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Endozoochory by white-tailed deer (*Odocoileus virginianus*) across a suburban/woodland interface

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Abstract

We examined the role of white-tailed deer (*Odocoileus virginianus*) in the dispersal of viable seeds in an intact forest bordered by medium-density housing in southern Connecticut. Estimated deer density on site was 23 deer/km^2 with higher local densities along the suburban/woodland interface. A total of 566 pellet groups were gathered in summers through early winters of 2002–2005. After vernalization at 5 °C for 60 days, pellet groups were placed in a growing medium in a temperature controlled greenhouse for 6 months. A total of 11,512 seedlings germinated from 61% of pellet groups, which included 86 taxa. Seeds of 40 species confirmed not native to the United States germinated from pellet groups. Given mean germination data of more than 20 germinants/pellet group and deer population estimate, each deer on site during the sampling interval had the potential to disperse over 500 viable seeds/day, which included approximately 350 seeds of exotic species. Median maximum travel distance of does for a 24-h period was 568 m with a maximum distance of 5932 m. Deer were likely consuming seeds in disturbed and/or edge habitats, which are often adjacent to residential housing, and transporting them into forested areas where exotic plants are not as prevalent. Birds, small mammals, and abiotic factors are known dispersal agents for plants. These results indicate that white-tailed deer are another important dispersal agent of seeds, particularly exotics. Thus, white-tailed deer may not only alter vegetation structure through direct browse damage of established plants, but also indirectly by lowering reproductive output of native plants and simultaneously distributing seeds of exotic species.
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1. Introduction

In eastern North America, white-tailed deer (*Odocoileus virginianus*) are the dominant large herbivore with a population that has been expanding exponentially since the turn of the 20th century (Conover et al., 1995) and is now estimated to be at least 16 million (McCabe and McCabe, 1997). For example, the deer population in Connecticut has grown from an estimated 12 animals in 1900 to nearly 80,000 presently (Ward, 2000; Gregonis, 2003). Research on the impacts of deer on local ecosystems has focused on the deleterious effects of browsing on herbaceous communities (Anderson et al., 2001; Fletcher et al., 2001; Carson et al., 2005) and forest regeneration (Alverson et al., 1988; Tilghman, 1989; Pedersen and Wallis, 2004).

Robertson et al. (1994) suggested that two major threats to natural preserves are browsing by overabundant white-tailed deer herds and exotic plant species. Nearly 100 threatened or endangered species are browsed by white-tailed deer (Miller et al., 1992), and forests with deer densities exceeding 8 deer/km^2 will have little, if any, natural regeneration (Tilghman, 1989). Deer browsing can lower reproductive output of native species by reducing plant size or by directly targeting flowers (Fletcher et al., 2001; Webster et al., 2001; Frankland and Nelson, 2003).

The adverse effects of deer browsing are compounded by the invasion of woody and herbaceous exotic species, especially in areas adjacent to suburban development (Waller and Alverson, 1997; Seabloom et al., 2006). Such areas have an abundance of

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edge habitat. Edge habitats were created on a small scale by natural disturbances in pre-colonial times and were quickly re-vegetated by forest interior species. However, development and agricultural practices have created patchwork-like forests surrounded by fields, roads, and development (Robertson et al., 1994).

Edge habitats are becoming more common throughout the U.S. as demand for development increases habitat fragmentation and road networks, which facilitate the establishment and dispersal of exotic plant species (Forman, 2000; Gelbard and Belnap, 2003). An estimated 21% of the forested area in Connecticut is within 400 m of development (Hurd et al., 2006). Fragmentation also impacts other wildlife species as forest interior birds were not detected in forest tracts smaller than 187 ha in southern Connecticut (Askins et al., 1987).

The suburban/woodland interface, the hard edge where the forest abruptly terminates and abuts residential areas, is ideal habitat for white-tailed deer, with an abundance of food and protection from hunting and predation (DeNicola et al., 2000). In addition, many residential gardens have a high proportion of exotic ornamental species (Ward, 2000). Flourishing deer populations in these areas not only cause severe damage to native plant populations by overbrowsing, but also foster the spread of exotic species (Williams and Ward, 2006). While some native species populations may recover following release from browse pressure (Anderson et al., 2002; Townsend and Meyer, 2002), the establishment of exotic species before deer population control will result in long-term, if not permanent, changes in community structure.

