Can seed dispersal by human activity play a useful role for the conservation of European grasslands?

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Article first published online: 4 MAR 2011

DOI: 10.1111/j.1654-109X.2011.01124.x

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Issue

Applied Vegetation Science

[Volume 14, Issue 3](#), pages 291–303, August 2011

Submitted version – pre-referreed.

Applied Vegetation Science

Human mediated seed dispersal for conservation in the European rural landscape

Journal:	<i>Applied Vegetation Science</i>
Manuscript ID:	AVS-A-00351
Manuscript Category:	Ordinary article
Date Submitted by the Author:	04-Aug-2010
Complete List of Authors:	Auffret, Alistair; Stockholm University, Department of Physical Geography and Quaternary Geology
Keywords:	Anthropocory, Conservation, Grassland, Long-distance dispersal, Restoration, Zoochory

Review – Human mediated seed dispersal for conservation in the European rural landscape

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Abstract

Objective: To summarise the recent research into human-mediated dispersal (HMD) in the European rural landscape.

Methods: A thorough literature search was undertaken to explore the potential for HMD vectors, both standard and non-standard, how they have changed through time, and their implications for conservation.

Results: Grazing animals provide an important source of propagules, but other, non-standard means of dispersal such as via clothing and motor vehicles can also transport seeds of many species. Dispersal is an important consideration for the conservation and restoration of species rich grasslands, and a lot can be gained by drawing inspiration from the past agricultural practices.

Recommendations: There should be a greater movement of grazing animals throughout the landscape, and the spreading of hay or dung from species-rich communities to target sites should be considered. There should be further investigation of the potential dispersal via human activities, and future research should be conducted at the landscape scale.

Keywords: Anthropocory, Conservation, Grassland, Long-distance dispersal, Restoration, Zoochory

38 **1. Introduction**

39 Throughout history, and at an accelerating rate recently, humans have influenced the dispersal of plant species
40 through their actions (Hodkinson et al. 1997). Human-mediated dispersal (HMD) has been recently defined as
41 dispersal directly by humans, as well as that by human associated vectors, such as transport and livestock
42 (Wichmann et al. 2009). Twelve years ago, Poschlod and Bonn (1998) described the changing dispersal
43 processes in the European rural landscape, and much of the empirical knowledge into how past and present land
44 practices aid or hinder the transport of species in the landscape has been gained since then.

46 European semi-natural grasslands are inherently influenced by man, maintained through the long term grazing
47 and mowing of areas within various agricultural systems, which started from around the Neolithic period (see
48 Poschlod et al. 2002). This continuous management over millennia has led to these habitats today being among
49 the most species rich in Europe, with over 40 plant species found per square metre in Swedish grasslands
50 (Eriksson et al. 1997, Eriksson et al. 2006), 63 in an Estonian wooded meadow (Kull et al. 1991), and 67 in a
51 Czech meadow (Klimeš et al. 2001). Cessation of management (abandonment), or conversion to arable land
52 during the past two centuries has been widespread across Europe, resulting in severely reduced area and
53 increased fragmentation (Adriaens et al. 2006, Bender et al. 2005a, Cousins et al. 2002, Fuller 1987, Johansson
54 et al. 2008, Luoto et al. 2003, Pärtel et al. 1999). In addition to the reduction in habitat area, large scale
55 fragmentation is often associated with biological impoverishment of remaining fragments (Harrison et al. 1999),
56 and the increasing amount of matrix in the agricultural landscape has created a barrier for the dispersal of
57 grassland plant species, which is essential for the maintenance of viable metapopulations (Hanski 1999).

59 Site history is embedded in the structure and function of all ecosystems (Foster et al. 2003), and exercises using
60 historical sources reveal that community composition in remaining and abandoned semi-natural habitats often

appears to be related to historical landscape configuration (but see Adriaens et al. 2006, Chýlová et al. 2008, Dahlström et al. 2006, Gustavsson et al. 2007, Helm et al. 2006, Lindborg et al. 2004, Maurer et al. 2003, Pärtel et al. 2007). This means that so-called ‘extinction debts’ (Tilman et al. 1994), where there exists a time delay between habitat destruction and species disappearance are fairly common in semi-natural landscapes. As well as the persistence of species in remaining grasslands, remnant populations can also be found in surrounding habitats such mid-field islets, road verges, field boundaries and abandoned farmland (Cousins 2006, Cousins et al. 2001, Cousins et al. 2008, Dahlström et al. published online, Hovd et al. 2005, Simmering et al. 2006, Smart et al. 2002).

