Natural History Note

Are Gastropods, Rather than Ants, Important Dispersers of Seeds of Myrmecochorous Forest Herbs?

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Submitted February 10, 2011; Accepted September 12, 2011; Electronically published November 22, 2011

Online enhancements: videos. *Dryad data:* http://dx.doi.org/10.5061/dryad.p3p0621d.

abstract: Seed dispersal by ants (myrmecochory) is widespread, and seed adaptations to myrmecochory are common, especially in the form of fatty appendices (elaiosomes). In a recent study, slugs were identified as seed dispersers of myrmecochores in a central European beech forest. Here we used 105 beech forest sites to test whether myrmecochore presence and abundance is related to ant or gastropod abundance and whether experimentally exposed seeds are removed by gastropods. Myrmecochorous plant cover was positively related to gastropod abundance but was negatively related to ant abundance. Gastropods were responsible for most seed removal and elaiosome damage, whereas insects (and rodents) played minor roles. These gastropod effects on seeds were independent of region or forest management. We suggest that terrestrial gastropods can generally act as seed dispersers of myrmecochorous plants and even substitute myrmecochory, especially where ants are absent or uncommon.

Keywords: myrmecochory, gastropodochory, Arion, slug, seed dispersal.

Introduction

Ant dispersal of seeds has strongly promoted plant diversification in angiosperms (Lengyel et al. 2010), with at least 11,000 plant species from 77 families thought to be adapted for seed dispersal by ants (Lengyel et al. 2010), many by means of a nutrient-rich seed appendage, the elaiosome (Sernander 1906). These so-called myrmecochores are found almost worldwide (Beattie 1985; Lengyel et al. 2010) and dominate plant communities in many habitats, in terms of both species richness and abundance (Sernander 1906; Ulbrich 1919; Handel et al. 1981). In a seminal study correlating the abundance and species richness of myrmecochores with the abundance of ants in 10 different forest types from West Virginia, Beattie and Culver (1981) found that ant abundance was generally positively correlated with the number of myrmecochorous species in these forests. There were, however, exceptions to this general pattern involving forests of high myrmecochore abundance but low abundance or even absence of ants. Similarly, in central Europe a diverse community of myrmecochores can be found in forests dominated by European beech (*Fagus sylvatica* L.), whereas ants can be rare and of low species diversity compared with that in other forest habitats (Seifert 1986; Wlodarczyk 2010). This suggests that seed dispersal of myrmecochores in European beech forests may well be ant limited.

In Europe, many forest myrmecochores are used as indicators of ancient woodlands (Wulf 1997; Orczewska 2010). However, such myrmecochores were recently found to colonize forests more rapidly than what would be possible if these plants relied solely on vegetative growth or if their seeds were not dispersed by animals (Brunet and von Oheimb 1998*a*; Verheyen and Hermy 2001; Orczewska 2009). This implies that animal vectors do transport diaspores of forest myrmecochores. If ants are rare, it may well be that other animals act as myrmecochore seed dispersers in beech forests. Rodents and insects other than ants are known to be seed predators of myrmecochores but are unlikely to disperse their seeds (Heithaus 1981; Ohara and Higashi 1987). Recently, several of us (Türke

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Am. Nat. 2012. Vol. 179, pp. 124–131.
DOI: 10.1086/663195

Video 1: Still photograph from a video (video 1, available online) showing a carabid beetle entering a seed depot (treatment with access to insects only) by crossing the slug-repellent paste, picking up a seed of wild ginger (*Asarum europaeum*), and leaving the depot with the seed. The video was recorded in an unmanaged beech forest.

et al. 2010) demonstrated that terrestrial gastropods consumed seeds of the two myrmecochores, wood anemone (*Anemone nemorosa* L.) and European wild ginger (*Asarum europaeum* L.), in an unmanaged beech forest in central Germany and that rates of seed removal by gastropods were higher than those for insects or rodents. In the laboratory, several slug species either consumed elaiosomes or swallowed seeds entirely. Because the viability of swallowed and defecated seeds was not reduced, these gastropods appear to act as seed dispersers rather than as seed predators (Türke et al. 2010). Moreover, the red slug (*Arion rufus* L.) may on average disperse seeds farther than ants (Türke et al. 2010). This suggests that gastropods could be important seed dispersers of forest myrmecochores and could account for their rapid colonization of forests.

