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Spatial heterogeneity in white-tailed deer activity increases seed dispersal of shade-intolerant plants near forest edges in fragmented forests¹

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Abstract. Seed dispersal structures plant populations and communities but may be affected by forest fragmentation. Recent work demonstrates that white-tailed deer (*Odocoileus virginianus* Zimmerman) can be important seed dispersers in North American forests, potentially moving seeds over long distances. However, little is known about the role of deer as seed dispersal agents in landscapes characterized by small, isolated forest patches. The objectives of this study were to (a) determine how habitat structure influenced the spatial distribution of deer activity, and (b) describe which plant species and traits were dispersed by deer in a highly fragmented, agricultural matrix. I collected deer fecal pellet groups from 10 forest patches in plots that ranged from 10 to 100 m from forest edge. Pellet groups were cold-stratified and planted in a greenhouse to quantify seeds dispersed by deer. The number of pellet groups collected was highest near forest edges but was not influenced by patch size or isolation; 258 seedlings from 15 species emerged from collected pellets, with three species contributing 80% of seedlings. Most seedlings emerging from deer pellets were herbaceous, nonnative plants with a foliage-as-fruit dispersal mode. Plants with these traits typically perform well in high-light habitats, such as forest edges, where deer are most active. These results suggest that while seed dispersal by deer is common in highly fragmented forest patches, it is most likely to benefit shade-intolerant herbaceous species, maintaining populations of those plants along forest edges.

Key words: agricultural landscape, edge effect, endozoochory, fragmentation, *Odocoileus virginianus*

In many temperate forests, seed dispersal has an important role in structuring plant population and community diversity (Zhou and Chen 2010, Pinto *et al.* 2014). However, changes in habitat structure resulting from habitat loss and fragmentation can alter plant species dispersal capacity (Damschen *et al.* 2008). Species that disperse poorly (*i.e.*, short mean or maximum dispersal distances) may be more likely to disperse into low-quality matrix habitat than suitable habitat as humans modify the biosphere through climate change and habitat loss (Cain *et al.* 2000).

Therefore, species with a reliable means of long-distance seed dispersal are most likely to persist under scenarios of high habitat fragmentation (Trakhtenbrot *et al.* 2005). Given the extreme extent of forest fragmentation across the biosphere (Haddad *et al.* 2015), identifying which species have sufficient dispersal capacity to persist in areas of intense habitat fragmentation remains a key conservation need.

Because animals are important agents of seed dispersal for many plant species, linking the behavior of seed dispersers to habitat structure can improve predictions of seed dispersal patterns in landscapes modified by human activity (McConkey *et al.* 2012). As forest is converted to other land uses, such as agriculture and development, forest patches become smaller and more isolated. Although dispersal agents often show high fidelity to certain habitat types (Carlo *et al.* 2013), many seed dispersers avoid small or isolated habitat patches (Cordeiro and Howe 2003). Additionally, forest fragmentation can increase the amount of forest edge (Villard and Metzger 2014) to which animals show variable responses. Edge habitat can facilitate the movement of some seed-dispersing animals (Levey *et al.* 2005, Bartuszevige and Gorchoy 2006) and impede others (Ness 2004). Whether or not seed dispersal agents preferentially move and disperse

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seeds into edges can have lasting effects on plant communities because seeds dispersed into edge habitats typically experience elevated temperatures, greater light penetration, and less moisture than forest interiors (Matlack 1993). This gradient in microhabitat conditions can favor the establishment of some seedlings, such as shade-intolerant herbs (Brothers and Spingarn 1992) and select against other species, including shade-tolerant herbs (Jules 1998, Jules and Rathcke 1999).