The existence of extinction debts and remnant populations is promising with regards to restoration potential, but seed-sowing experiments regularly find that grassland plant species dispersal or seed limited (Ehrlén et al. 2006, Franzén et al. 2003, Gross et al. 2005, Münzbergová 2004, Primack et al. 1992, Stein et al. 2008). The degree of dispersal limitation increases with isolation of the focal site (Ozinga et al. 2005), and therefore plant species may require long-distance dispersal (LDD) (Nathan 2006). LDD is thought to be most prevalent in open terrestrial landscapes, mediated by large animals (Nathan et al. 2008), as well as by non-standard dispersal vectors such as via human activity (Higgins et al. 2003). The potential therefore exists for successful dispersal of grassland plants in the fragmented agricultural landscape, largely by human associated vectors.

Research into dispersal mechanisms in grassland communities is therefore important, and here I will review HMD vectors in semi-natural landscapes throughout history, and discuss their implications for conservation. In Table 1 I have summarised the findings of the 22 research articles found via searching the ISI Web of Science®, plus studies referenced within, of seeds dispersed via human-mediated vectors under natural conditions (i.e. samples taken from vector without any seed addition) in Europe.

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2. HMD vectors in the rural landscape

2.1. Grazing animals

2.1.1.

Before the widespread introduction of agriculture, a woodland-grassland mosaic was maintained through the presence of large wild herbivores (Vera 2000). Species such as fallow deer (*Dama dama*), European bison (*Bison bonasus*), Red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*) have been found to be effective seed dispersers, both epi (outside)- and endozoochorously (inside the animal) (Jaroszewicz et al. 2009, Kiviniemi 1996, Schmidt et al. 2004, von Oheimb et al. 2005).

2.1.2. Epizoochory

In semi-natural grasslands, grazing livestock have taken over this role, and seeds adapted to epizoochorous dispersal can be very effective at travelling in the fur of grazing animals. Fischer et al. (1996) found that 100% of species with hooked diaspores, 86% of bristly and 85% of coarse surfaced diaspores present in the study area were found in the fur an experimental sheep. Even 52% of species with smooth seeds were represented in the fleece. In a Dutch experiment, ‘dummy’ sheep and cattle were found to carry the seeds of 13 out of 15 fruiting species in an experimental area of a nature reserve (Mouissie et al. 2005a). The potential for so-called non-adapted seeds to disperse in this way has been reported elsewhere, with around a quarter of species represented in germinable seeds found in the coats of donkeys, cattle and horses not specialised to any particular dispersal

vector (Couvreur et al. 2004a), and unappendaged seeds were found to have a higher attachment potential (% remaining after 1hr mechanical shake) than both elongated and flat seeds in cattle fur, and flat seeds in sheep fleeces (Römermann et al. 2005). An experiment looking at small-seeded species from Spanish grasslands (de Pablos et al. 2007) showed that unappendaged seeds had an attachment potential of 79.5%. It is thought likely that nearly all plant species have the potential to disperse epizoochorously (Couvreur et al. 2004b).

Attempts to quantify attachment times and distances for epizoochorous seed dispersal reveal the potential for seed transportation. Seeds of 12 species with varying morphologies in a nature reserve in Belgium found that at least 20% of seeds of all species applied remained on the fur of Haflinger horse after 3hr and Galloway cattle after 20 hours in natural conditions (Couvreur et al. 2005b). Studies in Sweden found maximum retention time of 35-195 minutes of 10-20 seeds of grassland species in the fur of domestic cattle, however the lethargic behaviour of the animals (4 metres movement per minute) resulted in projected distances of only a few hundred metres (Kiviniemi 1996, Kiviniemi et al. 1999). In reality however, the number of seeds transported on grazing animals can be very high indeed (see Table 1).

2.1.3. Endozoochory

Endozoochorous seed dispersal by grazers is another effective means of transporting species in semi-natural grasslands, with numerous seeds of many species found in their dung (Table 1). There is great also potential for long distance dispersal by this vector, not least because of the guaranteed transportation time associated with it, with mean retention of germinable seeds of 50-70 hours for cattle, sheep, horses and donkeys (Cosyns et al. 2005b). Larger mammals have a remarkable potential for seed dispersal, with approximately 1200000 seeds per individual per summer calculated for both cattle and horses in a coastal dune landscape in Belgium (Cosyns et al. 2005a), up to 2600000 seeds per year for cattle in the Netherlands (Mouissie et al. 2005b), and an estimated 1510 seeds per square metre per year deposited by grazing cattle in a Mediterranean wooded pasture (Malo et al.