We tested two hypotheses concerning seed dispersal of myrmecochores in beech forests. First, we tested the hypothesis that myrmecochore abundance is positively related to the abundance of gastropods rather than to the abundance of ants in beech forest sites of varying management types. Second, we tested the hypothesis that gastropods rather than ants are the most important seed dispersers of myrmecochores in beech forests by differentially excluding rodents, gastropods, and insects to the seeds of two abundant myrmecochores.

Material and Methods

Study Areas

The study was conducted in three regions of Germany within the framework of the Biodiversity Exploratories project (http://www.biodiversity-exploratories.de; Fischer et al. 2010): (1) the UNESCO Biosphere Reserve Schorfheide-Chorin in northeastern Germany (the northeastern region; 53°00′N, 13°76′E), (2) Hainich National Park and its surrounding areas (Hainich-Dün) in central Germany (the central region; 51°15′N, 10°47′E), and (3) the UNESCO Biosphere Area Schwäbische Alb (Swabian Jura) in southwestern Germany (the southwestern region; 48°43′N, 9°39′E). The exploratories comprise one hundred fifty 100 × 100-m experimental forest plots of different management types. We selected the 105 forest plots that were dominated by European beech.

Species Involved

European beech is a commercially and ecologically important tree species that is widely distributed over large parts of Europe; it is the most common—and on many sites the dominant—deciduous tree in Germany (Czajkowski et al. 2006). A great number of the herb species in mature beech forests are thought to be myrmecochores (Sernander 1906; Ulbrich 1919). In our seed-removal experiment, we used diaspores (referred to as seeds in the following) of two myrmecochorous spring geophytes, wood anemone (*Anemone nemorosa*) and European wild ginger (*Asarum europaeum*). Seeds of both plant species bear an elaiosome (Servigne 2008), although it is rather indistinct in wood anemone. Wood anemone forms dense carpets in forests in the central and southwestern regions but is less abundant in the northeastern region. Wild ginger is also common in the central and southwestern regions but was not recorded in the northeastern region. Ant nest densities in mature beech forests are often low and can mostly be attributed to the red ant (*Myrmica ruginodis* Nyl.) and the arboreal brown tree ant (*Lasius brunneus* Latreille; Seifert 1986; Wlodarczyk 2010). In contrast, beech forests harbor a diverse fauna of terrestrial gastropods (Müller et al. 2005), including a number of species that are large enough to potentially disperse seeds endozoochorously. Among these species, the abundant red slug (*Arion rufus*), growing to sizes of 10–20 cm, has been described as a seed disperser of wood anemone and wild ginger (Türke et al. 2010). Therefore, we focused on this species in our observational slug survey (see fig. A1 for an image of one consuming a seed of European wild ginger). However, we suggest—or at least cannot exclude—that other gastropods may disperse the seeds of myrmecochores, although direct evidence is unavailable for most species.

Vegetation, Ant, and Gastropod Surveys

In 2009, we recorded vegetation in a 20 × 20-m core area of each plot in both spring and summer/autumn. We identified all herbaceous vascular plants (excluding phanerophyte seedlings) and estimated their percentage cover. We classified species as ant dispersed according to Servigne's (2008) list of 260 European ant-dispersed plant species.

