Eycott AE, Watkinson AR, Hemami MR, Dolman PM (2007) The dispersal of vascular plants in
456 a forest mosaic by a guild of mammalian herbivores. *Oecologia* 154:107–18.

457 Gorchov DL, Henry MC, Frank P (2014a) Invasion of an exotic shrub into forested stands in an
458 agricultural matrix. *Invasive Plant Sci and Manag.* 7: 336-344.

459 Gorchov, DL Castellano SM, Noe DA. (2014b) Long-distance dispersal and diffusion in the
460 invasion of *Lonicera maackii*. *Invasive Plant Sci and Manag.* 7:464–472.

461 Gorchov D, Trisel D (2003) Competitive effects of the invasive shrub, *Lonicera maackii* (Rupr.)
462 Herder (Caprifoliaceae), on the growth and survival of native tree seedlings. *Plant Ecol*
463 166:13–25.

464 Gould A, Gorchov D (2000) Effects of the exotic invasive shrub *Lonicera maackii* on the
465 survival and fecundity of three species of native annuals. *Am Midl Nat* 144:36–50.

466 Guiden PWG (2014) The role of white-tailed deer (*Odocoileus virginiana*) in long-distance seed
467 dispersal of Amur honeysuckle (*Lonicera maackii*). Master thesis, Department of Biology,
468 Miami University, Oxford OH, USA.

469 Hartman K, McCarthy B (2008) Changes in forest structure and species composition following
470 invasion by a non-indigenous shrub, Amur honeysuckle (*Lonicera maackii*). *J Torrey Bot*
471 *Soc* 135:245–259.

472 Heilman G, Strittholt J (2002) Forest fragmentation of the conterminous United States: assessing
473 forest intactness through road density and spatial characteristics. *Bioscience* 52:411–422.

474 Hewitt DG (2011) Nutrition. In: Hewitt DG (ed) *Biology and Management of White-tailed Deer*.
475 CRC Press, Boca Raton pp. 75-105.

476 Hidayati SN, Baskin JM, Baskin CC (2000) Dormancy- breaking and germination requirements
477 of seeds of four *Lonicera* species (Caprifoliaceae) with underdeveloped spatulate embryos.
478 Seed Sci Res 10: 459–469

479 Hutchinson TF, Vankat JL (1997) Invasibility and effects of Amur honeysuckle in southwestern
480 Ohio forests. Conserv Biol 11:1117–1124.

481 Ingold J, Craycroft M (1983) Avian frugivory on honeysuckle (*Lonicera*) in southwestern Ohio
482 in fall. Ohio J Sci 83:256–258.

483 Janzen D (1970) Herbivores and the number of tree species in tropical forests. Am Nat 104:501–
484 528.

485 Jaroszewicz B, Pirożnikow E, Sondej I (2013) Endozoochory by the guild of ungulates in
486 Europe’s primeval forest. For Ecol Manag 305:21–28.

487 Jenks J, Leslie D (1989) Digesta retention of winter diets in white-tailed deer (*Odocoileus*
488 *virginianus*) fawns in Maine, USA. Can J Zool 67:1500–1504.

489 Johnson A, Hale P, Ford W (1995) White-tailed deer foraging in relation to successional stage,
490 overstory type and management of southern Appalachian forests. Am Midl Nat 133:18–25.

491 Johnston S, Henry M, Gorchov D (2012) Using advanced land imager (ALI) and landsat
492 thematic mapper (TM) for the detection of the invasive shrub *Lonicera maackii* in
493 southwestern Ohio forests. GIScience Remote Sens 49:450–462.

494 Kjær LJ, Schaubert EM, Nielsen CK (2008) Spatial and temporal analysis of contact rates in
495 female white-tailed deer. J Wildl Manag 72:1819–1825.

496 Knight TM, Dunn JL, Smith LA, Davis JA, Kalisz A (2009) Deer facilitate invasive plant
497 success in a Pennsylvania forest understory. Nat Areas J 29:110–116.