2000). As well as seeds being adapted for endozoochory, ungulates have been found to selectively forage flowers and fruits above leaves (Hulber et al. 2005). Like transportation in fur, germinable seeds in dung also contain species with a range of other dispersal adaptations (Bruun et al. 2006, Couvreur et al. 2005a), and a noteworthy proportion of the total species in grazed areas have been found in dung samples, between 21 and 72% (Bakker et al. 2003, Cosyns et al. 2005a, Cosyns et al. 2005c, Mouissie et al. 2005b).

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2.1.4. Complimentarity

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Not surprisingly, zoochorous seed dispersal is regarded as important for the diversity of the rural landscape, where animals can be described as ‘moving pieces of habitat’ (Fischer et al. 1996). In such fragmented landscapes, the negative impact of isolation can be partly explained by sheep fleece retention, whilst retention on cattle is significantly related to occupancy in grassland specialists (Adriaens et al. 2007). Both dung and fur are important vectors of specialist and red-listed species (Eichberg et al. 2007, Fischer et al. 1996, Wessels et al. 2008), and epi- and endozoochory have been found to complement one another with regards to species dispersed (Couvreur et al. 2005a). The contents of Table 1 also indicate a complimentarity between grazing animals in the grasslands, with the larger mammals transporting a large number of seeds internally, but sheep transporting far more on their coats than other animals. Investigations into both epi- and endozoochory in natural conditions have shown that each study herbivore species transports the diaspores of plant species not transported by any other herbivore study species (Cosyns et al. 2005a, Couvreur et al. 2004a). The act of dispersal can also be complimentary, where cow dung has a large total seed content, it is deposited in concentrated heaps in areas where the animal has been ruminating, whilst sheep drop numerous small dung pellets whilst in motion (Mitlacher et al. 2002). Bruun and Fritzboeger (2002) state that more two-thirds of plant species growing in Danish semi-natural grasslands today can be transported by cattle and sheep combined.

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152 2.1.5. History

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154 Despite this great potential for dispersal in the rural landscape, very little is now realised. In Early Modern
155 Europe, three-field rotation systems between pasture and arable cropping were the norm (Clout 1999). Villages
156 in many countries employed an in-outfield system, where livestock grazed communal land during the summer,
157 and enclosed on arable land post-harvest (Uhlir 1961, Whyte 1999). Fences between arable fields were also rare
158 due to the labour-costs involved (Bruun et al. 2002). These practices would have allowed for free dispersal of
159 plant species at the landscape scale, but by the start of the nineteenth century, the enclosure movement had swept
160 across Europe. Communally regulated systems were gradually eliminated and commonlands were abolished
161 (Clout 1999). The past system involved a lot of mixed grazing, though is now a much less common practice, and
162 livestock often spend the whole season grazing the same small pasture. Together with the destruction and
163 abandonment of grassland habitats in the twentieth century, the changes in livestock management practices over
164 time have taken their toll on grassland plant species. The more light-demanding a species is, there more likely it
165 is to be dispersed epi- or endozoochorously, or both (Ozinga et al. 2004), but these are the dispersal vectors
166 which are being denied since the modernisation of agriculture, and the species which are now most threatened.

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168 Transhumance, the seasonal movement of livestock between pastures was widespread for centuries (Whyte
169 1999), facilitating the movement of seeds between landscapes and even countries. This has also been
170 progressively abandoned as a result of economic development (Manzano et al. 2006). Studies of two of the few
171 remaining transhumance ovine drives, in Germany and in Spain found that experimentally attached seeds were
172 still attached at the end of the experiment, after travelling over 100km and 400km respectively (Fischer et al.
173 1996, Manzano et al. 2006). The reintroduction of transhumance and in-out land systems in Europe is unlikely

174 due to land ownership issues, but zoochorous seed dispersal can still occur over longer distances through the
175 transportation of grazing animals between isolated nature reserves (Couvreur et al. 2004a, Wessels et al. 2008).
176 Dispersal via grazing animals certainly has the potential for LDD, but only if the animals are allowed to move
177 long distances.

