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ORIGINAL ARTICLE

Early successional colonizers both facilitate and inhibit the late successional colonizers in communities of dung-inhabiting insects

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Abstract. The influence of early arriving species on the establishment and activity of later ones (the priority effect) is a key issue in ecological succession. Priority effects have been extensively studied in communities subject to autotrophic succession (plants, sessile animals), but only sporadically studied in communities subject to heterotrophic succession (e.g. dung or carrion inhabiting communities). We studied the influence of early successional colonizers on late successional colonizers by manipulating the successional processes in cow dung pats via delaying, and thus lowering, colonization by early successional insects. The decreased activity of early successional insects did not affect the species richness of late successional insects, but it did lead to increased abundance of colonizers. Late successional coprophagous beetles were facilitated by early successional species while larvae of late successional coprophagous flies were inhibited, presumably, by the larvae of early successional flies. We therefore propose that both facilitation and inhibition have a role to play in the heterotrophic succession of coprophilous insects. In addition, facilitation and inhibition among taxa seems to reflect their evolutionary relationships, with facilitation being prominent between phylogenetically distant lineages (early successional Diptera and late successional Coleoptera), and inhibition being more common between closely related lineages (early vs. late successional Diptera). These patterns are strikingly reminiscent of the situation in the autotrophic succession of plants.

INTRODUCTION

Succession is one of the most studied phenomena in community ecology, yet the mechanisms behind the patterns observed are still not completely known. Successional processes either lead to the establishment of a more or less stable community (autotrophic succession, e.g., formation of forests on lava islands), or to the disintegration of the resource and loss of all species from the community (heterotrophic succession, e.g. dung decomposition) (Begon et al., 2006).

How early colonizers influence the species richness and abundance of later ones (priority effects) is a major field of study in successional theory. Priority effects typically lead to one of three outcomes and are driven by distinct processes (Connell & Slatyer, 1977). The facilitation model predicts that early successional species enable the establishment of the late successional ones; the inhibition model predicts that early successional species prevent the establishment of late successional ones; and the tolerance model predicts late successional species to establish themselves irrespective of the activity of the early successional ones. Wootton (1993) refined these ideas and added two more scenarios describing the partial effect of early successional species; i.e., that the early successional species can support or hinder the establishment of the late successional species. This stands in contrast to a strict dichotomy between enabling and disabling establishment under the facilitation and inhibition models).

Successional mechanisms have traditionally (Clements, 1916; Gleason, 1926, 1927) and primarily been studied in the context of autotrophic plant communities and sessile animals, which have been long supposed to follow the inhibition or tolerance models (Connell & Slatyer, 1977). However, in all such communities, it is more typical to see a combination of several models during the course of succession, so that facilitation and inhibition often co-occur (Callaway & Walker, 1997; van der Putten, 2009; Walker et al., 2010; Maggi et al., 2011). For example, a nurse plant only facilitates seedlings within a limited distance (Dickie et al., 2005), or facilitation applies only under high levels of environmental stress (Vazquez et al., 1998). The level of facilitation also depends on the patristic evolutionary distances between plant species. Evolutionarily distant lineages tend to facilitate each other while closely related lineages tend to compete (Verdú et al., 2009; Castillo et al., 2010).

In contrast, there are still only a limited number of studies targeting the mechanisms behind heterotrophic succession, which was originally supposed to follow the facilitation model (Connell & Slatyer, 1977). The reality is, however, inevitably more complex with both facilitation and inhibition at work. Dung insect communities have shaped much of this thinking. For example, early successional dung beetles can facilitate the activity of late successional earthworms which hasten dung degradation (Holter, 1977, 1979). On the other hand, late successional dung beetles tend to be outcompeted by early successional ones to such a point that late beetles are more abundant in moths when early beetles are scarce (Davis, 1989). Moreover, early successional beetles are supposed to facilitate the invasion of late successional beetle predators and flies (Hammer, 1941; Mohr, 1943). In large carcasses, early successional larvae of blowflies (Calliphoridae) were reported to facilitate carrion degradation following the bloated stage (Pechal et al., 2014), and thus facilitate the invasion of late successional beetles (Sharanowski et al., 2008). On the other hand, elimination of some dominant early successional blowfly species increased the diversity of late successional flies from other families (Pechal et al., 2014). Furthermore, a high abundance of early successional blowfly is negatively correlated with the abundance of both early and late beetle and fly species (Kadlec et al., 2019). This cumulative evidence, however, stems from individual studies. To date, there has been no experimental focusing on interactions between early and late colonizers of ephemeral resource patches. Finally, it is not yet clear which process exactly determines the correlational trends seen between early successional and late successional species. This contrasts with studies of plant communities, where the level of facilitation depends on the patristic evolutionary distances between species (Verdú et al., 2009; Castillo et al., 2010).

