Evaluating the relative importance of habitat filtering and niche differentiation in shaping the food web of dung-inhabiting predator

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1 # Evaluating the relative importance of habitat filtering and niche

2 # differentiation in shaping the food web of dung-inhabiting predators.

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26 **Abstract**

27 Investigation into the mechanisms responsible for community assembly (habitat filtering, niche

28 differentiation) is essential for understanding the processes maintaining coexistence of species

29 rich natural communities. Studies of such mechanisms have up to now been almost exclusively

30 limited to communities of primary producers or consumers, and very few are focused on

31 coexistence of predatory communities. Top-down regulation by predators is on the other hand

32 essential in structuring communities of primary consumers. We therefore present a study

33 focusing on coexistence and assembly in a species rich community of dung-inhabiting

34 predators, investigating the potential effect of their temporal trends (succession, seasonality) on

35 lowering their negative interactions (competition and intra-guild predation). We used field

36 derived predator-prey co-occurrence data in combination with previous observations of trophic

37 interactions and morphological constraints to describe the potential food web of dung-

38 inhabiting insects. We used that food web to establish all combinations of negative interactions

39 among individual species. We then analyzed whether interaction between species successional

40 and seasonal optima could lower or eliminate their negative interactions. The predator prey

41 ratio increased throughout dung pat succession, remaining constant among seasons. We found

42 that the predator size decreased along the successional gradient, while similarly sized predators

43 were evenly distributed across seasons. The succession of dung-inhabiting predators therefore

44 displayed potential for environmental filtering. In contrast, seasonality niche differentiation

45 seems to promote coexistence of species co-occurring along succession. The interaction of both

46 species temporal patterns should significantly reduce or even eliminate the potential negative

47 interactions between dung-inhabiting predators and thus promote high species richness in

48 communities of dung-inhabiting insects.

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1. Introduction

54   Understanding species coexistence is crucial for understanding the composition of natural

55   communities. Mechanisms preventing species rich communities from collapsing into single

56   species dominions (Gause, 1934) are therefore among the most frequent studied topics in

57   community ecology.

58   Natural communities are believed to be assembled and maintained either through

59   species adaptation to environmental conditions – i.e., habitat filtering (Keddy, 1992; Kraft et

60   al., 2015), or through the avoidance of negative interactions such as competition and predation

61   – i.e., niche differentiation (MacArthur and Levins, 1967; Schoener, 1974). Habitat filtering

62   results in communities in which species share similar traits related to environmental conditions,

63   whereas niche differentiation results in communities composed of species differing in traits

64   related to resource acquisition (Maire et al., 2012). In addition, habitat filtering seems to apply

65   at larger spatial and evolutionary scales, while niche differentiation more often promotes

66   coexistence of more related, co-occurring species (Adams and Thibault, 2006; Arellano et al.,

67   2016; de Camargo et al., 2016; Wiescher et al., 2012). The role of both of these mechanisms

68   has   been   extensively   studied   in   plants   and   in   metazoan   primary   consumers

69   (herbivores/saprophages).

70   In contrast, studies focusing on the assembly of predatory communities, i.e. predators

71   *sensu stricto*, parasitoids, and parasites, remain rather scarce. Most such studies have focused

72   on predators from the perspective of their prey, targeting the assembly of their prey

73   communities (Giam and Olden, 2016; Paine, 1966) or prey control (Horenstein and Salvo, 2012;

74   Walsh and Cordo, 1997). Studies involving the coexistence of predators remain limited to pairs

75   of predatory species or small subsets of more diverse communities (Bischof et al., 2014; Droge

76   et al., 2017; Hawes et al., 2013; Wereszczuk and Zalewski, 2015).

77   Niche differentiation is considered to play a major role in the coexistence of predatory

78   species (Droge et al., 2017; Torretta et al., 2016), while some authors also discuss the potential

79   effects of habitat filtering (Wereszczuk and Zalewski, 2015). Coexistence of predators is

80   moderated by indirect and direct species interactions. Indirect interactions include competition

81   via the lowering of shared prey abundance (exploitation competition) (White et al., 2006).

