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## Conservational value of Aculeata communities in sand quarries during ecological succession --Manuscript Draft--

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<b>Abstract:</b>	<p>Sand quarries that are used occasionally and not subjected to rehabilitation are important biodiversity banks in both anthropogenic and semi-natural landscapes. However, their value for biodiversity preservation can change due to dynamic successional processes. We determined the responses of three Aculeata groups: herbivores (Apiformes), predators (Crabronidae, Sphecidae), and kleptoparasites (Apiformes, Chrysididae, Crabronidae) to successional transformations in 32 sand quarries, spanning 15 years of spontaneous succession. Responses to successional changes in vegetation differed depending on the trophic group. Values of community indices for herbivores and kleptoparasites reached the highest complexity at the middle stages of succession, whereas for predators, they remained stable. The arrival of new species, but not changes in dominance structure, significantly affected the community structure of all three Aculeata groups. However, only for predator species, turnover rates increased at the later successional stages. This was manifested by the rapid accumulation of new and rare species. In contrast, <math>\beta</math>-diversity of kleptoparasites decreased, and in the case of herbivores, it remained constant throughout the successional stages. Predators were also characterized by high numbers of prevalent species, present at all successional stages. We highlight that various patterns of species exchange can affect conservational values of sand quarries and provide information about preferences of predatory, herbivorous (pollinating), and parasitic Aculeata, including rare and threatened species, in respect of stages of ecological succession. The collected information will allow a more deliberate selection of protective measures through the implementation of suitable management strategies to facilitate the preservation of these valuable habitats.</p>
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November 9, 2020

Dear Editors,

Please find attached our manuscript entitled “Conservational value of Aculeata communities in sand quarries during ecological succession” that we would like to submit for publication in *Global Ecology and Conservation*.

In our work we address the issue of presenting sand quarries as sites of high biodiversity for insect, with considering dynamical successional changes of these ecosystems, which can have significant effect on conservation value of these sites. Our study concerns the responses of three groups of Aculeata with different life histories – herbivores (Apiformes), predators (Crabronidae, Sphecidae), and kleptoparasites (Apiformes, Crabronidae, Chrysididae) – to successional transformations in 32 sand quarries, spanning 15 years of spontaneous succession. The results show varied processes of species exchange and provide information about preferences of predatory, herbivorous (pollinating), and parasitic Aculeata, including rare and threatened species, in respect of stages of ecological succession in sand quarries. This will allow a more deliberate implementation of suitable management methods to improve the preservation of these valuable sites by maintenance of a mosaic of habitats at various stages of successional transformation.

This is an original piece of research carried out by the authors. All authors agree with the contents of the manuscript and its submission to the journal.

The manuscript is not being considered for publication elsewhere while publication in your journal is pending. All sources of funding are acknowledged in the manuscript, and all authors have declared any direct financial benefits that could result from publication. All appropriate ethics and other approvals were obtained, and the study was conducted after obtaining oral consent from managers of the land and in accordance with applicable law.

The manuscript has been proofread by a native English speaker, and we have enclosed a Language Quality Assurance Certification.

Thank you for your consideration of this manuscript; we look forward to hearing from you.

Sincerely,  
Corresponding author  
Piotr Szefer

1    **Highlights**

- 2        • Successional changes of Aculeata communities in sand quarries were studied.
- 3        • Herbivorous, kleptoparasitic, and predatory Hymenoptera were sampled.
- 4        • Conservational value changed during 15 years of vegetation succession.
- 5        • Aculeata communities changed due to the arrival of new species.
- 6        • Increase in rare or endangered species proportion was observed only for predators.

**1    1    Conservational value of Aculeata communities in sand quarries during ecological**  
**2    2    succession**

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## Abstract

Sand quarries that are used occasionally and not subjected to rehabilitation are important biodiversity banks in both anthropogenic and semi-natural landscapes. However, their value for biodiversity preservation can change due to dynamic successional processes. We determined the responses of three Aculeata groups: herbivores (Apiformes), predators (Crabronidae, Sphecidae), and kleptoparasites (Apiformes, Chrysididae, Crabronidae) to successional transformations in 32 sand quarries, spanning 15 years of spontaneous succession. Responses to successional changes in vegetation differed depending on the trophic group. Values of community indices for herbivores and kleptoparasites reached the highest complexity at the middle stages of succession, whereas for predators, they remained stable. The arrival of new species, but not changes in dominance structure, significantly affected the community structure of all three Aculeata groups. However, only for predator species, turnover rates increased at the later successional stages. This was manifested by the rapid accumulation of new and rare species. In contrast,  $\beta$ -diversity of kleptoparasites decreased, and in the case of herbivores, it remained constant throughout the successional stages. Predators were also characterized by high numbers of prevalent species, present at all successional stages. We highlight that various patterns of species exchange can affect conservational values of sand quarries and provide information about preferences of predatory, herbivorous (pollinating), and parasitic Aculeata, including rare and threatened species, in respect of stages of ecological succession. The collected information will allow a more deliberate selection of protective measures through the implementation of suitable management strategies to facilitate the preservation of these valuable habitats.

**Keywords:** Apiformes; Chrysididae; Sand quarry; Species turnover; Spheciformes, Succession

## 1. Introduction

Abandoned sand quarries and gravel pits can be colonized by various groups of species, including some threatened and rare taxa (Tropek et al., 2010; Heneberg et al., 2013, 2016; Twerd et al., 2019a). Hence, many publications provide evidence for the high conservation value of post-mining sites as habitats for numerous orders of arachnids (Tropek and Konvicka, 2008; Tropek et al., 2010) and insects (Brändle et al., 2000; Lenda et al., 2012; Lönnberg and Jonsell, 2012; Tichanek and Tropek, 2015; Harabiš, 2016; de Smedt and van de Poel, 2017), including bees and other aculeates (Krauss et al., 2009; Seitz et al., 2019; Twerd et al., 2019a, 2019b). Insect communities on post-mining sites present high conservation value but will undergo spontaneous ecological succession, which affects species richness and abundance. However, most studies have neglected the fact that changes in percentage contributions of individual insect species, caused by plant succession, can markedly influence their conservational value.

Temporal variability of insect communities during succession is, along with their abundance and species diversity, an important criterion of ecosystem value (Corbet, 1995; Asaad et al., 2017). In general, species richness and diversity of insect communities are expected to increase over time, but responses of individual species are often highly specific. In contrast, the dynamics of trophic groups (e.g., herbivores, predators, and parasites) can show more predictive patterns (Siemann et al., 1999) and is of high importance from the standpoint of the whole ecosystem (Christensen, 1995). For example, in the case of pollinators, habitat age has no effect on species abundance and



diversity in abandoned fields (Krauss et al., 2009), but this may not be the case for other trophic groups, such as predators, which depend strongly on the structural complexity of the ecosystem. In general, the proportion of herbivores in the community may decrease in favor of increasingly diverse and abundant predators and parasites (Corbet, 1995; Siemann et al., 1999).

