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Donkeys as mobile links for plant seed dispersal in coastal dune ecosystems

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Abstract

Long-distance seed dispersal is a key factor in vegetation dynamics, especially in highly dynamic ecosystems such as dune landscapes. To assess the role of large herbivores in long-distance seed dispersal in dunes, we examined epi- and endozoochory by free-ranging donkeys, released for grazing in a Flemish dune nature reserve. At least 29, respectively 53, plant species were dispersed epi- and endozoochorously by the donkeys. Comparison of the species with the local vegetation using dispersal-relevant plant traits, showed that epi- and endozoochory are additive and complementary dispersal mechanisms, epizoochory being restricted to a narrower range of dispersal-functional plant types. To estimate potential dispersal distances of the seeds, we used empirical studies of the movement and behaviour of the donkeys, in combination with experimental epi- and endozoochorous seed retention times of selected plant species in the dune reserve. The mean potential dispersal distances indicated that the donkeys disperse seeds over the entire 100ha nature reserve, hereby providing a mobile link function between fragmented dune habitats for at least 20% of the local plant species. The influence of large herbivores on dune vegetation dynamics through seed dispersal should be considered in nature management decisions.

Keywords: Endozoochory; Epizoochory; Grazing; Large herbivore; Long-distance dispersal; Nature management; dispersal distance.

Introduction

Vegetation dynamics in highly dynamic landscapes, such as dune ecosystems, partly depends on long-distance seed dispersal. Seed dispersal drives plant spatial dynamics by

influencing the distribution of populations and communities, both at local and regional scales (e.g. Cain *et al.*, 2000; Bullock *et al.*, 2002, Levin *et al.*, 2003, Ozinga *et al.*, 2004). Long-distance dispersal is an extremely important determinant of range shifts of plants, as demonstrated in the case of Holocene plant migrations (Clark *et al.*, 1998; Higgins and Richardson, 1999; Cain *et al.*, 1998; Pakeman, 2001), and in the context of actual and future plant migrations in response to land use changes (Poschlod and Bonn, 1998; Takahashi and Kamitani, 2004) and climate change (Watkinson and Gill, 2002).

To allow a successful colonization of newly formed suitable patches of dune habitat, the presence and functioning of long-distance dispersal vectors is crucial (Bossuyt *et al.*, 2003). Although wind is probably a major dispersal vector in dune landscapes, wind dispersal does – in general – not lead to a displacement of seeds further than a few metres, and is mostly confined to seeds with a low falling velocity (Bullock and Clarke, 2000; Tackenberg *et al.*, 2003). Whereas on open sandy patches wind dispersal may be very efficient (Poschlod and Bonn, 1998), it is likely that other dispersal mechanisms, such as zoochory, are more important in more densely vegetated parts of dunes. In the past agricultural history (Poschlod and Bonn, 1998; Pykälä, 2000; Bruun and Fritzbøger, 2002), Western European semi-natural landscapes e.g. coastal dunes have often been grazed by livestock (De Smet 1961, Massart 1908). Nowadays the use of large herbivores to maintain semi-natural vegetation is commonplace in nature management (Eggermont *et al.*, 1996). In addition, the ongoing debate about reintroduction of plants (Strykstra, 2000) to surpass certain bottlenecks for nature restoration – such as seed dispersal limitation (Zobel *et al.*, 2000; Turnbull *et al.*, 2000; Verheyen *et al.*, 2003) – urges for a better knowledge of dispersal possibilities of plants in endangered ecosystems.

Large herbivores can disperse seeds both externally (in fur or hooves) and internally (via the digestive tract). Both mechanisms – referred to as epizoochory and endozoochory, respectively – are considered very efficient long-distance dispersal modes, providing mobile link functions between habitats (see Lundberg and Moberg, 2003; Couvreur *et al.*, 2004a). In spite of the inherent difficulty of tracing zoochorous long-distance dispersal – which is influenced by complex animal behaviour – recent studies of epizoochory (Fischer *et al.*, 1996; Kiviniemi, 1996; Stender *et al.*, 1997; Kiviniemi and Telenius, 1998; Mrotzek *et al.*, 1999; Heinken, 2000; Graae, 2002; Heinken and Raudnitschka, 2002; Couvreur *et al.*, 2004ab, 2005ab) and endozoochory (Janzen, 1984; Welch, 1985; Gardener *et al.*, 1993; Malo and Suárez, 1995; Pakeman *et al.*, 1998; Heinken *et al.*, 2002; Cosyns, 2004; Cosyns *et al.*, in press; Couvreur *et al.*, 2005a) all point to the large potential of these mechanisms.

