University of South Bohemia in České Budějovice
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Heterotrophic succession of dung insect communities of the warmer part of European temperate region

Master thesis

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Annotation:
The mechanisms of dung inhabiting insects' heterotrophic succession were studied by preventing the colonisation of early successional insect. The early successional insect, predominantly the large larvae of Calyptratae Diptera, both facilitated and inhibited the later establishing insect. Whereas the removal of early successional species affected negatively the late successional Coleoptera (facilitation), the small late successional larvae of Acalyptratae Diptera were affected positively (inhibition). The patterns retrieved from the heterotrophic succession strongly resemble the patterns retrieved from the autotrophic – mostly plant – succession. Therefore it is possible to suggest, that similar mechanisms are behind both the autotrophic and the heterotrophic succession.

Prohlašuji, že svoji diplomovou práci jsem vypracoval samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.
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V Českých Budějovicích, 10. prosince 2012

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František Sládeček

Declaration & Acknowledgement

As the Supervisor and the co-author of the manuscript, presented here as the Master Thesis of František Sládeček, I hereby declare that:

František Sládeček is the sole author of project, both in idea and realization. He also identified all the material and carried out the statistical analyses. Finally, he contributed to the creation of the manuscript presented here by at least 95% amount of work.

Doc. Mgr. Martin Konvička, PhD.

I would like to thank to all who help me at any stage of my work, especially:
1) to God, because;

The LORD is my shepherd, I lack nothing.
2 He makes me lie down in green pastures,
he leads me beside quiet waters,
3 he refreshes my soul.
He guides me along the right paths
for his name's sake.
4 Even though I walk
through the darkest valley,
I will fear no evil,
for you are with me;
your rod and your staff,
they comfort me.

5 You prepare a table before me
in the presence of my enemies.
You anoint my head with oil;
my cup overflows.
6 Surely your goodness and love will follow me
all the days of my life,
and I will dwell in the house of the LORD
forever.

[Psalms 23,1-6]

2) to my father and family for support, bringing me up, and for patience with the bad son
3) to my fiancée, who I love
4) to my supevisor Martin Konvička and to my colleagues, especially Petr Klimeš and Jan Hrček, who taught to do science, and how to write papers
5) to Ziki who I owe a lot for having the patience with me
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Contents:

Introduction to the thesis

Succession is one of the most studied phenomena in community ecology. The successional turn-over could be classified according to its end-point as the i) autotrophic, leading to the more-or less stable community (plants, sessile animals); or the ii) heterotrophic, leading to the complete disintegration of the original habitat (ephemeral habitats such as animal droppings, carrions, rotting fruit and fruiting bodies of Macromycetes)(Finn, 2001; Koskela & Hanski, 1977).

One of the fundamental questions in successional theory is: "How the early successional (or early occurring) species affect the establishment of the late successional (or late occurring species)?" In 1977, Joseph Connell and Ralph Slatyer formulated the three models of successional mechanisms concerning the influence of the early successional species on the later occurring species (Connell & Slatyer, 1977). These models propose that the activity of early successional species: i) is necessary for the establishment of the late successional species (facilitation); ii) prevent the establishment of late successional species (inhibition); or iii) the late successional species are tolerant to the previous activity of early successional species, concurrently, however, being able to establish themselves irrespectively to the previous activity of early successional species (tolerance).

These models were based almost exclusively on the studies of autotrophic succession and were extensively studied in the communities subjected to the autotrophic succession in the next 35 years (e.g. Dickie *et al.*, 2005; Gallagher, Jumars & Trueblood, 1983; Maggi *et al.*, 2011; Walker *et al.*, 2010; Zanini, Ganade & Hubel, 2006). Up to now, there are probably dozens or hundreds of such studies in total.

Contrary, the communities subjected to the heterotrophic succession were up to now studied mostly in manner of species displacement over the successional gradient (e.g. Hanski & Koskela, 1977; Horenstein & Linhares, 2011; Kocarek, 2003; Lee & Wall, 2006; Yamashita & Hijii, 2007). In total, there is only one study of mechanisms behind the heterotrophic succession (Weslien *et al.*, 2011) comparable to the dozens of studies concerning the mechanisms behind the autotrophic succession (e.g. Callaway & Walker, 1997; Castillo, Verdu & Valiente-Banuet, 2010; Walker *et al.*, 2010).

This thesis had two primary aims; using the dung inhabiting insects, and cow dung pats as a model system:

1) The survey of the successional and seasonal patterns of dung inhabiting insects at selected study site as the pilot study for the examination of the successional mechanisms. This study was meant to be a regular part of this thesis; however, it has been already published (Sladecek *et al.*, 2013) and will be the main body of my RNDr. thesis.

2) The study of successional mechanisms behind the heterotrophic succession of insect inhabiting the dung pats, with regard to the Connell & Slatyer models. This study, in form of a manuscript formatted for *Journal of Animal Ecology*, is the main body of this thesis.

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Thesis main body

Succession of dung inhabiting insects parallels the competition and facilitation principles known from plant succession.

Sladecek, F.X.J., Konvicka M.

Abstract

1. Successional change in natural communities represents a prominent and much studied phenomenon in community ecology. However, after more than a century of studies targeting the mechanisms of autotrophic — predominantly plant — succession, heterotrophic succession remains remarkably understudied, limited to descriptions of species successional turn-over without disclosing the underlying mechanisms.
2. Here we present the first study of successional mechanisms behind the heterotrophic succession of coprophilous insects, using cow dung pats as a model system. We manipulated the successional processes using three exclusion periods, during which we prevented access of early successional colonisers to fresh dung pats.
3. In total 45,366 insect individuals were sampled. The exclusion of early successional guilds (predominantly the large larvae of calypratae Diptera) negatively affected the abundance of a coleopteran late successional guild; this applied especially for shorter periods of early guilds exclusion. Concurrently, it positively affected the abundance of late successional small larvae of acalyptratae Diptera. The abundances of the predatory guilds were independent of the previous activity of early successional guilds.
4. These results show that the heterotrophic succession of coprophilous insects does not follow a simple facilitative model of succession, in which earlier guilds facilitate the colonisation by later ones. Instead, both facilitative and inhibitory effects of the early successional species are present.
5. Some patterns observed in the coprophilous insect heterotrophic succession resemble patterns known from the autotrophic, mostly plant, succession, suggesting similar underlying mechanisms. Namely, facilitation occurs among phylogenetically distant lineages (early successional Diptera, late successional Coleoptera) while competition affects closely related lineages (early vs. late successional Diptera). Additionally, the facilitation was more prominent in dung pats from which early succsessional species

were excluded for shorter periods and which had maintained higher moisture, a stressful condition for the beetles, again resembling the patterns known from plant communities. We suggest that very similar patterns of species interactions underlay both animal and plant, i.e. both autotrophic and heterotrophic, succession.

Key words: coprophilous community, Diptera, dung beetles, ephemeral habitat, heterotrophic succession, inhibition

The rest of the thesis can not be placed online while it has been submitted to *Journal of Animal Ecology* (on 3rd December 2012) and it is still under review. However, the thesis will be available in full version in the library of University of South Bohemia in České Budějovice.