Hymenopterans in sand quarries do not necessarily follow the general predictions of classic successional theories advocating a continuous increase in diversity and abundance (Odum, 1969; Brown, 1984). According to general predictions, the abundance and diversity of aculeate Hymenoptera should increase over time, and there might be fewer rare species at the initial stages of succession (Gathmann et al., 1994; Corbet, 1995). However, bees and wasps are good ecological indicators (Odanaka and Rehan, 2019), and thus, their communities dynamically respond to even small changes in their environment. This is due to their high nesting and food requirements (Müller et al., 2006; Ricketts et al., 2008), resulting in a strong relationship with available floral resources (Alanen et al., 2011). Therefore, contrary to the above predictions, early successional stages of abandoned fields harbor diverse Hymenoptera communities because of a high abundance of annual plants (Parrish and Bazzaz, 1979; Alanen et al., 2011; Tschardt et al., 2011; Roberts et al., 2017). This also affects rare species, which can aggregate in the community because of a large variability of microhabitats (Tropé et al., 2010). Numbers of hymenopteran pollinator species (including rare ones) generally decrease with increasing density of plant cover (Rutgers-Kelly and Richards, 2013; Hendrychová and Bogusch, 2016). This is thought to be mainly driven by changes in vegetation characteristics, such as species richness or pollination strategies (Gathmann et al., 1994; Losapio et al., 2016). However, recent observations have shown

1 87 that responses of specialized oligolectic bees to successional processes may be more  
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3 88 complex (Twerd et al., 2019a). On the other hand, late successional stages are predicted  
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5 89 to harbor more diverse parasite and predator communities (Losapio et al., 2016), which  
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8 90 can boost numbers of rare species in older quarries.  
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11 91 Important aspects of community change may be missed when focusing only on  
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13 92 species numbers, in particular raw numbers of rare species. Conservational value will  
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15 93 generally change in the course of succession. However, temporal changes in the  
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17 94 abundances of some persistent species may reflect their important ecosystem value  
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19 95 (Harvey et al., 2017), and rare species may contribute little to functional diversity  
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21 96 within ecosystems (Jain et al., 2014, but see Lyons et al., 2005). Therefore, from the  
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23 97 conservational standpoint, estimates of shifts in contributions of individual species as  
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25 98 well as species turnover rates for different trophic groups in the course of succession in  
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27 99 sand quarries are needed.  
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33 100 In this study, we tested the hypothesis that the conservational value of sand  
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35 101 quarries, based on the aculeate Hymenoptera community, changes due to successional  
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37 102 processes. We expected a continuous increase in abundance and species diversity for  
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39 103 Aculeata communities, but supposed that the detailed patterns would depend on the life  
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41 104 history of individual trophic groups of aculeates. Herbivores (pollinators) were expected  
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43 105 to be the most diverse/abundant at the early and/or middle stages of succession. In  
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45 106 contrast, communities of predators and kleptoparasites would change more slowly, with  
46  
47 107 the accumulation of rare species at later stages of succession. We predicted that changes  
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49 108 in  $\beta$ -diversity would be caused mainly by the arrival of new species. Species turnover  
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51 109 rates would differ between groups presenting diverse trophic behaviors of larvae:  
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53 110 decreasing for herbivores (pollinators) and increasing for parasites and predators. The  
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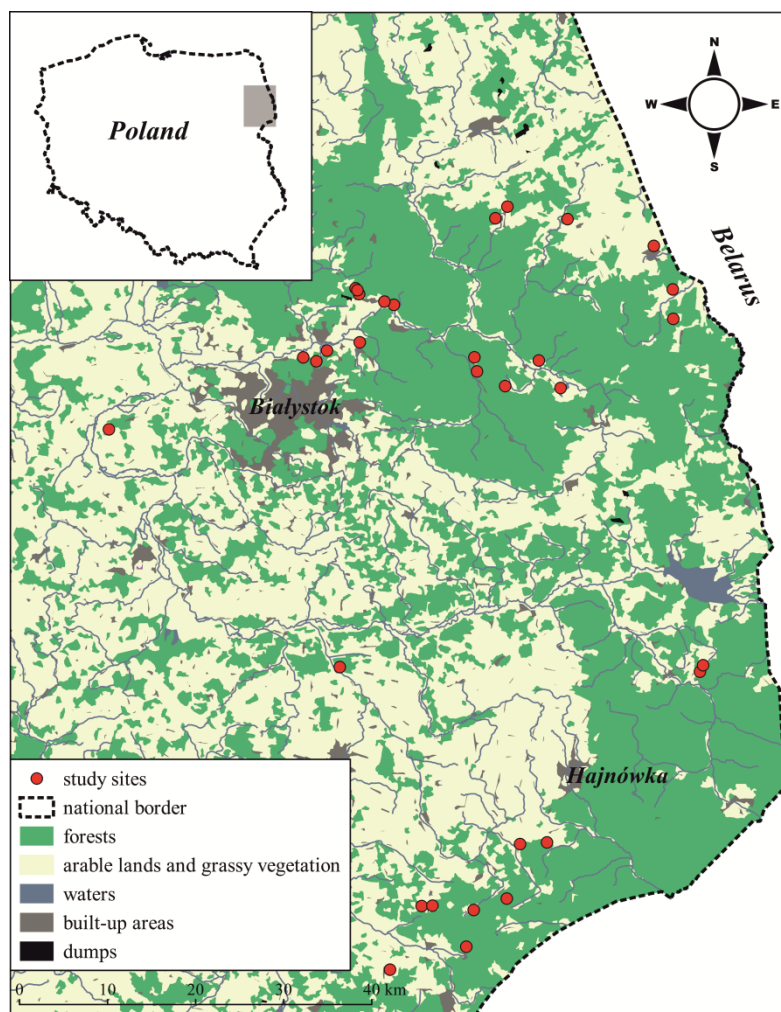
111 groups with more rapid changes in the balanced component of  $\beta$ -diversity would  
112 include higher numbers of rare species and of species characteristic of individual stages  
113 of plant succession. In contrast, fewer species were expected to show continuous  
114 changes in abundance in the course of succession.

## 115 2. Material and methods

### 116 2.1. Study sites

117 Field research was conducted in the Podlasie region (NE Poland), in the  
118 immediate vicinity of extensive woodlands of Białowieża Forest and Knyszyn Forest.  
119 This area is rich in natural deposits of sand and gravel, which result mostly from glacial  
120 and fluvioglacial or, albeit rarely, fluvial accumulation (Siliwończuk, 1985). As much as  
121 69% of the deposits have never been exploited or their extraction was stopped, while the  
122 other 31% are exploited permanently or periodically.

