Ant species dispersing the seeds of the myrmecochorous *Sternbergia colchiciflora* (Amaryllidaceae)

The evolutionary and ecological importance of myrmecochory (ant-mediated seed dispersal in plants) has become increasingly evident (Lengyel et al. 2009, 2010). Nevertheless, myrmecochory is likely the most understudied of the main seed dispersal syndromes (Bronstein et al. 2006) and its research is highly challenging (Bologna et al. 2017). In most cases, myrmecochorous seed dispersal of plants was assumed based on morphological traits: presence of elaiosome, a lipid-rich appendage on the seed (Lengyel et al. 2010), rather than on direct observations on seed dispersal events. Consequently, the specificity of this ant-plant interaction remains largely unexplored. However, myrmecochory may play a significant role in shaping the distribution and survival of plants. Understanding the mechanisms of myrmecochory is especially important in case of rare and threatened plant species, because conservation of their population is not possible without collateral conservation of ant populations.

Sternbergia colchiciflora Waldst. & Kit. (Amaryllidaceae) is a bulbous geophyte distributed from North Africa through Southern Europe and Asia Minor to the Caucasus and Ukraine (Pasche & Kerndorff 2002). The species is considered rare or sporadic in many countries within the distribution area. It is listed on CITES (Washington Convention) Appendix II [web1].

Although it has long been known that the elaiosome-bearing seeds of *S. colchiciflora* (Fig. 1.A) are dispersed by ants (Pénzes 1934), the identity of seed-dispersing ant species participating in the process has remained unknown. The aim of our study was to assess which ant species are responsible for myrmecochorous seed dispersal in this rare and threatened plant species. Our paper provides the first data on association of this threatened plant species and the elaiosome predatory ant species that are engaged/involved in the seed dispersal.

Thirty localities of *Sternbergia colchiciflora* (27 in Hungary, three in Serbia) have been visited in 2017 during the fruiting season (from 25 April to 19 May) to detect ant-mediated seed dispersal events. Every ant individual that was observed to carry seeds of *S. colchiciflora* has been collected. The collected material was stored in 50% EtOH in unique vials until determination. All ants have been identified based on keys by Seifert (1996) and Seifert & Galkowski (2016). We took morphological measurements using an Olympus SZX9 stereomicroscope at a magnification of 100×.

Seed dispersing ants were detected in seven Hungarian localities. Five ant species (*Camponotus piceus*, *Lasius alienus*, *Lasius bombycina*, *Lasius fuliginosus* and *Tapinoma erraticum*) were observed to disperse the seeds of *S. colchiciflora* (Table 1.).

Although fruiting plants were abundant in most localities, ants were observed only on a few plant individuals. However, foraging ants were detected in large numbers on these highly attractive fruits (Fig. 1.B & C). Ant workers were found on 3–7 cm high fruits with ripening, yellowish pericarp. Ants removed the seeds from the rifts of ripening fruits and carried them one by one.

Figure 1. Seeds of *Sternbergia colchiciflora* (A) and its ant dispersers: B – *Lasius alienus* (Várpalota-Inota). C – *Camponotus piceus* (Tihany). Photo credits: A–B: A. Molnár V., C – A. Mészáros. Scale bars represent 10 millimetres.

Table 1. Ant-mediated seed dispersal events in *Sternbergia colchiciflora* in 2017. Observers are indicated by abbreviations of their names (see authors).

Settlement: Locality	Observer	Day/ Month	Ant species (Subfamily)	Quantity of seed carrying ants observed
Tihany: Diósi-medows	AM	25.04.	*Camponotus piceus* (Leach, 1825) (Formicinae)	Numerous workers
Pécsely: Klárapuszta	AM	25.04.	*Lasius alienus* Förster, 1850 (Formicinae)	Numerous workers
Várpalota-Inota: graveyard	AMV	30.04.		
Várpalota-Inota: graveyard	AMV	02.05.		
Csór: graveyard	AMV	02.05.	*Tapinoma erraticum* (Latreille, 1798) (Dolichoderinae)	Single worker
Makó: Montág-puszta	GB	15.05.	*Lasius bombycina* Seifert & Galkowski, 2016 (Formicinae)	Numerous workers
Pusztaföldvár: graveyard	AMV	13.05.		Few workers
Battonya: Tompapuszta	AICs	19.05.	*Lasius fuliginosus* (Latreille, 1798) (Formicinae)	Single worker

