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Authors: Panter, Christopher J., and Dolman, Paul M.

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Original article

Mammalian herbivores as potential seed dispersal vectors in ancient woodland fragments

Christopher J. Panter & Paul M. Dolman

Europe's remaining ancient woodland is highly fragmented and many specialist woodland plants persist as isolated relictual populations. Their apparent dispersal limitation and failure to colonise more recently established secondary woodlands may reflect a loss of vectors and mechanisms for dispersal. This is in contrast to long-distance dispersal events evidenced both by paleoecology and some contemporary observations. Although increasing populations of deer are recognised as important dispersers of plant seeds, particularly for species with no apparent dispersal mechanism, the potential for deer to disperse ancient woodland plants has not been studied previously in the UK, where remaining ancient woodland fragments are frequently surrounded by arable landscapes. Viable seed content of 616 faecal samples collected from a guild of mammalian herbivores; red deer *Cervus elaphus*, fallow deer *Dama dama*, roe deer *Capreolus capreolus*, reeves' muntjac *Muntiacus reevesi* and brown hare *Lepus europaeus*, over five months and from four coppiced ancient semi-natural woodlands in eastern England, was assessed. Following cold stratification and sowing in a controlled greenhouse, 502 seedlings of 41 species germinated. Three species, constituting just 1.8% of the total individual seedlings recorded, were characteristic of woodland habitats, including only one ancient woodland indicator species, wood speedwell *Veronica montana*. Germinated plant species were instead characteristic of non-woodland habitats including grassland, arable and ruderal communities. The four most abundant species were the widespread grass common bent *Agrostis capillaris*, the ruderal greater plantain *Plantago major* and the two crop species, wheat *Triticum* spp. and rape *Brassica napus*. Mammalian herbivory in these ancient woodland fragments provided few dispersal benefits for the woodland plant community. Instead, larger free-ranging herbivores transported large volumes of propagules of ruderal agrarian and open-habitat species from surrounding habitats into ancient woodland fragments.

Key words: ancient semi-natural woodland, deer, endozoochory, herbivory, seed dispersal

Christopher J. Panter & Paul M. Dolman, School of Environmental Sciences, University of East Anglia, Norwich, NR4 7TJ, UK - e-mail addresses: c.panter@uea.ac.uk (Christopher J. Panter); p.dolman@uea.ac.uk (Paul M. Dolman)

Corresponding author: Christopher J. Panter

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The ancient woodland resource remaining in north-western Europe is highly fragmented and in many regions remaining fragments are small and isolated (Thomas et al. 1997, Wulf 2003). Many vascular plant species characteristic of ancient woodland are considered to be dispersal limited, forming relictual populations that persist in ancient woodland fragments, but fail to colonise secondary woodlands nearby (Peterken 1974, Verheyen et al. 2003). This contrasts with long-range dispersal events apparent in the paleoecological pollen record, suggesting that mechanisms and vectors of dispersal may have been lost (Reid's paradox; Clark et al. 1998).

Deer populations are increasing throughout most of Europe and are reestablishing in landscapes that have lacked large herbivores for much of the last millennia (Fuller & Gill 2001, Dolman & Wäber 2008). The important role vertebrates play as dispersers of plant seeds is well documented (Traveset et al. 2007). Furthermore, the specific role of large wild mammals, including wild boar *Sus scrofa*, bison *Bison bonasus*, deer and hare as dispersers of plant seeds, by both endozoochory and epizoochory, is increasingly recognised (Heinken et al. 2002, Schmidt et al. 2004, Oheimb et al. 2005, Eycott et al. 2007, Jaroszewicz et al. 2009). For example, deer

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dispersed 34% of all plant species known from a plantation forest landscape in eastern England, including many species that otherwise lacked any apparent physiological adaptation or mechanism for dispersal (Eycott et al. 2007). Although, effects of endozoochoric seed dispersal by deer within an ancient woodland context have been explored in Europe (Heinken et al. 2002, Schmidt et al. 2004, Oheimb et al. 2005), these studies were conducted in unfragmented forested landscapes or in large forest patches. In contrast, ancient woodlands in areas such as the UK survive as small fragments set in intensively modified, often arable, landscapes, and it is not clear whether seed dispersal by deer will be positive or detrimental in such contexts (Dolman et al. 2010). Rare events of ancient woodland species appearing in relatively young or secondary woodland are not fully explained (e.g. Jakubowska-Gabara & Mitka 2007), though Reid's paradox is predicted to have been influenced by herbivore endozoochorous dispersal (Pakeman 2001). In North America, uncharacteristic long distance dispersal events in the ant-dispersed plant species, white trillium *Trillium grandiflorum*, resulted from endozoochorous dispersal by white tailed deer *Odocoileus virginianus* (Vellend et al. 2003). In Britain, the consumption of the flowers and seed heads of ancient woodland species, including oxlips *Primula elatior*, wood anemones *Anemone nemorosa*, dog's mercury *Mercurialis perennis* and herb paris *Paris quadrifolia*, particularly by the introduced reeves' muntjac *Muntiacus reevesi* and naturalised fallow deer *Dama dama* (Tabor 2004, Cooke 2006), suggests the potential for deer to improve dispersal distances by acting as vectors for dispersal-limited woodland plants. However, grasses and ruderal herbaceous species are often common in endozoochorous and epizoochorous seed burdens of wild large herbivores (Heinken et al. 2001, Heinken & Raudnitschka 2002, Schmidt et al. 2004, Oheimb et al. 2005, Jaroszewicz et al. 2009). Thus, there is the possibility that increasing populations of deer and other herbivores may be introducing heavy ruderal seed rain into small ancient woodland fragments (Dolman et al. 2010). The relative role of herbivores as seed dispersers in ancient woodlands is, therefore, uncertain and requires study, particularly for small woodland fragments surrounded by ruderal and agricultural habitats.