The potential role of white-tailed deer in the dispersal of native, cultivated, and exotic seeds has been examined only recently. Vellend (2002) reported deer pellets contained viable seeds of honeysuckle (Lonicera sp.). Further analysis of the same pellets found viable white trillium (Trillium grandiflorum) seeds (Vellend et al., 2003). Myers et al. (2004) described deer as a long-distance dispersal mechanism for 72 species of plants. Williams and Ward (2006) reported deer dispersed viable seeds of 32 exotic species.

The original objective of this research was to document the number of seeds and diversity of species that germinated from deer pellets in southern New England. Because a high number of species and seeds germinated from the first year's sample, the study was continued to examine the potential role of endozoochory, seed ingestion and subsequent defecation, in distribution of native and exotic species in southern New England woodlands adjacent to residential development over four growing seasons. This provided an opportunity to determine if deer are facilitating the invasion of exotic species in woodlands adjacent to residential development.

2. Methods

2.1. Study site

The study was conducted in southern Connecticut on South Central Connecticut Regional Water Authority property (41°21′N, 72°46′W) in the town of North Branford. The property is privately owned, closed to the public, and covers an area of approximately 2800 ha including a 400 ha reservoir. The property is managed for water quality with some commercial timber harvesting. The research area was restricted to the 1550 ha bounding the reservoir to the south and extending several kilometers northward. The property, excluding the reservoir, is approximately 90% forested with some fields and a spruce (Picea spp.) plantation at the south end.

Dominant tree species on site were oak (Quercus spp.), sugar maple (Acer saccharum), tulip poplar (Liriodendron tulipifera), black birch (Betula lenta), and American beech (Fagus grandifolia). Because of high deer densities, woody understory vegetation was sparse except for sugar maple seedlings less than 10 cm tall, spicebush (Lindera benzoin), and non-natives such as Japanese barberry (Berberis thunbergii), winged burning bush (Euonymus alata), and wine raspberry (Rubus phoenicolasius). Autumn olive (Elaeagnus umbellata) was well established in abandoned fields and tree of heaven (Ailanthus altissima) thrived in disturbed areas.

2.2. White-tailed deer

A prohibition of legal hunting on site since the mid-1920s had fostered a large deer population. Based on four different censusing techniques (mark/recapture survey, walking line transect method, vehicle line transect method, aerial snow count), mean deer density was estimated at 23 deer/km^2 throughout the study area in 2003 with higher densities in the southern than northern section, 40 and 14 deer/km^2, respectively (S.C. Williams, unpublished data). Similar densities were reported in 1991 using pellet counts (Ward and Stephens, 1995). Medium-high density residential development (>100 residences/km^2) abutted the southern margin of the property. Southern female deer (does) were observed utilizing backyards and gardens as part of their range, while northern does seldom wandered into adjacent suburban areas.

In order to characterize movement patterns of deer on site, 10 adult does were tranquilized using an explosive-injection dart rifle equipped with a 4× scope (Pneu-Dart, Inc., Williamsport, PA) from a tree stand over established bait sites or opportunistically from a vehicle. Each dart contained 367 mg zolazepam hydrochloride/tiletamine hydrochloride (Telazol®) and 220 mg xylazine hydrochloride (Rompun®). Sedated deer were first blindfolded and Puralube® was applied to prevent desiccation of the cornea. All deer were ear-tagged and fitted with a global positioning system (GPS) collar (Lotek Wireless, Inc., Newmarket, Ontario) programmed to record locations every 2 h. The effects of Rompun® were reversed with a 6-mg injection of tolazoline hydrochloride (Tolazine®). Contact names and phone numbers were clearly placed on each identification item; both ear tags and GPS collars were labeled to identify captured deer to prevent consumption by humans until capture drugs could be fully metabolized. This capture system has been proven effective and has been used since the mid-1980s with less than 1% mortality. The Connecticut Agricultural Experiment Station's Institutional Animal Care and Use Committee approved the animal capture and handling

procedures (Permit # P08-00), in accordance with the principles and guidelines of the Canadian Council on Animal Care. Permission to capture deer was granted by the State of Connecticut Department of Environmental Protection's Wildlife Division (Permit # 6008).

