Seed mobility and connectivity in changing rural landscapes

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Abstract. The success or failure of many organisms to respond to the challenges of habitat destruction and a warming climate lies in the ability of plant species to disperse between isolated habitats or to migrate to new ranges. European semi-natural grasslands represent one of the world’s most species-rich habitats at small scales, but agricultural intensification during the 20th century has meant that many plant species are left only on small fragments of former habitat. It is important that these plants can disperse, both for the maintenance of existing populations, and for the colonisation of target species to restored grasslands.

This thesis investigates the ecological, geographical and historical influences on seed dispersal and connectivity in semi-natural grasslands, and the mobility of plants through time and space. Seed dispersal by human activity has played a large role in the build-up of plant communities in rural landscapes, but patterns have shifted. Livestock are the most traditional, and probably the most capable seed dispersal vector in the landscape, but other dispersal methods may also be effective. Motor vehicles disperse seeds with similar traits to those dispersed by livestock, while 39% of valuable grasslands in southern Sweden are connected by the road network. Humans are found to disperse around one-third of available grassland species, including several protected and red-listed species, indicating that humans may have been valuable seed dispersers in the past when rural populations were larger. Past activities can also affect seed mobility in time through the seed bank, as seeds of grassland plant species are shown to remain in the soil even after the grassland had been abandoned. Today however, low seed rain in intensively grazed semi-natural grasslands indicates that seed production may be a limiting factor in allowing seeds to be dispersed in space through the landscape.

Keywords: Biodiversity, Conservation, Functional connectivity, Historical ecology, Human-mediated dispersal, Invasive species, Landscape Ecology, Long-distance dispersal, Restoration, Seed bank, Seed dispersal, Seed rain, Structural connectivity.
Recommendations for grassland management.

- Grazing pressure must be appropriate for both seed production and colonisation. Over-grazed semi-natural grassland reduces seed availability for dispersal, while a low grazing intensity in former arable fields reduces the likelihood of colonisation by target species. A varied within or between year management timing and intensity might improve seed set within existing grasslands, while still providing enough management intensity to keep the landscape open.

- There should be a greater movement of grazing livestock in the landscape. Movement could be between existing semi-natural grasslands or directed from semi-natural grasslands towards restoration areas. Movement would be most beneficial to the recipient habitat at the time of highest seed availability in the middle to late summer.

- Boundaries between semi-natural grassland and adjoining areas for restoration should be opened up. This is another way to increase livestock movement and the spread of seeds, while larger pastures should result in a more heterogeneous grazing pattern, improving prospects for seed production and colonisation from both the seed bank and seed rain.

- Road verges should be managed in order to improve the habitat quality of these linear habitats which connect many grasslands. The timing and intensity of mowing should allow sufficient seed production for dispersal by motor vehicles.

- When managing rural landscapes, all major seed dispersal vectors should be considered with regard to their movement, abundance and relationship to the physical landscape. Combining the dispersal potential and structural connectivity of a landscape can help identify specific locations for potential management intervention, which can then be considered according to importance, feasibility and resource limitations.

- Finally, policy regarding agri-environment schemes must give land managers the required incentives and flexibility to implement such management strategies, despite the resulting changes in tree cover, grazing pressure and other metrics which are currently used as guidelines for subsidy provision.
Rekommendationer för Naturvård.

- Betestrycket måste tillåta både fröproduktion och eventuell etablering. Ett för högt betestryck i kvarstående naturbetesmarker minskar frömängden och ett för lägt tryck minskar förmågan för frön att etablera sig i restaurerade gräsmarker. En mer heterogen skötsel av gräsmarker i både tid och intensitet skulle kunna öka fröproduktionen i dagens betesmarker samtidigt som det skulle hålla landskapet öppet.

- Betesdjur bör röra sig mer genom landskapet. Ökad rörelse kan vara mellan dagens naturbetesmarker, eller mer riktad från artrika betesmarker till restaurerade områden. Fröspredningen gynnas mest om djuren flyttas under sensommaren.

- Gränser mellan närliggande naturbetesmarker och restaureringsobjekt kan öppnas. Det här är ett annat sätt att öka rörelsen av betesdjur och frön. Större betesmarker skulle göra betestrycket mer heterogent, och fröproduktion och etableringsmöjligheter kunde därmed öka.

- Vägkanter bör skötas för att förbättra kvalitetet på dessa habitat som redan ansluter till många gräsmarker. Slättertid och intensitet bör anpassas för att främja fröproduktion och för att öka möjligheter för spridning med motorfordon.

- Vid naturvårdande skötsel av ett område bör samtliga fröspredningssätt övervägas. Deras möjligheter att bidra till ökad artrikedom varierar med landskapets struktur. På så vis kan konkreta platser för naturvårdsåtgärder identifieras och prioriteras utifrån viktighet, genomförbarhet och tillgängliga resurser.

- Till sist måste jordbrukspolitiken bli mer flexibel och ge markägare och naturvårdshandläggare incitament att implementera dessa strategier, trots att de kan gå emot de parametrar som avgör jordbruksstödet idag.
Seed mobility and connectivity in changing rural landscapes

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List of papers *

This doctoral dissertation consists of this summary and the following papers, which are referred to by their Roman numerals in the text.


* Author contributions.

I Review written by AGA.

II Conceived and designed: AGA, SAOC. Performed experiment and analysed data: AGA. Wrote the paper: AGA, SAOC.

III Conceived and designed: AGA. Performed experiment and analysed data: AGA. Wrote the paper: AGA, SAOC.

IV Conceived and designed: AGA, SAOC. Performed experiment and analysed data: AGA. Wrote the paper: AGA, SAOC.

V Conceived and designed: AGA, JB, SAOC. Wrote the paper: AGA, JB, SAOC.
Introduction

Humans and the landscape

Across the world, humans and their activities interact with the landscape and the organisms which inhabit it. Unfortunately, the effects of human activity today are largely negative, and many now believe that we are in the midst of a human-induced sixth mass extinction of the world’s organisms (Barnosky et al., 2011). Habitat destruction by land-use change, and a climate which is warming due to human activity form the most serious threats to biodiversity worldwide (Sala, 2000; Baillie et al., 2004). Species the world over are forced to survive on isolated and ever-smaller patches of habitat (Fahrig, 2003), while their climatic range moves rapidly through space (Thomas et al., 2004). If the world’s organisms are to successfully respond to the challenges posed by global change, they must be able to move, or disperse. Dispersal is important both for maintaining populations at the local or regional scale (Hanski, 1999) and for tracking their climatic range to higher latitudes or altitudes (Thomas et al., 2004), while also being responsible for the build up of biodiversity in the first place (Eriksson et al., 2006; Vandvik and Goldberg, 2006). On the other hand, the ability to disperse is at the core of another currently much debated problem, the invasion of alien species into new regions (Baillie et al., 2004; Wilson et al., 2009), the increase of which is also linked to the increase of human activity and movement through time (Hulme, 2009).

It is clearly important to understand the process of dispersal, and how it relates to human activity and the physical environment in which it takes place. The response of plant species to global change has implications for other organisms (Berg et al., 2010), including the limitation of dispersal by insects depending on specific host plants (Menéndez et al., 2007; Müller et al., 2011). To move between increasingly isolated habitat patches, or to new areas or regions, plant species must disperse further than might be expected. The long-distance dispersal of plant species (Nathan, 2006) is therefore an important process for understanding the ecological responses to human-induced environmental change worldwide (Trakhtenbrot et al., 2005). In Europe, landscapes have been changing through human activity since the advent of agriculture around 8000 years ago (Renfrew, 2000), but the severity of recent habitat destruction is threatening the plant communities that humans have helped to shape.

Semi-natural grasslands

European semi-natural grasslands (Box 1) are among the most species-rich habitats worldwide at small spatial scales (Wilson et al., 2012). Formed and maintained by hay-cutting and livestock grazing over several hundreds to thousands of years, pastures and meadows are now an important habitat for a range of plant species (Poschlod and WallisDeVries, 2002; Eriksson, 2013). Today, more than 60 individual plant species can be found in one square metre of species-rich grassland (Poschlod and WallisDeVries, 2002; Eriksson, 2013). To move between increasing increasingly isolated habitat patches, or to new areas or regions, plant species must disperse further than might be expected. The long-distance dispersal of plant species (Nathan, 2006) is therefore an important process for understanding the ecological responses to human-induced environmental change worldwide (Trakhtenbrot et al., 2005). In Europe, landscapes have been changing through human activity since the advent of agriculture around 8000 years ago (Renfrew, 2000), but the severity of recent habitat destruction is threatening the plant communities that humans have helped to shape.
expected to support a higher number of species, and vice versa (the species-area relationship: Arrhenius, 1921; Drakare et al., 2006). Habitat fragmentation also involves an increase in the relative amounts of habitat edges in a landscape, which can affect plant communities in various ways (Ries et al., 2004). Further to the risks of the fragmentation of these grasslands, indirect effects of agricultural change such as nitrogen deposition are also causing long-term damage to grassland communities (Stevens et al., 2011; Isbell et al., 2013).