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179 2.1.6. Implications for management

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181 Changing practices within existing field systems could also benefit dispersal. As mentioned in section 2.1.4,
182 different herbivores complement each other with regards to seed dispersal methods and seeds transported. The
183 type of disturbances caused by different grazers can also be complimentary. Dung deposits by cows can give an
184 overly strong nutrient stimulus, leading to taller vegetation and light limitation if grazing pressure is not
185 maintained (Bakker et al. 2003). When it comes to pure physical disturbance, cows are preferred to smaller
186 herbivores because their large size leads to more disturbance and therefore gaps in the sward, benefitting
187 colonisation (Pywell et al. 2007). Herbivore diversity can lead to both additive and compensatory effects
188 (Ritchie et al. 1999), whereby different animals can selectively graze the same or different plant species.
189 Loucogarray et al. (2004) found that mixed grazing of cattle and horses in a French dune system yielded a
190 higher species richness than monospecific grazing due to a combination of additive and compensatory effects. A
191 metastudy of management in semi-natural grasslands (Stewart et al. 2008) found that grazing stock was less
192 important than grazing intensity for species richness. Historical records can be used to find out past grazing
193 practices (Bender et al. 2005b, Dahlström 2006), so the possibility exists to recreate conditions which can aid
194 dispersal and diversity. The combination of complementarity in disturbances, seeds dispersed and grazing
195 behaviour between different grazers suggests that an increase in grazer diversity in semi-natural landscapes, at an
196 appropriate density, would be of benefit for conservation.

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199 2.2. *Traditional haymaking*

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201 In order to feed livestock through the winter, it is necessary to provide hay. From Dahlström (2006), one can
202 calculate that four parishes in south-central Sweden in the 17th Century tended 1.17-1.9 ha traditional meadow
203 per head of cattle or equivalent, illuminating the vast extent of managed meadows required before agricultural
204 intensification.

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206 Haycutting is well known to result in high species richness (Hansson et al. 2000, Kull et al. 1991, Mitlacher et al.
207 2002), which is usually attributed to an increased light availability following cutting, which positively affects
208 grassland specialists. Dispersal is benefitted quite simply because more seeds are available for dispersal, as in
209 contrast to in pastoral fields, meadow plants are allowed to complete their reproductive cycle undisturbed, with
210 95% of plants having matured at the traditional hay-cut date in mid-August, increasing to 100% if management
211 was left as late as mid-September (Dahlström et al. 2008). Williams (1984) states that when the widespread and
212 abundant *Juncus* are excluded, haycutting in October instead of September doubles the seed set. The act of
213 haycutting itself can positively affect dispersal of anemochorous (wind-dispersed) seeds, with *Rhinanthus minor*
214 dispersal found to benefit from this management technique (Coulson et al. 2001).

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216 The potential number of seeds contained in hay is substantial, with an estimated 436 300 seeds contained within
217 one 21kg hay bale from a traditionally managed meadow in England (Smith et al. 1996). Edwards and Younger
218 (2006) found germinable seed densities to be an order of magnitude lower, however over 50% of species present

219 in the meadow were represented, despite the early hay cut date in early July. Traditional haymaking is another
220 practice which has declined during modern times, whereas previously hayseed was collected from the barns
221 where the hay was stored and distributed on meadows, the import of commercial grassland seed and even
222 roughage (Bruun et al. 2002, Poschlod et al. 1998) has reduced the dispersal potential of haymaking. The
223 mechanisation of haymaking has also meant that the process takes less time, and therefore finishes earlier now
224 than earlier in the twentieth century, also affecting seed set. Summing the maximum area of meadow in
225 Dahlström's (2006) four parishes between 1620 and 1850 gives a total of 9332 ha, more than the 8300 ha of
226 remaining meadowland in the whole of Sweden in 2008 (Jordbruksverket 2009).