Here, we present a study focusing on mechanisms that shape heterotrophic succession in communities of dung inhabiting insects. We experimentally delayed access to the dung resource for all insects for a period of five days and in doing so restricted the invasion of early successional colonizers (Sladecek et al., 2013). We then compared community development in such dung pats to those pats which were freely accessible to all insects throughout the experiment. Our approach is similar to that used to limit the dominant early successional colonizers in carrion, a comparable ephemeral resource (Kadlec et al., 2019). Any resultant increase or decrease in activity of late successional species in exclusion treatments revealed potential interactions between early and late successional species. This approach allowed an assessment of the successional mechanisms behind heterotrophic succession in dung-inhabiting communities. Communities of dung-inhabiting insects are both species-rich (Hanski & Koskela, 1977; Sladecek et al., 2013), and ecologically important for ecosystem services such as dung degradation (DeCastro-Arrazola et al., 2020). Dung insect communities are also threatened by land use changes (Buse et al., 2015) and the overuse of veterinary products with non-target effects (Tonelli et al., 2020). These threats mean that understanding dung community dynamics is of relevance to maintaining ecosystem services in conservation efforts (Cimon-Morin et al., 2013). Specifically, we address the following questions:

(1) Does delaying insect access, and therefore limiting access of early successional species, enable/disable (models sensu Connell) or improve/hamper (models sensu Wootton) the activity of late successional dung-inhabiting insects?

(2) Is there a preference of late successional groups of insects towards dung with previously high (controls) or low (treatment) activity of early successional species?

MATERIAL AND METHODS

Study site

The study was carried out on a 23 ha pasture, situated 10 km west of Ceske Budejovice, Czech Republic (48°59′2.4″N, 14°24′34.957″E), Central Europe. This pasture hosts a permanent herd of 30 adult cows and has been continuously grazed for decades. It is situated at 380 m a. s. l., in a region with a mean annual temperature of 8.1°C, mean annual precipitation of 620 mm, and a vegetation season spanning from March to October (Sladecek et al., 2013).

Insect sampling

Three sampling campaigns, covering the three main periods of coprophilous insect activity, were carried out in 2011: spring (18 April – 3 May); early summer (12–27 July) and early autumn (22 August – 6 September).

We used artificially created cow dung pats of 1.5 l volume (approx. 25 cm in diameter) to mimic naturally deposited pats. Fresh, recently defecated, un-colonized dung was obtained from a barn with permanently stalled cows. These cows were not treated with any veterinary drug that could affect insect colonization and establishment (Rodríguez-Vívas et al., 2020). No insects were found to colonize the dung in the barn, since fresh dung is cleared each day. We protected such dung from insect colonization before exposition. At the study site, we thoroughly mixed and homogenized the dung before creating the exposed pats. We artificially created dung pats (Fowler et al., 2020) because it was not possible to assure that the naturally dropped pats would not already be invaded by the eggs of earliest-occurring Diptera (Hammer, 1941). Following Barth et al. (1994), we assume that the insect communities sampled from artificially created dung pats do not substantially differ from those present in naturally dropped pats.

Insect invasion was prevented in treatment pats using simple covering constructions (Fig. 1). They consisted of a plastic basket of 30 cm diameter with 0.5 × 0.5 cm sized holes firmly covered with a 1 × 1 mm wire mesh. Similar constructions using a hard cage with a net (Pechal et al., 2014; Kadlec et al., 2019) or just a fine mesh (Lumaret & Kadiri, 1995; Lee & Wall, 2006; Tixier et al., 2015) are frequently used to exclude insects. The construction was firmly nailed to the ground to exclude crawling insects. The mesh within the basket did not touch the covered dung which eliminated potential insect (especially fly) oviposition. This covering was tested before the experiment and no insects were found to colonize covered pats before uncovering.

The sampling design consisted of treatment pats and control pats. The treatment pats were covered immediately after their

Fig. 1. Covering construction used in this study. The meshed plastic basket is of 30 cm diameter with 0.5 × 0.5 cm sized holes. The wired 1 × 1 mm mesh is situated within, thus protecting the dung pat from invading insects but allowing it to dry due to soil absorption and weather impact. This construction was firmly nailed to the ground to exclude crawling insects as well (in the photograph it is loosely placed on the ground). The mesh within the basket did not touch the covered dung to eliminate potential insect (especially fly) oviposition.

placement on the pasture and remained covered for five days. Afterwards, they were uncovered and exposed to colonizing insects for an additional one, two, three, five or seven days (exposition time). Therefore, there were five treatment pats per replication. The whole five-pat arrangement was replicated four times per sampling campaign. The four replicates were established during four successive days (one on each day) to minimize variation due to weather.

Control pats were placed on the pasture concurrently with treatment pats, but remained uncovered throughout their existence. We chose not to cover control pats with any cover device, since covering of control pats would alter the early successional species abundances. Control pats treated as such would thus also receive some form of insect exclusion treatment, instead of representing the natural and un-manipulated successional process. Similar uncovered controls have been used in most studies that have excluded insects in ephemeral habitats (Lumaret & Kadiri, 1995; Lee & Wall, 2006; Pechal et al., 2014; Tixier et al., 2015).