498 Mautz W, Petrides G (1971) Food passage rate in the white-tailed deer. *J Wildl Manag* 35:723–
499 731.

500 McConkey KR, Prasad S, Corlett RT, Campos-Arceiz A, Brodie JF, Rogers H, Santamaria L
501 (2012) Seed dispersal in changing landscapes. *Biol Conserv* 146:1–13.

502 McNeish RE, Benbow ME, McEwan RW (2012) Riparian forest invasion by a terrestrial shrub
503 (*Lonicera maackii*) impacts aquatic biota and organic matter processing in headwater
504 streams. *Biol Invasions* 14:1881–1893.

505 Miller KE, Gorchov DL (2004) The invasive shrub, *Lonicera maackii*, reduces growth and
506 fecundity of perennial forest herbs. *Oecologia* 139:359–75.

507 Murray KG (1988) Avian seed dispersal of three neotropical gap-dependent plants. *Ecol Monogr*
508 58:271–298.

509 Myers JA, Vellend M, Gardescu S, Marks PL (2004) Seed dispersal by white-tailed deer:
510 implications for long-distance dispersal, invasion, and migration of plants in eastern North
511 America. *Oecologia* 139:35–44.

512 Ng J, Nielson C, Clair CS (2008) Landscape and traffic factors influencing deer-vehicle
513 collisions in an urban environment. *Hum Wildl Confl* 2:34-47.

514 Nixon C, Hansen L, Brewer P, Chelsvig J (1991) Ecology of white-tailed deer in an intensively
515 farmed region of Illinois. *Wildl Monogr* 18:1-77.

516 Pfeiffer SS, Gorchov DL (2015) Effects of the Invasive Shrub *Lonicera maackii* on soil water
517 content in eastern deciduous forest. *Am Midl Nat* 173:38–46.

518 Quinn ACD, Williams DM, Porter WF (2013) Landscape structure influences space use by
519 white-tailed deer. *J Mammal* 94:398–407.

520 Rawsthorne J, Roshier DA, Murphy SR (2009) A simple parametric method for reducing sample
521 sizes in gut passage time trials. *Ecology* 90:2328–31.

522 Riitters KH, Coulston JW, Wickham JD (2012) Fragmentation of forest communities in the
523 eastern United States. *For Ecol Manag* 263:85–93.

524 Rooney TP (2001) Deer impacts on forest ecosystems: a North American perspective. *Forestry*
525 74:201–208.

526 Rooney TP, Waller DM (2003) Direct and indirect effects of white-tailed deer in forest
527 ecosystems. *For Ecol Manag* 181:165–176.

528 Rouleau I, Crete M, Ouellet JP (2002) Contrasting the summer ecology of white-tailed deer
529 inhabiting a forested and an agricultural landscape. *Ecoscience* 9:459–469.

530 Schaefer HM (2006) The role of chromatic and achromatic signals for fruit detection by birds.
531 *Behav Ecol* 17:784–789.

532 Schauber E, Storm D, Nielsen C (2007) Effects of joint space use and group membership on
533 contact rates among white-tailed deer. *J Wildl Manag* 155–164.

534 Shelton AL, Henning JA, Schultz P, Clay K (2014) Effects of abundant white-tailed deer on
535 vegetation, animals, mycorrhizal fungi, and soils. *For Ecol Manag* 320:39–49.

536 Stewart KM, Boyer RT, Weisberg PJ (2011) Spatial use of landscapes. In: Hewitt DG (ed)
537 *Biology and Management of White-tailed Deer*. CRC Press, Boca Raton pp. 75-105.

538 Storm DJ, Nielsen CK, Schauber EM, Woolf A (2007) Space use and survival of white-tailed
539 deer in an exurban landscape. *J Wildl Manag* 71:1170–1176.

540 Swift CE, Gross MK (2008) Preventing deer damage. Colorado State Univ. Extension
541 (<http://www.ext.colostate.edu>).

542 van Beest FM, Mysterud A, Loe LE, Milner JM (2010) Forage quantity, quality and depletion as
543 scale-dependent mechanisms driving habitat selection of a large browsing herbivore. *J*
544 *Anim Ecol* 79:910–22.