Despite these challenges, the observed negative effects of habitat destruction on biodiversity have been smaller – or at least slower – than expected, and many rural landscapes still support the kind biodiversity expected before habitat destruction and fragmentation. By comparing historical and present-day maps, it has been found that a landscape’s current
Table 1. Approximate mean and maximum distances seeds can be dispersed by various vectors.

<table>
<thead>
<tr>
<th>Dispersal vector</th>
<th>Known as</th>
<th>Approximate mean distances</th>
<th>Approximate max distances</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wind</td>
<td>Anemochory</td>
<td>9 m</td>
<td>500 m</td>
<td>Thomson et al. (2011)</td>
</tr>
<tr>
<td>Ballistic</td>
<td></td>
<td>1.4 m</td>
<td>60 m</td>
<td>Thomson et al. (2011)</td>
</tr>
<tr>
<td>Water</td>
<td>Hydrochory</td>
<td>538 m</td>
<td>4050 m</td>
<td>Thomson et al. (2011)</td>
</tr>
<tr>
<td>Ant</td>
<td>Myrmecochoxy</td>
<td>3.61 m</td>
<td>180 m</td>
<td>Thomson et al. (2011)</td>
</tr>
<tr>
<td>Vertebrates</td>
<td>Zoonochory</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>- Attachment</td>
<td>Epizoonochory</td>
<td>103 m</td>
<td>400 000 m</td>
<td>Thomson et al. (2011)</td>
</tr>
<tr>
<td>- Digestion</td>
<td>Endozoonochory</td>
<td>312 m</td>
<td>6 500 m</td>
<td>Thomson et al. (2011)</td>
</tr>
<tr>
<td>- Seed caching</td>
<td></td>
<td>23 m</td>
<td>22 000 m</td>
<td>Thomson et al. (2011)</td>
</tr>
<tr>
<td>Humans</td>
<td>Anthropochory</td>
<td>NA</td>
<td>5 000 m</td>
<td>Wichmann et al (2009), Pickering et al. (2011)</td>
</tr>
<tr>
<td>Motor vehicles</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>- Mud</td>
<td></td>
<td>NA</td>
<td>256 000 m</td>
<td>Taylor et al. (2012)</td>
</tr>
<tr>
<td>- Airflow</td>
<td></td>
<td>6 m</td>
<td>45 m</td>
<td>von der Lippe et al. (2013)</td>
</tr>
</tbody>
</table>

biodiversity is often better explained by the past rural landscape, when managed grasslands were much larger and better connected (Lindborg and Eriksson, 2004; Gustavsson et al., 2007; Cousins and Vankhovenacker, 2011). This phenomenon is known as the ‘extinction debt’ (Tilman et al., 1994), by which it is implied that extinctions will occur in the future in order to put the landscape and its diversity back in equilibrium according to the species-area relationship. Although biodiversity has been slow to respond to landscape change during the 20th century, shifts in plant species composition to more persistent species in fragmented habitats have been detected (Maurer et al., 2003; Lindborg et al., 2012).

So, even though semi-natural grasslands have become very much fragmented, they are still of great importance for local biodiversity. However, in order to maintain and support their high biodiversity and other values in the long-term and at a large spatial scale, plants must be able to move between fragmented grasslands (Hanski, 1999), and former habitat must be restored to increase the area of habitat in the landscape to ease the threat of the extinction debt (Kuussaari et al., 2009). For both these points, seed dispersal across the landscape is key.

Seed dispersal

In flowering plants, effective dispersal entails the establishment of new individual plants (Schupp et al., 2010), the culmination of a multi-step process from seed production through seed transport to seedling recruitment (Eriksson, 2000). Successful seed dispersal between two points can broadly be determined by geographical and biological conditions: structural and functional connectivity. Structural connectivity can generally be defined as the organisation of habitat features within a landscape, while functional connectivity refers to an organism’s response to the landscape’s structure (Taylor et al., 1993). In plants, functional connectivity involves the dispersal of seeds between landscape features with the help of a dispersal syndrome (adaptation) and a dispersal vector (carrier). The unassisted dispersal of plant species across a fragmented landscape is very slow (van Dorp et al., 1997), so in rural landscapes with isolated grasslands, the study of long-distance dispersal vectors is important. The definition of what constitutes long-distance dispersal is case-specific (Nathan, 2006), and in this thesis it is defined as dispersal between fragmented habitat patches, or at least dispersal which has the potential to cover the necessary distances.

How do seeds disperse?

Seeds have evolved to disperse in a number of ways (see Table 1; Box 2). Plant species can disperse long distances in the wind by having very small seeds, wings or parachute-like structures, while the explosive or ballistic dispersal of seeds can transport seeds a few metres away from their parent plant (van der Pijl, 1972). Seeds can also be dispersed in water, by being flushed or splashed away from the parent plant, or dispersed longer distances either floating on, or submerged in streams and rivers (van der Pijl, 1972). With the help of animals, plants can disperse their seeds in a more directed manner (Howe and Smallwood, 1982). Seeds with small, lipid-rich attachments (elaiosomes) which attract ants are present in many plant families (Lengyel et al., 2010), allowing seeds be ‘planted’ underground in the ants’ nest, usually up to a few metres away from the parent plant. Animals which have larger ranges are also able to disperse seeds longer distances, while their habitat preferences can allow seeds to arrive at suitable loca-
Box 2. Examples of the mechanisms of seed dispersal

Plant species have evolved a number of ways to disperse their seeds away from the parent plant. Most easily recognisable are those adaptations to wind dispersal such as winged seeds or those with parachute structures. Ballistic dispersal, whereby seeds are propelled short distances is another method for a plant to spread seeds through the air. Seeds can also be dispersed in different ways with the help of animals. Lipid-containing elaiosomes attract ants, while fleshy fruits attract birds and other small mammals. Larger herbivores such as wild ungulates eat a large amount of plant matter, and seeds are often found in their droppings. Animals can also disperse seeds unwittingly, as hairy and/or hooked seeds become attached to their fur.

- The small Dandelion (Taraxacum) seeds with their parachute structures allow them to travel long distances once they detach from the mother plant.
- Wych Elm (Ulmus glabra) seeds have winged appendages which help them to fly in the wind.
- Seeds of the invasive weed Himalayan Balsam (Impatiens glandulifera) ‘explode’ out of their pods, helping them reach nearby water for further transportation.
- A grass seedling emerging from the dung of a wild deer.
- Consumption of fleshy fruits such as the bilberry (Vaccinium myrtillus) results in the dispersal of seeds in the dung of the consumer.
- Hooks and hairs, such as those visible on different species of avens (Geum) allow for seeds to become attached to the fur of passing animals.

(tions (D’hondt et al., 2012; Carlo et al., 2013). Seeds with hooks, hairs or other appendages can disperse long distances by attaching to the fur of animals (Sorensen, 1986), although most plant species probably have the capability of being dispersed in this way (Couvreur et al., 2004a). Small, hard seeds can resist digestion to be dispersed in the droppings of animals (Janzen, 1984; Pakeman et al., 2002), while birds and rodents store (cache) seeds and subsequently forget about them (Vander Wall et al., 2005). There are many plant species which have seeds that do not appear to be specially adapted to any mechanisms of dispersal, but despite this can still be transported by a range different dispersal vectors (van der Pijl, 1972).

In addition to seeds dispersing in space, many species also have the capacity to disperse in time by remaining dormant for a period in the soil in seed
banks. This allows the seeds to 'wait' until suitable conditions for growth in unpredictable environments (Thompson and Grime, 1979), and traces of former plant communities can be detected in the seed bank for a very long time afterwards (Plue et al., 2008). Temporal seed dispersal might then be another useful strategy for plant species in a changing rural landscape, especially regarding the restoration of former habitats (Kalamees et al., 2012).

It is clear from Table 1 that seeds are able to travel long distances with their different vectors, however mean dispersal distances are relatively short compared to the maximum measured distances. The use of multiple vectors is possible to increase dispersal distances, and seeds can also travel long distances using dispersal vectors to which they are not necessarily adapted. These non-standard dispersal events are relatively regular providers of long-distance dispersal, which themselves have a disproportionately high importance for plant movement and dynamics (Higgins et al., 2003; Nathan, 2006). Humans are a regular and well reported non-standard means of long-distance dispersal, and the potential role of humans in seed dispersal has been recognised for some time (Woodruffe-Peacock, 1918; Clifford, 1959; Hodkinson and Thompson, 1997). Recently, human-mediated dispersal was defined as:

"...dispersal directly by humans, on their clothes or by human-associated vectors, including all means of human transport, pets and livestock, human equipment and food"

Wichmann et al. (2009)

As humans continue to affect all natural systems and their organisms, including the full range of seed dispersal vectors (even by indirectly affecting wind dispersal through climatic change - Bullock et al., 2012), the study of how human activity directly and indirectly affects seed dispersal is of great interest for biodiversity science worldwide. This is particularly relevant in rural landscapes, where human and landscape histories are so intertwined.