82   Direct interactions include physical contact (fighting or killing) among predators, (interference

83   competition) (Hawes et al., 2013) or direct predation among predators (intraguild predation,

84   IGP) (Holt and Huxel, 2007). Direct interactions are probably the most detrimental for

85   predatory species (Arim and Marquet, 2004; Gagnon et al., 2011; Raso et al., 2014). Predators

86   usually avoid potential competition/IGP via modifying their behaviour (Koivisto et al., 2016;

87   Mueller et al., 2016), host-specificity (e.g. Hrcek et al., 2013), or through spatio-temporal

88   segregations (Bischof et al., 2014; Droge et al., 2017; Opatovsky et al., 2016). Up to now,

89   almost all studies focused on coexistence of species predating on primary or secondary

90   consumers (herbivores and omnivores), while there is a lack of studies focusing on predator

91   preying on decomposers (i.e. dung or carrion-inhabiting insects).

92   Within the diverse insect assemblages colonising ungulate dung pats, the coexistence of

93   saprophages has been studied in detail (e.g. Finn et al., 1998; Hanski and Koskela, 1977; Holter,

94   1982; Sladecek et al., 2013), this is in contrast to predators, which constitute over a half of dung

95   insect species richness in both temperate (Koskela and Hanski, 1977; Sladecek et al., 2013) and

96   tropical (Guimaraes and Mendes, 1998; Walsh and Posse, 2003) conditions. Dung-inhabiting

97   predators are subjected to direct interactions (intra-guild predation (IGP) or interference

98   competition) as an increase in predator abundance does not result in an increase in the overall

99   predation rate (Fincher, 1995; Roth, 1982). The role of indirect interactions (exploitative

100   competition) is believed to play a less central role due to a high abundance of prey individuals

101   (Valiela, 1974), although dung-inhabiting predators can be highly voracious (Valiela, 1969).

102   The coexistence of dung-inhabiting predatory species within the community is thought to be

103   maintained primarily by spatial (Hanski and Koskela, 1979) and temporal (Koskela, 1972; Lee

104   and Wall, 2006) niche differentiation. Habitat filtering is thought to have only an occasional

105   role, mediated via seasonal temperature tolerances of beetle and fly predators (Sladecek et al.,

106   2017a) or size-based temporal segregation (Hanski, 1980; Sladecek et al., 2013). Apart from

107   observing these patterns, the mechanisms of co-existence of dung inhabiting insects have not

108   been further studied, and there has been no consideration of potentially existing competition in

109   the form of IGP.

110   This study focuses on the potential mechanisms shaping the coexistence of predatory

111   dung insects. To investigate this, we inferred their potential negative indirect (competition for

112   the shared resource) and direct (intra-guild predation and interference competition) effects,

113   using a combination of field-collected co-occurrence data and trophic links, inferred according

114   to the size ratio of predators to prey (assuming that predator generally eats smaller prey/predator

115   (Cohen et al., 1993; Kajita et al., 2014; Woodward et al., 2005). Our approach defines a

116   "hypothetical" food web, yet such size-based predictions could result in fairly accurate picture

117   of a real food web (Pomeranz et al., 2019). Using these negative interactions, we assess whether

118   two major temporal trends in dung-inhabiting predatory community, succession and season,

119   promote species coexistence and if there are result of niche differentiation or environmental

120   filtering (Keddy, 1992; Kraft et al., 2015; Silvertown, 2004).

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2. Materials and Methods

2.1 Study site and filed data sampling

We investigated predator's temporal patterns on 23 ha pasture, situated 10 km west of Ceske Budejovice, Czech Republic, Central Europe (48°59'2.4"N, 14°24'34.957"E, altitude 380 m, mean annual temperature: 8.1 °C, mean annual precipitation is 620 mm, vegetation season March – October). The site hosts a permanent herd of 30 adult cows and has been continuously grazed for decades (Sladecek et al., 2017a).