In 2008, ants and gastropods were sampled using three pitfall traps per plot; traps had a funnel diameter of 15 cm (see Lange et al. 2011 for general trap design). For all plots, samples were collected monthly from May to October. Ants and gastropods were counted in 4–18 samples (mean ± SE, 11.5 ± 0.3) per plot and in 1,211 samples in total. For some plots, fewer samples than intended (a minimum of 10 samples) were sorted because some traps were destroyed by large mammals. Pitfall traps provide evidence for the presence of seed-dispersing ants in the plot but not for their abundances because ants may recruit their nestmates by pheromone trails to the trap. Therefore, we used the proportion of pitfall trap samples with ants as a measure of ant abundance. Species of ants or gastropods were not identified.

Seed-Removal Experiment

For our seed-removal experiment, we collected ripe seeds of wood anemone and wild ginger in the central region and in deciduous forests around the city of Jena (coordinates: 50°56′N, 11°36′E) in May and June 2009, respectively. Seeds were stored at −20°C until the start of the experiment to prevent desiccation of elaiosomes. The seed-removal experiment was conducted in all three regions and in 47 plots representing different forest management types in each region. In each plot, we exposed seeds in batches of 10 on 10 × 10-cm wooden plates (seed depot), sheltered against rain by a 12.5 × 12.5-cm plastic roof supported by toothpicks. Seeds dropped by plants were exposed on the forest floor, similar to our seed depots. We offered seeds while our study species were fruiting; we exposed seeds from May 7 to June 11, 2009, for wood anemone and from June 29 to July 25, 2009, for wild ginger.

Video 2: Still photograph from a video (video 2, available online) showing a mature red slug (*Arion rufus*) swallowing wild ginger seeds (*Asarum europaeum*) after it had entered a seed depot with restricted access to gastropods and insects in an unmanaged beech forest.

Video 3: Still photograph from a video (video 3, available online) showing a worker of the black-backed meadow ant (*Formica pratensis*) carrying a seed of wild ginger (*Asarum europaeum*) over an ant bridge, leaving a seed depot with access to rodents and insects in the laboratory.

We applied four treatments as described by Türke et al. (2010): (1) all animals had access (control), (2) only rodents and insects had access, (3) only gastropods and insects had access, and (4) only insects had access. We excluded gastropods by outlining the wooden plate with slug-repellent paste (IRKA Schneckenabwehrpaste; R+M Gartenbedarf GbR). We excluded rodents by covering the seed depots with an 11 × 11 × 4-cm metal cage with a mesh size of 28 mm × 10 mm. We provided access for insects while excluding gastropods by using zinc-coated wire (18 cm long, 2.8 mm wide) to connect the seed depots on each of their four sides to the forest floor.

Differential effectiveness of the animal-exclusion techniques were confirmed in preliminary experiments (appendixes S5–S8 in Türke et al. 2010). We used video recordings to further evaluate the influence of exclusion methods on arthropods in the field (8-day observations in an unmanaged beech forest in the central region in July and August 2010) and on ants (the black-backed meadow