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229 2.3. *Motor vehicles*

230 2.3.1. Private vehicles

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232 Whereas movement of grazing animals within and between landscapes has reduced through time, the invention
233 of motor vehicles and agricultural machinery has introduced a new potential for seed dispersal in the rural
234 landscape (see Table 1). Despite their apparent simplicity, studies looking at mud carried by cars since Clifford's
235 (1959) work in Nigeria are few and far between. This mode does appear to be fairly effective at dispersing
236 species through the landscape, though it is often referred to in relation to the transport of alien species (Lonsdale
237 et al. 1994, Wace 1977). An experiment in three road tunnels in the Berlin area showed that of 204 species
238 found, exactly half were non-native to the region, including 39 listed as problematic aliens worldwide, and five
239 of particular concern in Germany (Von der Lippe et al. 2007). Despite their non-nativeness, over 70% of the
240 total plant species and 98.5% of the seeds collected were part of the regional roadside flora, of which many of

these species were found within 100m of the tunnel entrances. Not surprisingly, all published motor vehicle dispersal studies also state that most species transported are typical of local roadsides and ruderal land, though correlations between species abundance in samples and roadsides are rarely found (Clifford 1959, Hodgkinson et al. 1997, Schmidt 1989, Wace 1977, Zwaenepoel et al. 2006). This is probably due to the negative relationship between precipitation before sampling and seeds found (Zwaenepoel et al. 2006). From the tunnel experiment in Berlin (Von der Lippe et al. 2007), it can be assumed that seeds of most roadside species will be picked up by vehicles at some point during the year, and therefore that samples taken from vehicles driving mainly around the rural landscape should have a higher fraction of plants from rural habitats, and fewer aliens. Obviously no plant species has evolved to disperse via motor vehicles, but Zwaenepoel et al. (2006) found a significantly higher proportion of seeds with persistent seed banks were dispersed by this agent, indicating that this method can aid dispersal of species through space which are traditionally dispersed through time. The insides of cars are also thought to contain a large number of seeds (Wace 1977), which could then become attached to the occupants for later dispersal in the landscape.

2.3.2. Agricultural machinery

Mowing machinery operating in species-rich meadows has also been found to be an effective dispersal agent, where small subsamples of material collected post-mowing contained 27 of 52 species found in the meadow system (Strykstra et al. 1997). Cultivation machinery has also been shown to transport seeds between arable fields (Mayer 2000), though this would be of limited use in semi-natural grasslands. However, tractors were found to transport seeds the furthest due to the limited contact with the earth, and these vehicles are used in meadows and on pastures, where the physical disturbance can promote the generation of new seedlings, an effect documented on grassland with other heavy vehicles (Hirst et al. 2003).

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265 2.3.3. Implications for management

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267 As mentioned earlier, regularly managed road verges can act as remnant habitats for grassland specialists. They
268 have also been shown to allow colonisation of such species (Kiviniemi et al. 1999), especially with regular
269 mowing (Milberg et al. 1994). It has been argued that grassland plants use road and railway verges for dispersal
270 (Tikka et al. 2001), however a modelling exercise has calculated that the rates of migration along these habitats
271 are only in the order of a few metres per year, even in the widest corridors (vanDorp et al. 1997). The latter study
272 however only considered wind dispersal, and therefore predicted rates could be somewhat increased if vehicles
273 were included, though better data are needed. Road and railway verges should have the same mowing regimes
274 as ancient meadows. This would maintain species richness and allow plants to reach the reproductive stage
275 (Jantunen et al. 2007), in turn allowing the effectiveness of motor vehicles to disperse grassland species to aid in
276 grassland connectivity.

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278 2.4. *Humans*

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280 Humans themselves can also be effective dispersers of seeds through the landscape. A recent study from
281 Australia (Mount et al. 2009) has shown the capacity for clothing to disperse seeds, both native and alien, where
282 207 clothing samples yielded almost 25000 seeds of 70 taxa. The paper also contains a useful summary of the
283 few published clothing dispersal studies, which is dominated by work from the Southern Hemisphere focussing
284 on aliens (Healy 1943, Whinam et al. 2005). There is a clear absence of recent work from Europe quantifying the
285 number of seeds and species dispersed with humans, which is limited to Clifford's (1956) investigation of his

shoes and those of his colleagues, which were found to contain seeds of 44 species representing a range of dispersal adaptations, and Woodruffe-Peacock (1918), who identified mud from boots, as well as clothing and hair as the sources of seeds for a number of species colonising a newly created fox covert. There have been few attempts to quantify dispersal distances of seeds attached to humans, but seeds of three species in Costa Rica were calculated to have mean dispersal distances of 4.6-2420m on cotton trousers and shirts, depending on habitat (Bullock et al. 1977), and two species of *Brassica* were regularly found to remain attached to the mud on boots after 5km walking, which was almost fifty times further than the maximum value calculated for wind dispersal, which is their primary vector (Wichmann et al. 2009).

