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Dung beetles as secondary seed dispersers in a temperate grassland

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Abstract

The two-phase dispersal event in which dung beetles move seeds after endozoochory is often assumed to be advantageous for plant regeneration. Because seeds are expected to end up in favourable and safe germination sites, it is considered as an example of directed dispersal. However, literature so far is restricted to tropical rain forest ecosystems, while data for temperate regions are lacking. In this study, the effect of dung beetles on seedling establishment of endozoochorically dispersed seeds is evaluated for a temperate grassland ecosystem. We performed a field experiment in which cages excluded dung beetles from horse and cattle dung samples with mixed-in grass seeds. Seed germination from these samples was significantly higher than that from samples which were accessible to dung beetles. This indicates that the effect of dung beetles on short-term seedling establishment was negative, which contrasts with the patterns found for large-seeded species used in tropical studies. This is most likely attributed to the lack of roller species and the larger depth at which tunneling *Geotrupes* species bury seeds.

Zusammenfassung

Eine zweiphasige Ausbreitung, bei der Samen im Anschluss an endozoochoren Transport von Dungkäfern weiterbewegt werden, wird oft als günstig für die pflanzliche Regeneration angenommen. Da man vermutet, dass die Samen günstige und sichere Keimungsplätze erreichen, wird dies als Beispiel für eine gerichtete Ausbreitung angesehen. Die Literatur beschränkt sich auf tropische Regenwälder, während Daten für gemäßigte Regionen fehlen. In dieser Studie wird der Effekt von Dungkäfern auf die Etablierung von Keimlingen aus endozoochor verbreiteten Samen in einem Grasland-Ökosystem untersucht. Wir führten ein Freilandexperiment durch, bei dem die Dungkäfer durch Käfige von Pferde- bzw. Rinderdungproben, denen Grassamen beigemischt waren, ferngehalten wurden. Die Samenkeimung von diesen Proben war signifikant höher als die von Proben, die den Dungkäfern zugänglich gewesen waren. Dies deutet darauf hin, dass die Dungkäfer die Etablierung von Keimlingen im engeren Zeitrahmen negativ beeinflussten, was im Gegensatz zu Ergebnissen steht, die in tropischen Studien mit großsamigen Arten gefunden wurden. Höchstwahrscheinlich ist dies auf das Fehlen von Pillendrehern zurückzuführen, sowie auf die größere Tiefe, in die die grabenden *Geotrupes*-Arten die Samen verfrachten.

Keywords: Seed dispersal; Secondary dispersal; Diplochory; Seed burial; *Agrostis*; *Poa*

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Introduction

Acting as dispersal agents, animals may take plant seeds to non-random microhabitats that are well-suited for establishment and growth. This process, referred to as 'directed dispersal', was distinguished by Howe and Smallwood (1982) as one of three major advantages of seed dispersal, and is assumed to be more common than formerly thought (Wenny, 2001). Directed dispersal is considered to be a key step in diplochory (Vander Wall & Longland, 2004), in which seeds are dispersed in two successive phases, each involving a different dispersal agent. According to Vander Wall and Longland (2004), the benefits offered by the different phases differ: second phase dispersers (e.g. ants, rodents, corvids) take seeds to microsites that are more suitable for establishment than those reached by phase one dispersers (e.g. wind, herbivores). One particular case of diplochory occurs when dung beetles act as secondary dispersers of seeds contained in vertebrate dung.

Within the dung beetles (coprophilous species within the Scarabaeidae subfamilies Aphodiinae, Geotrupinae and Scarabaeinae [classification following Janssens, 1949, 1960]), three functional groups are distinguished: dwellers, tunnelers and rollers (Cambefort & Hanski, 1991). Aphodiinae are predominantly dwellers: these small-sized beetles (generally less than 10 mm in length) eat their way through the dung and deposit their eggs without constructing a nest or chamber. Geotrupinae and most Scarabaeinae are tunnelers: they dig a more or less vertical tunnel beneath a dung pat and move the dung to the shaft base. Many Scarabaeinae, specified as rollers, construct a dung ball and transport this over a distance prior to burying it (telecoprid nidification sensu Bornemissza, 1969). Dung beetles do not eat seeds (Andresen & Feer, 2005), so tunnelers and rollers may contribute to directed dispersal by moving and burying seeds along with the dung.

So far, studies on secondary seed dispersal by dung beetles and its influence on plant regeneration almost exclusively focused on tropical rain forest ecosystems. In a review, Andresen and Feer (2005) concluded that burial has both a positive impact through lower seed predation and a negative impact through decreased seedling emergence. Little is known, however, about the net outcome of these antagonistic effects. Only Andresen and Levey (2004) really followed the fate of seeds placed in dung until seedling establishment in a (Central Amazonian) rain forest ecosystem. Their results, concerning 11 large-seeded tree species and howler monkey dung, indicated that seeds buried by dung beetles were on average twice as likely to become seedlings than unburied seeds. In the only study investigating dung beetle mediated seed dispersal outside tropical regions we know about, Wicklow, Kumar, and Lloyd (1984) found a subtropical roller species (Kohlmann, 1991) to facilitate seedling establishment of a prairie grass species in North America.

More studies are needed to ascertain if this positive effect also holds for other climate regions and ecosystems (Andresen & Feer, 2005), because it is reasonable to assume that important differences in the dung beetle communities or the plant species involved may lead to deviant patterns. For instance, at lower latitudes dung beetle communities are dominated by rolling or tunneling Scarabaeinae, whereas the northern temperate regions are characterized by a dominance of the dwelling genus *Aphodius* (Aphodiinae), normally accompanied by one or a few species of tunneling Geotrupinae (Hanski, 1991).

In this study, we aim to test the hypothesis that dung beetle activity has an overall positive effect on successful germination of seeds present in dung in a temperate coastal dune ecosystem. A field experiment was constructed, in which the effect of dung beetle presence on short-term seedling establishment from horse and cattle dung was tested. This 'main experiment' was supplemented by some supplementary experiments, i.e. controls to evaluate the main setup in detail and a study of the dung beetle fauna present within.

Materials and methods

Study area and local dung beetle assemblage

The field experiment was set up in the nature reserve 'Westhoek' (Belgium, 51°04′50″N–2°34′19″E), consisting of over 340 ha of coastal dune landscape. It is characterized by a spatially heterogeneous mosaic of open dunes, grey dunes, grassland, shrub and woodland. Since 1996, part of the area is grazed by cattle and several equine breeds, restoring extensive grazing previously maintained by livestock. In a recent study of the associated dung beetle fauna, 15 species were found (Struyve, 2002), 12 of which belong to the dweller genus *Aphodius* Illiger. *Onthophagus similis* Scriba, *Geotrupes niger* Marsham and *Geotrupes spiniger* Marsham were the tunneler species found. No roller species were present in the area. Hence, functionally, the overall dung beetle fauna can be considered as typical of a temperate ecosystem (Hanski, 1991).

Main experiment

At each of two grassland sites within the study area, the effect of dung beetle activity on seed germination was assessed using the same experimental randomized block design. The sites consisted of preliminary mown grasslands located within livestock-excluding fences, the