123 This study was conducted in 32 periodically exploited or abandoned sand  
124 quarries (Table A.1, Fig. 1) subjected to spontaneous succession. The investigated sites  
125 varied in stages of ecological succession and were covered mostly with synanthropic  
126 herbaceous vegetation. Synanthropic plant species included e.g. *Anchusa officinalis* L.,  
127 *Ballota nigra* L., *Daucus carota* L., *Echium vulgare* L., *Lamium purpureum* L., and  
128 *Leonurus cardiaca* L. The dominant grass species in those habitats were *Calamagrostis*  
129 *epigejos* (L.) Roth, *Elymus repens* (L.) Gould, and *Poa pratensis* L., while among  
130 woody species, *Pinus sylvestris* L. was the most abundant one.



131

132 **Fig. 1.** Location of the study sites (sand quarries).



**Fig. 2.** Representative photographs of stages of plant succession in sand quarries: a, b = early succession; c, d = middle succession; e, f = late succession.

The analyzed sand quarries were divided into three groups, depending on the stage of plant succession (Fig. 2), namely stage I: 0–5 years, i.e., early succession (initial colonization by plants – 10 sand quarries): bare soil  $\geq 55\%$  of the area, herbaceous vegetation 20–45% of the area; stage II: 5–10 years, i.e., middle succession



(sward formation – 12 sand quarries): bare soil  $\leq$  45% of the area, herbaceous vegetation 35-80% of the area, woody vegetation  $\geq$  5%; stage III: 10–15 years, i.e., late succession (development of woody vegetation – 10 sand quarries): bare soil  $\leq$  5% of the area, herbaceous vegetation 15–40% of the area, woody vegetation  $\geq$  60%. Percentage contributions were estimated in relation to the total area of the sand quarry (Table A.1).

This study is a continuation of a project concerning the importance of sand quarries for wild bees, which was initiated in 2015. The material used here was collected in 2008, 2015–2016 (Twerd et al., 2019a, 17 sites), and in 2017 (15 sites). Research was conducted after obtaining oral consent from managers of the land and in accordance with applicable law.

## 2.2. Insect sampling

The insects were collected when the weather was favorable for Aculeata activity, i.e., with no or little wind ( $< 3$  on the Beaufort scale) (Krauss et al., 2009). During field research, the temperature was always above 16°C, and on most days, it did not exceed 25°C. Because the phenological periods in Eastern Poland are delayed by about 2 weeks in relation to the central part of the country, sampling was conducted in May and July to obtain the fullest possible number of both spring and summer species. In each sand quarry, the insects were caught along transects; each transect was 200 m long and 1 m wide (Banaszak, 1980). Each researcher surveyed one transect for 30 minutes and collected the selected group of Aculeata (Apiformes, Crabronidae and Sphecidae, Chrysididae). The transects were visited in a random order throughout the season to cover the entire period of Aculeata activity during the day. The number of delimited transects was adjusted to the size of sand quarries, in three categories: 0.5–1.0 ha (no

163 more than 4 transects), 1.0–3.0 ha (no more than 8 transects), > 3.0 ha (no more than 12  
164 transects). Information about numbers of surveyed transects, depending on site area, is  
165 presented in Table A1. To avoid self-replication, the sampled quarries were spaced  
166 more than 1.5 km apart. The collected specimens were pinned and identified to the  
167 species level. Species of the *Bombus lucorum* complex (Bossert, 2015) are not  
168 distinguishable by morphological features, and *B. lucorum* and *B. terrestris* are easily  
169 confused (Wolf *et al.*, 2010); therefore, data on the occurrence of bumblebees of the  
170 subgenus *Bombus* Latreille, 1802 = *Terrestribombus* Vogt, 1911 were pooled. Species  
171 names followed Bitsch and Leclercq (1993), Skibińska (2004), Puławski (2020),  
172 Wiśniowski (2015), and Kuhlmann *et al.* (2020) (Table A.2). We identified the status of  
173 threatened bee and wasp species according to the most recent editions of the Polish Red  
174 Lists provided by Banaszak (2004), Celary (2004), Skibińska (2004), and Wiśniowski  
175 (2015).

176         The Aculeata were divided into three groups representing diverse trophic  
177 behaviors of larvae (= life histories): herbivores (Apiformes), kleptoparasites  
178 (Apiformes, Chrysididae, Crabronidae), and predators (Crabronidae and Sphecidae).  
179 The group of herbivores was composed of bees, i.e., aculeates completely biologically  
180 linked with flower forage: imagines feed mostly on nectar, while larvae are fed with  
181 nectar and pollen. However, numerous bee species have adopted a kleptoparasitic way  
182 of life (Michener, 2007). Predators were represented by species of the families  
183 Crabronidae and Sphecidae. Most females of digger wasps hunt for insects or spiders as  
184 food for larvae, but there are some *Nysson* species (Crabronidae) that have lost their  
185 hunting instinct, becoming specialized in entering the nests of other species and laying  
186 their eggs on their host victims (Bohart and Menke, 1976). Adult digger wasps feed

187 mainly on nectar and aphid secretions, sometimes on their hosts (Blösch, 2000). Cuckoo  
188 wasps (Chrysididae) are a group of wasps that develop during the larval stage as  
189 kleptoparasites or parasitoids of mainly other hymenopterans (Paukkunen et al., 2015).

### 190 2.3. Statistical analysis

191 All analyses were performed in the R statistical environment (R Core Team,  
192 2019). We used generalized linear models (GLMs) to assess differences in species  
193 diversity, species richness, and community abundance. Error distribution for abundance  
194 was investigated with the use of a negative binomial model in the *MASS* package  
195 (Venables and Ripley, 2002); for species number, we used Poisson distribution. To study  
196 interactions between individual groups of aculeates at individual stages of succession,  
197 we conducted a post-hoc test with Tukey correction for multiplicity in the *emmeans*  
198 package (Lenth, 2019).

199 To verify if plant succession was responsible for changes in community  
200 structure, we performed redundancy analysis (RDA) with successional stage as an  
201 explanatory variable. Prior to the analysis, the matrix of abundance was subjected to  
202 Hellinger transformation (Legendre and Cáceres, 2013). To identify the species most  
203 strongly reacting to the stages of succession, we fitted the abundance of individual  
204 species to the defined RDA model, using the *envfit* function of the *vegan* package  
205 (Oksanen et al., 2019). The number of species with significant vs. non-significant  
206 responses in each group was summarized in a 3 x 2 contingency table, and the  
207 homogeneity of the contingency table was then tested with likelihood-ratio chi-square  
208 statistic ( $G^2$ ). To better understand the underlying relationships between species  
209 responses and trophic groups, we further decomposed the above table following the



rules of partitioning in Agresti (2012). Partitioning steps can be found in a supplementary R code (<http://tiny.cc/aryzsz>).