Few organisms have had such a sustained effect on North American forests as the white-tailed deer, *Odocoileus virginianus* Zimmerman (reviewed by Côté *et al.* 2004). The mechanisms by which deer alter plant communities are diverse: deer can suppress canopy tree species through herbivory (Horsley *et al.* 2003), change the outcomes of competitive interactions between plant species (Waller and Alverson 1997), and alter nutrient cycling (Murray *et al.* 2014). However, a growing body of literature demonstrates that wild ungulates, including deer, often have an underappreciated role as seed dispersers for many plant species (Myers *et al.* 2004, Williams and Ward 2006, Eycott *et al.* 2007, Williams *et al.* 2008, Blyth *et al.* 2013, Guiden 2013, Albert *et al.* 2015, Guiden *et al.* 2015). Although these studies identified which species were most likely to be dispersed by deer, we know little about where deer are most likely to disperse those seeds or what type of microhabitats emerging seedlings are most likely to encounter. Because germination and establishment are sensitive to both habitat size (van Ruremonde and Kalkhoven 1991) and proximity to habitat edges (Jules 1998), spatial variation in disperser activity can influence postdispersal establishment success (Fragoso *et al.* 2006).

Two factors suggest that deer could be important seed dispersers in isolated forest patches within predominantly agricultural landscapes. First, fragmented agricultural landscapes can sustain large deer populations that exceed pre-European settlement abundance (Foster *et al.* 2002), indicating that seeds will frequently be encountered and consumed by deer. Second, agricultural land does not impede deer movement (Walter *et al.* 2009). Even in highly fragmented landscapes, 7% of the seeds dispersed by deer are projected to move > 1 km from a seed source (Guiden *et al.* 2015), meaning that deer can likely disperse seeds among disjunct forest patches. The objectives of this study were to (a) determine how habitat structure

influences the spatial distribution of deer activity among and within fragmented forest patches, and (b) characterize the plant species dispersed by deer in a predominantly agricultural landscape. Together, these data provide insight into not only which species are dispersed by deer but also which species should benefit most from seed dispersal by deer.

Materials and Methods. **STUDY AREA.** This study was conducted in a 23 km² region of the midwestern United States (Darke County, OH: 40°05'36"N, 84°46'47"W), where agriculture accounted for > 80% of land cover (Guiden *et al.* 2015). Data were collected from 10 discrete, mesic, deciduous forest patches, which were surrounded by row crops (corn [*Zea mays* L.] and soy [*Glycine max* (L.) Merr.]) and sparse residential housing (for a detailed map of the study area, see Guiden *et al.* 2015). These 10 forest patches varied in size and isolation (see Results), allowing deer activity to be assessed over a gradient of forest-patch characteristics. Common canopy species included *Acer saccharum* (Marshall), *Fagus grandifolia* (Ehrh.), and *Prunus serotina* (Ehrh.), whereas *Aesculus glabra* (Willd.) and *Cornus florida* (L.) were common throughout the understories.

DATA COLLECTION. In July 2013, global positioning system (GPS) coordinates marking the corners of each forest patch were recorded. Nearest-neighbor distance and patch area, two simple and complementary metrics used to describe forest fragmentation (Calabrese and Fagan 2004), were determined for each patch using ArcMap 10.2 (Environmental Systems Research Institute, Redlands, CA). The GPS coordinates were also used to create two evenly spaced transects per patch. Transects began 10 m inside the forest edge and extended 100 m into the forest interior. Every 10 m, a 10 m × 2 m collection plot was established, with the exception of one forest patch in which a stream prohibited collection in five plots. The long side of each plot was parallel to the forest edge. Deer fecal pellet groups were collected from plots every 2 wk between September 2013 and December 2013 (Guiden *et al.* 2015). Pellet groups were stored at 5 °C for approximately 6 wk to break seed dormancy. After that time, pellet groups were planted on sterile vermiculite in a greenhouse (day/night: 24 °C/15 °C, 16 hr/8 h), where they received regular watering and ambient light (Wil-

liams and Ward 2006) for approximately 12 wk. Control pots, consisting of only sterile vermiculite and no pellet groups, were used to assess potential contamination of our samples from seed sources within the greenhouse. *Oxalis stricta* (L.) was found in both control pots and pots with deer pellets and was excluded from analysis.