The control and treatment pats existed on the pasture for the same number of days, but differed in the lengths of exposure to early successional insects. For example, the pat covered for five days and exposed for one day (six days after creation on the pasture) was compared with the control pat also exposed for six days.

Processing the samples

We extracted insects by floating the dung pat and a small portion of underlying soil in a bucket of water. Great attention was paid to ensure capture of all quickly escaping insects, so that the percentage of potential runaways was negligible. Each dung pat was floated for at least 45 min and the floated substrate was then hand-sorted to assure that all individuals were sampled (Fowler et al., 2020). The insects were preserved in 96% ethanol and taken to the laboratory for identification.

Insect identification and classification

All adult beetles were identified to species level, or to morphospecies within respective genera. The larvae were identified to species whenever possible, otherwise to genus or family levels (Table S1). The genus or family morpho-species were treated as regular species in the analyses. Singleton records were excluded from the analyses. One dung pat and its inhabitants represent one sample in further analyses.

First, we placed dung-inhabiting insect species into early and late successional categories. For adult beetles, we used the temporal preferences from our previous study, in which beetles formed two distinct successional groups (Sladecek et al., 2013). Specifically, beetles occurring in dung ≤ 4 days old were classified as early successional, beetles occurring in dung ≥ 5 five or more days old as late successional. For larvae and parasitoids, we used findings reported in the literature (Hammer, 1941; Laurence, 1954; Skidmore, 1985).

Second, we established groups of dung-inhabiting insects based on a combination of their ecology and taxonomy. For this classification, we took into account their trophic strategy (coprophagous / predatory), family (coprophagous / predatory larvae of Muscidae), and in the case of Hydrophilidae beetles, if they were dung-specialists or generalist saprophages (large / small Hydrophilidae) (Hansen, 1987). Full list of our groups is provided in Table 1.

The complete list of species sampled with their successional classification and group affiliation is provided in supporting information (Table S1).

Hypotheses and analyses

(1) Does delaying insect access and therefore limiting access of early successional species enable/disable (models sensu Connell) or improve/hamper (models sensu Wootton) the activity of late successional dung-inhabiting insects?

Connell & Slatyer (1977) predicted that early successional species either directly enable or disable the late successional species establishment. It follows that a lower number of early successional species in the treatment may lead to: (1) a lower number of late successional species (facilitation), (2) a higher number of late successional species (inhibition) or to (3) no difference between treatment and control (tolerance). To compare the number of species per pat between tretment and control, we used Generalized linear models with mixed effects computed with "glmer" function from package "lme4" (Bates et al., 2015) in R 4.0.3 (Team, 2020). We fitted three models with one of three response variables: (a) total species richness, (b) early successional species richness and (c) late successional species richness. Each model was fitted with treatment (treatment/control) as a focal explanataory variable and with a Poisson distribution of errors. In addition, dung age (6,7,8, 10 or 12 days) and sampling campaign (spring, early summer, early autumn) were included as factors with fixed effects. Affinity to replicative line within sampling campaign (1, 2, 3, 4) was a factor with a random effect. Resulting models were validated using the package "DHARMa" (Hartig, 2019) in R 4.0.3 (Team, 2020). If overdispersion was detected, we fitted a new model with observation level as a random effect (Harrison, 2014). Statistical significance of fixed effects were retrived using the function "Anova" in package "car" (Fox & Weisberg, 2019). Resultant figures were created using packages "effects" (Fox & Weisberg, 2019) and "ggplot2" (Wickham, 2016).

Wootton (1993) presented the idea that early successional species could not only strictly enable or prevent the activity of late successional species, but rather increase (facilitation) or decrease (inhibition) the activity of late successional species. It follows that a lower abundance of early successional species in the treatment pats should lead to: (1) lower abundance of late successional species (facilitation), (2) higher abundance of late successional species (inhibition) or to (3) no difference between treatment and control (tolerance). To compare the abundances of early and late successional species per dung between treatment and control, we used Generalized linear models with mixed effects computed

Table 1. Classification of dung-inhabiting insects used in this study. Trop. group / Order – trophic group and order; Coprophage – feeds solely on dung matter; Omnivore – switch between coprophagy (adult) and predation (larvae); Predators – feeds on living insects; Tax. group – taxonomic group (mostly families); Suc. cat. – successional category; early – mostly abundant in ≤ 4 days old dung; late – most abundant in ≥ 5 days old dung; Representative – representative genus / family; Abb. – abbreviation used in further analyses.