In this paper, we compile results on the seed-dispersing role of donkeys used as a management tool in a species-rich coastal dune nature reserve in Belgium. Our principal objectives were (1) to present a list of plant species dispersed by epi- and endozoochory, (2) to compare the zoochorous species with those present in the study area, using morphological and ecological plant traits relevant for dispersal, and (3) to estimate potential dispersal distances of the dispersed seeds. For these purposes, we use empirical data from recent studies by Couvreur *et al.* (2004b, 2005b), Cosyns *et al.* (2005), and Lamoot *et al.* (in press), and we highlight zoochory in the context of coastal dune management.

Material and methods

Study site and vegetation

The study site was the 100ha coastal dune nature reserve 'Houtsaegerduinen', in western Flanders, Belgium (51° 05' N, 2° 35' E) (Fig. 1).

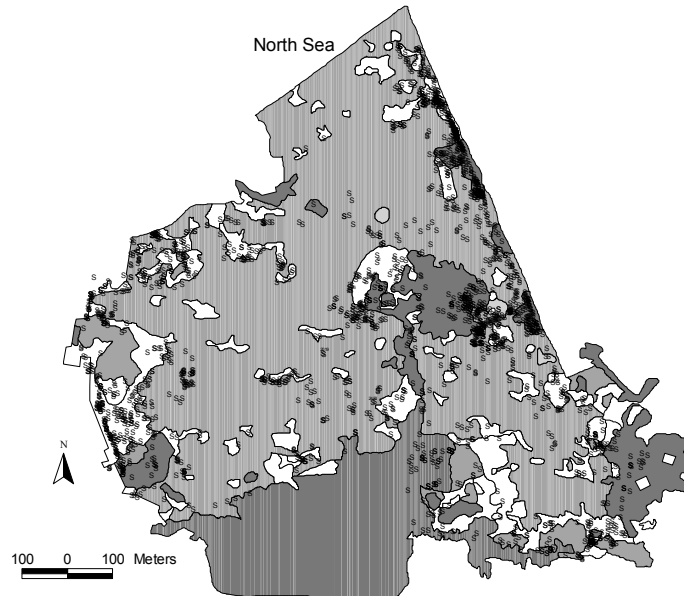


Fig. 1. Study site, the 100ha Flemish nature reserve 'Houtsaegerduinen' along the North Sea coast. Four main vegetation types are indicated with different colours (grassland and moss dune, white; tall herbage vegetation, light grey; shrub, intermediate grey; forest, dark grey). Black circles represent locations of donkeys, recorded with 15min intervals (see 'Material and methods').

The variation in abiotic conditions and the historical land use in this coastal dune ecosystem have led to relatively high plant species richness and a range of different plant communities. Although the dune landscape is dominated by *Hippophae rhamnoides* and *Ligustrum vulgare* shrubs, patches of herb-dominated vegetations are scattered within the scrub (which covers 58% of the area), as small and mostly species poor remnants of dune grassland and mossdune (13%) or as species poor *Calamagrostis epigejos-Arrhenatherum elatius* dominated tall herbage vegetation (4%), which established after scrub degradation. About 25% of the study site was forested with *Alnus glutinosa*, *Populus canescens* and *P. x canadensis* trees. Flowering and fruiting of the plant species in the study site is concentrated from April to October. For nature management purposes, six donkeys were released in the reserve in 1997. The herd comprised 15 animals in 2000, the time of data collection. Plant species nomenclature follows Lambinon *et al.* (1998).

Epi- and endozoochory: data collection and analysis

Epi- and endozoochorous material was collected in the field, using the donkeys in the study site as experimental animals. Their entire fur was brushed during 15 minutes with a fine horse brush, and freshly deposited excrements were collected. Sampling occurred in four different time periods between June and October 2000. In the case of epizoochory, 41 samples were collected: respectively 8, 11, 15 and 7 donkeys were brushed in each of the four time periods. In the case of endozoochory, the number of sampled donkeys was 4 in the first, and 8 in each of the three other periods. In the laboratory, the samples were sown on sterilized potting soil, and allowed to germinate in a greenhouse (see also Couvreur *et al.*, 2005a). During six months, species and seedlings were recorded, and immediately removed to prevent competition and flowering.

