Summary

Since 1900, huge areas of European heathlands and species-rich grasslands have been converted into arable land or pastures, comprising a serious loss of biodiversity. In addition remnants, that have been preserved, suffer from abandonment (leading to subsequent bush encroachment) desiccation, eutrophication and acidification. Many species-rich heathlands and grasslands on nutrient-poor soil are replaced by monocultures of fast growing perennial grasses. Hence, the ecological restoration of these plant communities has become an important issue, especially in densely populated countries with high-intensive farming.

Recent research has revealed that besides abiotic constraints also biotic constraints can hamper successful restoration of plant communities. After decades of agricultural practice, the soil seed bank of target communities has almost completely disappeared. Hence, in most cases, the success of ecological restoration depends on the transport of seeds from outside sources. In the current fragmented landscape, these sources are often hundreds or event thousands of metres away. Few plant species are able to reach such distances by wind. Large herbivores are expected to disperse many plant species over long distances, potentially enhancing the colonisation of ecological restoration sites (Chapter 1).

Indeed many plant species from grasslands and heathlands appear to be part of the diet of large herbivores and most of these species have at least some probability of surviving chewing and digestion. In total 61 species emerged in dung samples of free-ranging domestic herbivores and 15 species in dung samples of wild herbivores. The highest number of species was found in cattle dung (51 species), followed by horse dung (35 species), sheep droppings (31 species) (Chapter 3), fallow deer droppings (10 species), red deer droppings (9 species) and roe deer droppings (2 species) (Chapter 4). In a seed feeding experiment with 25 plant species fed to fallow deer, 24 plant species survived chewing and digestion (Chapter 5). Seed survival is negatively related to seed mass ($R^2 = 0.43$), positively related to the roundness of seeds ($R^2 = 0.32$) and positively related to seed longevity ($R^2 = 0.28$). Contrary to the ‘foliage-is-the-fruit hypothesis’ seed survival appears to be unrelated to palatability.

The observed number of species recovered from fur of sheep and cattle (Chapter 2) is much lower than the number of species recovered from dung samples. Only four
species attached to the fur of our real sheep and 13 species attached to cattle and sheep dummies. The low number of species that we observed must be due to the short period of possible attachment: three hours for the sheep and one minute for the dummies. Others have found a large number of species in the fleece of sheep and donkeys, cattle and ponies. Also seeds without hooks or other typical appendages classically associated to epizoochory were found in herbivore fur. Plumes ‘designed for’ wind dispersal may also enhance the probability of adhesive dispersal, but also many species without bristles or awns were dispersed. Seed attachment to sheep fur seems little selective in relation to the abundance of seeds in the vegetation. However, in short cattle fur intermediate-sized smooth seeds such as *Medicago lupulina* and large-sized smooth seeds such as *Iris pseudocorus* are not dispersed (Chapter 2).

Seed retention both in fur and in the alimentary tract is long enough to enable the large herbivores to move seeds towards ecological restoration sites hundreds or even thousands of metres away (Chapter 2, Box 6.1). However, especially smaller and more selective herbivores may not use the whole grazing area or avoid the habitat restoration sites (Chapter 3). In our study site, the ‘Dellebuursterheide’, Scottish highland cattle and Exmoor ponies used the whole habitat range from nutrient-poor grassland, heathland, nutrient-rich grassland and habitat restoration site, while sheep were almost entirely restricted to nutrient-poor grassland and heathland (Chapter 3).

As 13 Highland cattle and 18 Exmoor ponies used the site more or less homogenously (Chapter 2), seed input into the ecological restoration site was proportionate to its size: 12.5 % of the total grazing area. Consequently, an approximate total of 5.2 million seeds are deposited in the ecological restoration site per year, 4.1 million seeds in cattle dung and 1.1 million seeds in pony dung. Endozoochory comprises only about 0.2 % of the total seed production of the site (Chapter 3), while the remaining 99.8 % of seeds are mostly dispersed by wind and gravity. An estimation of seed input via epizoochory would be tentative, but is certainly lower than the number of seeds deposited in dung. The longest distance recorded for *Calluna vulgaris* seeds dispersed by wind is 80 m, whereas 94 % of seed dispersed via fur of sheep and 99 % of seeds ingested and defecated by cattle is dispersed beyond 100 m (Chapter 7).

The probability of plants to be dispersed via ingestion and excretion by free-ranging large herbivores appeared to increase with habitat fertility. This implies that more seeds are dispersed from nutrient-rich parts towards nutrient-poor parts of a grazing system than vice versa. Furthermore, in the open nutrient-rich habitat that dung pats create, seeds from nutrient-poor habitat do not germinate, while seeds from nutrient-rich habitat germinate well and grow rapidly. Hence, if heathlands are surrounded by former agricultural pastures, large herbivores can reduce the area occupied by heathland species (Chapter 3).

Simulations of a vegetation-grazer model in a spatially structured environment of feeding-station-sized cells showed that ruminants can create and subsequently maintain patterns of short and tall stands (Chapter 6). Many grazing herbivores prefer short stands irrespective of the availability of tall stands thus keeping short
stands in an immature state with high crude protein content, little structural carbon and high energy content. Simulated vegetation patterns change with herbivore size, stocking rate, productivity and season. However, in many cases patterns are maintained long enough to promote a transition towards grazing-resistant and light-demanding plant species. Plant establishment is higher in open patches than under tall canopy. While, large herbivores continuously visit short stands they disperse plant species throughout the area of short canopy.

When applied with care, large domestic herbivores can increase the availability of target seeds in ecological restoration sites. To achieve this, ecological restoration sites should be grazed in combination with target plant communities, but not with nutrient-rich soils harbouring non-target communities. Remaining heathlands and species-rich grasslands should not be included in the same grazing scheme with adjacent pastures until nutrient loads in such pastures are decreased to appropriate levels for the establishment of species from target communities. In nature reserves on a productivity gradient, plant communities with high conservation interest are best preserved with separate grazing or cutting management. Deer can connect habitat restoration sites with more distant plant communities than livestock. The creation of deer corridors is a more parsimonious measure than the creation of plant corridors, requiring less space and less specific abiotic site conditions. (Chapter 7).