DATA ANALYSIS. Regression analysis was used to determine the response of deer activity to habitat structure at both the patch and plot (within-patch) scales. The number of deer pellet groups per unit area provides an index of deer activity (Allan *et al.* 2010), and consequently, the number of deer pellet groups collected in an area was used as the response variable in all regression models. There are some potential limitations in using deer pellet groups as an index for activity. For example, a key assumption of pellet collection indices is that pellet deposition rate is constant, but the rate of deer pellet deposition might vary with diet (Rogers 1987). However, because all forest patches in this study area were embedded within corn and soy fields, deer in each forest patch likely had access to qualitatively similar diets (*i.e.*, a mix of woody plants and crops). Additionally, pellet group detection potentially suffers from observer bias (Neff 1968), but that source of error was eliminated by using only one observer throughout the study.

To understand the influence of forest patch characteristics on deer activity, I modeled the number of deer pellet groups in each patch (summed from all plots within the patch) as a function of forest area and nearest-neighbor distance using multiple regression. In addition, to understand the spatial variation in deer activity at a finer scale, the number of deer pellet groups collected in each plot was modeled as a function of plot distance to the forest edge. Because multiple plots were nested within a transect at a patch, I used a linear mixed-effects model with transect nested within patch as a random intercept term. The response variable (number of deer pellet groups collected) in the plot-scale model was log transformed to resolve issues of nonnormality because of a large number of zeroes (Ives 2015). All analyses were performed in R version 3.2.0 (R Core Team 2015), using the lme4 package for linear mixed modeling (Bates *et al.* 2014).

Seedling emergence was recorded weekly, and identified seedlings were removed from pots. Seedling nomenclature followed Gleason and

Cronquist (1991). To identify plant characteristics that predicted seed dispersal by deer in agricultural landscapes, three traits were recorded for each species growing out of deer pellet groups: dispersal mode (fleshy structures, winged structures, or foliage-as-fruit; *i.e.*, Janzen 1984), growth habit (grass, herb, shrub, or tree), and provenance (native or nonnative to Ohio). Those traits were selected to compare the species dispersed by deer in this study to those in similar studies (Myers *et al.* 2004, Williams *et al.* 2008, Blyth *et al.* 2013). Dispersal mode and growth habit traits were assigned according to Gleason and Cronquist (1991) and Holmgren (1998). Provenance was assigned using the PLANTS database (USDA NRCS 2004). Seedlings that died before being identified to species were not included in further analysis ($n = 4$).

Results. Forest patch area ranged from 1.5 to 12.8 ha (Fig. 1A), and forest patch isolation distance ranged from 70 to 509 m (Fig. 1B). Forest patch area and isolation distance were not significantly correlated ($r = -0.24$, $P = 0.51$, Pearson's product-moment correlation). A total of 74 deer pellet groups were collected from 48 of 195 plots (25%) in nine patches. Deer activity showed little response to habitat structure at the patch scale because the number of deer pellet groups found in a forest patch was not associated with patch size ($F_{1,7} = 1.73$, $P = 0.23$) or patch nearest-neighbor distance ($F_{1,7} = 1.12$, $P = 0.32$; Table 1). However, at the plot scale, the number of deer pellet groups found was greatest near the forest edge ($F_{1,175} = 8.15$, $P = 0.004$, Fig. 2).

From these pellet groups, 258 seedlings emerged in the greenhouse, representing 14 unique species and 11 families (Table 2). However, *Portulaca oleracea* (L.), *Solanum ptycanthum* (Dunal), and *Pilea pumila* (L.) together accounted for almost 80% of viable seeds dispersed by deer. Emerging seedlings were most often herbaceous (94%) and nonnative (71%) with the foliage-as-fruit dispersal mode (82%).