To gain insight in the selectivity of epi- and endozoochory, the resulting species list was compared with the local species pool. For this purpose, all 335 species in the study site were assigned to dispersal-functional plant types, resulting from cluster analysis based on dispersal-relevant plant traits, using Gower's Similarity Coefficient and the Sum of Squares method in the program Clustan Graphics 5.08 (Clustan Ltd. 2001). The used plant traits were seed weight, length and width, plant height, life span, dispersal strategy, reproduction type, group, and seedbank persistence, derived from Klotz *et al.* (2002) and Grime *et al.* (1988) (see Couvreur *et al.*, 2005a). Consequently, the species identified in the epi- and endozoochory samples were evaluated with respect to these functional plant types, to see whether certain plant types were overrepresented (see also Couvreur *et al.*, 2005a).

Animal movement and seed dispersal distance

Estimating zoochorous dispersal distances requires information on animal behaviour and seed retention times. Therefore, the movement rate and habitat preference of the donkeys in the study site were derived from observational data (see also Lamoot *et al.*, in press). The data were recorded during 32 observation sessions, conducted between May 2000 and June 2001, and more or less evenly distributed between morning (6-12h), afternoon (12-18h) and evening (18-24h). Each session consisted of a 5h45 min visual observation period on one randomly chosen focal animal, whose exact position was located on a map every 15min (total locations = 768; see Fig. 1). The mean distance travelled in 15min was calculated from the Euclidean distances between each pair of consecutive donkey locations. To estimate mean potential seed dispersal distances, the mean observed movement rate was multiplied with experimentally defined mean zoochorous retention times of seeds. In the case of epizoochory, retention data on horse fur were used, as measured by Couvreur *et al.* (2005b). This is justified since the behaviour of donkeys and horses is quite similar (Cosyns *et al.*, 2001) and since donkey fur is at least as suitable for seed dispersal as horse fur, given the fur characteristics of both animals (see also Couvreur *et al.*, 2004b). In the case of endozoochory, seed retention data in donkey gut as measured by Cosyns *et al.* (2005) were used.

Results

In total, 6675 seedlings of 66 plant species (Table I) were identified from the zoochory samples, covering 20% of the 335 species recorded in the study area. The endozoochory samples contained more species and seedlings (4349 seedlings of 53 species) than the epizoochory samples (2326 seedlings of 29 species). The most abundantly germinating species were *Urtica dioica* (70% of the seedlings in the endozoochory samples), *Cynoglossum officinale* and *Galium aparine* (41% and 31% of the seedlings in the epizoochory samples, respectively). The epizoochory samples contained relatively more grasses (Table I). Of the 66 species, 16 occurred in both epi- and endozoochory samples, 13 were exclusively present in the epizoochory samples and 37 exclusively in the endozoochory samples. Species dominant in the study area (e.g. *Calamagrostis epigejos*, *Arrhenatherum elatius*, *Rubus caesius*) as well as rare species (e.g. *Leontodon saxatilis*, *Myosotis arvensis*) were dispersed zoochorously.

Despite some shared species, the epizoochorously dispersed flora was complementary to the endozoochorously dispersed flora in terms of species composition and plant traits. This was shown by the different distribution of the epi- and endozoochorously dispersed species among the five clusters of dispersal-functional plant types represented in the study site (Table I). While the species exclusively dispersed by epizoochory were almost confined to one dispersal-functional plant type, the species exclusively dispersed by endozoochory belonged to a wide range of plant types. The species dispersed by both mechanisms showed an intermediate selectivity.

The mean distance covered by the donkeys in 15min was 41.9m, indicating a mean rate of 167.6m.h⁻¹. To assess the mean potential epizoochorous dispersal distances of the seeds, we used epizoochorous seed retention data of six species studied by Couvreur *et al.* (2005b), which were – in terms of seed characteristics – comparable to at least some of the epizoochorous species in the study site. In the case of endozoochory, gut retention data of five of the endozoochorously dispersed seeds were available from Cosyns *et al.* (2005). Combination of the donkey movement rate with the mean retention times of dispersed seeds (ranging between 0.29 and 1.52h in the case of epizoochory, and between 64.2 and 79.5h in the case of endozoochory), resulted in mean potential seed dispersal distances ranging between 50 and 250m in the case of epizoochory (Table II), and in the order of magnitude of 10 km in the case of endozoochory (Table III). However, as donkeys do not move in straight lines and are limited by the size of the fenced nature reserve, the realized dispersal distance must have been 1.4km at most. Although the donkeys' preferred habitat is grassland (Fig. 1; ratio of proportion of grassland visits and proportional grassland area is 2.5), they frequent all habitats in the study site (Fig. 1).