Mechanisation of agriculture has meant there are fewer humans working in the landscape, but the potential for dispersal by recreational walkers (and ecologists) remains. Many people walking through the modern landscape are accompanied by dogs, and these can also be effective dispersers of seeds (Graae 2002, Heinken 2000). Seeds transported on humans and their pets will also travel in cars and other modes of transport, increasing dispersal distances further. Recreational horse-riding combines the effectiveness of equine endozoochory with man's freedom to move throughout the landscape, although like motor vehicles, this has also been linked to the spread of alien species (Törn et al. 2010, Wells et al. 2007).

It would be difficult to incorporate seed dispersal directly by humans into any conservation plans, however 'Freedom to Roam' public access rights such as those enjoyed in the Nordic countries would be expected to benefit dispersal by this route, as well as a general promotion of recreation in semi-natural grasslands. Löfgren and Jerling (2002) found that islands in the Stockholm archipelago with a longer history of recreation exhibited a higher rate of immigration than those where recreation began more recently.

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3. The role of HMD in the restoration of abandoned or converted grassland

3.1.HMD and Restoration

The successful restoration of former grasslands has a positive impact on local biodiversity, and should also reduce the isolation of remaining ancient grassland fragments. A lot of research has been carried out on this subject, although a recent and comprehensive review is lacking (but see Walker et al. 2004 for a UK specific review of restoration from former arable fields). A common conclusion is that restoration of species rich grassland communities is seed limited. Seeds of grassland species are often transient, and therefore restoration of abandoned semi-natural grasslands in Europe cannot rely upon regeneration via the seed bank (Bakker et al. 1996, Bossuyt et al. 2008, Buisson et al. 2006, Edwards et al. 1999, Kalamees et al. 1998, Mitlacher et al. 2002, Wagner et al. 2003). Seed banks in grasslands on former arable fields are especially depleted (Bekker et al. 1997, Graham et al. 1988, Hutchings et al. 1996), and therefore propagule additions are required to aid colonisation of desirable species (Kardol et al. 2008, Lepš et al. 2007, Lindborg 2006, Öster et al. 2009, Pykälä 2003, Pywell et al. 2002, but see Ruprecht 2006, Smith et al. 2002, Stampfli et al. 1999).

Thus it is important that any restoration management focuses on dispersal, and just as with the remaining semi-natural grasslands, management inspired by traditional agricultural methods can be very effective, especially the use of mixed grazing, and the movement of livestock between pastures. If it is impossible or unfeasible to move the animals and the seeds they carry, then the high quantities of seeds in dung would suggest that the redistribution of manure to target areas might help species dispersal between grazing areas. However, seedling establishment in the field after endozoochory is often found to be lower than that measured in the greenhouse (Malo et al. 1995, Mouissie et al. 2005b, Pakeman et al. 2009). Kohler et al. (2006, 2004) similarly found a relatively negligible impact of dunging on colonisation compared to other disturbances such as mowing and

physical disturbance. A study based on rabbits, however, found that dung contributes to seed bank build-up (Pakeman et al. 1999), and even seeds with transient banks have been found in the soil below decomposed dung patches (Dai 2000). It may therefore be that the positive effects of manuring take time to manifest. The storage of dung has a negative impact on germinability (Edwards et al. 2006, Mayer 2000), and samples deposited can only be as species rich as what was eaten (Edwards et al. 2006), so in order for such a measure to work best, manure samples would have to be collected during summer grazing in species-rich pastures and redistributed directly to target areas. In a similar vein, the spreading of hay from species rich meadows (Donath et al. 2007, Edwards et al. 2007, Kiehl et al. 2006) and even the transplantation of turf from nearby grasslands (Pärtel et al. 1998) have been found to aid with the reestablishment of species rich target communities in former species-rich grasslands.