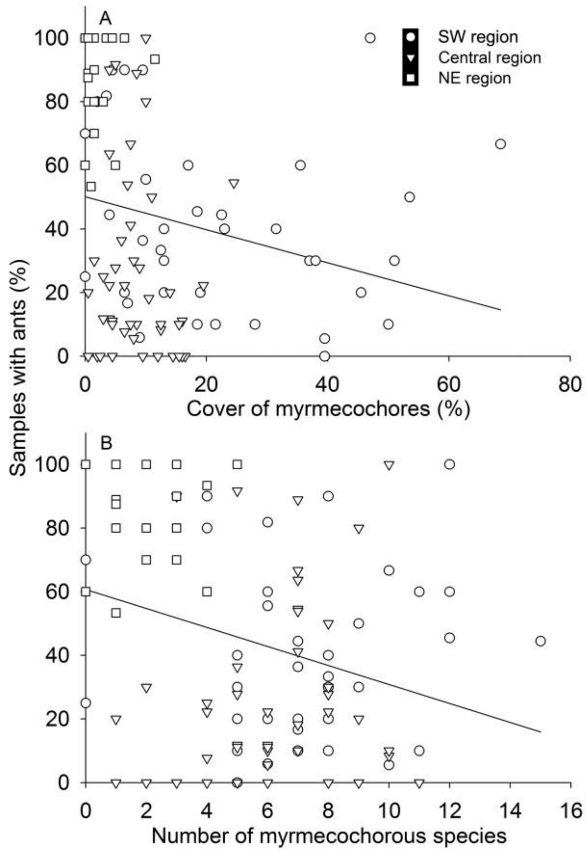

Figure 1: The proportion of pitfall trap samples containing ants decreased with increases in both the cover of myrmecochores (*A*) and the number of myrmecochorous species (*B*; $N = 105$ plots). Least squares regression lines are given to illustrate the trends. SW = southwestern, NE = northeastern.

ant [*Formica pratensis* Retzius], the small black ant [*Lasius niger* L.], and the common elbowed red ant [*Myrmica scabrinodis* Nyl.]) in the laboratory (48 h in August 2010). The video recordings in the field showed that elaiosome-feeding arthropods visited depots with slug repellent less often than depots without slug repellent. However, seed-removing arthropods (carabids) removed similar numbers of seeds from depots with or without slug repellent (for an example video, see video 1, available online). Thus, our methods might underestimate elaiosome damage by arthropods but not seed removal. Interestingly, in the field not a single ant was observed, whereas some seeds were removed by slugs (for an example video of *A. rufus* swallowing *A. europaeum* seeds, see video 2, available online). In the laboratory, ants removed most seeds of wild ginger from depots protected by slug repellent by means of the experimental bridges (for an example video of the black-backed meadow ant [*F. pratensis* Retzius], see video 3, available online), but no seeds of wood anemone were removed or elaiosomes consumed by ants.

The different treatments were applied to seed depots in the corners of two 4 × 4-m squares (subplots) per plot, which were situated in two opposite corners of each 100 × 100-m plot for a total of 752 seed depots (47 plots × two subplots × four treatments × two plant species). Three days after exposure we counted the remaining seeds and recorded feeding traces on seeds or elaiosomes. Eleven seed depots were destroyed by animals—most likely by wild boars—and were excluded from the analysis. We also excluded 19 seed depots where gastropod exclusion had failed, as indicated by mucus. Therefore, we analyzed data from 722 seed depots.

We additionally counted all red slugs we observed, walking a 10 × 10-m area in five transect lines with the subplot in its center. During the wood anemone experiment we counted slugs on four consecutive days in each subplot, and during the wild ginger experiment we counted slugs on the first and on the fourth day. Sampled individuals in each region were dissected for species identification.

Statistical Analysis

Statistical analyses were performed using R 2.8.0 (R Development Core Team 2011). We tested for a correlation between ant or gastropod abundance and the cover or species number of herbs or myrmecochores with Spearman's rank correlation. We used a linear mixed-effects model to analyze the variation between different treatments in the number of removed seeds and in the remaining seeds with consumed elaiosomes (fit by the Laplace approximation for binomial errors using the "lmer" function in the lme4 package). Plant species, regions, and treatments were treated as fixed effects, and plots and subplots nested in plots were treated as random factors. Multiple comparisons of means (Tukey contrasts) were performed using the function "glht" in the multcomp package. Means and SEs of variables are given throughout.

Results

Myrmecochore and Seed Disperser Relationship

We recorded 231 herb species in the 105 plots, of which 46 were classified as myrmecochores. The number of myrmecochores increased with the number of herb species ($r_s = 0.79$, $P < .001$, $N = 105$).