We calculated the rates of species exchange ( $\beta$ -diversity) on the basis of the transformed abundance matrices and assessed the character of changes in community structure between stages of succession for individual Aculeata groups. We used Bray-Curtis (BC) dissimilarity as a measure of  $\beta$ -diversity. According to Baselga (2013), we adopted the subdivision of  $\beta$ -diversity into two components: associated with changes in dominance structure of species (gradient component) and associated with arrival of new species (balanced component). We calculated both components for all possible pairs of sites at stages I and II as well as II and III. For comparisons of two successional stages, a site from an earlier stage was used as a random factor to account for local differences in community composition. For statistical analysis, we adopted an additional assumption concerning the permissible values of  $\beta$ -diversity, i.e., that no two stages can be completely different (BC = 1) or completely identical (BC = 0), and therefore, empirical values of  $\beta$ -diversity equal to 0 or 1 were replaced by 0.001 and 0.999, respectively. This allowed us to use the beta distribution in the statistical analysis. Statistical significance of changes in mean components of  $\beta$ -diversity for stages of succession and individual groups of species were calculated using the *glmmTMB* package (Brooks et al., 2017), and components of  $\beta$ -diversity were calculated using the *codyn* package (Hallett et al., 2019).

To determine the strength of association of species with successional stage, we calculated indicator values (*IndVal*) for each Aculeata species (Dufrêne and Legendre, 1997). The significance of *IndVals* was confirmed by a Monte Carlo test with 9,999 permutations. We summarized the results in a 3 x 3 contingency table for three

234 successional stages and the three trophic groups. As above, we used the  $G^2$  statistic to  
235 test for homogeneity, and individual partitioning steps can be found in a supplementary  
236 R code.

237 To calculate the probability of an individual belonging to any category of  
238 vulnerability for each trophic group at all three stages, we used binomial distribution  
239 with a logit link function. As above, the post-hoc Tukey test was used to assess  
240 statistical significance.

### 241 3. Results

#### 242 3.1. Wasp and bee species composition

243 In total, we recorded 8,230 individuals of 272 species of Aculeata. In respect of  
244 species richness, 51.47% (140 species) were herbivores, 25.37% (69 species) were  
245 predators, and 23.16% (63 species) were kleptoparasites. Expected species richness  
246 (Chao 1 estimator) was calculated for groups of Aculeata differing in trophic behaviors  
247 of larvae and for Aculeata found at individual stages of succession (Fig. A.1 and A.2).  
248 Simultaneously, 20.22% of the recorded species were threatened or rare (Table A.2);  
249 herbivores accounted for 9.93% (19.29% of the group), predators for 4.78% (18.84% of  
250 the group), and kleptoparasites for 5.51% (23.81% of the group) of all recorded species.

#### 251 3.2. Patterns in community characteristics

252 Total species richness (chi square test,  $p < 0.001$ ) and abundance (chi square test,  
253  $p = 0.019$ ) of Aculeata significantly increased with successional changes. In contrast,  
254 overall diversity did not change (Table A.3). This pattern was primarily due to a  
255 significant increase in abundance and species richness in parasites and herbivores at the

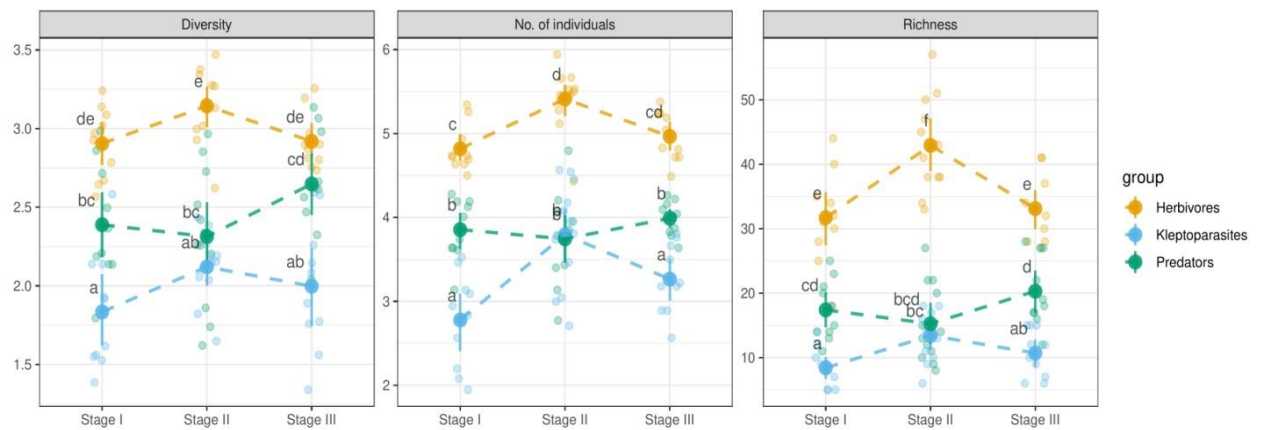
middle stage of succession (Table 1, Fig. 3). In the case of predators, we did not detect any changes in overall values of community indices. Species richness, abundance, and diversity were generally highest for herbivores and lowest for kleptoparasites. At the middle stage of succession, the indicators for kleptoparasites and predators were similar, and at the late stage, the diversity of predators was similar to that of herbivores.

**Table 1.** Mean values and their asymptotic 95% CIs for linear and generalized linear models for diversity (Shannon index), abundance, and species richness of three Aculeata trophic groups at three studied successional stages. Different letters in the last column indicate statistically significant differences (Tukey correction for multiplicity,  $\alpha > 0.05$ ). Successional stages: I = early; II = middle; III = late.

Index	Stage	Aculeata group	Mean value	Standard error	df	Lower 95% CL	Upper 95% CL	Significance
Diversity (Shannon index)	I	Herbivores	2.91	0.10	Inf	2.71	3.10	de
		Kleptoparasites	1.83	0.10	Inf	1.64	2.03	a
		Predators	2.39	0.10	Inf	2.19	2.59	bc
	II	Herbivores	3.14	0.09	Inf	2.96	3.33	e
		Kleptoparasites	2.12	0.09	Inf	1.94	2.30	ab
		Predators	2.31	0.09	Inf	2.13	2.49	bc
	III	Herbivores	2.92	0.10	Inf	2.72	3.12	de
		Kleptoparasites	2.00	0.10	Inf	1.80	2.20	ab
		Predators	2.65	0.10	Inf	2.45	2.85	cd
Species richness (Poisson)	I	Herbivores	3.82	1.78	Inf	28.50	35.52	e
		Kleptoparasites	8.42	0.92	Inf	6.75	10.38	a
		Predators	17.46	1.32	Inf	15.03	20.29	cd
	II	Herbivores	42.95	1.89	Inf	39.25	46.99	f
		Kleptoparasites	13.46	1.06	Inf	11.47	15.64	bc
		Predators	15.18	1.13	Inf	13.19	17.64	bcd
	III	Herbivores	33.12	1.82	Inf	29.67	36.97	e
		Kleptoparasites	10.70	1.03	Inf	8.85	12.94	ab
		Predators	20.29	1.43	Inf	17.64	23.34	d
Abundance	I	Herbivores	127.74	15.17	Inf	100.48	160.77	c

(negative binomial)	II	Kleptoparasites	17.46	2.41	Inf	13.33	22.87	a
		Predators	48.91	6.07	Inf	38.48	62.18	b
		Herbivores	235.09	25.22	Inf	190.57	290.04	d
	III	Kleptoparasites	51.42	5.79	Inf	41.26	64.07	b
		Predators	46.99	5.34	Inf	37.71	58.56	b
		Herbivores	148.41	17.52	Inf	116.75	186.79	cd