Overall, a reduction in the dominant plant species and an increase in vegetation diversity results from low or fluctuating herbivore populations (Olff & Ritchie 1998, Kirby 2001). However, abundant deer populations may negatively impact on herbaceous woodland plants, as well as reducing shrub layer vegetation and preventing woodland regeneration (Putman & Moore 1998, Cooke 2006). Current management guidelines often promote exclusion methods in ancient coppiced woodlands in an attempt to prevent impacts on coppice regeneration and ground flora. However, if herbivores act as dispersal vectors for ancient woodland species, keeping areas of established coppice and newly restored secondary woodlands open to deer might provide connectivity, import new species, allow access to sources of propagules and help restore mobility to relictual plant populations. In our study, we conducted germination trials using faeces from a guild of herbivores (comprising four deer species and brown hare *Lepus europaeus*) collected from four isolated ancient woodlands, in order to examine whether large and long-ranging herbivores act as dispersal vectors of ancient woodland species via endozoochory.

Material and methods

Study sites

We selected four ancient semi-natural woodlands, of varying size, in eastern England, each supporting regionally important communities of ancient woodland plant species. All woodlands were coppiced (with stands cut on rotation with multi-stem regeneration from cut 'stools'), but comprised a range of woodland types due to differing soils.

Our largest study site (1.25 km^2), Foxley Wood National Nature Reserve (52°45'31"N, 001°03'06"E) contains a combination of wet ash *Fraxinus excelsior*-maple *Acer* spp. woodland, pedunculate oak *Quercus robur*-hazel *Corylus avellana*-ash woodland and birch *Betula* spp.-pedunculate oak woodland (Goodfellow & Peterken 1981). Ashwellthorpe Wood (0.38 km^2; 52°32'15"N, 001°09'13"E) has predominantly clay soils that support plateau alder *Alnus glutinosa* woodland (Goodfellow & Peterken 1981). Within both of these sites, newly cut stands of rotational coppice are enclosed by electric fencing (for up to four years) to protect them from deer. Wayland Wood (0.32 km^2; 52°33'10"N, 000°50'25"E) lies on chalky boulder clay overlain by loam and sand, and consists predominantly of bird cherry *Prunus padus*-alder woodland (Goodfellow & Peterken 1981). Our smallest site, Honeypot Wood (0.09 km^2; 52°41'31"N, 000°51'30"E), lies on exposed boulder clay and supports acid pedunculate oak-hazel-ash woodland (Goodfellow & Peterken

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1981). Wayland and Honeypot woods do not have any fencing. Although the four woodlands we sampled were small, this is not atypical for ancient woodlands in the UK. For example, within south-eastern England, the ca 12,000 ancient woodland fragments recognised in the Ancient Woodland Inventory (Provisional) for England (available at: http://www.gis.naturalengland.org.uk/pubs/gis/GIS_register.asp; last accessed on 17 November 2011) have a mean area of only 0.103 km^2 ($\pm$ 0.263 SD). The landscape surrounding each of the four woodlands was dominated by arable and horticulture, with some grassland and additional woodland areas (Table 1). All four woodlands had the potential for dispersal of seeds from unshaded open habitats within the woodland (e.g. track margins and glades), from regenerating young growth, established coppice and high forest areas; while the two woodlands lacking any fencing also had potential for dispersal of seeds from ground vegetation in newly coppiced areas. All four woods had potential for dispersal from the wider landscape into the woodland.

Sampling methods

Faecal pellet groups from red deer *Cervus elaphus*, fallow deer, roe deer *Capreolus capreolus*, reeves' muntjac and brown hare were collected. European rabbit *Oryctolagus cuniculus* faecal pellets may contain large densities of seed (Eycott et al. 2007), but were not examined because the species was unlikely to act as a long-range dispersal agent. In contrast, brown hare range further (Bray et al. 2007), and thus, could potentially facilitate seed transfer among woodland blocks.

Faecal samples were collected from each site over a five month period, during spring and summer, from 4 April to 31 August 2008. This is a period of prolific seeding in a wide range of plants, and it includes the seed ripening period of early flowering ancient woodland species. Sampling at each site was carried out 15 times, approximately evenly spaced throughout the five months. Within each sampling period, all sites were visited on the same or following day, except during April when there was a maximum of five days between visits.

The time spent at each site and the sampling effort was consistent between visits and proportionate to site area. Faecal samples were obtained by walking paths used by herbivores, notable by trampling, tracks and browsing. Only fresh faecal groups were collected, following criteria defined by Eycott et al. (2007). Any adhering soil or plant material was removed from the faecal pellets, before placing them in a paper bag to air dry. Samples were not collected during or after periods of heavy rainfall, as this may have increased seed rain and potential contamination.