3.2 Economics

Restoration management can also form an economic benefit. Sowing species rich seed mixtures on former arable fields gave significantly higher hay yields than did the standard seed mixture recommended for agri-environment schemes, whilst also creating a vegetation layer resembling the species-rich target community (Bullock et al. 2001, Bullock et al. 2007). The perceived incompatibility of agricultural and environmental goals has recently been disputed. Kumm (2004) suggests how recreating large continuous pastoral mosaics can be of economic benefit, but (as Kumm also points out) it could equally be useful for conservation. Propagules could be dispersed by livestock over much larger areas than in modern, small-field systems, and areas formerly under arable land use or abandoned would benefit from the increased local species pool to aid in their restoration. Even if individual farmers could open up their pastures to connect those of different histories, the dispersal of grassland specialists in the landscape would be benefitted, although there would be a danger of dispersing more non-target species from nutrient rich to nutrient poor areas within these new pastures (Mouissie et al. 2005b), which in turn

356 could have implications for agro-environment subsidies and organic certification. If there are no direct financial
357 incentives for restoration management which aids dispersal, increasing subsidies is an option (Zechmeister et al.
358 2003), as is the alignment of conservation with other benefits to society such as flood protection, tourism and
359 health (Sutherland 2004). An increase in tourism would bring more people with more dogs and horses and
360 therefore more seeds, but this could also mean more aliens.

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362 Whichever methods are employed, restoration to target community takes a considerable amount of time, with
363 estimations in the order of decades, depending on initial conditions (Gibson et al. 1992, Klimeš et al. 2000,
364 Mitlacher et al. 2002, Smith et al. 2000). This more intensive management and directed dispersal must therefore
365 continue for some time to ensure the dispersal of target species to the site, and progress should be regularly
366 monitored to assess the success of the restoration work and adapt it to suit local conditions.

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369 **4. Dispersal and Conservation on the landscape scale**

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371 Throughout this review, the importance of considering the landscape has been implicit, from the importance of
372 historical landscape configuration and the value of remnant habitats and linear corridors, to the potential for
373 long-distance dispersal in semi-natural grasslands, and the movement of hay, manure and livestock between
374 grassland habitats across the landscape which can aid it. All the human mediated dispersal vectors discussed
375 show the potential for LDD, and understanding the geographical context of dispersal is vital if we are to
376 facilitate it for conservational goals.

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378 Experiments into grassland restoration from arable land in Britain are generally characterised by small blocks of
379 land within one field (e.g. Pywell et al. 2007, Smith et al. 2002), concentrating on the effects of different
380 management types at the expense of considering the landscape. The importance of considering the landscape is
381 highlighted by a rare example of spontaneous restoration of former arable fields, where it was the presence of
382 source habitats in the surrounding landscape which was most important for the successful recolonisation of
383 grassland specialists (Ruprecht 2006).

384

385 There is also little doubt that the facilitation of dispersal by the village scale grazing regimes and national and
386 international livestock drives contributed to the high species richness of these grasslands across Europe after the
387 elimination of native large herbivores. Although such management cannot easily be brought back, the movement
388 of livestock between fragmented pastures shows that modern management can still assist seed dispersal over
389 large distances (Couvreur et al. 2004a), and larger pastures can be of both an environmental and economic
390 benefit (Kumm 2004). Other conservation measures based upon historical landscape scale dispersal, such as hay
391 spreading (Edwards et al. 2007), hay exchange (Mayer 2000), and possibly even fresh manure exchange and
392 spreading could also be beneficial, and should be relatively simple to organise.

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394

395 5. Conclusions and further research

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397 In this review, I have highlighted the enormous potential for human-mediated seed dispersal of grassland plant
398 species in Europe. The studies summarised in Table 1 show that HMD can be an important in terms of both
399 number of seeds and species. It is clear, however, that modern land-use change and agricultural intensification
400 has negatively affected this potential. In order to preserve, conserve and restore high species richness in semi-
401 natural grassland landscapes, it is therefore important to draw inspiration from past land use and its dispersal
402 vectors, but equally important is not to overlook the potential of those that modern life and agriculture has
403 introduced. A great deal of research into human-mediated seed dispersal has been done during the past decade,
404 but there is still more to be done, and in the case of semi-natural grasslands, it is vital that both agricultural
405 history and the landscape scale are considered.