Trop. group / Order	Tax. group	Suc. cat.	Representative	Abb.
Coprophages				
Coleoptera	Scarabaeidae	early	*Onthophagus*	EScara
		late	*Aphodius*	LScara
	Staphylinidae	early	*Anotylus*	EStaCo
		late	*Platysthethus*, *Megarthrus*	LStaCo
Diptera	Muscidae	early	*Musca* larvae	EMusci
	Anthomyiidae	late	Anthomyiidae larvae	LAntho
	Acalyptratae	late	Sepsidae, Sphearoceridae larvae	LAcaly
Omnivores				
Coleoptera	Large Hydrophilidae	early	*Sphaeridium* adults	ESphAd
		late	*Sphaeridium* larvae	LSphLa
	Small Hydrophilidae	early	*Cercyon*	EHydSm
		late	*Cryptopleurum*	LHydSm
Diptera	Muscidae	early	*Mesembrina* larvae	EMesem
		late	*Mydaeinae* larvae	LMydae
Predators				
Coleoptera	Staphylinidae	early	*Ontholestes*	EStaPr
		late	*Philonthus*, *Atheta*	LStaPr
	Histeridae	late	*Hister*	LHiste
Hymenoptera	"Parasitica"	late	Figitidae	LParas

with "glmer" function from package "lme4" (Bates et al., 2015) in R 4.0.3 (Team, 2020). We fitted three models with one of three response variables: (a) total abundance, (b) early successional species abundance and (c) late successional species abundance. Further model setup followed that otlined for question one.

(2) Is there a preference of late successional groups of insects towards dung with previously high (controls) or low (treatment) activity of early successional species?

We tested the affinities of insect groups (sums of individuals belonging to these groups in each sample), occurring in at least ten samples, for treatment and control pats using redundancy analysis (RDA) computed in CANOCO for Windows 5 (Ter Braak & Smilauer, 2012). RDA is suitable for datasets where species display linear responses to environmental gradients (Leps & Smilauer, 2003). Data were log(x + 1) transformed prior to the analyses. Dung age, sampling campaign and affinity to the replicate line were treated as covariates (equivalent to factors with random effects). The statistical significance of the main RDA predictor was assessed using the Monte Carlo test (999 unrestricted permutations under the reduced model).

RESULTS

In total, the sampling amassed 15,814 insect individuals from 78 species and morphospecies (Table S1). Treatment pats differed visibly from control ones, yet all changes were induced by insect activity in control pats (i.e. perforated crust and galleries under the crust).

(1) Does delaying insect access and therefore limiting access of early successional species enable/disable (models sensu Connell) or improve/hamper (models sensu Wootton) the activity of late successional dung-inhabiting insects?

Both total species richness (estimate = –0.001, standard error = 0.042, z = –0.228, p = 0.820) and species richness of late successional species (estimate = 0.044, standard error = 0.045, z = 0.976, p = 0.329) did not differ significantly between control and treatment pats (Fig. 2A, C). Species richness of early successional species was significantly lower (estimate = –0.282, standard error = 0.103, z = –2.739, p = 0.006) in treatment pats than in control pats (Fig. 2B).

Total abundance of dung-inhabiting insects did not significantly differ between control and treatment pats (estimate = 0.141, standard error = 0.099, z = 1.415, p = 0.157) (Fig. 2D). Abundance of early successional species was lower (estimate = –0.561, standard error = 0.169, z = –3.321, p < 0.001) in treatment pats than in control pats (Fig. 2E). Abundance of late successional species was higher (estimate = 0.249, standard error = 0.103, z = 2.413, p = 0.016) in treatment pats than in control pats (Fig. 2F).

(2) Is there a preference of late successional groups of insects towards dung with previously high (controls) or low (treatment) activity of early successional species?

Larvae of Anthomyiidae were present in < 10 samples and were omitted from the analysis. Dung-inhabiting insect groups were significantly (F = 9.5, p = 0.001, all canonical axes explain 8.1% of variability) structured by treatment factor (Fig. 3). The vast majority (5/7) of early successional groups were associated with controls pats (notably the *Musca* larvae and *Sphaeridium* adults). Only early successional dung beetles and predatory Staphylinidae were associated with treatment pats.

Late successional groups were almost equally divided among control (4) and treatment (5) pats. Larvae of Acalyptratae flies, predatory Staphylinidae, larvae of *Sphaeridium* species, Histeridae and Hymenoptera parasitoids were associated with treatment pats. Dung beetles, coprophagous Staphylinidae, small Hydrophilidae and larvae of Mydaeiinae were associated with control pats.