Faecal pellet groups were assigned to herbivore species primarily on the basis of pellet size, as dimensions best distinguish species (Chapman 2004), and secondarily by other traits that may be less consistent, including pellet end morphology or striations, following Chapman (2004), Bang (2006) and Swanson et al. (2008). Faecal pellets from the colons of culled deer were also used as reference samples. Although overlap in pellet size can occur between species and is increased by the presence of calves (Swanson et al. 2008), we are confident that pellet groups of brown hare, reeves' muntjac and roe deer were consistently and reliably distinguished, and were also not confused with pellets of the two larger deer species. However, as it was not possible to confidently distinguish between red and fallow deer, samples from these two species were pooled in subsequent analysis (following Eycott et al. 2007).

In total, 616 faecal pellet groups were collected.

Table 1. Land-use composition (%) within 1-km buffers around each of the four semi-natural ancient woodland study sites. Land-use data derived from the Land Cover Map 2000 and habitat definitions of these are given in Fuller et al. (2002).

Broad habitats	Honeypot	Wayland	Ashwellthorpe	Foxley
Broad-leaf woodland	4.1	7	12.7	11.2
Coniferous woodland	0	0.4	0.3	0.2
Arable and horticulture	86.9	55.1	76.2	83.7
Improved grassland	4.3	3.5	3.9	2.8
Setaside grass	3	2.5	0	0
Neutral grassland	0	14.2	0	0
Calcareous grassland	1.7	1.2	4.8	1
Built up areas (incl. gardens)	0	16.1	2.1	1.1
Total	100	100	100	100

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Table 2. Number of individual faecal samples for each herbivore species at each site and mean dry weight (± SD) of a pellet group for each species. Means that share a superscript do not differ significantly (Tukey multiple comparison test, $P < 0.05$)

	Brown hare	Reeves' muntjac	Roe deer	Red/Fallow deer	Total
Honeypot	34	79	58	2	173
Wayland	47	44	27	8	126
Ashwellthorpe	4	90	60	109	263
Foxley	4	26	16	8	54
Total	89	239	161	127	616
Mean dry weight (g)	$3.1^{c} \pm 1.6$	$4.7^{c} \pm 2.5$	$9.2^{b} \pm 7.7$	$33.4^{a} \pm 23.1$	

Herbivore species and faecal dry mass were recorded for each pellet group. Samples of material from roe deer and reeves' muntjac were obtained from all woods. However, faecal pellet groups of brown hare were largely obtained from Honeypot and Wayland woods and material from red/fallow deer from Ashwellthorpe (Table 2). Pellet groups were placed in paper bags and left to air dry for seven days, then placed in a dark cold room for stratification at 4°C for 30 days, following Bullock (2006). Previous endozoochory studies used different temperatures and durations for the cold stratification, including no exposure (Vellend et al. 2003), and subsequently recording no germination; 0-1°C for one month (Eycott et al. 2007) and natural frost exposure (Schmidt et al. 2004, Oheimb et al. 2005). After stratification, we soaked samples in water, gently crushed to break open the pellets, and scattered onto a half full tray of compost, with additional sieved compost ($\leq$ 15 mm) placed on top; this depth was selected as intermediate compared to other studies (e.g. 0-25 mm depth in Eycott et al. (2007) and 0-60 mm in Jaroszewicz et al. (2009)). Soil-based compost was used in our study as peat-based compost may introduce contaminant seedlings, particularly rush *Juncus* spp. (Eycott et al. 2007). Samples were placed in trays, appropriate to their volume: samples weighing < 20 g were placed in trays of 15×25 cm, those between 20-40 g in trays of 25×30 cm and samples > 40 g in trays of 30×35 cm. Trays were placed in a greenhouse maintained at an 18 hour day length at 20°C and watered approximately every other day. The germination experiment continued, with trays monitored and watered until no further plants germinated. We also placed 10 control trays (25×30 cm) containing just compost in the same greenhouse and watered as sample trays. Seedlings were transplanted when possible and grown on until large enough for identification, following the guidelines of Ter Heerdt et al. (1996). Removal of seedlings provided some disturbance to soil, encouraging further germination. After two months, any developing plants were transplanted and the samples stirred to break up any algae or moss layer developing and stimulate germination of seeds from deeper in the sample (Ter Heerdt et al. 1996). This resulted in further germination.

Analysis

For each germinated species, attributes of their ecology, habitat association and dispersal strategy were assessed. Species were classified as a competitor, stress tolerator, ruderal or any combination of these strategies according to Grime et al. (2007). Mechanisms of dispersal were classified, following Grime et al. (2007) as: wind, animal ingestion, animal dispersal by mucilage, animal dispersal by awns and unspecialised. The habitat associations of each species was classified into one of three categories: grassland or open semi-natural habitats (including damp and dry habitats or open woodland rides), species dependent primarily on woodland habitats (including shade tolerant species) and species common in arable and/or other ruderal and disturbed habitats. These species associations were classified using a variety of sources (e.g. Hill et al. 2004, Rose & O'Reilly 2006, Grime et al. 2007), with reference to Ellenberg light values (Hill et al. 2004) and C-S-R strategies (Grime et al. 2007) to identify ruderals. Values for mean seed mass (mg) were taken from the LEDA Traitbase (Kleyer et al. 2008). Pellet group composition was also analysed in relation to the size of the woodland site (ranked 1-4, from smallest to largest).