Collars were recovered by recapture, natural mortality, or by remote release mechanism which included a charge that detonated and dropped the collar to the ground. Locational data were downloaded into Microsoft Office Excel (Microsoft Corp., Seattle, WA). Daily movements of animals were calculated by converting latitude/longitude coordinates into Universal Transverse Mercator coordinates using the LatLong function of the program Calhome (Kie et al., 1996). Pythagorean Theorem was then used to determine distance measurements for all combinations of data points gathered in a 24-h period, as it has been reported that the gut retention time of non-fibrous diets in white-tailed deer averages 23 h (Mautz and Petrides, 1971), but can be between 37 and 59 h for more fibrous material (Barnes et al., 1992). The maximum distance from any two data points was determined for 24-h periods for each animal. Does were collared intermittently from November 2000 (before pellet sampling began) through October 2004.

2.3. Pellet groups

Ninety pellet groups were collected from 13 September to 16 December 2002 throughout the site. An additional 236 pellet groups were collected from 2 June through 22 December 2003. In 2004, 124 pellet groups were gathered from 29 July through 11 December. In 2005, 116 pellet groups were gathered from 16 August to 30 December, totaling 566 pellet groups over four years. Coordinates of sampling locations were determined using standard 7.5 min topographic quadrangles. Only fresh pellet groups were collected to insure pellets had been deposited during the preceding week. Care was taken to gather only pellets; leaf litter and soil were brushed away to prevent seed contamination. The entire pellet group was collected, placed in an individual sampling bag, and vernalized at 5 °C for 60 days. A pellet group can be described as an aggregation of pellets, comprising one complete deer defecation.

After 60 days, pellet groups were removed and placed in and lightly covered with Promix® growing medium (Premier Horticulture, Inc., Rivière-du-Loup, Québec, Canada). The 326 samples from 2002 and 2003 were planted intact. The 240 samples from 2004 and 2005 were lightly crumbled and then planted. Pellet groups were kept in a temperature controlled greenhouse for 6 months and watered as needed. Seedlings were allowed to grow until they could be identified, at which time, they were removed from the tray and discarded. Germinants of unknown species were repotted to prevent crowding within trays and grown until they could be identified. One control tray was established for every four treatment trays (16 pellet groups) in 2002 and for every eight treatment trays (32 pellet groups) thereafter. These trays were filled with only Promix®. Control trays were placed among, and watered concurrently with trays containing pellet groups. We determined U.S. nativity status and seedling nomenclature using the

USDA Natural Resources Conservation Service's Plants Database (USDA, NRCS, 2004).

2.4. Vegetation survey

A vegetation study was initiated on the study area in fall of 2005. Plots were located in closed-canopy forests where pellet groups had been collected. Vegetation was sampled on 32 4-m² circular plots in the southern portion of the property, where deer were most abundant. Within each quadrat of each circular plot, the species and height class was recorded for all woody stems (excluding vines) with diameters less than 2.0 cm at 1.4 m above ground. Within each quadrat of each plot, the species and cover estimate (0, <2%, 10%, 25%, 50%, 75%, and 100%) were recorded for all herbaceous species and vines. On average, vegetation sample plots were 500 m from residential development.

2.5. Analysis

Species with viable seeds in white-tailed deer pellets were classified into three categories: woody, forb, and graminoid. For this study, frequency is defined as the proportion of pellet groups that had seeds which germinated. Density is defined as the number of seeds that germinated from pellet groups that had at least one seedling. Differences in frequency among months were determined using Pearson chi-square. Cochran's test of linear trend was used to determine if frequency increased from late summer through early winter (SPSS, 2000).