We carried out three sampling campaigns in 2011 (spring: 18 April – 3 May; high summer: 12–27 July; and early autumn: 22 August – 6 September), covering the seasonal turn-over of dung-inhabiting insects (Sladecek et al., 2013; Sladecek et al., 2017b).We sampled insect communities from artificially created dung pats (1.5 l volume) (Krell, 2007). We created such pats from fresh and un-colonized barn dung of permanently stalled cows and exposed them at the study site. There should be a little to no difference in insect communities between artificially created dung pats and naturally dropped ones (Barth et al., 1994). In each sampling campaign, we sampled the insects from pats exposed for 2, 3, 4, 5, 6, 7, 8, 9, 10, 11 and 12 days (successional age). We did not include very fresh (< 1 day old) and very old (from day 12 onwards) dung, since no beetle species or fly larvae reach their peak abundance in dung of such ages at our study site (Sladecek et al., 2013). Each successional age of dung was replicated four times per sampling campaign. Each replication therefore constituted of 11 dung pats (11 dung ages). Each replication was exposed on a single day. All replication were thus exposed on four consecutive days to minimize the effects of weather variation on the composition of samples. One sampling campaign thus contained 44 dung pats, amassing 132 dung pats in total for three seasonal sampling campaigns. Data used in this study were also utilized to compare the temporal patterns of fly larvae and beetles in our previous study (Sladecek et al., 2017a).

149   Insects were extracted by floating the dung pat and a small amount of the underlying

150   soil in a bucket of water. This floated substrate was then hand-sorted to assure that all insect

151   individuals were sampled. The insects were preserved in 96% ethanol and identified in the

152   laboratory. The community collected from a single dung pat represents one sample in all further

153   analyses.

154

155   2.2 Guild establishments

156   First, we classified dung-inhabiting insects into predator and prey categories. Predator is adult

157   (e.g. Staphylinidae, Histeridae) or larva (e.g. larvae of Hydrophilidae, larvae of

158   Muscidae:Mydaeinae) that feeds primarily on living prey (Koskela and Hanski, 1977;

159   Skidmore, 1985; Sowig, 1997). Prey is adult (e.g. Scarabaeidae, Hydrophilidae) or larvae (e.g.

160   Muscidae, Sepsidae) that feed on almost exclusively on dung and usually have some

161   modifications to do so (Holter and Scholtz, 2005).

162   To assess the potential indirect (competition) and direct (IGP and interference

163   competition) interactions between insect predators, we first established guilds of predators and

164   prey species based upon species sizes.

165   For classification of adult beetles, one of us (Zitek) weighed 20 adult individuals of

166   each dung-inhabiting beetle species present in our samples and calculated mean dry weights for

167   each species (Table S1). Guilds of adult beetles (both predator and prey) were distinguished

168   using Ward's hierarchical clustering, clustering the beetles according to their sizes, in R 4.0.3

169   (Team, 2020) and identifying the optimal number of guilds/clusters by K-means method.

170   For classification of prey larvae, we applied a different approach to sizing individuals.

171   Dry weight is not an optimal size measurement for larvae, due to high water content; dry weight

172   underestimates the size of larval individuals compared to adult beetle individuals. We *a priori*

173   classified the prey larval individuals according to their live size and ecological differences as

174   "large" (Calyptrate flies; e.g. Muscidae) and "small" (Acalyptrate flies, e.g. Sepsidae)

175   saprophage larvae (Hammer, 1941; Laurence, 1954).

176   Predatory larvae (carnivorous larvae of Muscidae, Hydrophilidae) are similarly sized,

177   forming a single guild. Predator size is practically irrelevant for prey selection in hymenopteran

178   parasitoids, so they formed a single guild of their own.

179

180   2.3 Prey spectrum assignment rules

181   The total prey spectrum was delimited primarily according to between predator and prey sizes,

182   as size is probably the main dimension affecting prey selection (Kajita et al., 2014; Woodward

183   et al., 2005). First, adult beetle guilds (predators) can prey upon similarly sized (saprophages)

184   or smaller adult beetle guilds (saprophages, predators), for which there is ample evidence

185   (Hammer, 1941; Laurence, 1954; Mohr, 1943; Valiela, 1969, 1974; Walsh and Cordo, 1997;

186   Wu et al., 2011; Wu et al., 2014). Second, all adult beetle predators can prey upon all parasitoids

187   and larvae (both saprophage and predatory) (Fincher, 1995; Hammer, 1941; Laurence, 1954;

188   Roth, 1982; Valiela, 1969). Finally, predatory larvae and parasitoids guild can prey only on

189   beetle and fly larvae, since carnivorous larvae are too sluggish to attack agile beetles, and

190   parasitoids only parasitize larvae.

191   In contrast to previous studies, we omit dung as a food source for predators (Valiela,

192   1974; Walsh and Cordo, 1997).