Connectivity and dispersal in rural landscapes

Connectivity, and the maintenance and restoration of existing habitats are important for the conservation of ecological communities under threat (Lindemayer et al., 2008; Hodgson et al., 2009). As mentioned earlier, dispersal and connectivity are inherently linked. Despite the importance of dispersal, plant communities are generally regarded as being seed or dispersal limited (Primack and Miao, 1992; Ehrlén and Eriksson, 2000; Stein et al., 2008). Furthermore, when a landscape becomes more fragmented, less connected and dispersal becomes more important, species find it more difficult to disperse. This increases dispersal limitation (Ozinga et al., 2005), eventually leading to dispersal failure and local extinctions (Ozinga et al., 2009), and the slow recovery of target communities after restoration (Öster et al., 2009; Helsen et al., 2013).

In the case of semi-natural grasslands, structural connectivity was greatly reduced during the 20th century, but small and linear landscape elements such as road verges and field boundaries can still contain grassland communities (Smart et al., 2002; Cousins, 2006). Functional connectivity through seed dispersal is also likely to have reduced over the same period. In the past, dispersal from the local to international scale was provided through the movement of grazing livestock, which are now largely confined to small pastures for the whole grazing season (Brumm and Fritzboger, 2002). Dispersal was also provided by other agricultural practices, such as hay-making and fertilising with manure, and most of the historical landscape was connected by these different dispersal processes (Poschlod and Bonn, 1998). As these traditional vectors have disappeared from the landscape, the dispersal of seeds between fragmented grasslands is more unlikely (Diacon-Bolli et al., in press), and the colonisation of grassland plants to different types of restored areas is also found to be limited by a lack of dispersal (Walker et al., 2004; Bossuyt and Honnay, 2008).

Despite the apparent threats to dispersal in grasslands, seeds arriving from different spatial scales, as well as those emerging from the seed bank are important contributors to local diversity when gaps in the vegetation become available (Pakeman and Small, 2005; Vandvik and Goldberg, 2006). In terms of potential restoration, seed banks also contain significant reserves of diversity in abandoned pastures (Plue and Cousins, 2013). Although dispersal (especially long-distance) is clearly important for conservation (Trakhtenbrot et al., 2005), it is generally not directly considered in conservation planning (McConkey et al., 2012). In rural landscapes, where for centuries human activity has shaped plant communities and had both direct and indirect effects on dispersal and connectivity, it is of interest to explore the interplay between historical and present-day land use and management, and their effects on the dispersal of plant species in these important habitats.
The aim of this thesis

The work described in this thesis studies how human activity and seed dispersal are linked in the rural landscape. Specifically, I investigate the ecological, geographical and historical influences on seed dispersal in fragmented semi-natural grasslands today. Concentrating mainly on the different seed dispersal vectors in the rural landscape, I focus on how mobile seeds are in time and space, using this to evaluate the potential for seeds to disperse successfully and effectively. In these valuable historical landscapes, I look at how seed mobility can be directly and indirectly influenced by past land use and management, exploring the changing roles of historical dispersal vectors, and the roles that new dispersal vectors can have in the landscape today. Specifically, I aim to identify the main seed dispersal vectors in the rural landscape, understand which types of plants and seeds they disperse, and evaluate their role in seed dispersal in the context of the conservation and restoration of semi-natural grasslands. Another important goal is to give concrete examples for how any findings can be applied in the conservation of semi-natural grasslands, with regards to improving structural and functional connectivity at the landscape scale.

The thesis is broadly laid out in three stages:

1. Assessment of current knowledge. Paper I is the result of an extensive literature search with the aim of collating what is known about how humans can mediate the dispersal of seeds in the rural landscape with a focus on the conservation and restoration of European semi-natural grasslands. Important dispersal vectors are identified, along with gaps in the knowledge and the need for more research.

2. Empirical investigation. Forming the main part of the thesis, Papers II–IV are the result of three investigations studying different aspects of seed dispersal in rural landscapes. Paper II describes an investigation of the mobility of seeds in time (through the soil seed bank) and in space (in seed rain), and how they relate to current or former land use, without directly considering the vector by which the seed arrived at the site. Papers III and IV consider three different dispersal vectors, with the aim of identifying which species can be dispersed long distances with the help of humans, and what attributes (life-history traits) of the seeds and plants of these species have. Paper III compares the potential role of a traditional long-distance seed dispersal vector (free-ranging livestock) with that of a modern one (motor vehicles). The structural connectivity of grasslands provided by present-day road networks is also investigated. Paper IV evaluates the role of humans themselves as seed dispersal vectors. Seeds dispersed from species-rich meadows are compared to the available species pools, and the past and present roles of humans in the dispersal of plant species in the rural landscape are discussed.

3. Future directions. Using the knowledge gained from the previous stages, Paper V looks forward by suggesting a way to broadly include dispersal in conservation planning. Here it is suggested that a knowledge of the landscape and its main seed dispersal vectors can form a basis for understanding the potential for seeds to cross between fragmented habitats.
Assessment of the current knowledge

(Paper I)

With the aim of capturing the state of the art with regard to how humans can affect seed dispersal in rural landscapes, a literature search was conducted for human-mediated dispersal studies in European grasslands. The following broad search terms were used in the ISI Web of Science (http://www.isiknowledge.com): anthropochor*, dispers* cloth*, dispers* footwear, human mediated dispersal, endozoochor*, epizoochor*, exozoochor*, motor vehicle* dispers*, zoochor* (see Table 1 for different types of dispersal and their names). Relevant publications found in the reference lists of resulting articles were also considered.

Three main vectors of human-mediated seed dispersal for European grassland plants were identified: grazing livestock, motor vehicles and human clothing (Box 3). Livestock had unsurprisingly received the most attention in the literature. Cattle can disperse a great deal of seeds and species in their manure, accumulating to over a million or more seeds per individual and year (Cosyns et al., 2005a; Mouissie et al., 2005), while seeds are also transported in their coats (Couvreur et al., 2004b). Sheep are also good at moving seeds, especially in their coat (Fischer et al., 1996; Wessels et al., 2008), and horses and donkeys complete the set of livestock studied (Cosyns and Hoffmann, 2005; Couvreur et al., 2005). Dispersal on the outside (epi-) and through the inside (endozoochory) of grazers are reported to be complementary with regards to the species transported (Couvreur et al., 2005). Different livestock can also complement one another, with sheep more successful epizoochorous and larger animals endozoochorous dispersers. With regards to dispersal distances, endozoochory can disperse seeds as far as the animal can move within two to three days (Cosyns et al., 2005b), while sheep can disperse seeds more than 400 km in their coats (Manzano and Malo, 2006).

Motor vehicles have also been found to disperse a lot of seeds. Private vehicles disperse seeds representative of the local roadside flora, but studies are concentrated in urban and suburban environments with a focus on ruderal and invasive species (Hodkinson and Thompson, 1997; Zwaenepoel et al., 2006; von der Lippe and Kowarik, 2007). In rural areas, where road sides contain grassland species in the vegetation and seed bank (Milberg and Persson, 1994; Cousins, 2006), the dispersal of grassland species across the landscape might be more common. Agricultural machines are more concentrated in rural environments, and the limited research regarding their ability to disperse seeds indicates they are also quite capable of transporting available seeds (Strykstra et al., 1997; Mayer, 2000).

Humans can also disperse seeds of many species on their clothes and shoes (Mount and Pickering, 2009). Investigations into this type of human-mediated dispersal have mainly been concerned with the spread of invasive species to sensitive areas (Healy, 1943; Whinam et al., 2005), and a study from Europe investigating which seeds and species are dispersed on clothing is lacking. Long distances are also possible using this vector, with seeds able to remain attached to footwear for the duration of a 5 km walk (Wichmann et al., 2009; Pickering et al., 2011).

Based on the literature search, it appears that along with the fragmentation of grassland habitat, a decline in dispersal has also occurred with agricultural change during the 20th century. Less movement of livestock, along with a declining rural population is likely to have reduced dispersal opportunities for grassland plants. It is, however, important that modern seed dispersal vectors such as motor vehicles are also considered, and that views of human-mediated dispersal in general are not biased towards the spread of invasive species. The review resulted in management recommendations, namely the need for more mixed grazing, and the increased movement of livestock across the landscape, both between pastures and to targets for restoration. The gaps in the knowledge which would manifest in the following section of this thesis were the need to study the potential of the three main human-mediated dispersal vectors (livestock, motor vehicles and humans) to provide connectivity in the modern rural landscape.
Empirical investigation

(Papers II–IV)

Methods

Studying and measuring seed dispersal is very difficult (Nathan et al., 2003; Bullock et al., 2006). Different methods can be employed according to the goals of the study. Unless a dispersal event is slow enough, or the distance short enough to be observed during the whole movement stage from parent plant to settled location, natural dispersal distances cannot realistically be measured. Instead, seeds generally have to be artificially attached to a vector, such as animals (e.g. Kiviniemi and Eriksson, 1999) and relocated after deposition. This can mean that seeds do not become attached to the vector as they might do in 'real life', and that for logistical reasons only one or a handful of species can be studied. Another approach is – depending on the studied vector(s) – to manually remove seeds from the vector (e.g. Couvreur et al., 2004b), collect deposited seeds (e.g. Cosyns and Hoffmann, 2005) or use seed traps to collect dispersed seeds (e.g. Jakobsson et al., 2006). This means that the source location of the seeds is not usually known, and therefore distances cannot be measured. However, this approach does allow for the identification of the species which can be dispersed in a certain way, and equally importantly, which species cannot. Both the described approaches (attaching and removing/collecting) yield different information, and both are useful in contributing to the understanding of long-distance seed dispersal. The empirical investigations in this thesis (Papers II–IV) use the latter method of sample collection, as the aim of the work
was to broadly understand the impacts of human activity and management on dispersal processes at the community and landscape level. Therefore, understanding which species and what kinds of species are dispersed was prioritised over how far seeds could disperse through human activity.