545 Vangilder L, Torgerson O, Porath W (1982) Factors influencing diet selection by white-tailed
546 deer. *J Wildl Manag* 46:711–718.

547 Vellend M (2002) A pest and an invader: white-tailed deer (*Odocoileus virginianus* Zimm.) as a
548 seed dispersal agent for honeysuckle shrubs (*Lonicera* L.). *Nat Areas J* 22:230–234.

549 Vellend M, Myers JA, Gardescu S, Marks PL (2003) Dispersal of *Trillium* seeds by deer:
550 implications for long-distance migration of forest herbs. *Ecology* 84:1067–1072.

551 Venables WN, Ripley B D (2002) *Modern Applied Statistics with S*. Fourth Edition. Springer,
552 New York.

553 Walter WD, VerCauteren KC, Campa H, Clark WR, Fischer JW, Hygnstom SE, Mathews NE,
554 Nielsen CK, Schauber EM, Van Deelen TR, Winterstein SR (2009) Regional assessment on
555 influence of landscape configuration and connectivity on range size of white-tailed deer.
556 *Landsc Ecol* 24:1405–1420.

557 Warner A (1985) Rate of passage of digesta through birds and mammals. *Nutr Abstr Rev Ser B*
558 51:789–820.

559 Wilfong BN, Gorchov DL, Henry MC (2009) Detecting an invasive shrub in deciduous forest
560 understories using remote sensing. *Weed Sci* 57:512–520.

561 Williams DM, Dechen Quinn AC, Porter WF (2011) Landscape effects on scales of movement
562 by white-tailed deer in an agricultural–forest matrix. *Landsc Ecol* 27:45–57.

563 Williams SC, Ward JS (2006) Exotic seed dispersal by white-tailed deer in southern Connecticut.
564 Nat Areas J 26:383–390.

565 **Table 1** A total of 82 white-tailed deer pellet groups were collected at two sites to investigate the
566 potential for deer to disperse *Lonicera maackii* seeds. Only pellet groups collected at the invaded
567 area contained germinable *L. maackii* seeds.

	Invaded Area	Invasion Front
Deer pellet groups collected	29	53
Deer pellet groups containing germinable <i>Lonicera maackii</i> seeds	9	0
Mean <i>Lonicera maackii</i> seeds per pellet group (± 1 standard deviation)	2.5 \pm 6.7	0

568 **Table 2** Forest patch and landscape characteristics that influence white-tailed deer movement
 569 and seed dispersal. Characteristics are compared across three study areas where white-tailed deer
 570 movement (“Movement Data”) or seed dispersal data (“Invasion Front” and “Invaded Area”)
 571 were collected.