193

194   2.4 Statistical analyses

195   2.4.1 Food web

196   To analyze the influence of predators' temporal trends on their indirect (competition) and direct

197   (IGP, interference competition) interactions, we first constructed the potential food web of

198   dung-inhabiting insects. The food web was constructed combining the prey spectra assignment

199   rules and predator-prey temporal co-occurrence, assuming that predators prey upon species with

200   which they co-occur in succession and season.

201   To quantify this co-occurrence, we computed the Spearman's correlation coefficient for

202   pair-wise predator and prey species abundance using the "rcorr" function in 'Hmisc' package

203   in R 4.0.3 (Harrel and Dupont, 2014). Predators received a trophic link to a prey species if that

204   prey species was in its prey spectrum (using our prey assignment rules) and both were

205   significantly (correlation significance $p < 0.05$) and positively correlated in our data. The final

206   web was visualized twice and basic network statistics were computed in package 'bipartite' in

207   R (Dormann et al., 2009; Dormann et al., 2008); one web sorted species by their successional

208   and the other sorted species by their seasonal optima (both for predators and prey species).

209   The successional and seasonal optima of dung inhabiting insects were retrieved using

210   Canonical Correspondence Analysis (CCA), a multivariate technique suitable for datasets with

211   a unimodal species` response to the gradient, i.e. displaying optima (Leps and Smilauer, 2003).

212   We computed two CCAs, one with succession and one with season as focal predictor, in

213   CANOCO 5 for Windows (Ter Braak and Smilauer, 2012). The affinity to a replicate line (four

214   dung pat lines per sampling campaign) and the second temporal variable (season in the analysis

215   with succession as focal explanatory variable, and *vice versa*) were treated as covariables

216   (random effect factors). We tested the significance of the CCAs using 999 Monte Carlo

217   permutations.

218

219   2.4.2 Establishment of potential negative interactions between predators co-occurring in

220   succession

221   After creation of the food web, we identified groups of predatory species that co-occur in dung

222   and thus have potential to interact through shared prey (indirect interactions) or interact directly

223   (IGP, interference competition). We clustered predatory species based upon their successional

224 optima. The successional gradient was chosen because we have more detailed data (11

225 consecutive points) than we have for seasonal gradient (3 separate points during year).

226 Predatory species were clustered using Ward's hierarchical clustering in R 4.0.3 (Team, 2020).

227 The optimal number of successional clusters was identified using K-means clustering.

228   Resultant clusters present species assemblages that would co-occur in dung if species

229 did not display a seasonal segregation. In each cluster, we establish the number of potential

230 indirect (shared food links among predators) and direct interactions between predatory species

231 (number of potential predator attacking predator interactions, based on species membership in

232 guilds – larger attacks smaller).

233

234 2.4.3 Effect of temporal trends on the amount of negative interactions

235 Finally, we analyzed whether any indirect or direct interactions occurring across succession

236 could be resolved by the seasonality of the species involved. To identify the seasonal patterns

237 (and seasonal abundance optima) of predatory species, we fitted a quadratic GLM for each

238 predatory species abundance (as a response variable) with quasipoisson error distribution (to

239 account for high overdispersion of our models, residual deviance was larger than the residual

240 degrees of freedom) and season as an explanatory variable in CANOCO 5 (Ter Braak and

241 Smilauer, 2012). We then compared the seasonal trends (GLM curves) among species presented

242 in each cluster (e.g. among species within cluster B, species within cluster C, etc.) to identify

243 whether indirect or direct interactions could be: a) resolved (species seasonal displacement =

244 predators had different seasonality or at least one of the pair had a distinct seasonality); b) or

245 not resolved (species co-occurrence = either both predators had the same seasonality or both

246 had no significant pattern of seasonal occurrence).

247

248 **3. Results**

249   3.1 Sampling results

250   In total, 4,935 predatory individuals, together with 17,516 potential prey individuals were

251   sampled. Singletons were *a priori* excluded from the dataset. Predators consisted primarily of

252   carnivorous Staphylinidae (4,500 individuals), supplemented by much rarer predatory larvae

253   (333 ind.), parasitoids (various families of Hymenoptera: 72 ind.) and Histeridae (30 ind.).

254   Among the prey species, Hydrophilidae beetles (8,419 ind.) and fly larvae (5,263 ind.) formed

255   the bulk of the samples, followed by saprophagous Staphylinidae (Staphylinidae:Oxytelinae:

256   2,508 ind.) and Scarabaeidae (1,326 ind.) (Table S1).