Cumulative plant species richness provided by faecal material from the different herbivore taxa was calculated as sample-based rarefaction in EstimateS (Colwell 2005). To compare the relative frequency of habitat association classes of germinated plant species among herbivore species, we used χ^2-tests (with Bonferroni correction applied). Overall proportional composition of samples from each herbivore taxa was related to herbivore species mean body mass

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(red/fallow deer = 85 kg, roe deer = 28 kg, reeves' muntjac = 14 kg and brown hare = 3.3 kg; Corbet & Harris 1991, Prior 2007) using Spearman's rank correlation. Due to low replication (just four herbivore taxa) these tests have weak statistical power and are therefore conservative, detecting only the strongest trends. Statistical analyses were conducted in SPSS version 16.0 (SPSS INC, Chicago, Illinois, USA).

Results

Overall germination was low, with only 24.8% of faecal pellet groups producing one or more seedlings, while overall seedling density was also low (0.07 plants/gram). No seedlings were recorded in the control trays and, therefore, no contamination was suspected to have occurred via the compost or ventilation. Pellet group dry masses (see Table 2) differed significantly between herbivore species ($F_{3, 612} = 206.56$, $P < 0.001$).

Comparison of seed dispersal among herbivore species

Larger herbivores dispersed more plants and more species, with red/fallow deer samples dispersing more seedlings than all other herbivore species (Fig. 1; 77.2% of plants from 33 plant species dispersed). However, number of seedlings germinating per gram of faecal material did not differ between red/fallow and reeves' muntjac (Table 3). Rarefaction curves had not saturated, thus more species would be detected with greater sample sizes. The asymptote of species richness curves for each herbivore was: brown hare, six species (95% confidence interval (CI): 1.5-10.5); reeves' muntjac, 19 species (CI: 11.6-26.4); roe deer, 17 species (CI: 10.5-23.5); red/fallow deer, 33 species (CI: 26.5-39.5) (see Fig. 1). A greater number of plant species were potentially distributed by red/fallow deer than by the other herbivore species, with no overlap in confidence intervals of rarefaction curves.

Fewer seedlings germinated per pellet group for brown hare than for any of the deer taxa; however, deer taxa did not differ (see Table 3). There were also greater densities of seedlings per gram of faecal material for reeves' muntjac and red/fallow deer compared to brown hare, with roe deer intermediate due to large variance. Controlling for herbivore taxa, seedling density was not affected by wood area (seedlings/pellet group: $F_{1, 611} = 0.399$, $P = 0.528$; seedlings/gram $F_{1, 611} = 1.919$, $P = 0.167$, respectively).

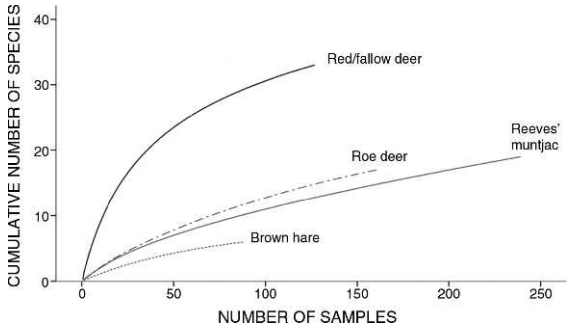


Figure 1. The cumulative number of plant species recorded for each herbivore species from sample based rarefaction.

Plant ecology

A total of 502 individuals of 41 plant species germinated, with only one seedling dying before identification (for details of plant species, see Appendix I). Germinated species were predominately unspecialised in their dispersal mechanisms (169 individuals from 19 plant species). Dispersal mechanisms of other plant species were, in order of abundance: wind (114 individuals of nine species), animal dispersal by ingestion (87 individuals of three species), animal dispersal by mucilage (81 individuals of three species) and animal dispersal by awns (51 individuals of seven species).

Rank abundance plots (Fig. 2) showed that the germinated assemblage was dominated by only a few species, with five species (common bent *Agrostis capillaris,* greater plantain *Plantago major,* wheat *Triticum* spp., rape *Brassica napus* and great willowherb *Epilobium hirsutum*) comprising the majority (50.9%) of seedlings. Of the germinated plant species, 22% were only recorded as single individuals.