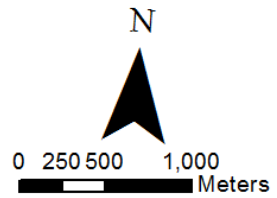
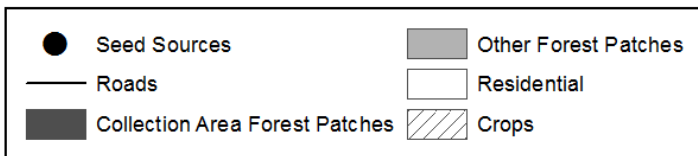
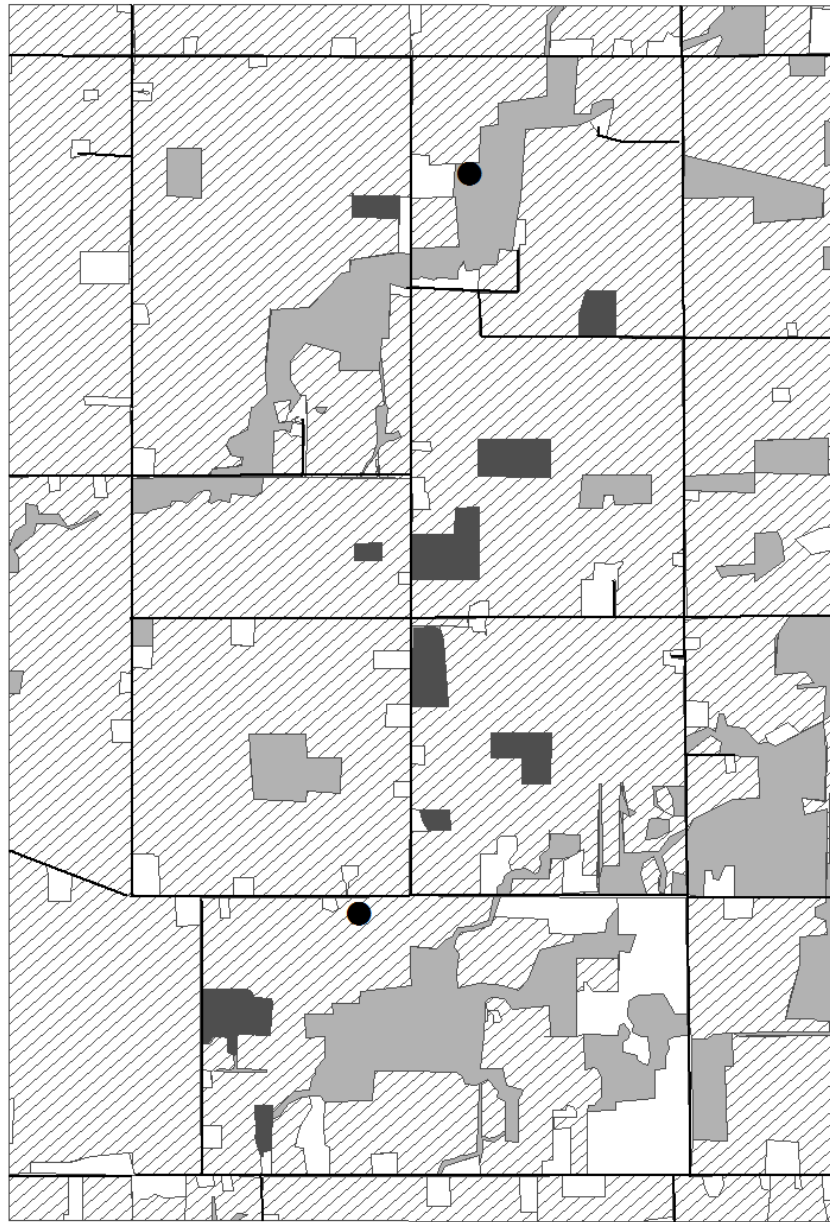
	Movement Data	Invasion Front	Invaded Area
Location	Illinois	Ohio	Ohio
<i>Lonicera maackii</i> abundance	Low	Low	High
Area-weighted Shape Index	9.38 ± 1.97	2.55 ± 0.67	8.99 ± 2.10
Nearest neighbor (m)	124.2 ± 181.3	214.3 ± 189.6	55.3 ± 36.2
Patch area coefficient-of-variation	423.9	180.7	354.1
Road Density (km km ⁻²)	1.22	1.36	1.43

572 **Figure Captions**

573 **Figure 1** Map of Darke County, Ohio study area, showing forest patches where white-tailed deer
574 pellets were collected (dark gray) and surrounding land use (Forest: light gray, Crops: hatch,
575 Residential: white, Road: black). Two *L. maackii* seed sources (black circles) in the landscape
576 are also shown. Forest patches southeast of this landscape also contained reproducing *L. maackii*.