Table I. Distribution of the different categories of zoochorously dispersed species over the five dispersal-functional plant types represented among the 335 species in the study site (adapted from Couvreur *et al.*, 2005a). Between brackets are the number of seedlings and the number of animals carrying the species

	Tall woody perennials with large, heavy seeds (berries or wind-dispersed) and a transient seedbank (n=74)	Biennial grasses and herbs with intermediately long seeds adapted to epizoochory (n=63)	Biennial herbs with light seeds adapted to dispersal by wind and ants (n=51)	Perennial herbs with short seeds and various dispersal strategies (n=77)	Biennial or perennial grasses, sedges and herbs with unspecialized seeds, often also reproducing vegetatively (n=70)
sp. excl. in epi (n=13)	0	10	3	0	0
		<i>Cynoglossum officinale</i> (95/32)	<i>Oenothera biennis</i> (70/6)		
		<i>Arctium minus</i> (137/6)	<i>Cerastium semidecandrum</i> (4/3)		
		<i>Arrhenatherum elatius</i> (30/9)	<i>Sonchus asper</i> (1/1)		
		<i>Myosotis arvensis</i> (24/11)			
		<i>Bromus hordeaceus</i> (2/1)			
		<i>Phleum arenarium</i> (2/2)			
		<i>Bidens tripartita</i> (1/1)			
		<i>Dactylis glomerata</i> (1/1)			
		<i>Geum urbanum</i> (1/1)			
		<i>Rumex obtusifolius</i> (1/1)			
sp. excl. in epi+endo (n=16)	0	5	3	2	6
		<i>Galium aparine</i> (712/19; 60/13)	<i>Lythrum salicaria</i> (6/2; 25/4)	<i>Urtica dioica</i> (103/17; 3010/10)	<i>Poa trivialis</i> (18/11; 168/12)
		<i>Anthriscus caucalis</i> (211/14; 1/1)	<i>Senecio jacobaea</i> (18/7; 9/5)	<i>Epilobium ciliatum</i> (1/1; 1/1)	<i>Poa pratensis</i> (1/1; 60/14)
		<i>Phleum pratense</i> (2/2; 63/13)	<i>Sonchus oleraceus</i> (2/2; 9/6)		<i>Holcus lanatus</i> (10/9; 89/9)
		<i>Plantago major</i> (1/1; 43/3)			<i>Artemisia vulgaris</i> (1/1; 68/4)
		<i>Poa annua</i> (2/2; 24/7)			<i>Agrostis capillaris</i> (3/2; 29/8)
					<i>Festuca rubra</i> (3/2; 29/2)
sp. excl. in endo (n=37)	2	6	9	12	8
	<i>Calamagrostis epigejos</i> (26/5)	<i>Galium mollugo</i> (54/2)	<i>Oenothera glazioviana</i> (19/3)	<i>Veronica chamaedrys</i> (64/10)	<i>Carex arenaria</i> (187/14)
	<i>Rubus caesius</i> (3/3)	<i>Juncus bufonius</i> (16/7)	<i>Arenaria serpyllifolia</i> (13/6)	<i>Galium verum</i> (60/6)	<i>Agrostis stolonifera</i> (41/5)
		<i>Plantago lanceolata</i> (16/4)	<i>Silene latifolia subsp. alba</i> (3/2)	<i>Trifolium repens</i> (20/3)	<i>Stellaria media</i> (7/5)
		<i>Trifolium dubium</i> (11/3)	<i>Chelidonium majus</i> (2/2)	<i>Juncus articulatus</i> (17/7)	<i>Geranium molle</i> (5/2)
		<i>Aira praecox</i> (3/2)	<i>Conyza canadensis</i> (2/2)	<i>Achillea millefolium</i> (4/3)	<i>Koeleria albescens</i> (3/2)
		<i>Plantago coronopus</i> (1/1)	<i>Crepis capillaris</i> (2/2)	<i>Eupatorium cannabinum</i> (4/3)	<i>Chenopodium album</i> (1/1)
			<i>Hypochaeris radicata</i> (2/1)	<i>Cerastium fontanum</i> (3/2)	<i>Sagina procumbens</i> (1/1)
			<i>Capsella bursa-pastoris</i> (1/1)	<i>Epilobium hirsutum</i> (2/1)	<i>Vicia cracca</i> (1/1)
			<i>Solanum nigrum</i> (1/1)	<i>Epilobium montanum</i> (1/1)	
				<i>Leontodon saxatilis</i> (1/1)	
				<i>Ranunculus repens</i> (1/1)	
				<i>Rumex crispus</i> (1/1)	