257   The proportion of predators in the community increased during succession from 6.1%

258   of total community abundance on day two (predator:prey ratio = 1:15.4) to ~45% of total

259   abundance on days 11 and 12 (predator:prey ratio = 1:1.2) (Fig. 1A). Across seasons the

260   proportion of predators in the community increased only slightly from spring, when they formed

261   19% of the total community abundance (predator:prey ratio= 1:4), towards summer (23-24%

262   of total community abundance, predator:prey ratio = 1:3) (Fig. 1B).

263

264   3.2 Predator and prey guilds

265   Clustering of adult beetle species based on their weights identified six predatory guilds and five

266   prey guilds (Table 1) (Fig. S1). After including larval and parasitoid guilds, we obtained eight

267   predatory guilds and seven prey guilds (Table 1). See Table S1 for guild membership of

268   individual species.

269   Table 1: Predator and prey guilds of dung-inhabiting insects based on size of individual

270   members.

271   Size = dry weight of adult beetle, N.Species = number of species within guild (asterisk* marks

272   if morphospecies, e.g. Figitidae spp., are included), Representative = species or morphospecies

273   with highest abundance

274

Guild	Size	N. Species	Representative
predatorI	>100 mg	1	*Emus hirtus*
predatorII	20-35 mg	1	*Hister unicolor*
predatorIII	8.5-15 mg	5	*Philonthus splendens*
predatorIV	3.72-7.9 mg	4	*Philonthus politus*
predatorV	1.35-2.9 mg	10	*Philonthus coprophilus*
predatorVI	< 1.15 mg	10	*Atheta longicornis*
preadatory larvae		3*	Muscidae:Mydaeinae *spp.*
parasitoids		4*	Figitidae *spp.*

	Size	N. Species	Representative
preyI	>100 mg	0	
preyII	20-35 mg	3	*Aphodius fossor*
preyIII	8.5-15 mg	4	*Aphodius fimetarius*
preyIV	3.72-7.9 mg	8	*Onthophagus ovatus*
preyV	1.35-2.9 mg	4	*Aphodius haemorrhoidalis*
preyVI	< 1.15 mg	14	*Cryptopleurum minutum*
large larvae		3*	*Musca autumnalis*
small larvae		4*	*Saltella spondylii*

275 3.3 Succession and seasonality effects on predators' coexistence

276 3.3.1 Food web

277 The abundance of most predatory species was significantly correlated with at least one prey

278 species from their potential prey spectra. Significant ($p<0.05$) correlation coefficients (*r*)

279 between predators and their prey were, however, generally not very high (mean = 0.314, max

280 = 0.61) (Table S2). The final web consisted of 34 predatory and 33 prey species with a total

281 sum of 186 links (Fig 2). Temporal patterns of predator and prey species thus resulted in a

282 relatively small number of realized links (connectance = 0.17) and revealed niche partitioning

283 among predatory species (niche overlap = 0.18, mean number of shared partners = 1.53).

284 Among prey, Hydrophilidae beetles received the highest number of links (73), followed by

285 small fly larvae and saprophagous Staphylinidae (37 and 35, respectively), and finally by large

286 fly larvae and Scarabaeidae beetles who received the least amount of links (21 and 20,

287 respectively).

288   The community of dung-inhabiting predators and prey was significantly structured by

289 both succession (F = 18.7, p = 0.001, succession explains 12.8% of variability) and season (F

290 = 20.1, p = 0.001, 13.6% of variability) (Fig. S2). When species were sorted by their temporal

291 position on temporal CCA axes, webs sorted by species succession and seasonality displayed

292 differing patterns (Fig. 2).

293   The web sorted by successional optima revealed two groups of predators: the early-

294 successional group containing the vast majority of larger predators (I-IV), along with a

295 significant number of predV species; and the late-successional group, containing primarily the

296 smaller predVI species along with less predV and very few large predatory species (Fig. 2A).

297 Moreover, the weight of predatory species declined significantly when plotted against species

298 successional optima (linear regression; $t_{1,32}$ = -4.68, p < 10^{-5}, R^2 = 0.39).