Overall, the dispersed assemblage comprised plant

Table 3. Mean number of seedlings (± SD) for each herbivore taxa, per pellet group and per gram. Means that share a superscript do not differ significantly (Tukey multiple comparison test, $P < 0.05$)

	Brown hare	Reeves' muntjac	Roe deer	Red/Fallow deer	F	P
Seedlings/pellet group	$0.12^{b} \pm 0.42$	$0.26^{a} \pm 0.57$	$0.26^{a} \pm 0.59$	$3.06^{a} \pm 8.52$	17.643	< 0.001
Seedlings/gram	$0.0294^{a} \pm 0.1134$	$0.0575^{a/b} \pm 0.1659$	$0.0346^{a} \pm 0.0810$	$0.0952^{b} \pm 0.1888$	5.119	0.002

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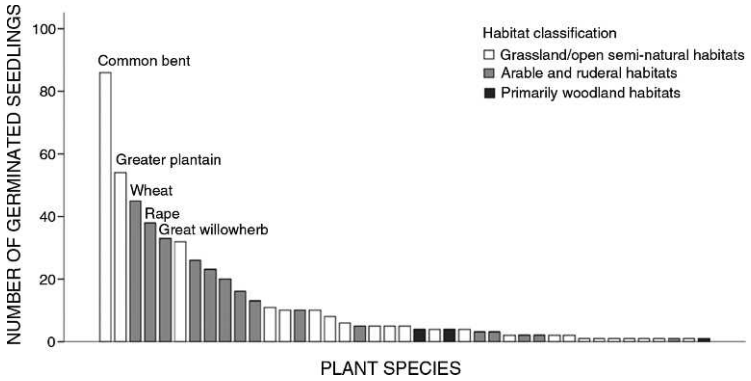


Figure 2. The rank abundance of plant species recorded from all herbivores, classified by their habitat type (with the five most abundant species labelled).

species characteristic of arable, ruderal and grassland habitats. The dispersed species were mainly from open habitats and shade intolerant, with the five most abundantly dispersed species all characteristic either of grassland and/or open semi-natural habitats, or of arable and ruderal habitats (see Fig. 2). Of the 20 most abundant plant species, which constitute 90.8% of dispersed species, none were associated primarily with woodland (see Fig. 2). In total, only three woodland-associated species were observed from all faecal samples: 1) tufted hair-grass *Deschampsia cespitosa*, a widespread species recorded in a range of habitats, which is shade tolerant and an important element in ancient woodland flora (Peterken 1993, Grime et al. 2007), 2) wild strawberry *Fragaria vesca*, occurring in grasslands as well as woodland or scrub, but regarded as a weak ancient woodland indicator (Peterken 1993, Rose & O'Reilly 2006) and 3) wood speedwell *Veronica montana*, an almost exclusively woodland species, regarded as a good ancient woodland indicator (Peterken 1993, Rose & O'Reilly 2006).

Representation of plant species associated with different habitats was not uniform among herbivore taxa (Figs. 3 and 4). The proportion of seedlings germinating differed significantly among the herbivore species for both arable ($\chi^2 = 26.1$, $P < 0.001$) and woodland ($\chi^2 = 32.5$, $P < 0.001$) habitat classes; both tests remain significant after Bonferroni correction. Brown hare was not recorded as dispersing any species characteristic of arable or ruderal habitats, and dispersed a greater percentage (27%) of woodland species than the other herbivores. Conversely, no species characteristic of woodland habitats were dispersed by the largest herbivores, red and fallow deer, for which seedlings largely comprised species of arable and ruderal habitats (56%). Percentage composition of ruderal and grassland plant species increased with greater herbivore body mass ($r_s = 0.340$, $P < 0.001$ and $r_s = 0.187$, $P < 0.001$, respectively). Conversely, the percentage composition of woodland species marginally decreased ($r_s = -0.067$, $P = 0.096$; see Fig. 4).

The majority of plant species (65%) and individual seedlings (50%) recorded were classified as ruderal in all or part of their C-S-R established strategy (e.g. shepherd's-purse *Capsella bursa-pastoris,* greater plantain; see Appendix I).

Seed mass of dispersed plants were generally low, mean 4.6 mg (SD ± 12.5); however, with large variance. Mean seed mass did not differ significantly among herbivore taxa ($F_{3,\ 498} = 2.336$, $P = 0.073$) though seeds dispersed by reeves' muntjac (1.1 ± 5.6 mg) appeared smaller; brown hare: mean 3.2 ± 9.2 mg; roe deer: 3.1 ± 10.5 mg; red/fallow deer: 5.4 ± 13.4 mg.

Differences in plant species and their ecologies were observed between the largest woodland block (Foxley wood) and the small fragments (all < 38 ha; Ashwellthorpe, Wayland and Honeypot). However, these observations were confounded by differences in the herbivore community encountered, with red and fallow deer material primarily collected from Ashwellthorpe (see Table 2).

Discussion

Our findings add to the growing evidence that deer can be important vectors for plant species that otherwise lack apparent morphological mechanisms for dispersal. However, we found that deer were primarily dispersing plant species of open farmland or ruderal habitats into these ancient woodland fragments, rather than acting as dispersers of woodland species.