Inf = infinite; CL = confidence limit

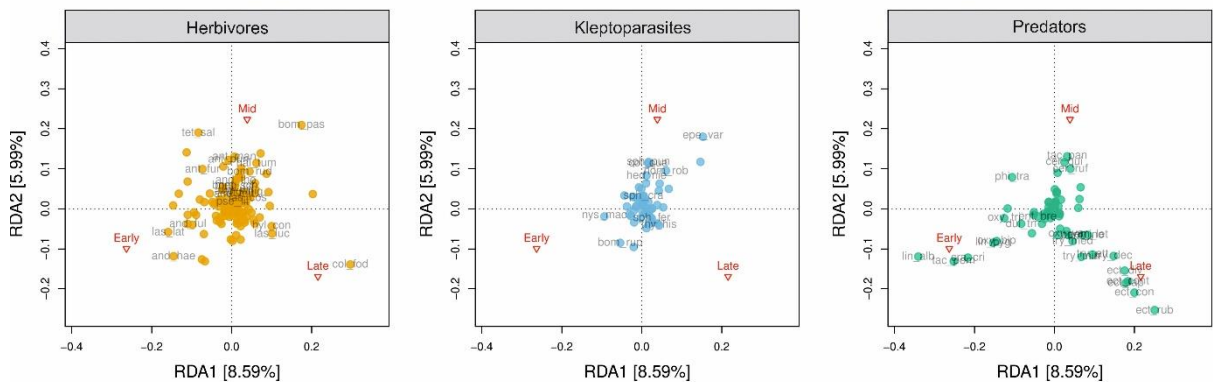


**Fig. 3.** Diversity, abundance, and species richness of Aculeata at the three distinguished stages of succession. Abundance was subjected to logarithmic transformation to better visualize the differences among groups. Transparent points denote empirical values. Different letters represent statistical significance at  $\alpha = 0.05$ , adjusted for multiplicity (Tukey correction).

### 3.3. Community structure as a response to successional transformation

Successional stages significantly affected the structure of aculeate communities (permutation test, 999 replications,  $F = 2.47$ ,  $p < 0.001$ ), and the RDA model explained 14.58% of the variation (adjusted  $R$ -square). Among 272 species of Aculeata, 55 (20.2%) significantly responded to successional transformation. In this group,

contributions of herbivores and predators were similar (38.2 and 43.6%, respectively), while kleptoparasites accounted for 18.2%. The species that most strongly reacted to successional transformations are listed in Supplementary Table A.4 and Figure 4. The analysis of 272 species, summarized in a 3 x 2 contingency table, revealed significant relationships between the Aculeata group and the number of species significantly responding to the RDA model ( $G^2 = 11.223$ ,  $df = 2$ ,  $p = 0.004$ ). Herbivores and kleptoparasites had similar low-percentage contributions of species significantly reacting to the successional stages (15 and ~16%, respectively,  $G^2 = 0.025$ ,  $df = 1$ ,  $p = 0.873$ ). Predatory species had a significantly higher (nearly 35%) percentage of species that significantly reacted to successional stages ( $G^2 = 11.197$ ,  $df = 1$ ,  $p < 0.001$ ).



**Fig. 4.** Plot of redundancy analysis (RDA) ordination with stage of succession as a discrete explanatory variable. For better visualization, the points are marked separately for individual trophic groups.

### 3.4 Changes in $\beta$ -diversity in the course of successional transformation

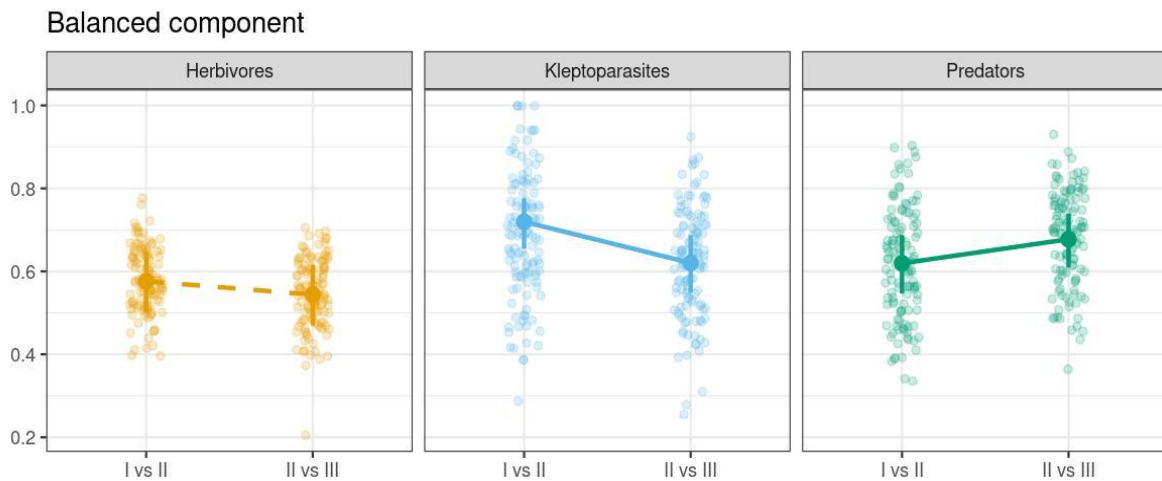
Species turnover rate (the balanced component of  $\beta$ -diversity) for herbivorous aculeates was stable (lack of significant differences between stages I and II and between II and III), but differed for predators and kleptoparasites. For predators, species turnover

rate increased, whereas for kleptoparasites, it decreased (Tables 2 and A.5, Fig. 5). In contrast, changes in dominance structure (gradient component) were small and similar for all three groups of Aculeata (Fig. A.3).

**Table 2.** Estimated means and 95% confidence intervals (CIs) for beta generalized linear models (GLMs) of species turnover rates for the analyzed successional stages and different trophic groups of Aculeata.

Component	Group	Prediction	Lower 95% CL	Upper 95% CL	Stages
Balanced	Herbivores	0.576	0.502	0.647	I vs. II
		0.544	0.470	0.616	II vs. III
	Kleptoparasites	0.719	0.655	0.776	I vs. II
		0.620	0.548	0.687	II vs. III
	Predators	0.619	0.547	0.687	I vs. II
		0.677	0.609	0.739	II vs. III
Gradient	Herbivores	0.034	0.025	0.047	I vs. II
		0.036	0.026	0.050	II vs. III
	Kleptoparasites	0.036	0.026	0.049	I vs. II
		0.035	0.025	0.047	II vs. III
	Predators	0.037	0.027	0.051	I vs. II
		0.037	0.027	0.051	II vs. III
Bray-Curtis	Herbivores	0.608	0.535	0.677	I vs. II
		0.575	0.502	0.646	II vs. III
	Kleptoparasites	0.754	0.694	0.806	I vs. II
		0.658	0.588	0.721	II vs. III
	Predators	0.659	0.589	0.723	I vs. II
		0.715	0.650	0.772	II vs. III

CL = confidence limit



**Fig. 5.** Means and 95% confidence intervals (CIs) for the balanced component of  $\beta$ -diversity for the three trophic Aculeata groups at two transitional stages: I vs. II and II vs. III. Solid lines indicate statistical significance of the mean differences at  $\alpha = 0.05$ . Points indicate empirical values.