Ants were trapped in 44% ± 3% of the traps per plot, ranging from 0% (11 plots) to 100% (11 plots). The proportion of pitfall trap samples with ants (i.e., our measure of ant abundance) was independent of the cover of all herbs ($r_s = -0.15$, $P = .12$) and of the total number of

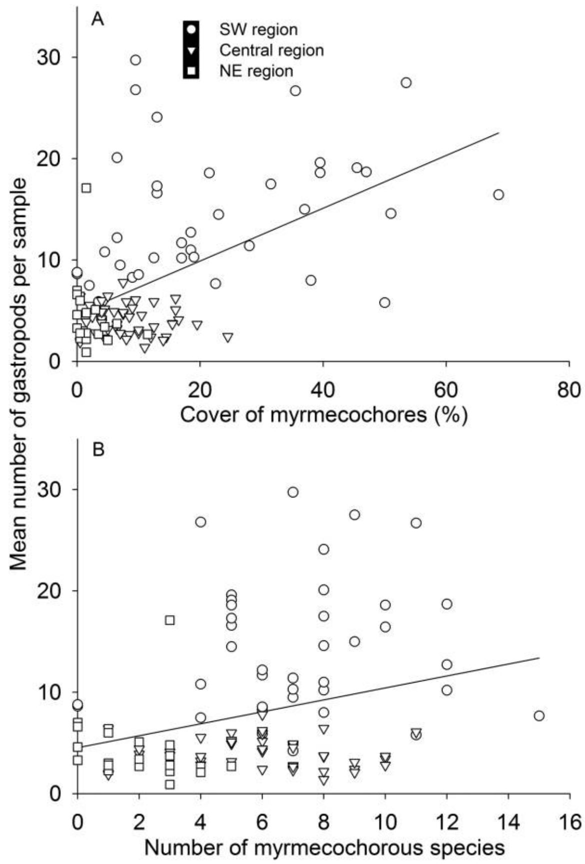

Figure 2: The abundance of gastropods increased with increases in both the cover of myrmecochores (*A*) and the number of myrmecochorous species (*B*; $N = 105$ plots). Least squares regression lines are given to illustrate the trends. SW = southwestern, NE = northeastern.

herb species ($r_s = -0.05$, $P = .59$). However, it was significantly negatively—rather than positively—correlated with the cover of myrmecochores in plots ($r_s = -0.33$, $P < .001$; fig. 1*A*) and with the number of myrmecochorous species ($r_s = -0.26$, $P = .007$; fig. 1*B*).

The mean number of gastropods per pitfall trap sample (7.9 ± 0.6; range = 0.9–29.7 individuals/sample × plot) increased with increases in the cover of both myrmecochores ($r_s = 0.42$, $P < .001$; fig. 2*A*) and all herb species ($r_s = 0.33$, $P < .001$) and with the number of myrmecochorous ($r_s = 0.25$, $P = .011$; fig. 2*B*) and all herb species ($r_s = 0.23$, $P = .020$).

Seed-Removal Experiment

In total, 26% of all seeds were removed from depots, fewer of wood anemone (598 seeds [17%]) than of wild ginger (1,299 seeds [35%]; generalized linear mixed model [GLMM]; $z = -20.53$, $P < .001$; fig. 3). Ten percent of the seeds that remained in depots had feeding traces on elaiosomes, again fewer of wood anemone (109 seeds [3%]) than of wild ginger (631 seeds [17%]; GLMM for the sum of removed seeds and remaining seeds with elaiosome damage; $z = -32.26$, $P < .001$).

Seed removal differed significantly between treatments (GLMM with Tukey post hoc tests; $P < .001$; fig. 3). Insects contributed only marginally to seed removal and elaiosome damage (fig. 3). Moreover, there was no difference between the treatments where rodents and insects had access and only insects had access ($z = 1.27$, $P = .57$; fig. 3), indicating that the impact of rodents on seeds was negligible. This pattern was consistent throughout regions and management types.

Red slugs were observed in 85% of the plots at the time of the experiment, ranging from 0 to 15 specimens (0.78 ± 0.04) per 100 m^2, and 48% of the seed depots without restricted entrance for gastropods had unambiguously been visited by gastropods, as indicated by mucus or feces. Within seed depots, we recorded 78 snails and 39 slugs, including 29 red slugs.