Table II. Mean retention time in horse fur (comparable to donkey fur) of seven experimental plant species as measured by Couvreur *et al.* (2005b). The retention times were used to assess the mean potential dispersal distances of the seeds by epizoochory, based on a mean movement rate of 167.6m.h⁻¹ of donkeys (see 'Results'). In the last two columns, a brief description of the seeds is given, as well as some epizoochorous species in the study site with comparable seed morphology

Experimental epizoochorous species	Mean retention time on horse fur (h)	Mean potential dispersal distance (m)*	Seed description	Comparable epizoochorous species in study site
<i>Anemone nemorosa</i>	1.19	199.4	Intermediate size, not adhesive	<i>Arrhenatherum elatius</i>
<i>Geum urbanum</i>	1.52	254.8	Intermediate size, adhesive	<i>Arctium minus</i> , <i>Anthiscus caucalis</i> , <i>Cynoglossum officinale</i> , <i>Galium aparine</i> , <i>Senecio jacobea</i>
<i>Ranunculus acris</i>	0.98	164.2	Intermediate size, not adhesive	
<i>Prunella vulgaris</i>	1.18	197.8	Very small, not adhesive	<i>Myosotis arvensis</i> , <i>Lythrum salicaria</i>
<i>Centaurea jacea</i>	0.63	105.6	Small, elongate, not adhesive	<i>Holcus lanatus</i> , <i>Festuca rubra</i> , <i>Poa trivialis</i>
<i>Oenothera biennis</i>	1.43	239.7	Very small, not adhesive	<i>Oenothera biennis</i> , <i>Cerastium semidecandrum</i> , <i>Urtica dioica</i>
<i>Heracleum sphondylium</i>	0.29	48.6	Large, flat, not adhesive	

* this distance is not the realized dispersal distance, since animals do not move in one direction and since the size of the nature reserve does not allow dispersal over more than 1.4km.

Table III. Mean retention time in donkey gut of five plant species as measured by Cosyns *et al.* (2005). The retention times were used to assess the mean potential dispersal distance of the seeds by endozoochory, based on a mean movement rate of 167.6m.h⁻¹ of donkeys (see 'Results'). In the last two columns, a brief description of the seeds is given, as well as some endozoochorous species in the study site with comparable seed morphology

Experimental endozoochorous species	Mean retention time in donkey gut (h)	Mean potential dispersal distance (m)*	Seed description	Comparable endozoochorous species in study site
<i>Agrostis capillaris</i>	69.0	11564.4	Intermediate size, not adhesive	<i>Agrostis stolonifera</i> , <i>Holcus lanatus</i> , <i>Festuca rubra</i>
<i>Carex arenaria</i>	68.7	11514.1	Intermediate size, slightly adhesive	
<i>Plantago lanceolata</i>	64.2	10759.9	Intermediate size, adhesive (mucus)	<i>Plantago major</i> , <i>Plantago coronopus</i>
<i>Poa pratensis</i>	66.0	11061.6	Very small, not adhesive	<i>Poa trivialis</i> , <i>Poa annua</i>
<i>Trifolium repens</i>	79.5	13324.2	Small, not adhesive	<i>Trifolium dubium</i>

* this distance is not the realized dispersal distance, since animals do not move in one direction and since the size of the nature reserve does not allow dispersal over more than 1.4km.