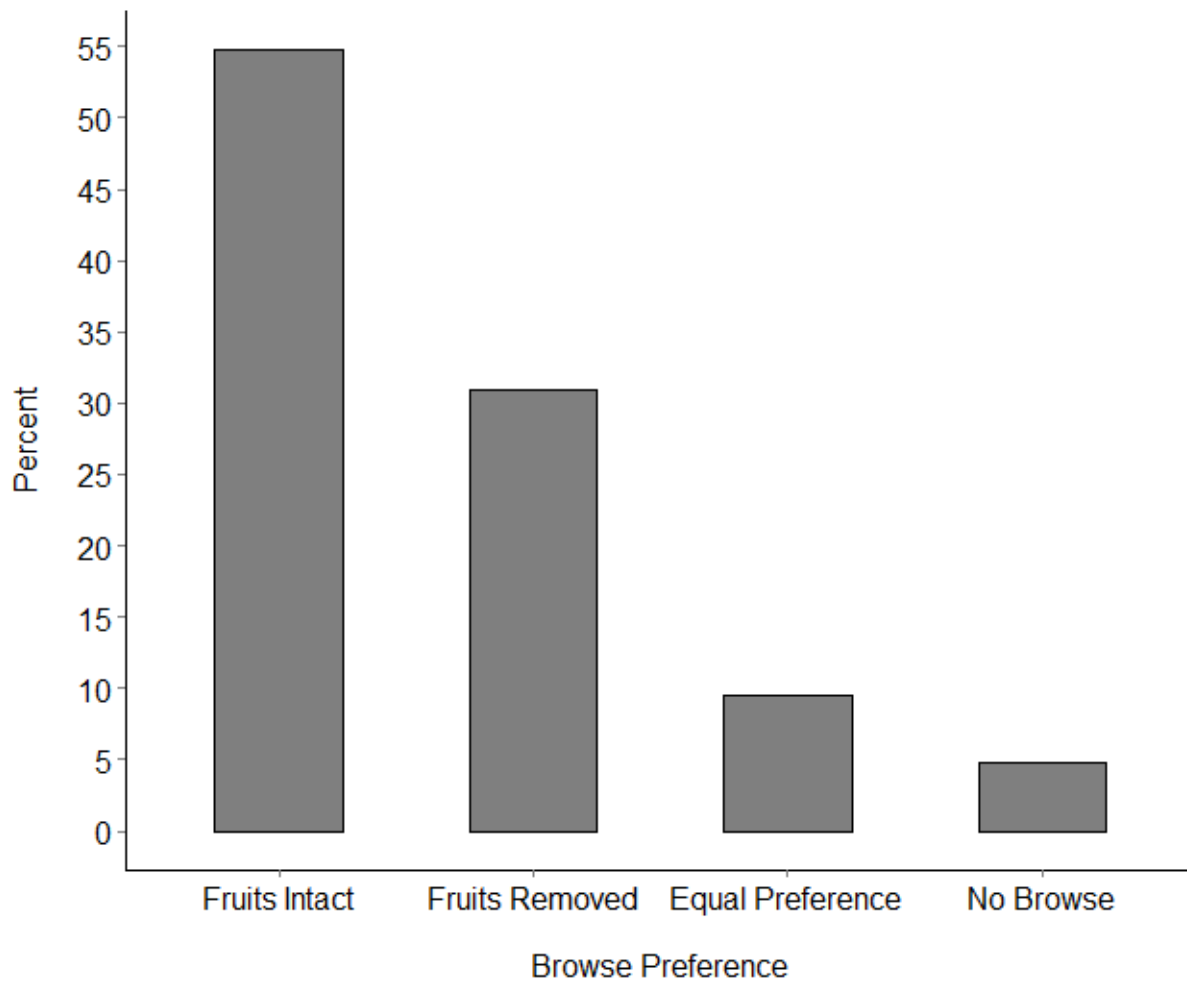
577 **Figure 2** White-tailed deer preference among 42 pairs of *L. maackii* shrubs assigned to fruit
578 removal treatments and control treatments (fruits left intact). Within each pair, the shrub with
579 more woody tissue consumed by white-tailed deer was considered to be preferred.

580 **Figure 3** Projected seed shadows for dispersal of *L. maackii* seeds by 25 female white-tailed
581 deer. Bars represent the probability that a *L. maackii* seed will be dispersed to each 100 m
582 distance class. The median and mode of projected seed dispersal distances was 300 m away from
583 a seed source, but rarely seed dispersal was projected to occur up to 7900 m away from a seed
584 source. Minor tic marks represent 200 m intervals.