Discussion

Our results, along with earlier published evidence, suggest that dispersal by gastropods may be common and more important than dispersal by ants for myrmecochores in central European beech forests. First, ant and myrmecochore abundances were negatively related to each other (fig. 1). Mature shaded beech forests are rather moist and cool, whereas most ants prefer warm habitats (Seifert 2007). Only a few ant species exist in shaded beech forests (Seifert 1986; Wlodarczyk 2010). Moreover, their nest densities are low. In contrast, some very common myrmecochores in beech forests, such as wood anemone or bear's garlic, depend on moisture (typical for most mature beech forests; Tutin 1957; Shirreffs 1985). Thus, at least in European beech forests, habitat requirements of ants and myrmecochores differ profoundly. In contrast, gastropods—in particular, slugs—depend on sufficient humidity (Barker 2001).

Second, myrmecochores in beech forests inevitably require animal vectors for dispersal. Dispersal of seeds of wood anemone by gravity will be a few centimeters only, and its annual clonal growth is less than 3 cm per year (Shirreffs 1985). Such distances are much too short to account for observed migration rates (Brunet and von Oheimb 1998*a*; Orczewska 2009). The importance of animal vectors for myrmecochore dispersal is also emphasized by studies from temperate deciduous forests showing that the majority of seeds or elaoiosomes on seeds fall prey to seed predators when there is no dispersal or when ro-

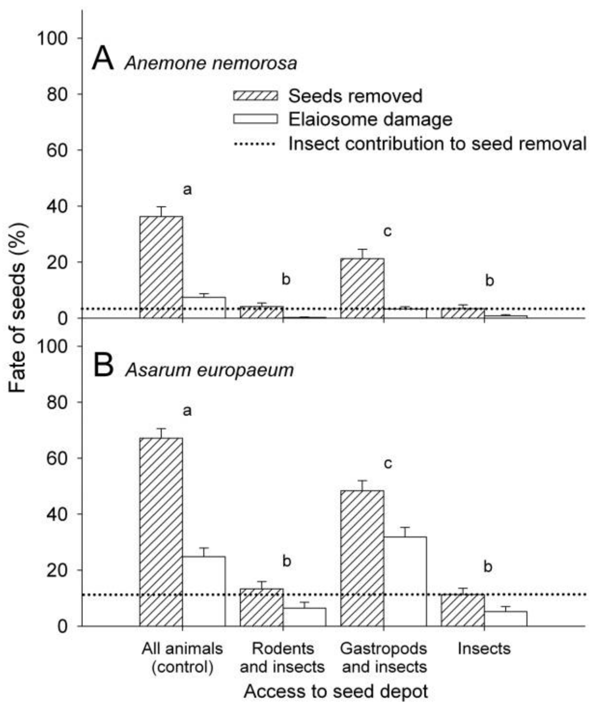

Figure 3: Fate of seeds of *Anemone nemorosa* (*A*) and *Asarum europaeum* (*B*) exposed in 47 beech forest plots with restricted access of certain animal taxa. Notice the negligible removal by insects and the major role played by gastropods. Values are given as means ± SE. Results of a generalized linear mixed model (Tukey contrasts) are shown for comparisons of treatments according to the number of removed seeds (the sum of removed seeds and seeds with elaiosome damage showed the same results); treatments with different letters differ significantly at $P < .001$.

dents or carabids are abundant (Heithaus 1981; Ohara and Higashi 1987).