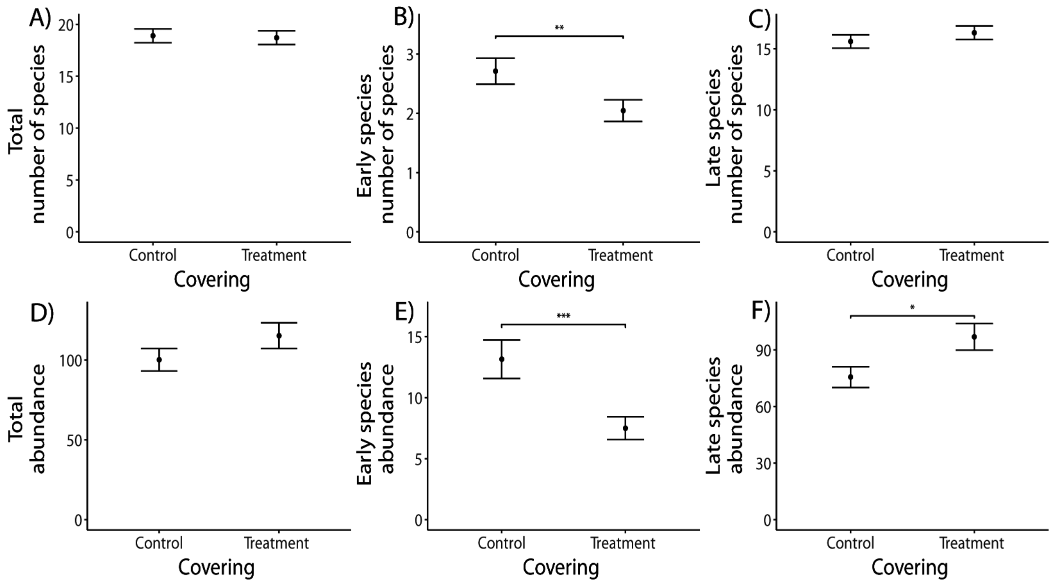

Fig. 2. Effects of delaying early insect invasion on development of dung-inhabiting insect's community abundance and species richness. Control – dung pats with normal insect invasion; Treatment – dung pats with insect invasion delayed by five days via their covering. A – total number of species per dung pat; B – number of early successional species (species with optima in dung < 4 days old) in the dung pat; C – number of late successional species (species with optima in dung > 4 days old) in the dung pat; D – total abundance in the dung pat; E – abundance of early successional species in the dung pat; F – abundance of late successional species in the dung pat. Middle points represent the model defined estimate of value per dung pat, error bars represent the standard error of mean. Horizontal lines denote statistical significance; * – p < 0.05, ** – p < 0.001, *** – p < 0.001.

DISCUSSION

Early successional species

As expected, delaying insect colonization effectively lowered the species richness and abundance of early successional species. Abundance and species richness of early successional species is generally very low under natural conditions in dung older than four days (Sladecek et al., 2013). It is therefore interesting, that treatment pats had even lower abundance and species richness of early successional species than control pats. A possible explanation could be the changes in dung-emitted volatiles (Sladecek et al., 2021a), which are the primary cue for insects inhabiting ephemeral resources when searching for their food sources (Frank et al., 2018; Weithmann et al., 2020). Dung-emitted volatiles are mostly produced by microbes (Saito et al., 2018), whose communities change with pat aging (Perez-Valera et al., 2019). Although dung beetles were always considered the prime catalyst for such changes (Lussenhop et al., 1980), it seems that any soil fauna could start this process (Perez-Valera et al., 2019). An intriguing result was the preference of early successional dung beetles and predatory Staphylinidae for treatment pats rather than controls.

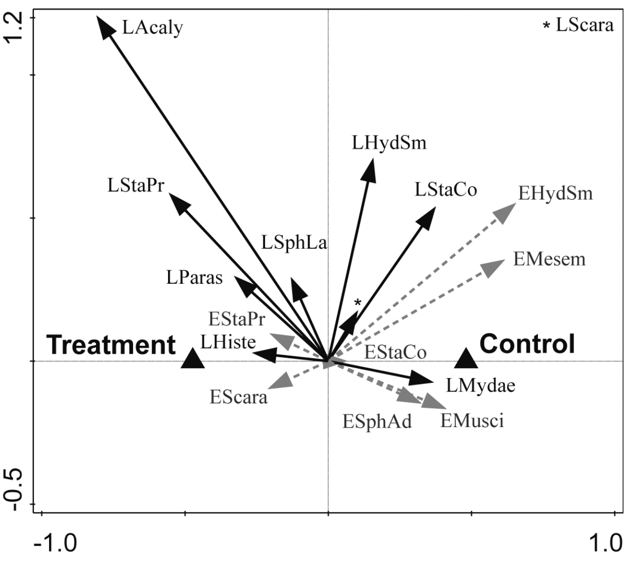

Fig. 3. Effects of delaying early insect invasion on abundance of dung-inhabiting insect's trophic and taxonomic groups. Control – dung pats with normal insect invasion; Treatment – dung pats with insect invasion delayed by five days via their covering. Late successional groups (species with optima in dung > 4 days old) are indicated by black solid arrows and black labels starting with "L". Early successional groups (species with optima in dung < 4 days old) are indicated by grey dashed arrows and grey labels starting with "E". For individual groups abbreviations see Table 1.

For dung beetles, this could mean that they compete with two other major groups, *Musca* larvae and Hydrophilidae species, even though dung beetles are generally considered to be top competitors in dung, especially in comparison to fly larvae (Ridsdill-Smith et al., 1986). The earliest successional dung beetles are dung relocating beetles in our study, and therefore could avoid dung pats with higher fly larvae abundance. There is a similar relationship between relocating burying beetles and blowflies in carrion (Kadlec et al., 2019).