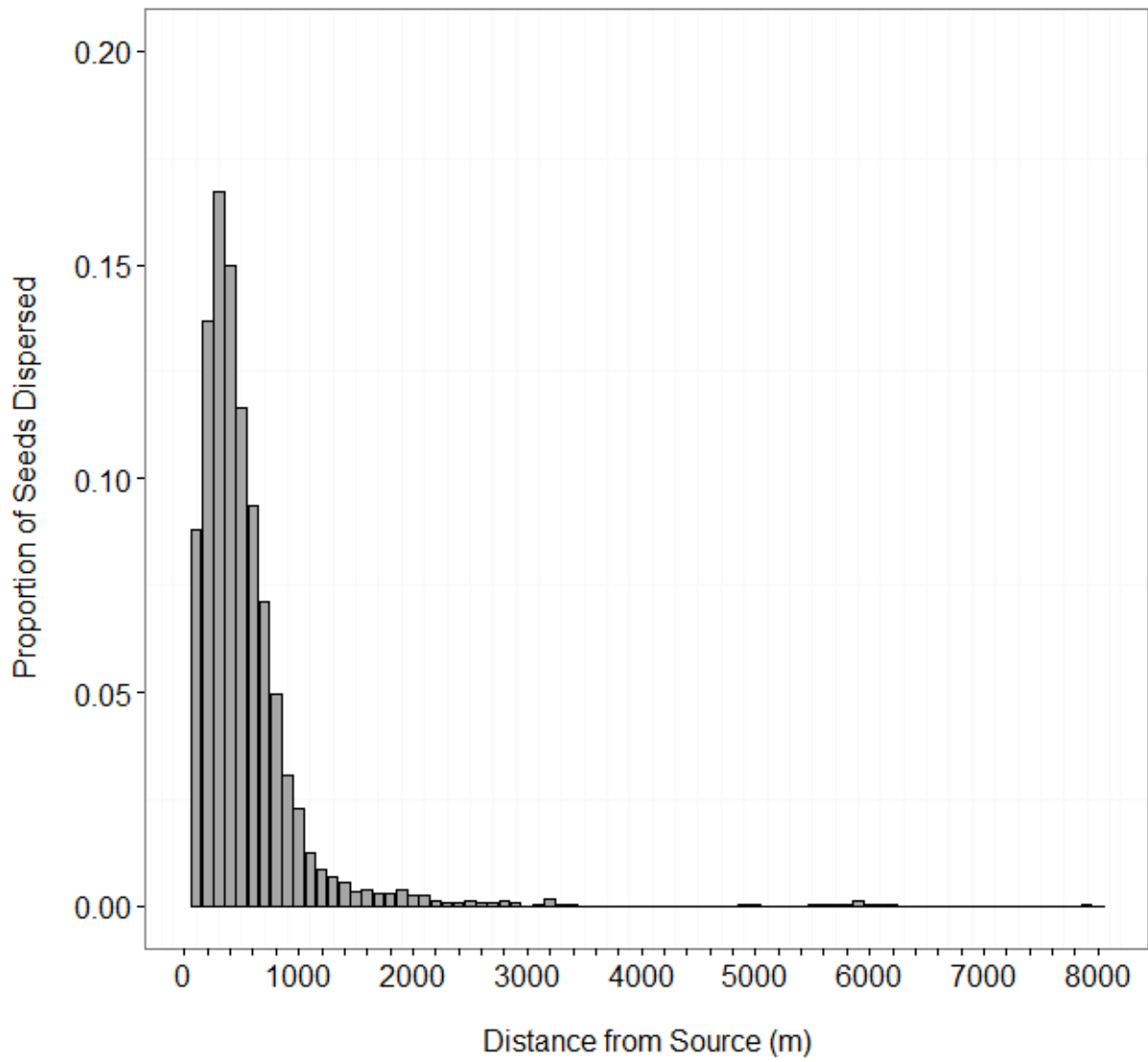
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586 Figure 1