Our study provides the first data on ant species that disperse the seeds of *S. colchiciflora*. Four out of the five ant species observed to remove seeds of *S. colchiciflora* are known to disperse elaiosome-bearing seeds of different plants [*C. piceus* (Manzaneda et al. 2007, Bas et al. 2009), *L. alienus* (Culver & Beattie 1978, Beattie et al. 1979), *Lasius fuliginosus* (Reifenrath et al. 2012), *T. erraticum* (Garrido et al. 2002, Manzaneda et al. 2007)]. Seed removal activity of the recently described (Seifert & Galkowski 2016) *Lasius bombycina* is reported here for the first time.

Although these omnivorous ant species obviously play a role in seed dispersal in *Sternbergia*, we speculate that the interactions between *S. colchiciflora* and these ants are facultative. Myrmecochory is a mutual interaction between plants and ant species (Bronstein et al. 2006). Myrmecochorous plant species increase their dispersal ability by attaching lipid and protein-rich elaiosomes to the seeds that are attractive to ants. Both lipids and proteins are essential sources of nutrients for developing ant larvae, hence elaiosomes containing these components in a larger proportion are highly preferred by foraging ant workers at the peak of larval production, in the spring. After removing the elaiosomes, ants drop the seeds, which remain fertile, far from the parental plant (e.g. waste disposal area), where the seed can germinate. The benefits of this interaction are obvious for each side. Our observations showed that the presence of elaiosomes on the seeds did not attract workers from a distance, because upon the first finding of seeds, ants contacted all parts of the seed equally. Although ants are mass-recruiting species, we never observed any recruitment or trail-laying behaviour towards seeds. Upon contacting seed items, the antennation, manipulation and seed retrieval behaviour of ants strongly varied depending on the species.

All ant species detected as seed dispersal vectors of *S. colchiciflora*, except for *Lasius fuliginosus*, prefer open, thermophilous habitats, although there are remarkable differences in their habitat preference within this broad category. *L. alienus* occurs in grasslands, on limestone or dolomite bedrock, whereas *L. bombycina* is abundant on loess substrates.

Our results provide some evidence for the phenological matching of seed production/maturation in *S. colchiciflora* and the seed dispersal activity of ants. The time period of seed maturation (end of April and early May) in *S. colchiciflora* coincides with the peak of the larval biomass of both *Lasius alienus* and *L. bombycina*. The nuptial flight of these ant species takes place in July to September (Seifert 1992), so in next May, their colonies contain rapidly growing sexual larvae. These species may thus be considered a principal contributor to seed dispersal in *Sternbergia*. In contrast, the association of *S. colchiciflora* and the arboricular *Lasius fuliginosus* might be accidental. This species nests in forests (mostly *Populus* spp.) and its nuptial flight takes place in May, thus, mostly pupae or imagos can be found in the nest at the time of seed maturity. Finally, in the two other species found on the sites, *Camponotus piceus* (on volcanic bedrock) and *Tapinoma erraticum* (on loess substrate), the nuptial flight coincides with the time of seed maturity, and thus both are beyond the peak of larval biomass production.

Our results suggest that the observed ant-mediated seed dispersal in *S. colchiciflora* is not a species-specific interaction with ants. Although *L. alienus* and *L. bombycina* appear as ideal seed dispersal agents, each detected species is dominant and abundant in sites with certain bedrock properties. Because seed maturity may or may not coincide with the larval biomass peak, other species can also play a role in seed dispersal, although probably to a smaller extent. Our results, however, agree with previous reports that typically only one or only a few ant species disperse most of the myrmecochorous seeds in any given locality (Rico-Gray et al. 2007). Future studies are thus essential before we can fully understand the nature and specificity of ant-mediated seed dispersal.

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