Few of the plant species that germinated (7%) were classified on the basis of their morphological

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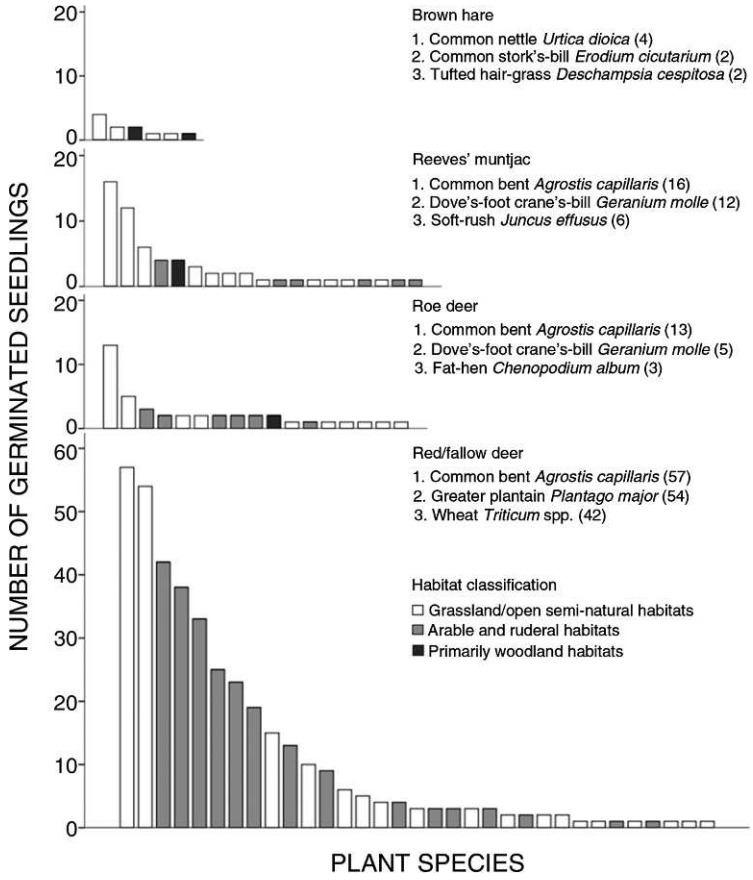


Figure 3. Rank abundance of plant species recorded, from faecal samples shown separately for each herbivore taxa, also showing the habitat classification of plant species. For each herbivore, the three most abundant species are listed.

structures as being primarily dispersed by animal ingestion (Grime et al. 2007). Our study and other recent work (Eycott et al. 2007) show that plants lacking any morphological specialisation or mechanism for dispersal can be prolifically dispersed via endozoochory. The abundance of plants with unspecialised dispersal mechanisms is expected, given the 'foliage is the fruit' hypothesis (Janzen 1984) and it is frequently observed in endozoochorous studies (Bruun & Poschlod 2006). Of the 41 species that germinated in our study, 34 were also detected in other studies of endozoochorous seed dispersal by deer or brown hare in Europe (e.g. Malo & Suárez 1995, Heinken et al. 2001, Schmidt et al. 2004, Oheimb et al. 2005, Eycott et al. 2007). Species novel to our study were: great willowherb, common stork's-bill *Erodium cicutarium*, wild strawberry, hedge bedstraw *Galium mollugo,* timothy *Phleum pratense,* groundsel *Senecio vulgaris* and pink water-speedwell *Veronica catenata*.

Woodland species were recorded very infrequently in the herbivore faecal samples and no ancient woodland species were recorded from deer samples;

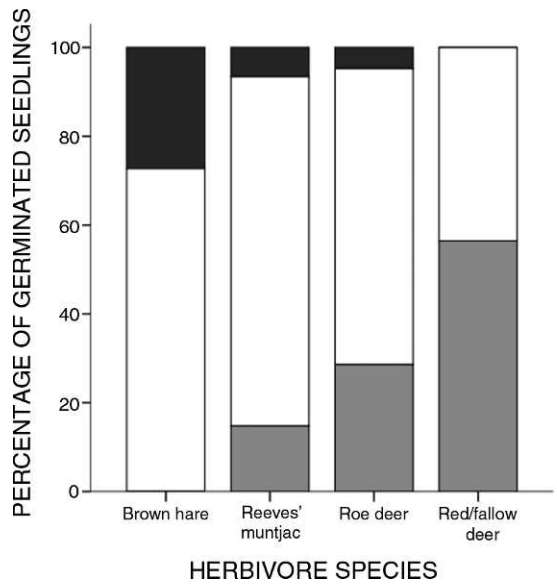


Figure 4. Habitat classifications of plants identified from faecal samples of four herbivore taxa: primarily woodland habitats (black), grassland/open semi-natural habitats (white) and arable and ruderal habitats (grey).

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as also observed in European studies (Heinken et al. 2002, Schmidt et al. 2004, Oheimb et al. 2005). Most of the species and the vast majority of individual seedlings that germinated were associated with open grassland, arable and/or ruderal habitats but may also have originated from open woodland rides. Germinated species were generally ruderal in their established strategy while stress tolerant strategists, including those typical of woodland habitats, were poorly represented. However, these observations suggest that herbivores may have the potential to disperse rare arable species. We were confident in the identification of deer faecal material between roe deer, reeves' muntjac and the two larger deer species (pooled).