299   In the web sorted by season, there were also two groups (early and late, i.e., spring and

300 summer/autumn), however, there was no obvious size separation among adult beetles (Fig. 2B),

301 reflected in the fact that no trend was apparent when species weights were plotted against their

302 seasonal optima (linear regression; $t_{1,32}$ = 0.57, p = 0.572, R^2 = 0.01). Individual species within

303 the guilds of adult beetles seemed to be evenly distributed, thus avoiding one another along the

304 seasonal gradient. The same applied for parasitoids and predatory larvae.

305

3.3.2 Establishment of potential negative interactions between predators co-occurring in succession

The successional clustering of dung-inhabiting predators resulted in six clusters (A-F; A = very early successional, F = very late successional), of which A contained a single predator species and was therefore omitted from further analyses. Each of the remaining clusters contained 6-7 species. The clusters were highly variable in terms of the numbers of indirect (competition) interactions (72 in B, 14 in F) while displaying 12-19 direct relations (IGP, interference competition) (Table 2). See supplementary material (Fig. S3, Appendix S1) for species affiliations to individual clusters. The vast majority of species displayed a significant seasonal trend (Appendix S1).

316

3.3.3 Effect of temporal trends on the amount of negative interactions

The seasonal separation of species within successional clusters considerably reduced the number of potential indirect and direct intearctions. The number of potential indirect relations within successional clusters was significantly lower for all but cluster F (Table 2). In clusters B-E the number of indirect interactions in succession decreased by 77-96% when species seasonality was included, while in cluster F only 43% of indirect interactions could be avoided. There was a significant seasonal reduction in direct interactions in all clusters (Table 2). The number of direct interactions that could be avoided through seasonality reached even between 80-100% (cluster F and E respectively).

Table 2: Number of indirect and direct interactions between dung-inhabiting predatory species co-occurring in succession and their potential seasonal resolution

Cluster = successional cluster of dung-inhabiting predators (B = early succession, F = very late succession), Indirect = indirect species negative interactions (exploitative competition), Direct

330 = direct species negative interactions (IGP and interference competition). An asterisk* marks

331 significant avoidance of either direct or indirect interactions (χ^2 test; unresolved / avoided).

332

	Amount of negative interactions		Interactions unresolved by species seasonality		Interactions avoided by species seasonality	
Cluster	Indirect	Direct	Indirect	Direct	Indirect	Direct
B	72	12	16 (22%)	2 (17%)	56 (78%)*	10 (83%)*
C	26	18	1 (4%)	3 (17%)	25 (96%)*	15 (83%)*
D	21	12	3 (14%)	2 (17%)	18 (86%)*	10 (83%)*
E	23	17	4 (17%)	0 (0%)	19 (83%)*	17 (100%)*
F	14	15	8 (57%)	3 (20%)	6 (43%)	12 (80%)*

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342 **4. Discussion**

343 Our results suggest that succession of dung-inhabiting predators seems to be driven by habitat

344 filtering. This can be traced to the number of predators per prey individual increasing with dung

345 age (thus increasing potential competition pressure among predators) as well as their body size

346 decreasing, i.e. clustering species with similar traits (body weight here), which is a signature of

347 habitat filtering (Keddy, 1992; Kraft et al., 2015). In contrast, predator:prey ratio remained

348 almost identical among seasons (hinting at species turnover in season), and similarly sized

349   predators were segregated in season (again pointing out to turnover of potential competitors).

350   Such segregation of similar competitors is a signature pattern of niche differentiation

351   (MacArthur and Levins, 1967; Schoener, 1974).

352   Moreover, a combination of both successional and seasonal species turn-over might provide

353   extreme potential for facilitation of species coexistence in dung-inhabiting predators, as the vast

354   majority of potentially negative interactions (competition, IGP and interference competition) in

355   predator community seem to be avoided through temporal segregation.

356

357   4.1 Environmental and niche interpretations of temporal trends in predatory dung insects

358   Coexistence of dung-inhabiting predators has long been attributed to their successional and

359   seasonal patterns (Hanski and Koskela, 1977; Hanski and Koskela, 1979). There has been

360   general consensus that species avoid each other along these temporal gradients in order to lower

361   the potential competition. Our results suggest, however, that successional and seasonal patterns

362   of dung-inhabiting predators might in fact be driven by different assembly mechanisms.