406

407 The research and conservation of European semi-natural grasslands should be considered at the landscape scale.
408 Empirical experiments at the landscape scale are generally lacking (de Blois et al. 2002, Hanski et al. 2003,
409 Harrison et al. 1999), particularly in relation to semi-natural grasslands. Research into endo- and exozoochory in
410 livestock is generally limited to a few research groups, and therefore more experiments should take place in
411 semi-natural landscapes across Europe, looking to quantify both the potential and the realised transportation by
412 these routes. Experiments looking at more modern dispersal agents such as humans and motor vehicles are very
413 rare, though these can be seen as the agents which have the free access to the landscape which animals no longer
414 do. Long distance dispersal events can often be caused by non-standard means (Higgins et al. 2003), and there
415 are several examples of this in this review. Measuring the seed dispersal that actually happens should therefore
416 be a priority, removing the bias of how we think seeds should migrate instead of how they do migrate. The
417 ability for a non-adapted seed to survive digestion is not useful if the seeds are never eaten. Once data have been
418 collected on the many routes of seed dispersal through the semi-natural landscape, robust, landscape scale
419 models can be built. Landscape scale empirical studies require a great deal of time and resources, but they are
420 essential if we are to understand dispersal processes in fragmented semi-natural landscapes

Finally, management practices should reflect what the research has found out, and conservation and restoration should be regularly monitored, modified and reported, in line with evidence-based conservation (Sutherland et al. 2004). Species-rich semi-natural grasslands took centuries to develop, and it is only through continual, long term and appropriate management that they can be conserved and restored for the future.

Acknowledgements

My thanks go to Sara Cousins and Ove Eriksson for their helpful comments on previous versions of the manuscript.

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760

Table 1. Human-mediated seed transport in natural conditions in the European rural landscape. Methods vary widely between studies.

	Reference	Country	Vector	Number of replicates ¹	Total seeds ¹	Number of identified species*
Epizoochory	Couvreur et al. 2004a	Belgium	Cattle	125	3692	63
			Donkey	46	2483	33
			Horse	30	210	20
Endozoochory	Couvreur et al. 2005a	Belgium	Donkey	41	NA	29
	Fischer et al. 1996	Germany	Sheep	16	8511	85
	Wessels et al. 2008	Germany	Sheep	41-63	9420	56
	Bakker and Olff 2003	Netherlands	Cattle	30	6124	35
	Bruun and Poschlod 2006	Germany	Cattle	48	14703	56
	Cosyns et al. 2005a	Belgium	Cattle and Horse	51	59049	117
	Cosyns et al. 2006	Belgium	Cattle	12	18974	50
			Horse	12	10808	49
			Horse	56	53493	106
	Cosyns and Hoffmann 2005	France/Belgium	Horse	56	53493	106
	Couvreur et al. 2005a	Belgium	Donkey	14	NA	53
	Dai, 2000	Sweden	Cattle	30	393	26
	Eichberg et al. 2007	Germany	Sheep	32	2669	28
	Kuiters and Huiskes 2010	Belgium/Netherlands	Sheep	24	11130	72
	Malo and Suarez 1995	Spain	Cattle (Spring)	8	1373	46
		Spain	Cattle (Winter)	8	17	5
	Mitlacher et al. 2002	Sweden	Cattle and Sheep	29	1504	44
	Mouissie et al. 2005b	Netherlands	Cattle	50	1161 (kg ⁻¹)	51
		Netherlands	Cattle	10	4605 (kg ⁻¹)	34
		Netherlands	Cattle	15	1095 (kg ⁻¹)	39
		Netherlands	Horse	10	661(kg ⁻¹)	35
		Netherlands	Sheep	10	527 (kg ⁻¹)	31
		Netherlands	Sheep	12	359 (kg ⁻¹)	21
Motor Vehicles	Pakeman et al. 2002	UK	Sheep	12	359 (kg ⁻¹)	21
	Hodkinson and Thompson 1997	UK	Car	201	367	37
			Tractor ²	1	6	4
			Plough ²	1	1945	35
	Mayer 2000	Germany	Heavy cultivator ²	1	844	28
			Rotary tiller ²	1	320	30
			Rotary harrow ²	1	658	25
			Curry comb ²	1	460	11
			Curry comb ²	1	460	11
	Schmidt 1989	Germany	Car	4	3926	124
	Strykstra et al. 1997		Mowing machinery	7		27
	Zwaenepoel et al. 2006	Belgium	Car	240	690	33
Humans	Clifford 1956	Ireland	Boots	Unknown (22.1g)	65	11
	Wooderuffe-Peacock 1918	UK	Clothes	3		19

¹ As far as can be deduced from the text. This includes both replication and pseudoreplication, i.e. 75 could mean either 75 individuals, or one individual sampled 75 times. Epizoochorous units are animals, endozoochorous are “samples”.

² In this study, machinery was driven through mud of varying soil dry matter, but species lists are not given. Displayed here are the individual runs that yielded the most seeds and species.

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