3. Results

3.1. White-tailed deer

GPS data were recorded for 10 does, resulting in movement data for 3888 deer days. For analysis of the movement data in terms of potential long-distance seed dispersal, data for the four month period of September to December (for multiple years) were used. There were 1167 days of observation from seven individual does during this period. Median maximum travel distance for a 24-h period was 568 m with a maximum distance of 5932 m (Fig. 1). Maximum travel distance for a 24-h period was at least 2000 m for 4% of observations and at least 4000 m for 1% of observations.

3.2. Pellet groups

A total of 11,512 seeds germinated from 61% of pellet groups, comprising 86 plant taxa. Seventy-two taxa positively identified to the species level accounted for 97% of seedlings (Table 1). Two percent of seedlings died before identification was possible. Sixteen taxa could only be identified to the genus (0.9% of seedlings). Forbs (48 species or genera) accounted for 92% of germinated seeds; graminoids (21 species or genera) and woody plants (17 species or genera) accounted for 3% and 5% of germinated seeds, respectively. Three species, Canadian horseweed (*Conyza canadensis*), yellow wood sorrel (*Oxalis*
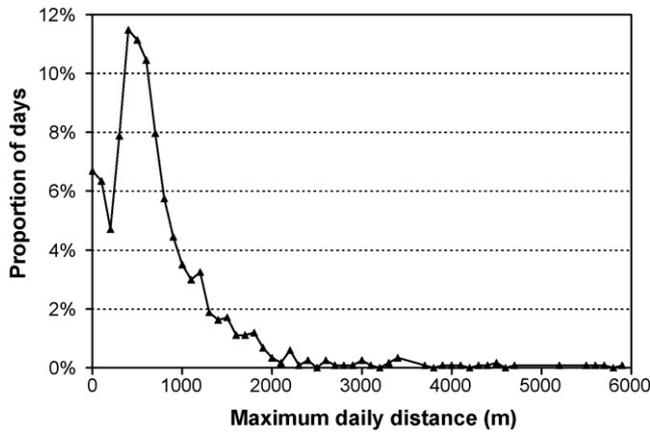
Fig. 1. Distribution of the maximum travel distance of white-tailed deer for 24-h periods (n = 1167) during the months of September through December.

stricta), and small spotted sandmat (*Chamaesyce maculate*) were found in both control and treatment trays. These species were excluded from analysis because it could not be determined if individual seedlings originated in a pellet or were the result of contamination.

Table 1

Total number of seedlings (density) and number of pellet group occurrences (occurence) for germinated seeds

	Density	Occurrence
Forbs		
Portulaca oleracea*	7,209	44
Chenopodium album*	199	12
Lotus corniculatus*	54	13
Solanum nigrum*	47	12
Veronica officinalis*	8	6
Trifolium pratense*	8	4
Securigera varia*	6	4
Trifolium sp.*	5	5
Polygonum caespitosum*	4	1
Chenopodium pumilio*	3	3
Polygonum persicaria*	3	3
Veronica persica*	3	3
Vicia sp.*	3	1
Artemisia vulgaris*	2	2
Nepeta cataria*	2	2
Trifolium repens*	2	2
Sonchus asper*	2	1
Capsella bursa-pastoris*	1	1
Capsicum sp.*	1	1
Cerastium fontanum*	1	1
Lychnis alba*	1	1
Petunia sp.*	1	1
Solanum dulcamara*	1	1
Solanum physalifolium*	1	1
Stellaria media*	1	1
Phytolacca americana	868	30
Solanum carolinense	647	101
Pilea pumila	621	61
Ludwigia palustris	332	2
Polygonum hydropiperoides	276	14
Amaranthus albus	136	12
Polygonum pensylvanicum	69	13
Plantago major	24	9
Mollugo verticillata	22	8

Table 1 (Continued)