Study area
The main study area for this work (Papers II–III) was the rural landscape around the parishes of Ludgo and Spelvik in the county of Södermanland, southern Sweden (58° 54’ N, 17° 00’ E; Figure 1; Box 4). Like much of southern Sweden, the region has a long history of anthropogenic influence. Historical maps from the 17th century show that at that time, most of the landscape was covered in open or semi-open pasture or meadow. By the beginning of the 20th century, a lot of grassland close to the settlements had been turned into arable fields as technology had progressed to allow heavier soils to be ploughed. Another period of agricultural change took place during the 20th century. Farming shifted from being sustenance-based to commercial, resulting in a more rationalised and intensive agriculture. In the 1950s many wooded grasslands were planted with coniferous forest. Surplus arable land was converted to improved grassland or planted spruce forest, while a lot of the less-productive semi-natural grassland pasture was abandoned to become secondary forest. In addition to the main land uses, small and remnant habitats exist on mid-field islets, road verges and field strips. There are around 15 farms in the area, and just over 200 other houses, many of which are summer cottages, and mostly concentrated in the village of Aspa.

Paper III also uses semi-natural grasslands from the whole of the south of Sweden for a structural connectivity study, while data collection for Paper IV takes place in hay meadows from across a large area of Sweden (Figure 1).

Historical and present-day maps and GIS tools
Sweden has an excellent archive of detailed historical maps dating back through the past few centuries, which has given researchers the opportunity to analyse land use and related ecological change (e.g. Cousins, 2001; Gustavsson et al., 2007). In this thesis, historical map data were used to select sites for Papers II and III, by following land-use trajectories in order to find habitats with different land-use histories for Paper II, and historical semi-natural grasslands for Paper III. Historical maps were georeferenced, interpreted and digitised to create digital maps over the main study area. Present-day land-use data were extracted from Sweden’s general land-use map (Översiktskartan) and the property map (Fastighetskartan). The freely available map data over Swedish Board of Agriculture’s (Jordbruksverket) database of valuable grasslands (TUVA, http://www.sjv.se/tuva) was also used in the classification of today’s semi-natural grassland.

In Paper III, the structural connectivity of remaining semi-natural grasslands by road verges in southern Sweden was assessed. First, the number of grasslands from the TUVA valuable grassland database lying adjacent to a public road were identified, before the distances between nearby grasslands along the road network and Euclidean distances were compared. In Paper IV, approximate potential dispersal distances between meadows and the postal areas of participants’ home addresses were calculated.

Throughout the thesis, data visualisation, manipulation and map creation was done using either ArCGIS 9.3–10.1 or Quantum GIS 1.6–1.7. Geographical analyses were carried out with PostGIS 1.5.3 (Holl and Plum, 2009), with the additional package PgRouting 1.03.

Figure 1. Map showing study areas and sites for Papers II-V.
To assess the impact of agricultural land use on the seeds which are found buried in the soil, ten replicates of the following four habitat types were used:

[i] semi-natural grassland pasture, [ii] pasture which has previously been cultivated (former arable field), [iii] secondary woodland on abandoned semi-natural grassland and [iv] mid-field islets (see Box 4). In each of these ten replicates, 30 $1 \times 1$ m plots were laid out.
randomly in a $10 \times 10$ m grid (total 1200 plots). One $8 \times 8 \times 10$ cm soil sample was taken from the centre of each plot, with the top layer of vegetation and soil removed to leave only seeds forming part of the permanent seed bank.

Samples were dried and cold stored, before the soil was concentrated according to Ter Heerdt et al. (1996). Concentrated samples were then spread thinly on a layer of potting soil and grown in a greenhouse until germination was judged to have finished. Emerging seedlings were identified and counted, with unidentified seedlings replanted and grown until identifiable.

Seed rain (Paper II)

In each of the seed bank plots described above, a seed trap filled with potting soil, measuring $8 \times 8 \times 10$ cm was placed in the ground in the early summer 2008 and left out until early winter. After collection, the contents of the seed trap were spread onto a layer of compost and greenhouse grown according to the method described above for the seed bank samples.

Grazing livestock (Paper III)

Seven semi-natural grasslands in the study area were used to investigate endozoochorous dispersal by grazing livestock. Each month between May and September 2009 (five occasions), the pastures were visited, and manure samples collected from each of the livestock types present. Two litres were collected for cattle and horses, while 1 L was collected for sheep. In total, 31 samples were collected, of which 24 were from cattle, four from horses and three from sheep. These samples were dried, chilled and concentrated similarly to the seed bank samples, before being grown in a greenhouse, and emerging seedlings identified and counted.

Motor vehicles (Paper III)

The five farms which owned and managed the semi-natural grasslands from the manure study were also used to investigate seed dispersal by motor vehicles. On the same sampling days as the livestock investigation, plus once in April before the livestock were let outside, mud was collected from vehicles in the farm yard. This generally involved one car and one all-round tractor from each farm, but all vehicles present in the farmyard which had been used between sampling periods were sampled. In total, 17 samples from cars and 31 samples from tractors were collected. After collection, samples were processed and grown using the same method as were used for the grazing livestock samples.

Clothing and footwear (Paper IV)

In July–September 2010, members of 38 groups of the Swedish Society for Nature Conservation (Naturskyddsforeningen) managing 48 species-rich meadows across Sweden took part in an investigation of seed dispersal by humans on their clothing. Each participant was asked that on returning home after the hay-cutting, they should remove their outer clothes, shaking them and brushing them down, emptying pockets, picking visible plant material and emptying and banging together footwear. All resulting material was placed in one plastic bag and posted to me before being examined under a microscope and any seeds in the sample were identified and counted. A total of 214 samples were received.

Species available for dispersal

In order that the seeds dispersed could be put into the context of which species were available and which did not disperse, and which life-history traits (plant and seed attributes) might contribute to dispersal, the local species pool was identified. This was collected in different ways for the different investigations. To assess how the established vegetation affected the seed bank and seed rain (Paper II), an inventory of each of the 1200 $1 \text{ m}^2$ plots was undertaken to identify which plant species were available at the plot level. The plot data were then pooled for each of the 40 sites to identify the species pool at the site level.

In Paper III, seeds were dispersed by livestock, motor vehicles and farming machinery with access to several habitats in large areas of the landscape. Therefore the available species pool for this study was taken from the local plant atlas (Rydberg and Wanntorp, 2001), where all species present in the two $5 \times 5 \text{ km}$ grid squares covering the study area were included.

A mixture of sources provided the species pools for 36 of the 48 meadows from Paper IV. Species lists came mostly from the groups managing the meadows, but when these were not available, data were either extracted from the Swedish Species Gateway (Artportalen, http://www.artportalen.se/), or from local or regional plant atlases. Meadows in the vicinity of Stockholm where species lists were not otherwise available were inventoried especially for the investigation.

Data analysis

A mixture of statistical techniques was used to analyse the dispersal data at both the species and community level. Lists of dispersed species were compared to lists of grassland specialists, nationally pro-
Table 2. Descriptions of the different categories of species used in this thesis to evaluate positive vs negative effects of human-mediated seed dispersal.