363   Mechanisms of habitat filtering are the most prominent in successional patterns of dung-

364   inhabiting predators. The first evidence is that the ratio of predators to prey increases along the

365   gradient of dung pat ageing, which increases the density of negative interactions among

366   predators due to their aggregation. This aggregation contradicts the mechanisms of niche

367   differentiation (Schoener, 1974; Silvertown, 2004). Further evidence comes from the separation

368   between "large" and "small" predators along the successional gradient. Therefore species with

369   similar traits (size), and thus probably similar niches (Cohen et al., 1993; Woodward et al.,

370   2005), are aggregated, which again contradicts expectations derived from niche differentiation

371   (MacArthur and Levins, 1967; Schoener, 1974), in favour of habitat filtering (Keddy, 1992;

372   Kraft et al., 2015).

373   The first explanation for such size-based successional patterns could be related to the

374   lethality of fresh and very moist dung for beetles (Whipple et al., 2013). Although there is no

375   specific evidence for moisture lethality in dung-inhabiting predators, the most abundant

376   predators, i.e. Staphylinidae, are resource generalists and do inhabit dung, carrion, humus, and

377   similar substrates (Freude et al., 1964, 1974; Matuszewski et al., 2010). These generalists are

378   unlikely to be adapted for surviving high dung moisture. The majority of predators thus colonize

379   dung in later development stages (Koskela, 1972) when dung more closely resembles humus

380   and has lost a greater portion of its moisture (Gittings and Giller, 1998). The large bodied early

381   successional species represent an exception in tolerating high dung moisture. These large

382   bodied species were recorded in early successional dung in almost all studies (e.g. Koskela and

383   Hanski, 1977; Sladecek et al., 2013), and occur early in succession also in other ephemeral

384   habitats, such as carrion (Kocarek, 2003; Matuszewski et al., 2011). Early successional large-

385   sized predators possibly invade dung before the crust forms on its surface, thus disallowing

386   them to enter the dung pat (Skidmore, 1991), while smaller late-successional predators might

387   use the holes in the crust drilled by smaller dung-feeding beetles (Mohr, 1943).

388   In contrast, seasonal trends are more parsimoniously explained by niche differentiation.

389   The almost equal ratios of predator and prey species among seasons strongly suggest a turnover

390   of predatory species, diminishing the potentially negative interactions. The turnover of species

391   is evident from the seasonal food web, as similarly sized species are seasonally separated. Still,

392   the effect of habitat filtering within seasons cannot be entirely ruled out, because the turnovers

393   might be driven partly by species-specific temperature requirements, as it is in saprophagous

394   prey species (Landin, 1961).

395

396   4.2 How do dung-inhabiting predators avoid exploitative competition, intra-guild predation and

397   interference competition?

398   To date, intra-guild predation and interference competition has not been specifically targeted in

399   dung-inhabiting predators. Still, there are indices that an increase in predator abundance beyond

400   a certain predator:prey ratio (1:17 - 1:25) does not increase predation (Fincher, 1995; Roth,

401   1982), calling for intra-guild predation and interference (Michel et al., 2016; Woodward and

402   Hildrew, 2002).

403   In this study, such ratios were achieved on day two of succession and in all seasons.

404   This points out to increased potential for negative interactions among the predators present.

405   However, temporal displacements should lead to strong reduction or even elimination of

406   potential intra-guild predation (IGP) and interference competition, allowing for large species

407   richness in dung-inhabiting communities (Hanski and Koskela, 1977). The remaining

408   potentially negative interactions, i.e. those not avoided by temporal segregations among the

409   predators, might be avoided by spatial segregation between such temporally co-occurring

410   species. Dung-visiting predators seem to have distinct preferences for habitat types where dung

411   pats are placed (e.g. forest types, open-field) (Hanski and Koskela, 1979; Koskela, 1972; Wu

412   et al., 2011). Dung-inhabiting predators would therefore follow the same ways of avoiding

413   negative interactions in space and time as other predatory communities or species with intra-

414   guild predation, including carrion-inhabiting communities (Galindo et al., 2016), dragonflies

415   (Crumrine, 2005; Harabis et al., 2012) or predatory mammals (Bischof et al., 2014; Droge et

416   al., 2017).