	Density	Occurrence
Amaranthus retroflexus	20	9
Stellaria pubera	13	4
Anaphalis margaritacea	7	1
Aster sp.	2	2
Solidago graminifolia	2	2
Solidago rugosa	2	2
Solidago sp.	2	2
Epilobium sp.	2	1
Galium sp.	1	1
Plantago aristata	1	1
Polygonum sagittatum	1	1
Polygonum sp.	1	1
Potentilla canadensis	1	1
Symphyotrichum puniceum	1	1
Unknown herb	1	1
Forbs total	10,620	x
Woody		
Rubus phoenicolasius*	467	36
Rosa multiflora*	33	14
Lonicera japonica*	10	3
Elaeagnus umbellata*	6	6
Phellodendron japonicum*	5	2
Ampelopsis brevipedunculata*	3	2
Malus sp.*	2	2
Fragaria sp.	6	3
Betula alleghaniensis	5	4
Rubus odoratus	5	1
Lonicera sp.	4	4
Ostrya virginiana	4	3
Prunus serotina	2	2
Rubus occidentalis	1	1
Rubus sp.	1	1
Smilax glauca	1	1
Tsuga Canadensis	1	1
Woody total	556	x
Gaminoids		
Microstegium vimineum*	7	3
Poa compressa*	4	3
Panicum miliaceum*	2	2
Agrostis tenuis*	1	1
Elymus repens*	1	1
Pennisetum glaucum*	1	1
Sorghum halepense*	1	1
Zea mays*	1	1
Muhlenbergia sp.	49	20
Digitaria sanguinalis	17	13
Carex sp.	12	8
Deschampsia flexuosa	7	7
Poa sp.	7	2
Juncus tenuis	6	3
Muhlenbergia schreberi	5	3
Dichanthelium clandestinum	5	2
Agrostis palustris	2	2
Agrostis perennans	2	2
Panicum capillare	2	2
Scirpus atrovirens	2	2
Calamagrostis canadensis	1	1
Unknown grasses and sedges	201	77
Grass total	336	x
Combined species total	11,512	x

An [*] indicates a plant species exotic to the United States.

Nativity status was determined for all identified species as well as some identified only to the genus. Plants not native to the U.S. accounted for 70% of seedlings. United States nativity was determined for 80 taxa, of which 40 (50%) were exotic. Cultivated species such as corn (*Zea mays*), blue petunia (*Petunia* sp.), and green pepper (*Capsicum* sp.) were considered U.S. exotics. Species that were classified as "native and introduced" by USDA, NRCS were also considered U.S. exotics for this analysis.

The 10 most abundant species included both exotic and native species (Table 1). Exotics included little hogweed (*Portulaca oleracea*), wine raspberry, and lambsquarters (*Chenopodium album*). United States natives included Carolina horsenettle (*Solanum carolinense*), American pokeweed (*Phytolacca americana*), Canadian clearweed (*Pilea pumila*), marsh seedbox (*Ludwigia palustris*), swamp smartweed (*Polygonum hydropiperoides*), prostrate pigweed (*Amaranthus albus*), and Pennsylvania smartweed (*Polygonum pensylvanicum*).

Frequency of occurrence was the proportion of samples with a given species (Table 1). The 10 most frequently occurring species also contained both U.S. exotics and natives. Exotics included little hogweed (8%), wine raspberry (6%), multiflora rose (*Rosa multiflora*) (2%), and bird's-foot trefoil (*Lotus corniculatus*) (2%). Native species included Carolina horsenettle (18%), Canadian clearweed (11%), American pokeweed (5%), swamp smartweed (2%), hairy crabgrass (*Digitaria sanguinalis*) (2%), and Pennsylvania smartweed (2%).

Other species of interest that germinated from samples included Japanese corktree (*Phellodendron japonicum*), autumn olive, Nepalese browntop (more commonly referred to as Japanese stiltgrass) (*Microstegium vimineum*), corn, blue petunia, green pepper, eastern hemlock (*Tsuga canadensis*), black cherry (*Prunus serotina*), apple (*Malus* sp.), and yellow birch (*Betula alleghaniensis*) (Table 1). Japanese corktree had not been previously documented as an escaped exotic in Connecticut (USDA, NRCS, 2004).