### 3.5. Species characteristic of individual successional stages

We identified 41 indicator species, including 15 herbivores, 21 predators, and 5 kleptoparasites (Table 3). Most of the indicator species were characteristic of the middle stage of succession (17 species), compared to 10 in the early stage and 14 in the late stage. In the middle stage, herbivorous species prevailed (58.8%), whereas predators dominated in the early and late stages (80.0 and 71.4%, respectively) (Table 3). We evaluated the original 3 x 3 contingency table of 41 indicator species and found significant relations between successional stage and trophic group ( $G^2 = 15.453$ ,  $df = 4$ ,  $p = 0.004$ ). Herbivorous and kleptoparasitic species had similar patterns of characteristic species throughout the successional stages, with the highest proportion of indicator species in the middle stage ( $G^2 = 1.243$ ,  $df = 2$ ,  $p = 0.537$ ). In contrast, for predators, the

proportion of indicator species was significantly higher in the early ( $G^2 = 4.640$ ,  $df = 1$ ,  $p = 0.031$ ) and late successional stages ( $G^2 = 9.569$ ,  $df = 1$ ,  $p = 0.002$ ).

**Table 3.** Associations of individual species of Aculeata with successional stages: I = early, II = middle, and III = late.

Stage	Aculeata	Species	IndVal	p
I	Predator	<i>Crabro cribrarius</i>	0.77	< 0.001
	Predator	<i>Tachysphex pompiliformis</i>	0.76	< 0.001
	Predator	<i>Oxybelus bipunctatus</i>	0.66	< 0.001
	Predator	<i>Lindenius pygmaeus</i>	0.63	0.001
	Predator	<i>Lindenius albilabris</i>	0.62	0.016
	Herbivore	<i>Andrena haemorrhoa</i>	0.56	0.004
	Predator	<i>Oxybelus trispinosus</i>	0.47	0.011
	Herbivore	<i>Andrena fulva</i>	0.41	0.031
	Predator	<i>Diodontus tristis</i>	0.40	0.011
	Predator	<i>Entomognathus brevis</i>	0.30	0.048
II	Kleptoparasite	<i>Epeolus variegatus</i>	0.65	< 0.001
	Herbivore	<i>Bombus pascuorum</i>	0.60	< 0.001
	Herbivore	<i>Tetraloniella salicariae</i>	0.57	0.031
	Predator	<i>Cerceris quinquefasciata</i>	0.52	0.018
	Herbivore	<i>Andrena dorsata</i>	0.51	0.028
	Kleptoparasite	<i>Sphecodes puncticeps</i>	0.50	0.002
	Kleptoparasite	<i>Hedychrumniemeali</i>	0.50	0.001
	Herbivore	<i>Megachile maritima</i>	0.50	0.038
	Predator	<i>Tachytespanzeri</i>	0.48	0.004
	Herbivore	<i>Anthidium punctatum</i>	0.47	0.015
	Herbivore	<i>Bombus ruderarius</i>	0.47	0.047
	Herbivore	<i>Halictus tumulorum</i>	0.46	0.039
	Herbivore	<i>Anthophora furcata</i>	0.43	0.032
	Herbivore	<i>Andrena thoracica</i>	0.42	0.007
	Predator	<i>Cerceris ruficornis</i>	0.40	0.019
	Herbivore	<i>Anthidium manicatum</i>	0.40	0.016
	Kleptoparasite	<i>Coelioxys quadridentata</i>	0.33	0.028
III	Predator	<i>Ectemnius rubicola</i>	0.88	< 0.001
	Predator	<i>Ectemnius confinis</i>	0.88	< 0.001
	Predator	<i>Ectemnius dives</i>	0.78	< 0.001
	Predator	<i>Ectemnius continuus</i>	0.72	< 0.001
	Predator	<i>Trypoxylon deceptorium</i>	0.70	< 0.001
	Predator	<i>Ectemnius lapidarius</i>	0.68	< 0.001
	Predator	<i>Trypoxylon attenuatum</i>	0.56	0.003
	Predator	<i>Pemphredon lethifer</i>	0.54	0.002
	Predator	<i>Trypoxylon minus</i>	0.52	0.006



Herbivore	<i>Colletes fodiens</i>	0.51	0.037
Predator	<i>Pemphredon inornata</i>	0.50	0.002
Herbivore	<i>Lasioglossum lucidulum</i>	0.39	0.027
Herbivore	<i>Hylaeus confusus</i>	0.36	0.027
Kleptoparasite	<i>Thyreus histrionicus</i>	0.30	0.046

Only statistically significant indicator values are shown (*IndVal* > 0.25).

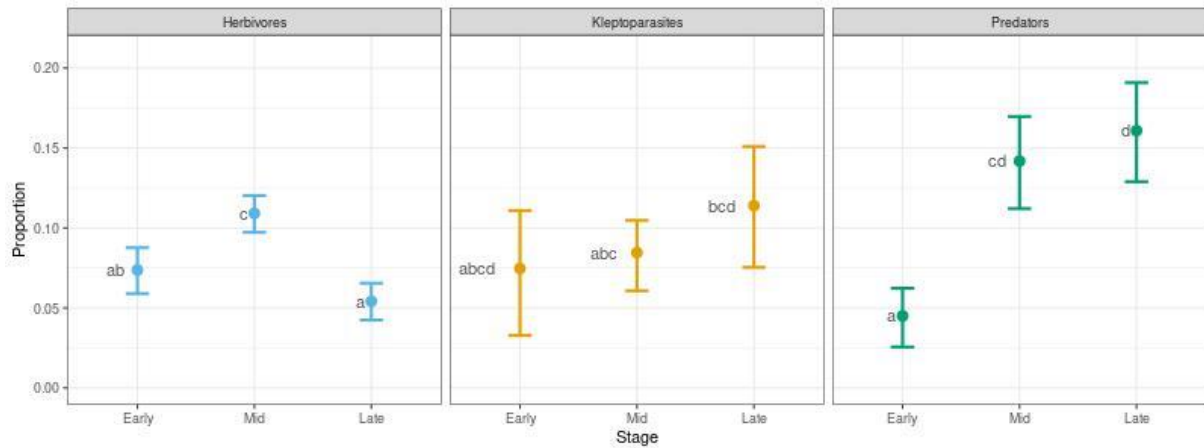
### 3.6. Rare and threatened species at individual successional stages

Rare and threatened species jointly accounted for 20.22% of all species. This concerned mostly herbivores (19.29% of the group) and kleptoparasites (23.81% of the group). For the cumulated Aculeata community and for herbivores, the probability of recording rare and threatened species was highest in stage II (Fig. A.4). For predators, probability values were highest in stages II and III, and for kleptoparasites, no significant differences between the stages were found (Table 4, Fig. 6).