Discussion

Epi- and endozoochory

Donkeys are clearly able to contribute to long-distance dispersal through epi- and endozoochory in coastal dune ecosystems. At least one fifth of all species (66 of 335 species) in the study area was dispersed by the donkeys, and it is likely that more intensive sampling would reveal more species (see Cosyns *et al.*, in press). Despite 13 species in common, the epizoochorous species composition was additive and complementary to the endozoochorous one in terms of species trait syndromes. The exclusively epizoochorous species were almost exclusively confined to one of the five dispersal-functional plant types represented among the species in the study site (*i.e.* the biennial grasses and herbs with intermediately long seeds adapted to epizoochory), while the exclusively endozoochorous species were spread over all five plant types, and the shared species showed an intermediate behaviour (Table I).

Dispersal distances

In terms of seed dispersal distances, epizoochory and endozoochory present an interesting contrast. Seed retention in guts includes an extended lag prior to defecation of at least 12h in the case of donkeys (Cosyns *et al.*, 2005). In contrast, seeds that are attached to fur immediately start to fall (*e.g.* Couvreur *et al.*, 2005b). This difference in time lag explains the calculated mean potential seed dispersal distances in the case of epi- and endozoochory (Tables II and III). However, these mean potential dispersal distances only confirm that the donkeys disperse seeds over the entire study site, as it is obvious that animals do not move in straight lines. Moreover, the suggested shorter dispersal distances of epizoochorous seeds are biased since few very adhesive seeds were used as experimental seeds (while the abundant species observed in donkey fur were very adhesive, *e.g.* *Cynoglossum officinale*, *Anthriscus caucalis*, *Arctium minus*, *Galium aparine*). In fact, there is no theoretical maximum to epizoochorous dispersal distances. Seeds can remain in fur until an animal molts or dies, but in practice the turnover of seeds is relatively fast (Couvreur *et al.*, 2005a). The potential for long-distance endozoochory depends on the survival of seeds ingested by the dispersers and the effects of the digestive system on the mean retention time of germinable seeds. Our field study shows the germination of many seedlings of a wide variety of grassland species. This implies that a large number of seeds must have been consumed to compensate for the generally low germination success after gut passage (Cosyns *et al.*, 2005). In fact, the efficiency of endozoochory for most temperate grassland species may be questioned, since the process of mastication and gut passage appears to impose a high cost. Furthermore, seeds dispersed in animal faeces experience a very different post-dispersal environment compared to seeds that fall on bare ground (Bakker and Olff, 2003). However, the fact that zoochory is an explicit long-distance dispersal mechanism will increase the chance of escaping density-dependent mortality (Connel, 1971; Janzen, 1970), and is hypothesized to result in directed dispersal (Wenny, 2001). As the donkeys' preferred habitat is grassland (Fig. 1 and Results), most species may indeed have a greater chance to be dispersed in grassland. Nevertheless, the donkeys also connect other habitat types, as they frequent all habitats in the study site (Fig. 1).

More detailed modelling of the complex mechanism of zoochory could yield estimations of realized seed shadows (see Vellend *et al.*, 2003 in the context of endozoochory; Higgins *et al.*, 2003 and Couvreur *et al.*, unpublished, in the context of epizoochory). For testing such models, seed numbers observed on animals are invaluable as an independent source of data (Levin *et al.*, 2003).

Implications for nature conservation and management

The present study highlights the relevance of donkeys as long-distance seed dispersal vectors. For ecosystem conservation and restoration purposes, the dispersal possibilities of plants are of crucial importance, especially in view of the present degree of habitat deterioration and fragmentation, leading to dispersal limitation. Therefore, our results contribute to the scientific basis required to guide decisions concerning the introduction of large domesticated herbivores for nature management purposes. As dispersal vectors, they provide a critical ecosystem function in a conservation context by linking fragmented patches of natural habitat (see Pykälä, 2000; Lundberg and Moberg, 2003; Couvreur, 2004a), with a reasonable chance of directed dispersal (cf. Wenny, 2001). In our study site, a 100ha coastal dune landscape, the donkeys disperse seeds among all habitat types throughout the reserve. To utilize the full seed dispersal potential of both wild ungulates and domesticated herbivores in fragmented habitats on a larger scale, connections between different patches of similar habitat as well as connections between nearby coastal dune nature reserves should receive attention. Especially in the context of climate change (Watkinson and Gill, 2002), it might be crucial to allow plant species to migrate across the limits of the nature reserves in which they might not much longer be able to survive.

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