Predatory Staphylinidae have always been considered to be one of the primary predators of Muscidae larvae (Walsh & Posse, 2003). However, this study in combination with our recent study on food webs (Sladecek et al., 2021b) strongly suggests that Staphylindae instead prey on other fly families (e.g., the adults and larvae of Sepsidae and Sphaeroceridae). Indeed, Staphylindae may not be the effective regulators of pestiferous (Krasfur & Moon, 1997) Calyptrate flies they are assumed to be.

Late successional species

Connell & Slatyer (1977) emphasised the total exclusion of early successional species. This is unfortunatelly not completely possible in insect communities inhabiting ephemeral resource patches (Lee & Wall, 2006; Pechal et al., 2014), in contrast to sessile communities of marine organisms and plants (van der Putten, 2009; Maggi et al., 2011). Nevertheless, per pat the number of early successional species (by approximately 33%) and their abundances (by almost 50%) were significantly lower in our treatment pats. Furthermore, control pats were probably invaded by numerous early successional species after their exposition, which had already vacated the dung (Sladecek et al., 2013). We therefore consider our manipulation to have significantly reduced or even negated the activity of early successional species in treatment pats. This reduction of early successional species enabled us to make interpretations using the models of succession proposed by Connell & Slatyer (1977).

Contrary to predictions made by Connell & Slatyer (1977), and earlier studies on the dung microhabitat (e.g. Holter, 1977), we found no straightforward facilitation (exclusion of early species results in absence of late species) between early and late successional species during the heterotrophic succession of the coprophilous insect community. Lower activity of early successional insects did not translate into lower species richness of late ones. In fact, there was a trend in treatment pats to host even more late successional species than control ones (approximately two more species per pat). Based on our data, the succession of the coprophilous insect community follows the tolerance model proposed by Connell & Slatyer (1977), tending even towards the inhibition models. Our results thus contrast sharply with earlier studies from ephemeral resource patches (Lumaret & Kadiri, 1995; Lee & Wall, 2006; Pechal et al., 2014). However, the majority of such studies primarily tested the effects of early successional species on habitat degradation, rather than within-community dynamics. Previous studies tended to decrease the number of early successional colonizers, which reduced the rate of habitat degradation, which led the authors to suggest facilitation as a model for succession (Holter, 1977, 1979; Lumaret & Kadiri, 1995; Pechal et al., 2014).

Based our observations, we therefore suggest that the succession of the coprophilous insect community is better described by Wootton's models (1993), which predicted the numerical (enhance/hinder) rather than the strict (enable/disable) effect of early successional species upon colonization of late ones. In our study, the treatment pats hosted higher abundance of late successional species (by approximately 25–30%) when compared to the control pats. This higher abundance (when taken at the community level) points toward strong inhibition of late successional species by early successional ones. The situation is, however, more complex at the level of individual groups of late successional insects.

The late successional coprophagous dung beetles (*Aphodius* spp.) and coprophagous Staphylinidae displayed a pattern suggestive of facilitation by early successional species. This may be a result of their relationship with either or both early successional larvae of Muscidae or Hydrophilidae beetles (*Sphaeridium* spp.), which are very abundant in freshly exposed dung (Sladecek et al., 2013). Despite the fact that *Sphaeridium* beetles tend to invade dung pats in high numbers during its initial exposition, their overall presence in dung is fairly limited due to their quick oviposition, as their larvae feed on the larvae of Diptera (Sowig, 1997). In contrast, larvae of Diptera have a more lasting presence in dung (Laurence, 1954). We therefore assume that the observed facilitative relationship between early successional species and late successional dung beetles could be attributed to high abundances of early successional larvae of Muscidae. This result is certainly controversial, since most studies to date focusing on the beetles versus fly larvae interactions have reported a negative relationship between the two (Hirschberger & Degro, 1996; Kadlec et al., 2019). Late successional dung beetles should avoid oviposition where there is a high abundance of fly larvae (Hirschberger & Degro, 1996) in sheep droppings, which are very small and provide less food and space for their inhabitatnts (Sowig, 1994). In contrast, in cow dung, which is large and contains high dung moisture (Gittings & Giller, 1998), adult late successional dung beetles could be facilitated by activity of fly larvae, since such beetles mostly prefer the drier parts of the dung pats (Holter, 1982). Alternatively, fly larvae might speed up the interchange between dung and soil microbiota, a process that should increase emission of beetle attractant volatile cues (Sladecek et al., 2021a). Moreover, Lee & Wall (2006) reported that numbers of *Aphodius* larvae were also highest in uncovered pats or pats covered for a very short period of time (and therefore exposed to free fly larvae activity). In combination with Lee & Wall (2006) the results of suggest that the relationships between late successional dung beetles and dung flies are probably not as straightforward as has currently thought. We encourage the collection of more manipulative data, which are needed to fully understand the relationships between *Aphodius* beetles and flies.

In common with dung beetles, coprophagous late successional Staphylinidae (Oxytelinae and Proteininae) also displayed a preference for control pats. These Stapyhylinidae beetles are actually saprophilous as opposed to strictly coprophilous (Koskela, 1972; Hammond, 1976). We therefore expected Stapyhylinidae to benefit from dung pat drying, a process hastened by the larvae of early successional Diptera. In addition, they may be attracted by increasing volatile emissions released by higher numbers of larvae (Sladecek et al., 2021a).