**Table 4.** Parameter values for the binomial generalized linear models (GLM) evaluating the proportion of individuals belonging to rare and endangered species at different successional stages and depending on the Aculeata trophic group. Successional stages: I = early, II = middle, and III = late.

Stage	Group	Proportion	<i>N</i>	SE	Lower 95% CL	Upper 95% CL
I	Herbivores	0.074	1,275	0.007	0.059	0.088
II		0.109	1,478	0.006	0.097	0.120
III		0.054	2,822	0.006	0.042	0.065
I	Kleptoparasites	0.075	174	0.020	0.033	0.111
II		0.085	272	0.011	0.061	0.105
III		0.114	615	0.019	0.075	0.151
I	Predators	0.045	489	0.009	0.026	0.062
II		0.142	541	0.015	0.112	0.170
III		0.161	564	0.016	0.129	0.191

CL = confidence limit



**Fig. 6.** Proportion of rare and/or threatened species in the Aculeata community for different trophic groups at different successional stages. Dots and whiskers represent predicted mean values and 95% CIs, respectively. Different letters represent statistical significance at  $\alpha = 0.05$ , adjusted for multiplicity (Tukey correction).

#### 4. Discussion

Our results confirm that occasionally used sand quarries, gradually colonized by plants, are important habitats for various groups of Aculeata with different life histories (Apiformes, Spheciformes, and Chrysididae). The significance of spontaneously overgrown extraction sites for biodiversity preservation has also been reported previously (Tropék et al., 2010; Řehounková et al., 2011; Prach et al., 2013). However, such habitats are subject to dynamic processes of ecological succession, which markedly influence their value for biodiversity preservation. The high conservation potential of such sites is confirmed by the fact that about 20% of the species recorded there are rare or threatened. We found that the arrival of new species, rather than changes in their dominance structure, significantly affected species exchange in communities of all three Aculeata groups. This significantly affected the occurrence of rare and threatened species and – as a consequence – also the conservation value of the studied habitats. Taking into account the cumulated Aculeata community, the value

354 decreased at early stages of succession. However, the character of these changes  
355 depends on the considered trophic group.

356 In our study, the Aculeata community reached the highest complexity level at  
357 the middle stage of succession. The sites in the late stage were characterized by the  
358 lowest values of the analyzed indices; this pattern was primarily due to a significant  
359 increase in abundance and species richness of herbivores and parasites. This is  
360 consistent with previous studies (Steffan-Dewenter and Tscharnkte, 2001; Potts et al.,  
361 2003; Rutgers-Kelly and Richards, 2013) in which Apiformes richness was proportional  
362 to bee food resources and tended to increase in the first years of successional  
363 transformation, followed by a decline.

364 Undoubtedly, the availability of bee forage plants and the presence of suitable  
365 nesting sites are factors determining bee occurrence in the environment (Ricketts et al.,  
366 2008; Ritchie and Johnson, 2009). In the case of herbivores, this can be associated with  
367 modification of habitat structure, linked with the colonization of the substrate at the first  
368 stage of succession and the appearance of new bee food plant species. The major  
369 reasons for the decline in bee diversity in wooded habitats include simplification of  
370 vegetation structure, loss of food resources, and disappearance of suitable nesting sites  
371 (Winfrey et al., 2007). The studied sites were mostly covered with synanthropic  
372 vegetation, also ruderal species, which attests to a high level of human impact (Twerd et  
373 al., 2019a) as such species often colonize transformed and degraded sites (Kuzmič and  
374 Šilic, 2017).

375 Another important factor is the rate of succession, depending on substrate type.  
376 Succession on poor, dry, and sandy soils is slow, whereas on fertile and moist soils,  
377 succession is generally faster (Ejrnaes et al., 2003). In our study, the rate of species

turnover for herbivores seemed to remain constant throughout successional stages, with a higher proportion of rare species in the middle stage of succession. This pattern was possibly due to highly specialized oligolectic bees, usually associated with ruderal plant species, which dominated at the sites in the middle stage of succession (Twerd et al., 2019a). In the case of kleptoparasitic communities, their species turnover slowed down in the course of succession, possibly following the patterns of their hosts (i.e., mainly wild bees).

In the case of predators, we did not detect any changes in values of community indices. We found, however, that changes in the community structure of predators accelerated at the later stages of succession, and this was mainly driven by the rapid accumulation of new and rare species. This resulted from the simultaneous presence of species preferring open habitats, e.g., *Cerceris arenaria* (L., 1758), *Lindenius albilabris* (F., 1793), and *Philanthus triangulum* (F., 1775), as well as stenotopic species associated with wooded habitats, e.g., *Ectemius continuus* (F., 1804) and *E. rubicola* (Dufour and Perris, 1840). Many of them are rare and threatened with extinction in Poland, e.g., *Bembecinus tridens* (F., 1781), *Harpactus laevis* (Lat., 1792), and *Lestica alata* (Panzer, 1797). A similar relationship was observed during research on the attractiveness of another type of anthropogenic habitats, namely Solvay process waste beds rich in calcium (Twerd et al., 2017). The cited study showed that the most favorable stage of succession in the waste beds was their colonization by woody vegetation, as the bee community included then species characteristic of open habitats as well as stenotopic species associated with wooded habitats (Twerd et al., 2017). In the present study, this was possible because the analyzed sand quarries are exploited only periodically. Because of the small scale of exploitation of the sand quarries, they

are subject to spontaneous succession. As a result, various microhabitats are formed within them, including both bare sandy soil and areas colonized by vegetation, including forest communities. Besides, in some of the sand quarries, exploitation ceased in 2006; the sites were not rehabilitated and were only subject to spontaneous succession. At present, they are dominated by *Pinus sylvestris*. In this case (late stage of succession), the proportion of herbaceous vegetation reached 15–40%, while that of woody vegetation exceeded 60%. Anyway, in most such sand quarries, part of deposits remained uncovered. This was due to the fact that when industrial exploitation ceased, the local inhabitants often started to use them illegally, which does not allow complete colonization by plants. However, this creates conditions for the coexistence of species with different habitat preferences and thus increases the conservation value of these sites (Kerbiriou et al., 2018).

Communities of herbivores, in contrast to kleptoparasites and predators, greatly differed among the successional stages, which leads us to infer that random factors play a significant role in their variability (Ponisio et al., 2017). On the other hand, in contrast to our expectations, predator communities maintained some degree of structural coherence, in spite of the faster species turnover rate. This is reflected in a relatively high number of persistent species, present in all stages of succession suggesting that these species are keystone species in trophic networks (Piraino et al., 2002). From the conservation standpoint, special attention is paid to rare and threatened species. However, they do not necessarily perform an important function in ecosystems, and their increased contribution to the community can be due to habitat size (Krauss et al., 2009) and the proximity of natural habitats (Novák and Konvička, 2006). The role of rare species in the communities is still unclear, but our study assessed changes taking

place in Aculeata communities and suggests that the overall variability of communities should be taken into account, with numbers of rare and threatened species, when determining protection priorities.