<table>
<thead>
<tr>
<th>Category</th>
<th>Definition</th>
<th>Source</th>
<th>Used in</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grassland specialist species</td>
<td>Over-represented in semi-natural grassland vegetation compared to abandoned grasslands, mid-field islets and grazed former arable fields in Ludgo-Spelvik.</td>
<td>Paper II</td>
<td>Paper II Paper III</td>
</tr>
<tr>
<td>Protected species</td>
<td>Protected by Swedish law. There are different levels of protection, covering some or all of the following restrictions: picking flowers, uprooting the plant, removing seeds and doing any of the above for commercial reasons.</td>
<td>Species Protection Act – Statute 2007:845</td>
<td>Paper II Paper III Paper IV</td>
</tr>
<tr>
<td>Red-listed species</td>
<td>Plant species judged to be at risk of extinction, according to the following scale: LC = least concern, NT = near threatened, VU = vulnerable, EN = endangered, CE = critically endangered, RE = regionally extinct.</td>
<td>Gårdenfors (2010)</td>
<td>Paper II Paper III Paper IV</td>
</tr>
<tr>
<td>Internationally invasive species</td>
<td>Non-native species worldwide whose introduction or spread threatens biodiversity in a country other than Sweden.</td>
<td>Centre for Agricultural Bioscience International – <a href="http://www.cabi.org/isc">http://www.cabi.org/isc</a></td>
<td>Paper IV</td>
</tr>
</tbody>
</table>

In Paper II, the capacity for the available established species to predict dispersal in time or space was assessed using co-correspondence analysis (Ter Braak and Schaffers, 2004). This method involves taking a predictor and response community from the same set of plots. A model is created relating the communities from all but one plot, which is then used to try to predict the response community from the predictor community in that remaining plot. This is carried out for each plot in turn to assess how well the response community can be predicted. The method was used to evaluate how well the species dispersed in the seed bank and seed rain were predicted by the available species in the surrounding vegetation. Ecological community similarity of dispersed species was calculated between each habitat type to assess if species available in the seed bank or seed rain were more related to the established vegetation in the habitat from which they were collected, or to another habitat. At the species level, indicator species analysis (Dufrêne and Legendre, 1997) was used for the vegetation data to identify characteristic species of the semi-natural grassland habitats which could then be used to see if these ‘specialists’ were present in the seed bank or seed rain of the four habitats.

Comparison of the dispersed and available species communities was carried out at the trait level in Papers III–IV, as well as being discussed in terms of percentage of the available species which were dispersed. Data regarding seed number, seed mass (mg) and seed releasing height (m), along with those relating to the ability to form a seed bank (persistent or transient), attach to animals (seed morphology, hooked, otherwise appendaged or not appendaged) or disperse in the wind (terminal velocity m s\(^{-1}\)) were extracted from the LEDA trait database (Kleyer et al., 2008). These traits were then used to compare dispersed and available species, to see which traits could explain whether a seed was dispersed by livestock, manure, both or neither (multinomial logistic regression, Venables and Ripley, 2002; Paper III), or by humans or not (quasibinomial logistic regression, Paper IV). Community similarity of dispersed and available species was calculated for the meadows in Paper IV, with linear regression used to assess how the number of samples received from a meadow affected how well the dispersed species represented the available species.

Differences between the species dispersed by manure and motor vehicles in Paper III were further
compared using permutational multivariate analysis of variance, while the individual species responsible for any differences were identified using indicator species analysis. Differences in the number of seeds and species dispersed by the vectors through the season were compared using Monte-Carlo random sampling. All numerical analyses in this thesis were carried out in the statistical environment R 2.11.0–2.14.1 (R Development Core Team, 2011).

Results and discussion

Dispersal in relation to available species

Across all three empirical investigations, 123,122 seeds or emerging seedlings were counted. Three-hundred and seven species were positively identified as being mobile in time or space, while many more were grouped into aggregates or to the genus level. From now on, all such groups are counted as species.

A total of 54,357 seedlings emerged from the seed bank and seed rain samples (Paper II), representing 188 species. The inventory of the established vegetation found 277 species, with a total of 296 species identified in the whole investigation. The co-correspondence analysis revealed that seed bank and seed rain communities were generally not very well predicted by the surrounding vegetation. The best prediction was provided for the seed bank of the semi-natural grassland, but seed bank and vegetation appeared to be out of synchrony in the other habitat types. This was supported by the similarity analysis, which showed that seed banks in the former grassland habitats (mid-field islets and abandoned grasslands) were more similar to the established semi-natural grassland communities (Figure 2). The existence of semi-natural grassland communities in the seed banks of abandoned habitats is not in line with the common assertion that semi-natural grasslands do not form permanent seed banks (Bossuyt and Honnay, 2008), but instead indicate that as well as current diversity patterns in the vegetation (Lindborg and Eriksson, 2004), seed bank communities are also largely influenced by their past management. The strength of this influence has since been found to relate to the time since the grassland was abandoned (Plue and Cousins, 2013). The results from the seed rain experiment showed how current management influences seed availability in the landscape, as the seed rain in lightly-grazed former arable fields and ungrazed abandoned habitats was most similar to the surrounding established vegetation (Figure 2). Seed rain in semi-natural grasslands was actually most similar to vegetation in former arable fields, possibly because the intensive grazing in these species-rich habitats only allows the most common and widespread species to grow and produce a detectable seed rain.

The 31 samples (total volume 57.6 L) of manure collected from livestock grazing semi-natural grassland pasture produced 31,793 seedlings of 108 species (Figure 3). A similar number of species emerged from mud attached motor vehicles, where 12,618 seedlings of 110 species emerged from 48 samples (35.1 L). Sixty-nine species were shared between the two vec-

Figure 2. Similarity of seed bank and seed rain communities to the habitat-type vegetation to which they were most similar, where ABA, abandoned semi-natural grasslands; FAF, former arable fields; MFI, mid-field islets; SNG, Semi-natural grasslands. Different line formats are used for the different habitat types to facilitate the following of arrows between the boxes.

Available species

Figure 3. Visualisation of emerging species identified from samples of manure from livestock grazing semi-natural grassland and cars and tractors driving around the rural landscape. For simplicity, invasive and protected species available in the plant communities are not considered.
Figure 4. Density (boxplots) and total species richness per month (line) of [a] manure samples and [b] motor vehicle samples throughout the grazing season. Boxes represent the upper and lower quartiles, thick lines show the median, and the whiskers indicate the range of the dataset without outliers. Outliers (open circles) are where an observation falls outside the quartiles +/−(1.5× the interquartile range). Letters in common represent no significant difference of species density (a-b) and seedling density (x-z) within vector, while * shows significant differences between vectors for a particular month from the monte-carlo analysis.

The clothes and shoes of humans were also found to disperse a considerable fraction of the available species. A total of 24354 seeds of 197 species were identified, 34% of the 514 species from the meadow inventories (Figure 5). Of the 214 samples received, 211 (99%) contained seeds, indicating the ubiquity of dispersed species.
of seed dispersal on clothing and footwear. The more samples which were received from a meadow resulted in a higher number of species and a better representation of the community in the source meadow (Figure 6). Potential dispersal distances with humans were found to be very long, ranging from 1.3 km to 110 km, with an average distance of 13.4 km. This shows how modern transportation methods can greatly increase the dispersal distances previously measured on humans walking in the landscape (Pickering et al., 2011; Wichmann et al., 2009).

Specialist, protected, red-listed and invasive species

The indicator species analysis identified 22 grassland specialist species in the study area for Papers II and III (Box 5). Seeds of many these specialists were found to be mobile in time and space. All but two specialists were found in the seed bank samples, five of which were found in the seed banks of the former grassland habitats despite not being available in the established vegetation. This, along with the similarity of the abandoned seed bank communities to the semi-natural grassland vegetation provides further evidence that semi-natural grassland plants are able to disperse in time.

Fifteen specialists were found to be dispersed by livestock grazing semi-natural pastures in the study area. It is perhaps not surprising that animals grazing grasslands disperse grassland specialist species, but specialists were also found to be mobile in other parts of the landscape. Four specialists not present in the vegetation of former arable fields were nevertheless found in the seed bank or seed rain in these pastures, while eight were found in the motor vehicle samples. Although seeds of specialist species were present in smaller concentrations compared to the manure samples, the dispersal of more than one-third of the area’s specialist species by motor vehicles is quite remarkable. Dispersal by motor vehicles is generally considered in the context of invasive species (von der Lippe and Kowarik, 2007; Taylor et al., 2012), but only four invasive species emerged from the samples, and these were introduced to the study area before the invention of motor vehicles (Rydberg and Wanntorp, 2001).

Plant species protected by Swedish law (Species Protection Act: Statute 2007:845), and those on the national red list of threatened species (Gärdenfors, 2010) were also found to be mobile. Three protected or red-listed species were found in the seed bank or seed rain, although this seemed to be quite an under-representation compared with what was available in the vegetation. Seven such species were found on the footprint and clothing of volunteers cutting species-rich meadows, and the fact that 34% of all the species recorded in the sites (many of which are designated protected areas) were dispersed by humans indicates...
Box 5. Grassland specialists, protected and red-listed species

The presence of grassland specialist species is an important goal in schemes regarding the conservation and restoration of grassland habitat, but definitions of what specialist species actually are can be unclear and sometimes inappropriate. In Paper II, a list of local grassland specialist species in Ludgo-Spelvik was created by comparing species present in the semi-natural grassland sites with those present in the other habitat types. These species are listed below, in descending order from the strongest to weakest specialists. The results from Paper II and III showed that many of these specialists are mobile in time and space in the study landscape. All but two were found in the seed bank, and five remained in the soil after disappearance from the established vegetation (remnant seed bank). In addition to these specialists, 8 nationally protected and/or red-listed species were identified in Papers II-IV. Invasive species were not often found to be dispersed by the investigated vectors, and those that were found are already very widespread common species which were introduced to Sweden several hundreds of years ago.