In contrast to the coprophagous beetles, the late successional small Acalyptratae Diptera (Sepsidae, Sphaeroceridae) larvae are most likely to be subject to competition (inhibition) with the early successional larvae of Calyptratae Diptera. The large Calyptratae Diptera larvae share their main food source with small Acalyptratae Diptera (Dowding, 1967). Calyptrate Diptera, due to their size (up to 1 cm) and density in the dung (up to 400 individuals per 1.5 liters), accelerate dung desiccation, thus destroying the habitat, and also diminishing the supply of their shared food source, bacteria (Lussenhop et al., 1986). Although there is no direct evidence, competition for space is considered to be an important factor in structuring the communities of dung beetles (Hirschberger, 1998; Finn & Gittings, 2003), and it could probably also affect fly-fly relations.

Our study primarily proposed and tested successional mechanisms among species that could compete with each other, e.g., the coprophagous species. Nevertheless, ephemeral resource patches such as dung or carrion facilitate studies of the effects of early successional colonizers even on competitively unrelated species, i.e., predators and omnivores. The late successional omnivores, who were more abundant in control pats, consisted mainly of saprophilous Hydrophilidae species (*Cryptopleurum* spp., *Cercyon* spp.) (Hansen, 1987). Presumably these insects also benefitted from the activity of early successional species (namely fly larvae), as did late successional dung beetles. In contrast to previous studies (Hammer, 1941; Mohr, 1943), the activity of late successional predators and parasitoids is not facilitated by the activity of early successional species, such as perforating the dung crust. The higher abundance of late successional predators and parasitoids in treatment pats could be attributable to high abundance of Acalyptratae Diptera larvae (mainly Sepsidae), which represent their main prey items (Valiela, 1974). Finally, the higher abundance of predatory *Sphaeridium* larvae could be explained by their rapid development (Sowig, 1997), i.e., being offspring of the few *Sphaeridium* adults visiting the treatment pats. Another explanation could be the potential density-dependent egg laying behavior of *Sphaeridium*, parents typically lay eggs when the presence of their kin is low, since larvae often display harsh cannibalism (Sowig, 1997).

Based on our results, we refute facilitation as the main successional mechanism in communities of dung-inhabiting insects. Previously, facilitation has been proposed for all ephemeral habitats (Connell & Slatyer, 1977) and seen as less important for dung-inhabiting communities (Holter, 1977, 1979; Slade et al., 2007). In contrast we propose that the successional processes in dung-inhabiting insects are defined by the interplay of facilitative and inhibitive relations, in common with carrion communities (Pechal et al., 2014).

With both inhibitive and facilitative effects of early successional species present, our results point to mechanistic similarities between heterotrophic succession in the coprophilous insect community and autotrophic succession in communities of plants (Callaway & Walker, 1997; van der Putten, 2009; Walker et al., 2010), sessile animals and algae (Maggi et al., 2011). Another pattern suggestive commonalities across heterotrophic and autotrophic succession is the phylogenetic relatedness of the species involved. During autotrophic succession of plants, facilitative relationships mostly occur among phylogenetically distant species, whereas competition occurs among closely related ones (Verdú et al., 2009; Castillo et al., 2010). In the dung microhabitat, the early successional larvae of Calyptratae Diptera (Muscidae) facilitated the phylogenetically distant Coleoptera (Scarabaeidae, Styphylinidae), while inhibiting the phylogenetically closer small Acalyptratae Diptera larvae (mostly Sepsidae).

We are aware that the conclusions we present here are based upon a single study, therefore future experimental studies involving other communities subjected to heterotrophic succession (necrophilous insects, coprophilous fungi) are needed to support our findings. For further validation, there is also a great need for studies that would directly manipulate the individual groups or taxa. In any case, the results presented here suggest that the mechanisms shaping heterotrophic and autotrophic succession be similar, or even identical.

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Table S1. List of species sampled and their respective insect group affiliations. Sum – sum of all individuals per particular group or species; Succ – successional optimum of a species or a group (early – optimum in < 4days old dung; late – optimum in > 4 days old dung); Trophic – trophic strategy of a species or a group [coprophages – both adult and larva coprophagous, predators – both adult and larva predatory, omnivores – trophic shift between adults and larvae (e.g. adult coprophagous, larvae predatory)]; Group – species affilation to a particular group in the analyses, combination of successional preference, taxonomic group and trophic strategy within the taxonomic group (e.g. LStaPr – late successional Staphilinidae predators). See Table 1 for group delimination.