3.3. Seasonal variation

Viable seeds germinated in pellet groups gathered throughout the June to December sampling period (Fig. 2). There was a marked difference among months in the proportion of samples (frequency) that had viable seeds ($\chi^2 = 47.36$, d.f. = 6, $p < 0.001$) with a pattern of increasing frequency from June through December (Cochran's linear trend = 16.03, d.f. = 1, $p < 0.001$). Forb frequency peaked in November and graminoid frequency peaked in October. No seasonal trend was observed for woody species.

There was a striking contrast in the seasonal pattern of native species compared with exotics. From June through August, exotic species were found in a much higher proportion of pellet groups than native species (Fig. 3). Not only were exotic species more frequent during this period, but seedling density (seedlings per pellet group) was several orders greater (Fig. 4). From September through December seedling frequency and density of native species was similar to exotic species.
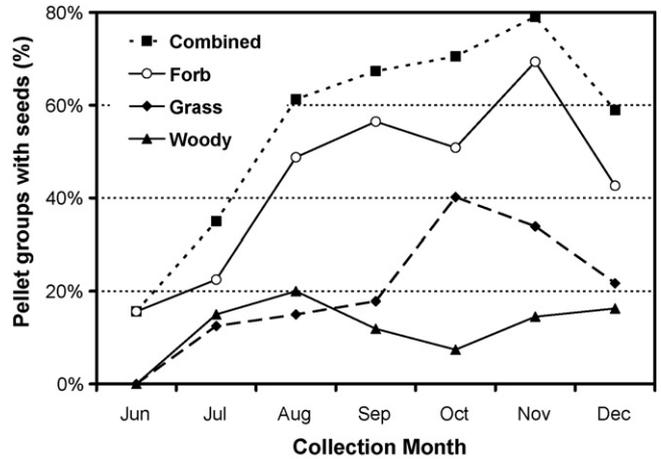

Fig. 2. Changes in frequency of pellet group samples with seedlings germinating by collection month in southern New England. Frequency is the proportion of pellet groups that had at least one seedling.

3.4. Vegetation plots

There were 70 taxa positively identified to the species level in the vegetation sampling plots. Seven taxa could be identified
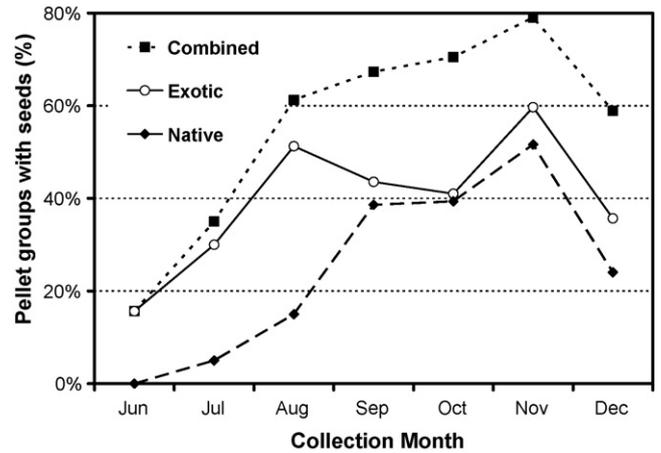

Fig. 3. Changes in frequency of pellet group samples with seedlings of native and exotic species germinating by collection month in southern New England. Frequency is the proportion of pellet groups that had at least one seedling.
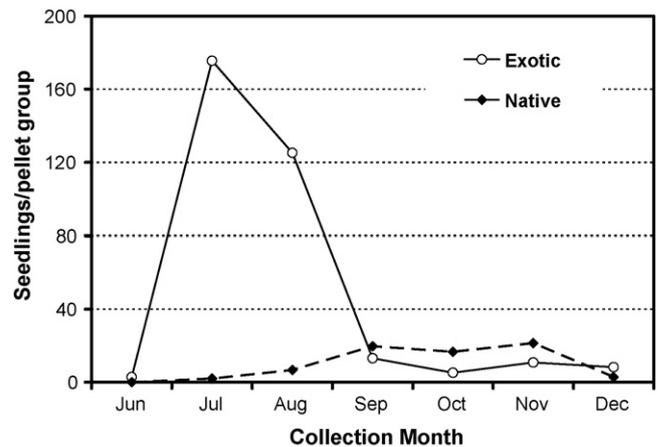

Fig. 4. Changes in mean number of seedlings/pellet group of exotic and native seedlings germinating by collection month in southern New England.

to the genus. Eleven species and one genus were exotic to the U.S. There were 1531 stems of woody species on the plots, 238 (16%) of which were exotic. Exotic woody species included Japanese barberry, multiflora rose, wine raspberry, winged burning bush, Norway spruce (*Picea abies*), and apple.