Seed mobility of local grassland specialists in Ludgo-Spelvik

<table>
<thead>
<tr>
<th>Species</th>
<th>Remnant seed bank</th>
<th>Grazing livestock</th>
<th>Motor vehicles</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Plantago lanceolata</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>2. Lotus corniculatus</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>3. Filipendula vulgaris</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4. Campanula rotundifolia</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>5. Pimpinella saxifraga</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6. Trifolium arvense</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>7. Rumex acetosa</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>8. Viola canina</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9. Veronica chamaedrys</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>10. Trifolium pratense</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>11. Anthoxanthum odoratum</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12. Alchemilla spp</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>13. Ranunculus auricomus/bulbosus</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>14. Arabidopsis thaliana</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>15. Scleranthus annuus</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>16. Festuca ovina</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>17. Carex spicata</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>18. Primula veris</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>19. Potentilla argentea</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>20. Veronica officinalis</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>21. Ajuga pyramidalis</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>22. Erophila verna</td>
<td></td>
<td></td>
<td>X</td>
</tr>
</tbody>
</table>

The dropwort (Filipendula vulgaris) was found to be a strong grassland specialist in Ludgo-Spelvik, but was not particularly mobile in time or space.

Seeds of Birds-foot Trefoil (Lotus corniculatus) were found in the seed banks of all studied habitats in Paper II, as well as being dispersed by cattle.

The endangered Field Gentian (Gentianella campestris) was dispersed by clothing and footwear from three of the four meadows where it was known to grow.

that many typical grassland species can be dispersed in this way. Only three invasive species were found in the clothing and footwear samples, but 71 (36%) of species found are considered invasive in other countries, highlighting the risk of invasions associated with long-distance travel to sensitive areas (Ware et al., 2011; Chown et al., 2012).

Dispersal traits

The plant trait analyses revealed that life-history and dispersal traits can to some extent determine how species can be moved around the landscape by different human-mediated dispersal vectors (Table 3). Both motor vehicles and livestock manure were found to disperse small and persistent seeds. This has
Table 3. Species life history and dispersal traits significantly (P<0.05) associated with dispersal via manure, motor vehicles and clothing and footwear. A plus indicates an increased likelihood for a species having a particular trait to be dispersed via a given vector compared to the available species pool, a minus indicates a negative effect. Brackets means a near-significant tendency. A multinomial logistic regression of the dispersed species compared to the available landscape species pool used the analysis for manure and motor vehicles, whereas a quasibinomial logistic regression of dispersed seeds compared to available species in the studied meadow habitats was used for analysis of the clothing and footwear.

<table>
<thead>
<tr>
<th>Seed bank</th>
<th>Seed mass</th>
<th>Hooked seeds</th>
<th>Appended seeds</th>
<th>Seed number</th>
<th>Seed release height</th>
<th>Seed terminal velocity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Manure</td>
<td>+</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Motor vehicles</td>
<td>+</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Manure &amp; Motor vehicles</td>
<td>+</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Clothing &amp; footwear</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>(−)</td>
<td>−</td>
<td>−</td>
</tr>
</tbody>
</table>

been previously reported for both vectors separately (Pakeman et al., 2002; Bruun and Poschlod, 2006; Zwaenepoel et al., 2006; von der Lippe and Kowarik, 2012). In addition, both vectors were found to disperse relatively low growing (seed releasing) species, which probably reflects the short vegetation in the pastures and road verges of the rural landscape. In another study, seeds adapted to dispersal by wind have been found to disperse in the slipstream of cars without becoming attached (von der Lippe et al., 2013). Comparing traits between vectors, it was found that motor vehicles were more likely to disperse species which produce many seeds. Together with the findings that the two vectors generally disperse species with quite similar traits, this indicates that dispersal by motor vehicles merely requires that the seeds are available to be dispersed. Unlike grazing animals who consume and defecate vast quantities of seeds every day (Cosyns et al., 2005a), attachment to motor vehicles more stochastic, and therefore species producing more seeds can reasonably be expected to attach more regularly.

Species that are able to form persistent seed banks were also found to be dispersed in clothing and on footwear. Along with the results from grazing livestock and motor vehicles, it shows how human-mediated dispersal can move seeds through space which also have the ability to disperse in time. Motor vehicles and humans might be expected to disperse seeds with persistent seed banks as the mud attaching to vehicles and shoes will contain seeds in the seed bank. With grazing livestock, the persistence required to form seed banks is also required to survive gut passage, while seed-containing mud can also attach to the hooves of large herbivores (Heinken and Rauchnitschka, 2002; Picard and Baltzinger, 2012). The tendency of seeds from lower growing plants to disperse with humans indicates that even in relatively open habitats, smaller herbs are probably more likely to be dispersed. Additionally, seeds with hooks and other appendages were more likely to disperse on the clothing of volunteers. In this respect, humans can act just like other animals with regards to seed dispersal by attachment (Römermann et al., 2005; Hovstad et al., 2009), although a lack of humans in the modern rural landscape compared to in the past means that this kind of dispersal is relatively rare.

Management of structural, functional and temporal connectivity

The results from the empirical investigations indicate that seeds in the rural landscape have the potential to be mobile in both time and space. Both semi-natural grassland communities and local specialists were found in the soil of abandoned grasslands and mid-field islets. In addition, seeds were found in all manure samples, 99% of clothing and footwear samples, and all but the very smallest of samples of mud from motor vehicles. Around a quarter to one-third of available species were found to be potentially dispersed by the studied vectors, including species with a range of dispersal traits. Several grassland specialist, protected and red-listed species were present, and relatively few invasives.

As the investigations were concerned with human-mediated dispersal vectors, the potential for this mobility to be realised lies to some extent in the hands of humans managing the landscape. The need for better connectivity and dispersal is clear, as it was found that only 3.4% of the more than thirty-thousand valuable grasslands in southern Sweden have another grassland less than 100 m away, which is the distance reasonably covered by wind dispersed species (Schleicher et al., 2011). Around 40% of valuable grasslands are structurally connected to each other via road verges on the public road net-
work, which provides a great potential for improving dispersal between fragmented grasslands. Despite containing grassland species (Cousins, 2006), road verges are by no means strips of semi-natural grassland, and they must be managed effectively to promote opportunities for colonisation of and seed production by grassland species for long-distance dispersal via motor vehicles (Kiviniemi and Eriksson, 1999; Jantunen et al., 2007).

Despite the potential for dispersal via motor vehicles, any successful dispersal events would be quite rare and unpredictable. Livestock were found to disperse more grassland specialists, and at much higher concentrations than motor vehicles. Therefore, to ensure a more dependable supply of seeds, the potential of livestock for long-distance dispersal should be managed through the increased movement of livestock around the landscape. This could be achieved both by moving livestock between fragmented species-rich habitats (Auffret et al., 2012), or by opening up boundaries between species-rich pastures and restoration areas (Kumm, 2004). Movement should be concentrated in the late summer, around the time of highest seed availability (Figure 4), and the risk of spread of unwanted species back into the species-rich pasture must be weighed up against the dispersal benefits (Mouissie et al., 2005).

Human-mediated dispersal of seeds on people’s footwear and clothing can hardly be managed for conservation purposes. However, the good representation of the available flora dispersed on clothes, along with the increase in potential dispersal with more samples (Figure 6) indicates how humans might have once been regular and effective seed dispersal vectors in the rural landscape when rural populations were larger. I have only focussed on the passive dispersal by humans, but historical farming practices also included the active spread of grassland seeds, for example via the spreading of hay (Poschlod and Bonn, 1998; Edwards et al., 2007). Since the modernisation of agriculture resulted in a rural-urban migration (Satterthwaite et al., 2010), the reduction of humans working in the landscape might have contributed to the dispersal failure evident in fragmented rural landscapes today (Ozinga et al., 2009). On the other hand, the number of species identified which are invasive in other countries shows how effective measures are needed to reduce the unintentional dispersal of invasive species into sensitive areas by increasingly mobile humans.

The work in this section of the thesis has generally been concerned with the movement stage of dispersal, the mobility of seeds in time and space. The results from Paper II also gave some implicit indications of how human management can benefit the other stages of effective dispersal. The incongruence between the established vegetation and the seed rain in semi-natural grasslands indicates that the grazing intensity in these pastures was too high to allow the species present to set enough seed for future dispersal in the landscape or for seed bank replenishment. In former arable fields, the grazing intensity was apparently too low, as several grassland specialists were found in the seed bank and seed rain, but were never present in the established vegetation. A lack of microsites for colonisation has previously been identified as a further limitation for restoration of these habitats (Oster et al., 2009), to which a low grazing intensity could be a contributing factor. In addition to increasing seed dispersal by livestock, the removal of boundaries between species-rich and restored pastures might also result in a more heterogeneous disturbance regime which could benefit both seed production and colonisation. Further, the strategic selection of sites for conservation and restoration management should be considered with regard to abandoned and remnant habitats which can contain populations of grassland communities in both the vegetation and the seed bank. More recently abandoned sites contain more diversity in the seed bank (Phue and Cousins, 2013), and these remnants can act as sources of diversity for the relatively seed-poor former arable fields. Managing habitats to facilitate seed production and colonisation is an important complement to other measures which might improve the dispersal of seeds in the landscape which have been found here to be highly mobile.