The deer species ranged in their feeding strategy from concentrate selectors to intermediate feeders or grazers (Hofmann 1989). Red and fallow deer are primarily bulk feeders and grazers, which frequently feed in open habitats and are highly mobile, travelling 3-4 km/day (Carranza et al. 1991). The dominance of grassland and arable species in the faecal material from these deer species was therefore expected, and is in accordance with observations from Europe (Heinken et al. 2002, Schmidt et al. 2004, Oheimb et al. 2005). However, the absence of any woodland species from faecal material of these herbivores was unexpected given their known diet includes herbaceous vegetation and browse (Corbet & Harris 1991, Putman 1986a); however, we must acknowledge that exclusion from newly coppiced stands may have influenced this result. In contrast, roe deer and reeves' muntjac are more versatile in diet preference (Putman 1986a). Both are frequently regarded as woodland browsers, but better considered mixed strategists or concentrate selectors. They feed on shrub browse and herbaceous material, including developing seed heads, but will also feed in arable fields and open habitats (Putman 1986b, Forde 1989, Corbet & Harris 1991, Cooke 2006). It is unclear whether the absence of ancient woodland species from faecal material of these two deer species was due to them feeding on unripened seed heads or whether seeds of these plants are less able to survive passage through the gut. In contrast to the ungulates, faecal samples from brown hare contained the greatest content of woodland species. This is often regarded as a species of open arable or grassland landscapes, but woodland is important for shelter (Corbet & Harris 1991), and brown hare may achieve high densities in heterogeneous forest landscapes that include areas of young growth (P. Dolman, pers. obs.).

Seed size is important in explaining which species are dispersed by endozoochory (Bruun & Poschlod 2006). However, seed mass of species dispersed did not differ significantly among herbivore taxa. Dispersed seeds were generally small, as typical of plants of open habitats (Hodkinson et al. 1998), but some larger-seeded species were also dispersed, particularly of cultivated plants. Therefore, although ancient woodland plants frequently have relatively heavy seeds (Brunet et al. 2000) this is unlikely to have precluded their dispersal by endozoochory.

Germination rates were generally low in comparison to other studies of deer and brown hare (e.g. Schmidt et al. 2004, Oheimb et al. 2005, Eycott et al. 2007). Depth of soil may have inhibited germination of some species. In the field, colonisation success of endozoochorically dispersed plants may be low compared to controlled germination experiments (Pakeman & Small 2009).

The dominance of open habitat species in the faecal material, particularly the high representation of arable and ruderal species, is understandable as the surrounding landscape composition was dominated by arable land and horticulture (see Table 1). Though a 1-km buffer is a small area compared to daily movements of red deer (3-4 km/day; Carranza et al. 1991), it is far greater than the typical home range of reeves' muntjac (Chapman et al. 1993). Small fragment sizes in our study, likely gave deer ready access to external habitats. Even the more territorial and sedentary species (reeves' muntjac and roe deer) may forage beyond the woodland boundary while the larger species (red and fallow deer) are highly mobile across the wider landscape and preferentially feed on farmland.

These results suggest implications for the long-term composition and character of the woodland ground flora. The importation of ruderal seedlings into the ancient woodland may alter community composition. Heliophytes either dispersed by endozoochory, epizoochory or wind dispersal will not persist as canopy closure occurs, unlike shade-tolerant perennial woodland specialists. However, they may compete with specialist woodland plants in the open-canopy phases following coppicing, an important stage for the proliferation and regeneration of woodland specialists (Ash & Barkham 1976, Brunet et al. 1996). At high deer densities, trampling and poaching reduce ground cover and increase bare ground (Kuiters et al. 1996, McEvoy et al. 2006), offering further opportunities for ruderal establishment. Both white clover *Trifolium repens* and broad-leaved dock *Rumex obtusifolius*, as well as all of the

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grass species recorded in our study, were recorded from woodlands grazed by livestock in Northern Ireland, and were regarded as indicators of intensive woodland grazing (McEvoy et al. 2006). In Bradfield Woods, an ancient woodland site in eastern England, ground flora of young coppice exposed to grazing by deer had higher plant species diversity than coppice protected from deer by wire fencing, but included a large proportion of ruderal plants (Stone et al. 2004). Furthermore, herbivore dispersal is also suspected as a factor contributing to the increase of ruderal species recorded at ancient woodland edges (Willi et al. 2004). High densities of Kerama deer *Cervus nippon keramae* in Japan contributed to the expansion of cultivated, non-woodland and grassland species into open habitats within woodland (Yamashiro & Yamashiro 2006). Herbivore-mediated seed dispersal may therefore exacerbate impacts of woodland fragmentation, further reducing the distinctiveness of woodland plant communities relative to that of surrounding habitats. However, effects are dependent upon the study system and grazing has been observed to aid dispersal of ground flora in Mediterranean open woodland (Malo & Suárez 1995) and native subalpine grassland species (Iravani et al. 2011), and may aid the dispersal of rare ruderal plant species (Boulanger et al. 2010).

Highly infrequent and rare dispersal events can be important to plant dispersal and establishment, but such events are difficult to capture in a faecal germination study (Boulanger et al. 2010). Furthermore, our study was limited by the exclusion of the two largest deer species from newly coppiced stands in the woodland in which they were most abundant. Although it is not expected that these bulk feeding grazers of farmland habitats will offer important dispersal benefits to woodland species, further investigation is recommended.