There were 29 species or genera of forbs; cover averaged 15%. Exotic forb cover was only 0.2% and included common wormwood (*Artemisia vulgaris*), common gypsyweed (*Veronica officinalis*), and Queen Anne's lace (*Daucus carota*). Combined cover of the eight species or genera of graminoids averaged 19%. Exotic graminoid cover was over 1% and included Nepalese browntop and barnyard grass (*Echinochloa crus-galli*). Combined cover of the vine species averaged 8%. Oriental bittersweet (*Celastrus orbiculatus*) was the only observed vine species not native to the United States. Combined cover of the five fern species averaged 12%; all were native to the United States.

4. Discussion

We found that white-tailed deer can distribute viable seeds of 86 taxa in southern New England. Myers et al. (2004) documented 72 taxa germinated from pellet groups in northern New York. Interestingly, there was minimal cross-over, and the combined data sets represent at least 134 unique plant taxa in the eastern United States whose seeds remain viable after passing through the digestive tract of white-tailed deer. Only 19 of the 87 unique genera were found in both studies. Seed dispersal by cervids is not limited to eastern North America, but has also been reported in Asia (Dinerstein, 1989; Yamashiro and Yamashiro, 2006) and Europe (Malo and Suárez, 1998; Mouissie et al., 2005). Ascertaining the common characteristics of plant species dispersed by cervids would help increase the understanding of the potential spread and maintenance of both native and exotic species in areas with high or increasing cervid populations.

Seeds of many species are probably ingested unintentionally by deer as they browse. Janzen's (1984) "foliage is the fruit" hypothesis suggests that the primary mode of long-distance dispersal for species with inconspicuous seeds proximate to palatable foliage is incidental ingestion and subsequent defecation by large herbivores. This hypothesis has been used to describe endozoochory by both wild and domesticated herbivorous species including: cattle (Malo and Suarez, 1995; Mouissie et al., 2005; Bruun and Poschlod, 2006), sheep (Mouissie et al., 2005; Ramos et al., 2006), ponies (Mouissie et al., 2005), gopher tortoise (*Gopherus polyphemus*) (Birkhead et al., 2005), and European rabbit (*Oryctolagus cuniculus*) (Malo and Suárez, 1995).

A long-distance dispersal mechanism can greatly enhance spread of invasive exotic species across and within landscapes (Vellend et al., 2003; Myers et al., 2004). While flight enables birds to serve as an efficient long-distance seed dispersal mechanism (Willson, 1986; Malmborg and Willson, 1988), the majority of seeds are deposited relatively short distances from parent plants (Fuentes, 2000; Williams, 2006). Deer may be a more efficient mechanism for long-distance seed dispersal,

especially given their exponential growth rates in the Northeast over the past several decades. However, there may be an antagonistic relationship between deer as seed dispersers and their ability to negatively impact plant populations via herbivory as populations continue to increase over the landscape (Vellend et al., 2006).

Median maximum travel distance for white-tailed deer on site during 24-h periods was 568 m and for 4% of deer days, animals traveled at least 2000 m (Fig. 1). These movement data are similar to those of a seed shadow model for white-tailed deer developed by Vellend et al. (2003). Adult male deer (bucks) range over larger areas than does and have the potential to transport seeds up to 20.9 km (Marchinton and Hirth, 1984). By comparison, tapirs (*Tapirus terrestris*) dispersed American oil palm (*Maximiliana maripa*) seeds up to 2000 m (Fragoso, 1997).