Future directions
(Paper V)

Seed mobility and movement ecology

The previous sections of this thesis have presented evidence that human-mediated seed dispersal vectors are potentially very capable dispersers, and providing they are present, should allow ample opportunity for the movement of plant species through the rural landscape. Papers I–IV and the references therein have shown how human-mediated dispersal vectors can disperse seeds of target species and communities long distances, representing a range of life-history traits. While recommendations can and have been made which might improve the potential of human-mediated seed dispersal, connections between dispersal and conservation practice are generally lacking (Trakhtenbrot et al., 2005; McConkey et al., 2012).
The uncertainties regarding where seeds actually end up is an obstacle to fully understanding how human-mediated dispersal vectors can provide connectivity between fragmented grassland habitats. The movement ecology paradigm (Nathan et al., 2008) identifies the importance of knowing how seeds are moved by their vectors, and recent work has indeed found that the behaviour of animals results in a directional dispersal of seeds to suitable areas for establishment (Carlo et al., 2013; Perea et al., in press). The interaction between different seed dispersal vectors and their environment is clearly an important factor when considering long distance seed dispersal, but a broad approach is needed if practitioners are to be able to identify dispersal processes in a landscape with a focus on conservation. A useful step forward could be to redirect the focus away from species and seeds, and onto the landscape and the dispersal vectors which inhabit it.

**Dispersal geography**

Paper V describes a new approach to broadly deal with dispersal in conservation management. It involves a combination of movement ecology (Nathan et al., 2008) and time geography (Hägerstrand, 1970). Time geography is a theoretical framework developed in the field of human geography to describe human movement and the spread of information, based around the fact that people can only be in one place at one time, and that they follow relatively predictable and repetitive patterns of movement constrained by external factors. Applying the concept of time geography to human-mediated dispersal vectors and how geographical features of the landscape can explain or constrain their movement (Figure 7), might allow for the broad identification of dispersal patterns in a landscape, and how structural and functional connectivity can be managed to improve dispersal between fragmented habitats patches.

**Figure 7.** Maps showing the an area of Ludgo parish, southern Sweden in 1900 and today. The geographical features of the landscape which can influence the movement of dispersal vectors can broadly be split into two groups. Polygons can represent areas of habitat, matrix or former/potential habitat, while their boundaries can limit movement between landscape features. Linear features such as paths, roads and field boundaries can provide structural connectivity between habitats, while governing the movement of dispersal vectors such as motor vehicles, humans and livestock. A clear reduction of semi-natural habitat has occurred between time steps, although the amount of roads has increased. Linear features other than roads and rivers which might influence dispersal are not shown on the available maps, and such limitations of available data should always be noted.
### Table 4: Shifts in the mobility and numbers of seed dispersal vectors in the rural landscape between 1900 and today.

<table>
<thead>
<tr>
<th>Vector</th>
<th>Daily prism</th>
<th>Explanation</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Humans</td>
<td>Not only was there a higher population density in rural areas compared to today, but also a shift in the distribution of population. Human movements were mostly local, limited to short distances.</td>
<td>1900: Södermanland county board. Present: Nyköping municipality (data for 2013).</td>
<td></td>
</tr>
<tr>
<td>Motor vehicles</td>
<td>Cars</td>
<td>Travel long distances, constrained by time and land use.</td>
<td>Present: Statistics Sweden (data for 2011).</td>
</tr>
<tr>
<td>Livestock</td>
<td>Cattle</td>
<td>Previously, livestock were vital for both labour and food production, with freedom to roam the landscape.</td>
<td>1900: Swedish Board of Agriculture. Present: Swedish Board of Agriculture (data for 2010).</td>
</tr>
<tr>
<td>Wild animals</td>
<td>Elk, Fallow deer, Roe deer, Red deer, Wild boar</td>
<td>Wild animals have largely the same freedom to move as before, but are present at much higher numbers today.</td>
<td>1900: Swedish Association for Hunting and Wildlife Management. Present: Swedish Association for Hunting and Wildlife Management and Södermanland county board (number of animals shot during the 2011/12 hunting season).</td>
</tr>
</tbody>
</table>
The dispersal geography of a case landscape

To illustrate this idea, the study area from Papers II–III was used, with two time layers (today and the beginning of the 20th century) used to compare polygon and linear features in contrasting landscapes (Figure 7). Like most of Europe, there has been a huge reduction in semi-natural grassland habitat during the past 100 years. Linear landscape features (roads) have increased according to the map, although there has actually been a general trend in Sweden, and probably much of Europe for the reduction in linear features such as footpaths, hedgerows, ditches and field boundaries in rural landscapes (Ihse, 1995). Table 4 illustrates the changing movement patterns and populations of four dispersal vectors at the two time steps. The time geography framework’s daily prisms of movement give an indication of when and how far the different vectors move in the landscape, and data regarding the populations of the vectors were collated. This allows for an assessment of the main dispersal vectors which are active in the landscape, and the changes of dispersal potential provided by different vectors between two landscapes or two time periods can be broadly identified. Along with the main dispersal vectors identified in Paper I (humans, livestock and motor vehicles), free-ranging wild herbivores were also considered, as they have also been identified as long-distance dispersal vectors in the landscape, often dispersing species of open grassland habitats in their fur, hooves and dung (Heinken and Raudnitschka, 2002; Eycott et al., 2007; Jaroszewicz et al., 2009). Although not strictly human-mediated vectors, their movements can be influenced by land use and populations are controlled by hunting.

The landscape and the movement of its dispersal vectors were then combined to visualise the landscape in terms of dispersal potential and limitation (Figure 8). While the historical map shows a well-connected landscape with much dispersal potential, the physical and human geographical constraints mean that dispersal in today’s landscape is much more limited. However, the exercise facilitates the identification of areas where management to improve dispersal through increasing structural and functional connectivity can be implemented. Recommendations for management from the earlier studies in this thesis, such as the management of road verges to improve seed production and dispersal (Paper III), the rotational grazing of livestock between semi-natural pastures (Paper III) and the opening up of boundaries between semi-natural grassland and for-

![Image of dispersal patterns](https://example.com/image.png)

**Figure 8.** Visualisation of dispersal patterns in a rural landscape in southern Sweden in two time steps based on livestock movement in semi-natural grasslands, wind dispersal (100 m) and linear features. Letters indicate areas where dispersal is constrained and/or management could be altered to improve dispersal. (A) shows how much dispersal is largely limited to within-habitat movement of livestock. Linear features such as road verges (B) can connect fragmented grasslands, while boundaries exist between adjacent habitat and potential habitat (C) which limit movement of vectors between them. Purely functional connectivity could be achieved by moving livestock between fragmented pastures (D).
A.G. AUFFRET

mer arable field (Paper II) can now be clearly identified geographically. Comparing two different landscapes, be it in time or space, can also be useful with regard to the populations and movement of dispersal vectors in the landscape. In this case study, there have been increases in some dispersal vectors, but decreases in others, while their mobility through the landscape has also changed (Table 4). It can be valuable to identify these differences, and where possible manage landscapes and vectors accordingly. Not all vectors can be managed for dispersal, but populations of wild animals can be maintained at healthy levels as well as allowing areas of shelter to grow on existing habitat may facilitate some semi-directed, rare long-distance dispersal events. Humans can also not be managed to facilitate dispersal today, but in other areas such tourist hotspots where invasive species can be a threat, the number and mobility of humans in the landscape can be a very important factor for conservation.

Concluding remarks

The work presented in this thesis has provided evidence that seeds in the rural landscape are highly mobile, in both space and time. Three main human-mediated dispersal vectors, livestock, humans and motor vehicles, were identified and found to move many seeds of many species, potentially long distances. Seed dispersal by human-mediated vectors was near ubiquitous, with very few samples from motor vehicles and human clothing not containing any seeds at all. The human-mediated vectors investigated were generally found to disperse more grassland specialists and/or protected and red-listed species than invasive species. Seeds were found to attach to humans just as they would to any other animal, and motor vehicles have the potential to disperse the same kinds of species as livestock disperse in their manure. Especially with regard to dispersal by motor vehicles and directly by humans, I hope that this work will help to remove any bias with regards to human-mediated dispersal, which is often studied in the context of invasive alien species. There has certainly been a shift in dispersal patterns in the rural landscape, from the well-connected former landscapes with a free movement of vectors, to today’s landscape of small and isolated habitat patches, with reduced numbers of historical vectors more confined in their movements. New vectors have arrived, but in landscapes where structural connectivity has been lost, it is important that all human-mediated seed dispersal vectors, both old and new, are managed to translate seed mobility into effective dispersal and functional connectivity.

I believe that looking at the movement ecology of seed dispersal vectors is an important forward step in the ecology of plant dispersal. The dispersal geography concept presented here may not be the definitive path, but identifying the importance of the interaction of dispersal vectors and the landscape is certainly something to consider alongside gaining further understanding of different stages of human-mediated seed dispersal, from attachment to detachment and colonisation. Looking at the movement and behaviour of human-mediated seed dispersal vectors in relation to their environment should aid the understanding of their contribution to the build-up of biodiversity in historical landscapes, as well as the important role they may play in facing current and future ecological challenges.