417   Exploitative competition is thought to have very little effect on coexistence of predators

418   (Valiela, 1974). Our results support this view, as competitive links were mostly significantly

419   omitted by temporal species level trends. The only exception was the cluster of very late

420   successional species. The small-sized late successional predators likely prey heavily upon mites

421   and Collembola, both very abundant during the latest phases of dung development (Laurence,

422   1954) but not considered in this study. Nevertheless, almost nothing is known concerning the

423 numbers of prey individuals a dung-inhabiting predator can consume, especially for the large

424 early successional species. The only study covering this topic revealed relatively high levels of

425 predation for a predator which would fall in our predV guild (Valiela, 1969). Therefore the

426 contribution of exploitative competition in structuring dung-inhabiting predator communities

427 remains unknown, until quantitative data on prey consumption by dung-inhabiting predators

428 are available.

429

430 4.3 Food web of dung-inhabiting insects

431 The food web presented here for a dung-inhabiting community should serve primarily as a

432 hypothesis regarding the prevalence of competition and IGP among dung-inhabiting predators.

433 However, as there are very few food webs published for dung-inhabiting communities (Valiela,

434 1974; Walsh and Cordo, 1997), we comment on several patterns occurring in the hypothetical,

435 but highly probable, web. Our approach to the food web's construction reflected the general

436 need for time-specific webs (Rasmussen et al., 2013; Valverde et al., 2016), which unlike static

437 webs contain only those trophic relations that can occur in the real world due to predator and

438 prey co-occurrence (Olesen et al., 2008). Although the result is technically a static web instead

439 of multiple webs for each successional day or season, our approach using predator and prey

440 correlations could be used as an example how to create a static web with time-specificity already

441 implemented. In agreement with previous studies, we found dung-inhabiting predators to be

442 prey generalists, not having a strong correlation (max $r = 0.61$) with any prey species (Valiela,

443 1974; Walsh and Cordo, 1997). In contrast to former studies, the larvae of flies (large and small

444 larvae in our study), do not seem to be the most frequent prey (Valiela, 1974), as Hydrophilidae

445 beetles received considerably more links. In contrast to studies focusing on their bio-control

446 (e.g. Roth, 1982), the larvae of Calyptrate flies (large larvae) seem not to be a frequent prey for

447 dung-inhabiting predators, probably because they finish their development before the majority

448   of predators arrive. However, we did not consider eggs of the flies, which could be preyed upon

449   more frequently than larvae (Fincher, 1995; Roth, 1982). Finally, our results highlight the

450   importance of saprophage beetles (Staphylinidae, Scarabaeidae), as potential prey for dung-

451   inhabiting predators, since predation on this guild is usually overlooked (Young, 2015).

452

453   4.4 Study limitations and future perspectives

454   To the best of our knowledge, our study for the first time explores the potential role of temporal

455   trends in the reduction of negative relations among dung-inhabiting predators, and thus in

456   promoting their coexistence. Its biggest limitation is the theoretical establishment of trophic

457   links, although size-based trophic links have been used in other systems (Pomeranz et al., 2019;

458   Woodward et al., 2005). The main achievement is therefore establishment of a hypothetical

459   background for future experimental studies of trophic interactions among organisms inhabiting

460   dung, or other ephemeral habitats such as carrion.

461   In a future, the following approaches may yield fruitful insights:

462   1) Establishing more realistic food web relations between predators and prey, preferably via

463   feeding trials or metabarcoding technologies, including quantitative information on how much

464   of prey an individual predatory species can process. This study should also include using

465   feeding trials to establish IGP and interference relations between dung-inhabiting predators.

466   2) Exploring the environmental filtering effect of dung moisture and chemistry on individual

467   predatory species.

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660   Fig. 1: Percentage representation of dung-inhabiting predators (pred) and prey abundance along

661   successional and seasonal gradients.

662   A) successional gradient, B) seasonal gradient (1 = early spring, 2 = high summer, 3 = early

663   autumn)

664

665   Fig. 2: Food web of dung-inhabiting insects

666   Rows (labels starting with B) represent prey species, columns (labels starting with A) represent

667   predatory species. Species position in the web (rows = from up down, columns = from left to

668   right) is established on species successional (A) or seasonal optima (B) (left/up position = very

669   early, right/down position = very late).

670 red = trophic interaction between prey and "large" predator (size < 3.72 mg; guilds

671 I+II+III+IV), green = with "medium" sized predator (size = 2.9 - 1.135 mg; guild V), blue =

672 "small" predator (size < 1.15 mg; guild VI), grey = predatory larvae and black = parasitoid For

673 individual species abbreviations see Table S1.

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