Discussion. Wild ungulates, including white-tailed deer, provide a potentially important but often overlooked source of seed dispersal for many plant species (Myers *et al.* 2004). However, much of our understanding about seed dispersal by deer comes from studies conducted in single forest patches (Myers *et al.* 2004, Williams and Ward 2006, Williams *et al.* 2008), which used nonran-

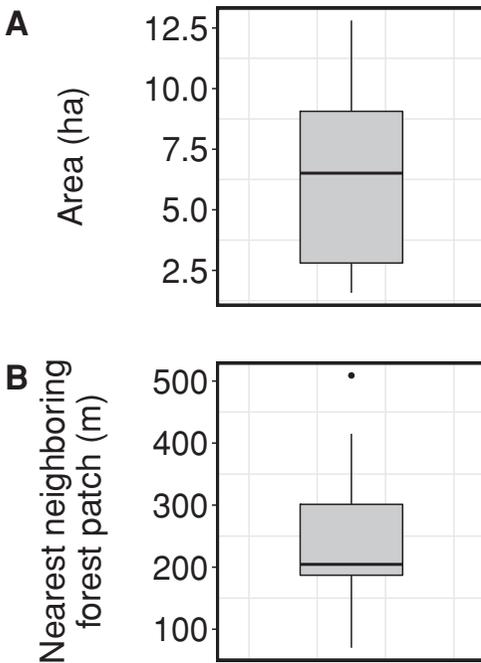


FIG. 1. Deer pellet groups were collected from 10 discrete forest patches (each represented here by a single point). Forest patches spanned (A) an eightfold gradient in area, from 1.5 to 12.8 ha; and (B) a sevenfold gradient in isolation distance (measured as the Euclidean distance to the closest neighboring patch) from 70 to 509 m. Forest patch area and isolation distance were not significantly correlated ($r = -0.24$, $P = 0.51$). Thick lines represent median values, and the top and bottom box hinges represent 75% and 25% percentiles of the data, respectively.

dom sampling to collect deer fecal pellets. Although this practice maximizes the number of samples collected, it may overlook spatial heterogeneity in disperser activity that could influence postdispersal seedling establishment. By sampling deer fecal pellet groups from a series of plots nested within small, isolated forest patches that varied in size and isolation distance, I show that deer activity is correlated with proximity to forest edge but not to metrics of larger-scale habitat structure, such as patch size or isolation. Thus, the few shade-intolerant plant species commonly dispersed by deer should benefit from the affinity of deer to forest edges. These results could help improve predictions of where deer are most likely to disperse seeds, including seeds from herbicide-resistance agricultural weeds and nonnative invasive plants.

Table 1. Regression table describing the relationship between deer activity (measured as the number of deer fecal pellet groups collected) and habitat structure at the patch scale, including patch area and patch isolation distance.

Predictor	Degrees of freedom	F	P
Patch area	1	1.73	0.23
Isolation distance	1	1.12	0.33

It seems paradoxical that most seeds dispersed in forests by deer are poorly adapted to forest habitats (Blyth *et al.* 2013). However, accounting for fine-scale spatial heterogeneity in deer activity may help resolve that paradox. At the plot scale, deer were more active near forest edges than forest interiors. Telemetry studies show that deer often use edge habitats in agricultural landscapes (Rohm *et al.* 2007). However, the implications of this edge use for seed dispersal by deer have not been explored. Seed dispersal by deer near forest edges likely exposes shade-intolerant species (*e.g.*, *P. oleracea*) to increased light and warmer temperatures (Brothers and Spingarn 1992, Matlack 1993), which promotes germination of shade-intolerant herbs, such as *P. oleracea* (Singh 1973). This suggests that high deer activity, and hence seed dispersal, near forest edges results in greater establishment of deer-dispersed, shade-intolerant plants. However, shade-intolerant herbs will not benefit from seed dispersal to forest edges when

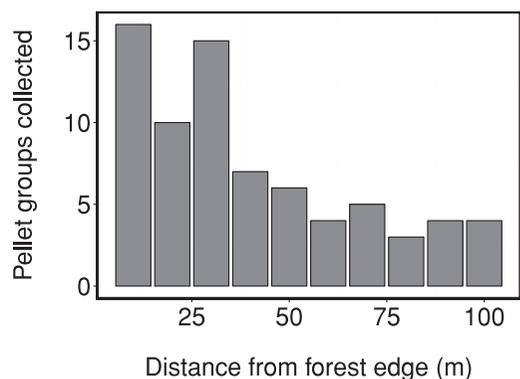


FIG. 2. Histogram describing the spatial distribution of seed dispersal by white-tailed deer in relation to forest edge. Forest patches were embedded in a predominantly agricultural matrix. The number of deer pellet groups collected in a plot was highly variable, but declined significantly as distance from the forest edge increased (ANOVA: $F_{1,175} = 8.15$, $P = 0.004$).