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References


SEED MOBILITY AND LANDSCAPE CONNECTIVITY


Summary of papers

Paper I

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

A.G. Auffret

Humans have influenced the dispersal of plant species throughout history. In the European rural landscape, where species-rich semi-natural grasslands have resulted from a long history of management, dispersal is now thought to be a limiting factor for the conservation and restoration of grasslands which have become fragmented due to agricultural change. This paper reviews the recent research into human-mediated dispersal in the European rural landscape, and explores the potential positive aspect of human-mediated dispersal for grassland conservation, in contrast to its common association with the spread of invasive species. A literature search was undertaken to identify the different human-mediated dispersal vectors operating in rural landscapes, and for the assessment of their dispersal potential in the historical and modern landscape. Grazing animals are important dispersers, transporting a high percentage of available species pools on their fur and in their manure. However, the reduced movement of livestock through the landscape has also meant a reduction in seeds dispersed in this way. To address this problem, there should be a greater movement of grazing animals throughout the landscape, either within larger grazing areas or between existing grasslands. Where this is not possible, other, more directed dispersal of seeds from species-rich communities to target sites should be considered. Other, non-standard human-mediated dispersal vectors can also transport seeds of many species. Both private vehicles and agricultural machinery have been found to disperse seeds with a variety of dispersal specialisations, but further investigation is required to understand their role in rural landscapes where road verges can host grassland specialist communities. Humans and their pets are also identified as capable seed dispersers, but European-based research into the topic is severely lacking. The potential of non-standard human-mediated seed dispersal vectors to make a positive contribution to biodiversity should be considered, but more research into all types of human-mediated vectors is important if we are to fully understand their role in the dispersal of plant species in fragmented landscapes.

Paper II

Past and present management influences the seed bank and seed rain in a rural landscape mosaic

A.G. Auffret, S.A.O. Cousins

Seed banks represent a plant’s ability to disperse in time, while seed rain represents dispersal in space. Both have the potential to be important sources of diversity in the rural landscape, where fragmented habitats are linked by their historical land uses. In this paper, seed bank, seed rain and established vegetation were sampled in four habitat types: abandoned semi-natural grassland, grazed former arable field, mid-field islets and grazed semi-natural grassland in a rural landscape in southern Sweden. The results from this large-scale experiment then examine whether community patterns can be distinguished at large spatial scales and whether seed bank and seed rain are best explained by current, past or intended future vegetation communities. We counted 54,357 seedlings of 188 species from 1,190 seed bank and 797 seed rain samples. Seed bank, seed rain and established vegetation communities all differed according to the habitat they were sampled in, but despite these differences, several species characteristic of managed grassland vegetation were present in the seed bank, seed rain and vegetation of the other three habitats. The seed banks of semi-natural grassland and the seed rain of the former arable fields were generally better predicted by their surrounding vegetation communities than were the other habitat types. The seed rain was generally most similar to the surrounding vegetation, except for the semi-natural grasslands where the seed rain most resembled the vegetation in the former arable fields. On the other hand, seed banks were most similar to the vegetation in semi-natural grassland in all habitats except for the former arable fields, and grassland specialist species remained in the seed banks of the abandoned grasslands and mid-field islets even after they had disappeared above-ground. This indicates that semi-natural grassland communities are able to form seed banks which survive land-use change and abandonment, but today’s grasslands are not setting enough seed for dispersal at the local and landscape scale. Despite today’s grazing management, gap availability and seed input could be limiting the colonisation of target species in former arable fields, which were sometimes present in the seed bank and seed rain.
but were not in the established vegetation. Meanwhile, remnant populations in the seed banks indicate that abandoned grasslands and mid-field islets could be valuable sources of future diversity in the landscape after restoration. By connecting existing grasslands with restoration targets, increased disturbance in the target habitats would allow for colonisation via the seed bank or seed rain, while decreased grazing intensity would benefit seed production in the source grasslands. Otherwise, landscape-wide propagule availability might increase with a more varied timing and intensity of management.

Paper III

Grassland connectivity by motor vehicles and grazing livestock

A.G. Auffret, S.A.O. Cousins

In addition to habitat loss and fragmentation, agricultural change has led to a change in seed dispersal processes in the rural landscape through a loss of structural and functional connectivity. In rural landscapes, human-mediated dispersal vectors are prevalent, and in this paper, we explored whether the loss of connectivity via free-ranging livestock could be mitigated by the increase in roads and motor vehicles. We found that 39% of all valuable semi-natural grassland habitats in southern Sweden are adjacent to public road verges, with a typical distance of around 1 km between grasslands along verges. In the rural landscape, where road verges are often considered to be suitable habitat for grassland species, this could provide useful structural connectivity between grassland patches. Additionally, by collecting mud attached to cars and farming machinery and manure from livestock (cattle, horse, sheep) grazing semi-natural grassland pasture, we found that motor vehicles are also capable seed dispersers. A similar number of species were dispersed by both livestock and motor vehicles, although the composition of samples was quite different. Motor vehicles dispersed more grassland specialists than invasive species, although in much lower abundances than did grazing livestock. Despite these differences, motor vehicles were found to be able to disperse species with the same kinds of dispersal traits as livestock, with low-growing plants, as well as those with small seeds and persistent seeds over-represented in the samples. A high number of seeds, species and specialists in manure samples means that greater movement of livestock is desirable to increase functional grassland connectivity. However, effective management could improve the suitability of roadsides as grassland corridors and increase the availability of seeds for long-distance human-mediated dispersal via cars and tractors. Our results suggest that in many rural landscapes, connectivity by road networks could help mediate habitat loss and fragmentation of grasslands. However, such effects can be context dependent, and the connectivity provided by roads could have serious negative consequences in other regions where invasive species are more of a threat.

Paper IV

Humans as long-distance dispersers of rural plant communities

A.G. Auffret, S.A.O. Cousins

Humans are known for their capacity to disperse organisms long distances. Long-distance dispersal can be important for species threatened by habitat destruction, but research into human-mediated dispersal is often focussed to few and/or invasive species. In this paper, we use citizen science to identify the capacity for humans to disperse seeds on their clothes and footwear from a known species pool in a valuable habitat, allowing for an assessment of the fraction and types of species dispersed by humans in an alternative context. We collected material from volunteers cutting 48 species-rich meadows throughout Sweden. Almost all (99%) of the 214 samples contained seeds, with a total of 24 354 seeds of 197 species counted. This represented 34% of the available species pool including several rare and protected species. However, 71 species (36%) are considered invasive elsewhere in the world, highlighting the risk of human-mediated dispersal in sensitive areas. Trait analysis showed that as with other animals, seeds with hooks or other appendages were more likely to be dispersed by humans, while seeds with a persistent seed bank were also over-represented. The more samples received from a meadow resulted in more dispersal, both in terms of the total number of species and representation of the meadow’s source community. The use of motor vehicles by participants resulted in longer dispersal distances than previously recorded for clothing and footwear, with an average distance of 13 km. We consider humans capable seed dispersers, transporting a significant proportion of the plant communities in which they are active, just like more traditional vectors such as livestock. When rural populations were larger, people might have been regular and effective seed dispersers, and the urbanisation resulting in a reduction in humans in the landscape may have exacerbated the dispersal failure evident in declining plant populations today.
With the fragmentation of habitat and changes in land use resulting from agricultural change, and the increased mobility of humans worldwide, the dispersal role of humans may have shifted from providers of regular local and landscape dispersal to providers of much rarer long-distance and regional dispersal, and international invasion.

**Paper V**

**Dispersal geography: a new concept for managing seed dispersal in rural landscapes**

*A.G. Auffret, J. Berg, S.A.O. Cousins*

The difficulties of understanding the mechanics of seed dispersal with regards to attachment, detachment, distance and direction means that dispersal is not often taken into account in conservation planning. Recently, the movement and behaviour of seed dispersal vectors in combination with the landscape they inhabit have been found to aid the prediction of where seeds disperse to. In human-dominated landscapes however, seed dispersal is largely human-mediated and often occurs by non-standard vectors. Human-mediated vectors are very capable of dispersing seeds of a wide range of plants long distances, and despite uncertainties in the whole dispersal process, their movements follow fairly predictable patterns. Here we present a method of visualising seed dispersal processes, where geographical features are used in combination with knowledge of dispersal vectors to identify dispersal potential and limitations in real landscapes, using data which should be readily available to practitioners. To illustrate the approach, we compare dispersal between two time periods in a rural landscape in southern Sweden. As habitat patches have become smaller and more isolated, there has also been a shift in the available seed dispersal vectors, their populations and their movement patterns. Visualising these changes has allowed us to identify concrete management recommendations in specific areas of the landscape. Although our focus was conservation in traditional landscapes, the method could also be used to compare different landscapes, and in the identification of dispersal pathways of invasive species. The need for including dispersal in conservation measures is clear, and we believe it is timely to consider a more general approach, shifting the focus from individual seeds to dispersal vectors, and their interactions with the landscape which surrounds them.
Thank you

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