Conclusion

Mammalian herbivores, including four deer species, did not appear to provide any significant seed dispersal service to ancient woodland plant species. These findings are even more pronounced than previous European endozoochoric and epizoochoric studies (Heinken et al. 2002, Schmidt et al. 2004, Oheimb et al. 2005), most likely due to the smaller size and highly fragmented nature of forest patches studied. Woodland managers wishing to conserve characteristic woodland understory plant assemblages and vegetation, including specialist and relictual species, frequently control and/or exclude deer (Dolman et al. 2010). The consequences of such deer management appear very unlikely to include the loss of dispersal opportunities for specialist woodland plants. Our evidence suggests that failure to manage deer in such ways may result in changes to ground flora composition of open stages through the importation of ruderal seed from the wider landscape in which ancient woodland fragments are set. These are in addition to the more widely recognised direct herbivory impacts on understory vegetation. Accepting the influence of low to moderate levels of deer activity may alter woodland structure and composition, but whether this is regarded as damaging or enhancement depends on the reference point used.

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Appendix I. Attributes of plant species identified from faecal material of different herbivore taxa

The habitat classifications for each plant species recorded in our study: G = grassland or open semi-natural habitats, W = species dependent primarily on woodland habitats, R = species common in arable and/or other ruderal and disturbed habitats. The number of seedlings germinated in samples from each herbivore taxa is also listed. Established strategy and agency of dispersal categories were taken directly from Grime et al. (2007) and defined as follows: Established strategy: C = competitor, R = ruderal, S = stress tolerator, CR = competitive ruderal, SR = stress tolerant ruderal, SC = stress tolerant competitor, CSR = CSR strategist.

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Agency of dispersal: U = unspecialised, Am = dispersal through secretion of mucilage, Aa = dispersal with awn, or spiny calyx teeth, Ai = an ingested berry, Uag = unspecialised but dispersed widely as a result of agricultural practices, Ww = wind, seeds winged or strongly flattened, Wc = wind, seeds small and shed from capsule, held above surrounding vegetation, Wp = wind, dispersule plumed or wrapped in woolly hairs. Seed mass (mg) is taken from the LEDA Traitbase (Kleyer et al. 2008), except for wild strawberry, for which values were taken from Fitter & Peat (1994; available at: http://www.ecoflora.co.uk).

Plant species	Habitat	Established strategy	Agency of dispersal	Seed mass (mg)	Brown hare	Reeves' muntjac	Roe deer	Red/Fallow deer
Agrostis capillaris	G	CSR	U	0.064	0	16	13	57
Agrostis stolonifera	G	CR	U	0.048	0	3	1	6
Brassica napus	R	-	A	4.392	0	0	0	38
Capsella bursa-pastoris	R	R	Ww	0.099	0	0	0	23
Centaurium erythraea	G	SR	Wc	0.013	0	1	0	0
Chenopodium album	R	CR	U	0.647	0	1	3	9
Chenopodium rubrum	R	CR	U	0.126	0	4	2	4
Deschampsia cespitosa	W	CSR/SC	Aa	0.211	2	0	2	0
Epilobium ciliatum	R	R/CSR	Wp	0.074	0	0	2	3
Epilobium hirsutum	R	C	Wp	0.128	0	0	0	33
Epilobium obscurum	R	R/CSR	Wp	0.068	0	0	0	3
Epilobium tetragonum	R	R/CSR	Wp	0.095	0	1	0	19
Erodium cicutarium	G	R/CSR	Aa	1.41	2	1	0	1
Fragaria vesca	W	S/CSR	Ai	0.31	0	4	0	0
Galium mollugo	G	C/CSR	U	0.732	0	0	0	1
Geranium molle	G	R/CSR	Aa	1.086	0	12	5	15
Holcus lanatus	G	CSR	U	0.407	0	2	1	3
Juncus bufonius	R	R/SR	Am	0.025	0	1	2	13
Juncus effusus	G	C/SC	Am	0.019	1	6	2	2
Lolium perenne	G	CR/CSR	Uag	1.975	0	1	1	3
Lotus corniculatus	G	S/CSR	U	1.403	0	0	0	2
Medicago lupulina	G	R/CSR	U	1.78	0	1	0	0
Persicaria maculosa	R	R/CR	Uag	2.12	0	0	0	3
Phleum pratense	G	CR/CSR	Aa	0.588	0	0	0	1
Plantago major	G	R/CSR	Am	0.268	0	0	0	54
Poa annua	G	R	Uag	0.224	0	2	2	4
Poa pratensis	G	CSR	Uag	0.273	0	0	0	10
Rumex acetosella	G	CSR	U	0.36	0	0	0	1
Rumex obtusifolius	G	C/CSR	Aa	1.155	0	1	1	2
Senecio vulgaris	R	R	Wp	0.269	0	0	1	1
Sonchus asper	R	R/CR	Wp	0.28	0	1	0	25
Stellaria media	G	R	Uag	0.385	0	0	0	5
Trifolium repens	G	CSR/CR	Aa	0.59	0	0	1	0
Tripleurospermum inodorum	R	R	Uag	0.29	0	0	0	2
Triticum spp.	R	-	A	43.75	0	1	2	42
Urtica dioica	G	C	Aa	0.18	4	0	0	1
Veronica arvensis	R	SR	U	0.119	0	0	0	1
Veronica catenata	G	R/CR	Wc	0.032	0	0	0	1
Veronica montana	W	SR/CSR	U	0.407	1	0	0	0
Veronica officinalis	G	SR/CSR	U	0.123	0	2	0	0
Vicia sativa	G	R/CR	U	31.047	1	0	1	0
Total number of seedlings					11	61	42	388

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