SPECIES	Sum	Succ	Trophic	Group
COLEOPTERA				
Histeridae				
Atholus duodecimstriatus	7	late	predators	LHiste
Hister unicolor	11	late	predators	LHiste
Margarinotus purpurascens	9	late	predators	LHiste
Margarinotus ventralis	3	late	predators	LHiste
Hydrophilidae				
Cercyon castaneipennis	39	early	omnivores	EHydSm
Cercyon haemorrhoidalis	29	early	omnivores	EHydSm
Cercyon impressus	29	early	omnivores	EHydSm
Cercyon lateralis	1279	late	omnivores	LHydSm
Cercyon melanocephalus	20	early	omnivores	EHydSm
Cercyon pygmaeus	434	early	omnivores	EHydSm
Cercyon quisquilius	25	early	omnivores	EHydSm
Cryptopleurum crenatum	660	late	omnivores	LHydSm
Cryptopleurum minutum	2330	late	omnivores	LHydSm
Megasternum concinuum	4	late	omnivores	LHydSm
Sphaeridium bipustulatum	44	early	omnivores	ESphAd
Sphaeridium lunatum	42	early	omnivores	ESphAd
Sphaeridium scarabaeoides	4	early	omnivores	ESphAd
Sphaeridium spp. larvae	226	late	omnivores	LSphLa
Scarabaeidae				
Scarabaeinae				
Onthophagus coenobita	3	early	coprophages	EScara
Onthophagus joanne	49	early	coprophages	EScara
Onthophagus ovatus	121	early	coprophages	EScara
Aphodiinae				
Aphodius ater	5	early	coprophages	EScara
Aphodius erraticus	1	early	coprophages	EScara
Aphodius fimetarius	346	late	coprophages	LScara
Aphodius fossor	42	late	coprophages	LScara
Aphodius granarius	1	late	coprophages	LScara
Aphodius haemorrhoidalis	79	late	coprophages	LScara
Aphodius pusillus	4	late	coprophages	LScara
Aphodius rufus	16	early	coprophages	EScara
Oxyomus silvestris	58	late	coprophages	LScara
Staphylinidae				
Aleocharinae				
Autalia rivularis	312	late	predators	LStaPr
Atheta longicornis	570	late	predators	LStaPr
Atheta sp. 1	80	late	predators	LStaPr
Atheta sp. 2	691	late	predators	LStaPr
Atheta sp. 3	49	late	predators	LStaPr
Atheta sp. 4	62	late	predators	LStaPr
Aleochara brevipennis	21	late	predators	LStaPr
Aleochara intricata	188	late	predators	LStaPr
Aleochara sparsa	12	late	predators	LStaPr
Oxytelinae				
Anotylus rugosus	25	early	coprophages	EStaCo
Anotylus tetracarinatus	1164	late	coprophages	LStaCo
Platystethus arenarius	258	late	coprophages	LStaCo
Paederinae				
Rugilus similis	43	late	predators	LStaPr
Lathrobium fulvipenne	17	late	predators	LStaPr
Proteninae				
Megarthrus denticollis	51	late	coprophages	LStaCo
Megarthrus depressus	56	late	coprophages	LStaCo

Staphylininae: Staphylinini				
Emus hirtus	1	early	predators	EStaPr
Ontholestes murinus	13	early	predators	EStaPr
Philonthus coprophilus	984	late	predators	LStaPr
Philonthus cruentatus	154	early	predators	EStaPr
Philonthus marginatus	12	early	predators	EStaPr
Philonthus politus	114	late	predators	LStaPr
Philonthus rectangulus	31	late	predators	LStaPr
Philonthus rotundicollis	15	late	predators	LStaPr
Philonthus sanguinolentus	156	late	predators	LStaPr
Philonthus spinipes	1	late	predators	LStaPr
Philonthus splendens	10	early	predators	EStaPr
Philonthus varians	575	late	predators	LStaPr
Philonthus varius	663	late	predators	LStaPr
Quedius cinctus	2	late	predators	LStaPr
Staphylininae: Xantholinini				
Gyrohypnus fracticornis	75	late	predators	LStaPr
Gyrohypnus angustatus	15	late	predators	LStaPr
Tachyporinae				
Cilea silphoides	6	late	predators	LStaPr
Tachinus lignorum	1	late	predators	LStaPr
Tachinus signatus	20	late	predators	LStaPr
Tachyporus nitidulus	2	late	predators	LStaPr
DIPTERA				
Anthomyiidae				
Anthomyiidae spp. larvae	157	late	coprophages	LAntho
Muscidae				
Muscinae				
Musca autumnalis larvae	726	early	coprophages	EMusci
Mesembrina meridiana larvae	41	early	omnivores	EMesem
Mydaeinae				
Mydeinae spp. larvae	38	late	omnivores	LMydae
Sepsidae				
Sepsis spp. larvae	730	late	coprophages	LAcaly
Saltella nigriceps larvae	24	late	coprophages	LAcaly
Saltella spondylii larvae	1644	late	coprophages	LAcaly
Sphaeroceridae				
Sphaeroceridae spp. larvae	25	late	coprophages	LAcaly
HYMENOPTERA				
Diapriidae spp.	5	late	predators	LParas
Figitidae spp.	45	late	predators	LParas
Proctotrupidae spp.	3	late	predators	LParas
Scelionidae spp.	7	late	predators	LParas