Third, it is known that a variety of arthropods as well as gastropods not only feed on elaiosomes of myrmecochorous seeds but also transport seeds and possibly disperse them (Mesler and Lu 1983; Gunther and Lanza 1989; Ohkawara et al. 1996; Türke et al. 2010), a fact that we observed in our video observations, too. In North American forests, several predatory wasps (*Vespula* spp.) compete with ants for seeds and disperse greater numbers of *Trillium* spp. seeds (Jules 1996; Zettler et al. 2001; Bale et al. 2003). Several studies in temperate forests in both Europe and North America have reported seed dispersal by gastropods. For gastropods feeding on fruits of strawberry (*Fragaria*), bilberry (*Vaccinium myrtillus*), huckleberry (*Vaccinium parvifolium*), and other fleshy-fruited plants, "accidental" consumption of tiny seeds has been frequently reported (Müller 1934; Müller-Schneider 1967; Gervais et al. 1998). Slugs have also been shown to swallow the relatively large seeds of wood anemone and wild ginger (Türke et al. 2010). Moreover, seeds of wood anemone, yellow anemone (*Anemone ranunculoides* L.), sedges (*Carex* spp.), and bear's garlic were observed in the feces of wild-caught red slugs (Türke et al. 2010; M. Türke, unpublished data), and seeds consumed by gastropods, including those of wood anemone, are capable of germinating after gut passage (Müller 1934; Müller-Schneider 1967; Gervais et al. 1998; Türke et al. 2010).

Fourth, it is also noteworthy that average seed dispersal distances of slugs can be considerable. Red slugs disperse seeds about five times farther than do ants (4.4 m vs. merely 0.87 m; data from the Northern Hemisphere; reviewed by Gómez and Espadaler 1998; Türke et al. 2010). In fact, the magnitude of seed dispersal by red slugs is compatible with the observed spread and abundance of myrmecochores in European deciduous forests (Brunet and von Oheimb 1998*a*, 1998*b*; Orczewska 2009). In our study, the abundance of myrmecochores was positively correlated with the abundance of terrestrial gastropods (fig. 2) but not of ants (fig. 1). This further suggests that gastropods are important dispersers of myrmecochorous seeds. Although not all gastropods caught by pitfall traps may act as seed dispersers, gastropod species other than red slugs might be effective dispersers, too.

Fifth, while we found large differences in removal rates between different animal-exclusion treatments, the results were consistent in that the influence of insects and rodents on seed removal was low, and most seed removal could be attributed to gastropods (fig. 3). Because rodents are prominent postdispersal seed predators in temperate regions (Hulme 1998), their abundances may have been low during our study because of the early season in which the experiments were conducted (Hulme and Kollmann 2005). Finally, it has to be emphasized that the actual fate of removed seeds in our experiment is unknown, and we can only speculate on whether they had been dispersed.

Conclusions

Our results support the hypothesis that myrmecochores can be abundant in mature, shaded beech forests where ants are rare or absent because gastropods act as substitutes for ants as seed dispersers. Thus, we question the traditional view of ants as being the only vector of "myrmecochorous" plant species, and we encourage further study of the role played by gastropods in the dispersal ecology of herbs in other ecosystems. Surprisingly, gastropods might have been overlooked for decades in the dispersal ecology of myrmecochores. Given the increasing abundance of invasive gastropods (Chichester and Getz 1973; Martin 2000; Shea 2006, 2007), many of which are large enough to potentially disperse seeds, it will be interesting to study whether seed dispersal by gastropods may become even more pervasive globally.

Acknowledgments

We thank J. Hutchinson and H. Reise for slug species identification. We also thank the technicians of the University of Göttingen and the Max Planck Institute for Biogeochemistry in Jena for permission to use the facilities of a climate tower where the video recording experiment was conducted and for assistance. The work was funded by the DFG Priority Program 1374 "Infrastructure-Biodiversity-Exploratories" (WE 3018/9-1, FI 1246/6-1). We thank the central management office and the local managers and local management teams of the Biodiversity Exploratories project for support. Two anonymous reviewers helped improve the manuscript. Fieldwork permits were given by the responsible state environmental offices of Baden-Württemberg, Thüringen, and Brandenburg (according to §72 BbgNatSchG).

APPENDIX

Figure A1: Red slug (*Arion rufus*) consuming a seed of European wild ginger (*Asarum europaeum*). Photograph by Manfred Türke.

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Natural History Editor: Craig W. Benkman