Our study found deer dispersed large numbers of exotic and native seeds across the landscape. Estimated white-tailed deer defecation rates range from 20 to 35 pellet groups per day (Rollins et al., 1984; Rogers, 1987). We found an average of 20.3 successful germinants per pellet group. By comparison, an average 27.2 germinants per pellet group were reported in New York (Myers et al., 2004). Using conservative estimates of 25 defecations per day and 20 germinants per pellet group, each deer potentially dispersed over 500 viable seeds per day. More than 70% of the seedlings in our study were exotic to the U.S. Therefore, each deer potentially dispersed approximately 350 viable exotic seeds per day from July through December. Using the estimated density of 23 deer/km^2, deer on site were dispersing nearly 15,000 viable exotic seeds per hectare for the 6-month period from July through December. Actual number of seeds dispersed at other locations will vary depending on local densities of exotic species, availability of alternative forage, and deer density. Additionally, Myers et al. (2004) reported the number of seeds per pellet group peaked in January and February, two months we did not sample. This suggests that we underestimated the actual numbers of exotic seeds dispersed by white-tailed deer.

While a high proportion (50%) of species germinating from pellet groups were confirmed not native to the U.S. (Table 1), only 18% of species (excluding ferns) found on vegetation sampling plots were exotic. Two of the exotic species found on vegetation plots and in pellet groups, Nepalese browntop and common wormwood, are aggressive invasives that can quickly dominate a site and exclude native species. The capacity of deer to transport viable seeds thousands of meters (Fig. 1) confounds the problem of controlling these, and other, exotic invasive species at a local stand level. Effective eradication will require control measures to be implemented at least one kilometer from preserve boundaries to minimize reestablishment of new infestation points of deer dispersed seeds.

The number and density of exotic species in the forest vegetation samples probably would have been higher if plots had been placed in recent canopy gaps, rather than under intact canopy. Many of the exotic species that germinated from pellet groups require full sun for development (Saunders et al., 1991; Brothers and Spingarn, 1992). Brothers and Spingarn (1992)

reported exotic plant species abundance was lower within the forest interior than in edge habitats. They suggested that this may be the result of limited dispersal or lower light conditions. Our study indicates that deer can transport seeds into forest interiors (Fig. 1). This suggests that the low light conditions within forest interiors is the limiting factor slowing the spread of exotic plant species in areas of high deer abundance. However, canopy gaps will inevitably form as trees senesce, creating the higher light conditions favorable for exotic species development. Seeds that do not germinate when deposited in forest interiors will form part of the seed bank. Seeds of many species can persist for years or decades (Burnside et al., 1996). The fact that these seeds, both native and exotic, are already on site will give them a competitive advantage over seeds that arrive after gap formation.

Fragoso et al. (2003) noted that plant species aggregations can be formed from defecation patterns. In contrast, our findings revealed that deer can deposit seeds not only on the order of several kilometers, but throughout their range within the forest interior as deer do not concentrate defecations in latrines as do tapirs (Fragoso et al., 2003) and raccoons (*Procyon lotor*) (Giles, 1939). Bartuszevige et al. (2006) reported that Amur honeysuckle (*Lonicera maackii*) in woodlot interiors were not older than individuals along the edge, suggesting rapid seed transport into forested interiors. Thus, in systems where endozoochory results in a widespread diffuse pattern of deposited seeds, aggregations are more likely at the scale of disturbance events (e.g., multi-tree canopy gaps) or underlying edaphic conditions.

5. Summary

White-tailed deer play an important role in shaping plant community structure, especially in forests adjacent to development and associated edge habitat. Deer are capable of long-distance transport of seeds, including those of exotic invasives that are deleterious to native ecosystems. Continued forest fragmentation will increase the amount of edge habitat where white-tailed deer and exotic plant species thrive, and the proportion of intact forest within the range of suburban deer. Minimizing the influx of exotic seeds by deer to natural areas cores will require a forested buffer of 500–1000 m – corresponding to an area of 100–400 ha. Thus, protection of larger forested tracts will minimize seed input of exotic species by deer and also provide habitat suitable for forest interior birds and other wildlife species.

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