Table 2. White-tailed deer dispersed seeds of 15 species in 10 fragmented forest patches embedded within a predominantly agricultural landscape. Abundance of emerging seedlings and detailed traits for each species are provided.

Species	Family	Abundance	Dispersal mode	Habit
Nonnative species				
<i>Portulaca oleracea</i>	Portulacaceae	130	Foliage-as-fruit	Herb
<i>Persicaria maculosa</i>	Polygonaceae	13	Foliage-as-fruit	Herb
<i>Chenopodium album</i>	Chenopodiaceae	10	Foliage-as-fruit	Herb
<i>Poa pratensis</i>	Poaceae	6	Foliage-as-fruit	Grass
<i>Amaranthus palmeri</i>	Amaranthaceae	5	Foliage-as-fruit	Herb
<i>Potentilla recta</i>	Rosaceae	2	Foliage-as-fruit	Herb
<i>Galinsoga quadriradiata</i>	Asteraceae	1	Wind	Herb
<i>Urtica dioica</i>	Urticaceae	1	Foliage-as-fruit	Herb
Total		168		
Native species				
<i>Solanum ptycanthum</i>	Solanaceae	37	Fleshy	Herb
<i>Pilea pumila</i>	Urticaceae	32	Foliage-as-fruit	Herb
<i>Boehmeria cylindrica</i>	Urticaceae	4	Wind	Herb
<i>Rubus allegheniensis</i>	Rosaceae	1	Fleshy	Shrub
<i>Celtis occidentalis</i>	Ulmaceae	1	Fleshy	Tree
<i>Gleditsia triacanthos</i>	Fabaceae	1	Wind	Tree
Total		76		

forest edges support dense shrub growth, such as invasive shrubs, which limit light penetration (McKinney and Goodell 2010). Conversely, even though deer disperse seeds of shade-tolerant forest herbs (e.g., *Trillium* spp.) over long distances (Vellend *et al.* 2003), the affinity of deer for forest edges makes it unlikely that seeds will establish after dispersal because of the poor adaptation of those plants to forest edges (Jules 1998). Hence, seed dispersal by deer most likely maintains populations of early successional plant species along forest edges, with relatively little effect on plant communities in core forest habitat (Blyth *et al.* 2013).

The affinity of deer for forest edge observed here is similar to that of many seed-dispersing birds (Levey *et al.* 2005, Bartuszevige and Gorchoy 2006). However, frugivorous birds primarily disperse species with brightly colored, fleshy fruits (Schaefer 2006), whereas deer primarily disperse species whose fruit lacks specialized dispersal morphology (Myers *et al.* 2004). Therefore, although these disperser guilds display similar behavioral responses to habitat structure, there is likely limited overlap in the suite of plant species that benefit from seed dispersal by deer and birds, implying that seed dispersal by these animals is complementary rather than redundant (McConkey *et al.* 2012).

We found no evidence that forest patch size or isolation distance influenced seed dispersal by deer. The area of forest patches in this study area

ranged from 1.5 to 12.8 ha, and the isolation distance ranged from 70 to 509 m, but these habitat characteristics did not predict deer activity at the patch scale. Because animal responses to fragmentation can be nonlinear (With and Crist 1995), it is possible that patch area and isolation are important predictors of deer activity and seed dispersal, but critical thresholds lay beyond the range of patch size and isolation investigated in this study.