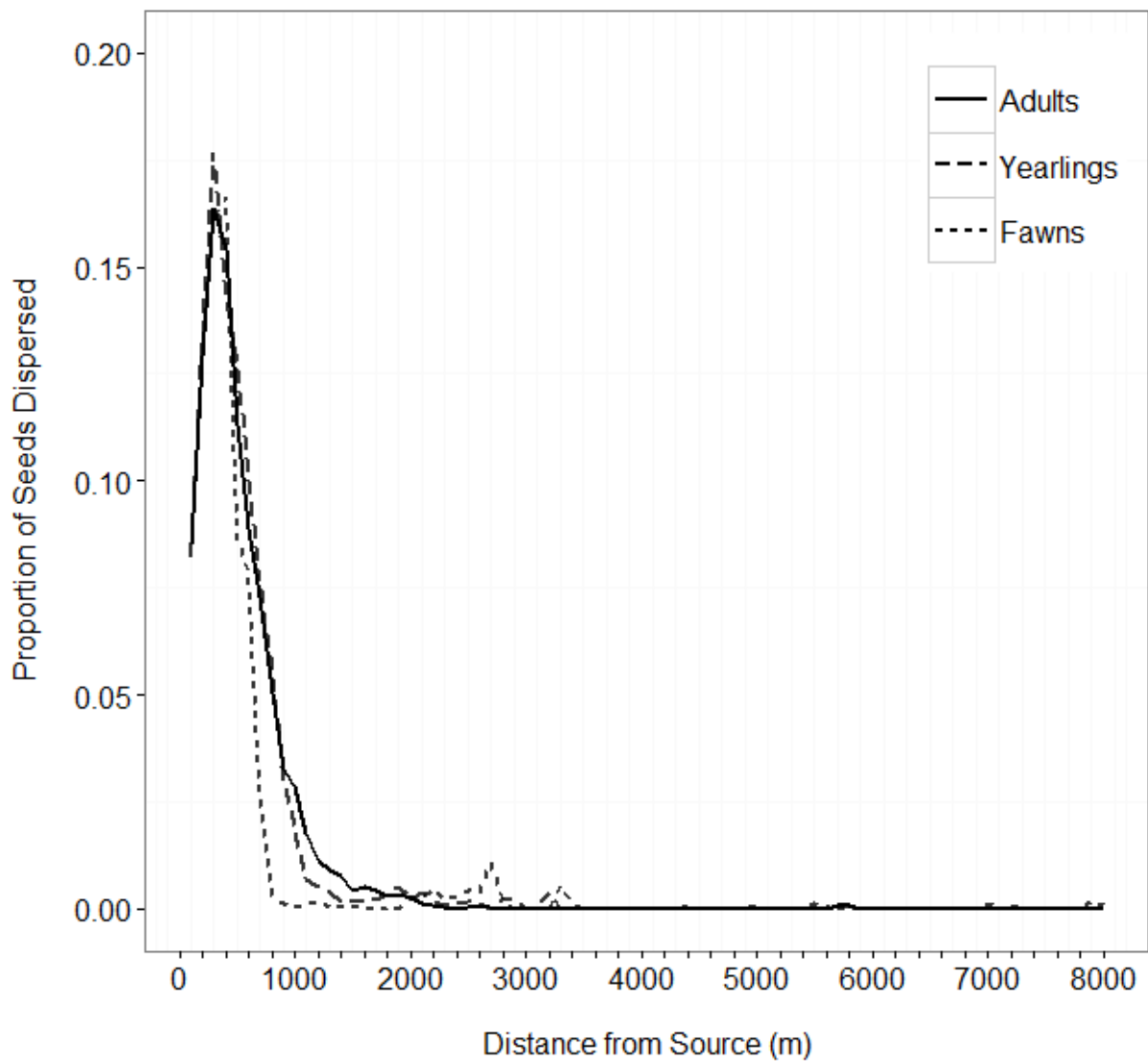
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588 Figure 2



589

590 Figure 3



592

593 Fig A1: Seed shadows projections for deer separated by age class, including fawn (n=1), yearling
594 (n=8), and adults (n=16). Minor tic marks represent 200 m intervals.