Although deer are generalist herbivores that can ingest fruits of woody (Guiden *et al.* 2015) and herbaceous plant species (Ruhren and Handel 2003), only a few species with similar traits were dispersed by deer in this study. Generally, deer are most likely to disperse nonnative, annual herbs that thrive in open habitats (Myers *et al.* 2004, Williams and Ward 2006, Eycott *et al.* 2007, Williams *et al.* 2008, Blyth *et al.* 2013, Albert *et al.* 2015). In this study, three species comprised most of the seeds dispersed by deer: *P. oleracea* (53% of all seedlings emerging from collected deer pellets), *S. ptycanthum* (15%), and *P. pumila* (13%). Several of the species dispersed by deer, including *P. oleracea* and *S. ptycanthum* are common agricultural weeds (Vencill *et al.* 2012). Previous greenhouse studies indicate that deer commonly disperse many seeds from a single species: Myers *et al.* (2004) found that *Chenopodium glaucum* (L.) accounted for 83% of all emerging seedlings, whereas Williams *et al.* (2008) found that *P. oleracea* made up 62% of all emerging seedlings. Previous studies suggest that

the few species dispersed by deer in this study was not a product of the methods employed (Williams and Ward 2006, Guiden 2014). Rather, because the number of plant species dispersed by deer is constrained by the plant species diversity in a landscape (Albert *et al.* 2015), the few species dispersed by deer was more likely a product of the species-poor forest herb layer that is characteristic of intensively modified agricultural landscapes (van Ruremonde and Kalkhoven 1991). Additionally, because deer pellet groups were only collected from September to December, species that set fruit in spring and summer are underrepresented in these data. However, that is unlikely a major source of bias in the present study because deer pellet groups collected in spring and summer have fewer germinable seeds representing fewer plant species, compared with pellet groups collected in fall and early winter (Myers *et al.* 2004, Williams *et al.* 2008).

These results have several practical implications for land managers. Organisms that connect multiple habitat types are seldom accounted for in management strategies but can have a strong influence on plant community composition (Lundberg and Moberg 2003). Here, I show that deer can connect agricultural fields and small forest patches by dispersing seeds of shade-intolerant plant species (often agricultural weeds) to forest edges. Because the average and maximum distances that deer disperse seeds often exceed other agents of seed dispersal (Vellend *et al.* 2003, Guiden *et al.* 2015), seed dispersal by deer could have a large effect on plant community and genetic diversity (Cain *et al.* 2000). In this study, deer pellets were only collected in forest patches, but future studies should consider collecting pellets in agricultural fields to determine whether deer might contribute to the spread of herbicide-resistant genes in weedy species (Chomas and Kells 2004) or whether the seed dispersal of those species to forest edge improves crop yield (*e.g.*, Villamagna *et al.* 2013). In addition, many conservation plans call for the establishment of small “islands” or forest corridors to connect larger forest patches (Saura *et al.* 2014). Here, I show that deer will likely disperse seeds into forest patches regardless of size or isolation but that deer are unlikely to disperse plant species of conservation concern (but see Vellend *et al.* 2003). Moreover, other studies show that deer disperse invasive woody plants (Vellend 2002, Myers *et al.* 2004, Williams and Ward 2006, Guiden *et al.*

2015), although I found no evidence of invasive plant dispersal in this study. The frequency of seed dispersal by deer near forest edges presented here suggest that when deer disperse seeds of invasive species in highly fragmented landscapes, most invasive seeds will likely be dispersed along forest edges. Therefore, land managers may be able to most efficiently stop new invasions by monitoring forest edges for seedlings of invasive plants, rather than forest interiors.

More work is needed to understand the complex effect of landscape context on seed dispersal by deer, and several exciting research questions remain unanswered. For example, deer abundance can influence which species are consumed by deer (Horsley *et al.* 2003), but it is unknown whether density-mediated changes in foraging behavior could translate into altered seed dispersal. In addition, forest gaps provide a similar high-light microhabitat to forest edges, which can benefit some species and influence the dispersal patterns of nonnative species (Driscoll *et al.* 2016), especially if seeds dispersed by deer enter the seed bank (Blyth *et al.* 2013). Future studies could determine whether tree-fall gaps alter deer activity similarly to forest edges and whether those disturbances provide transient habitat for shade-intolerant species dispersed by deer. Because of the increased abundance of deer and their potential to move seeds over long distances, continuing to develop an understanding of how habitat structure alters deer behavior will help predict the role they have in structuring plant communities along edges.

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