## **6. Conclusions**

Spontaneously colonized sand quarries can play an important trans-regional role in nature conservation as favorable sites for rare insect species and as substitute habitats for threatened species in Europe. However, their protective values for individual taxa and groups differing in life history vary widely, and therefore, a multi-taxon approach is needed for the development of adequate management plans for such sites. The problem of the simultaneous protection of species with different ecological requirements can be solved by allowing spontaneous succession in abandoned mines. Because of species substitution, which takes place during natural succession, active protection measures must also be implemented. Such measures should aim at the maintenance of a mosaic of habitats in various stages of successional transformation.

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**Fig. 1.** Location of study sites (sand quarries).

**Fig. 2.** Representative photographs of stages of plant succession in sand quarries: a, b = early succession; c, d = middle succession; e, f = late succession.

**Fig. 3.** Diversity, abundance, and species richness of Aculeata at the three distinguished stages of succession. Abundance was subjected to logarithmic transformation to better visualize the differences among groups. Transparent points denote empirical values. Different letters represent statistical significance at  $\alpha = 0.05$ , adjusted for multiplicity (Tukey correction).

**Fig. 4.** Plot of redundancy analysis (RDA) ordination for stage of succession as a discrete explanatory variable. For better visualization, the points are marked separately for individual trophic groups.

**Fig. 5.** Means and 95% confidence intervals (CIs) for the balanced component of  $\beta$ -diversity for the three trophic Aculeata groups at two transitional stages: I vs. II and II vs. III. Solid lines indicate statistical significance of the mean differences at  $\alpha = 0.05$ . Points indicate empirical values.

**Fig. 6.** Proportion of rare and/or threatened species in the Aculeata community for different trophic groups at different stages of succession. Dots and whiskers represent predicted mean values and 95% CIs, respectively. Different letters represent statistical significance at  $\alpha = 0.05$ , adjusted for multiplicity (Tukey correction).

**Table 1.** Mean values and their asymptotic 95% CIs for linear and generalized linear models for diversity (Shannon index), abundance, and species richness of three Aculeata trophic groups at three studied successional stages. Different letters in the last column indicate

statistically significant differences (Tukey correction for multiplicity,  $\alpha > 0.05$ ). Successional stages: I = early, II = middle, III = late.

**Table 2.** Estimated means and 95% confidence intervals (CIs) for beta generalized linear models (GLMs) of species turnover rates for the analyzed successional stages and different trophic groups of Aculeata.

**Table 3.** Associations of individual species of Aculeata with successional stages: I = early, II = middle, and III = late.

**Table 4.** Parameter values for the binomial generalized linear models (GLMs) evaluating the proportion of individuals belonging to rare and endangered species at different successional stages and depending on the Aculeata trophic group. Successional stages: I = early; II = middle, and III = late.

Figure 1

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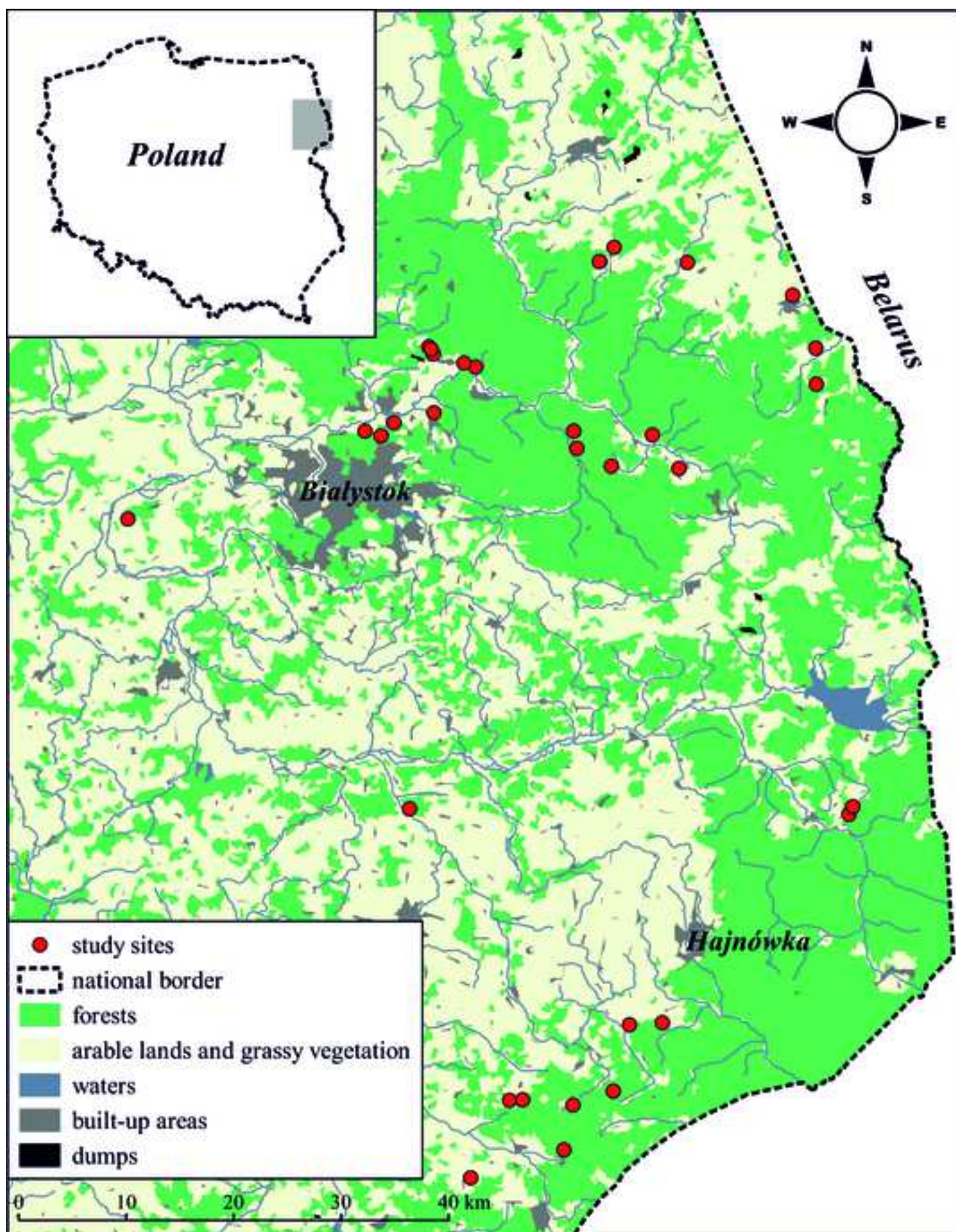




Figure 2

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Figure 3

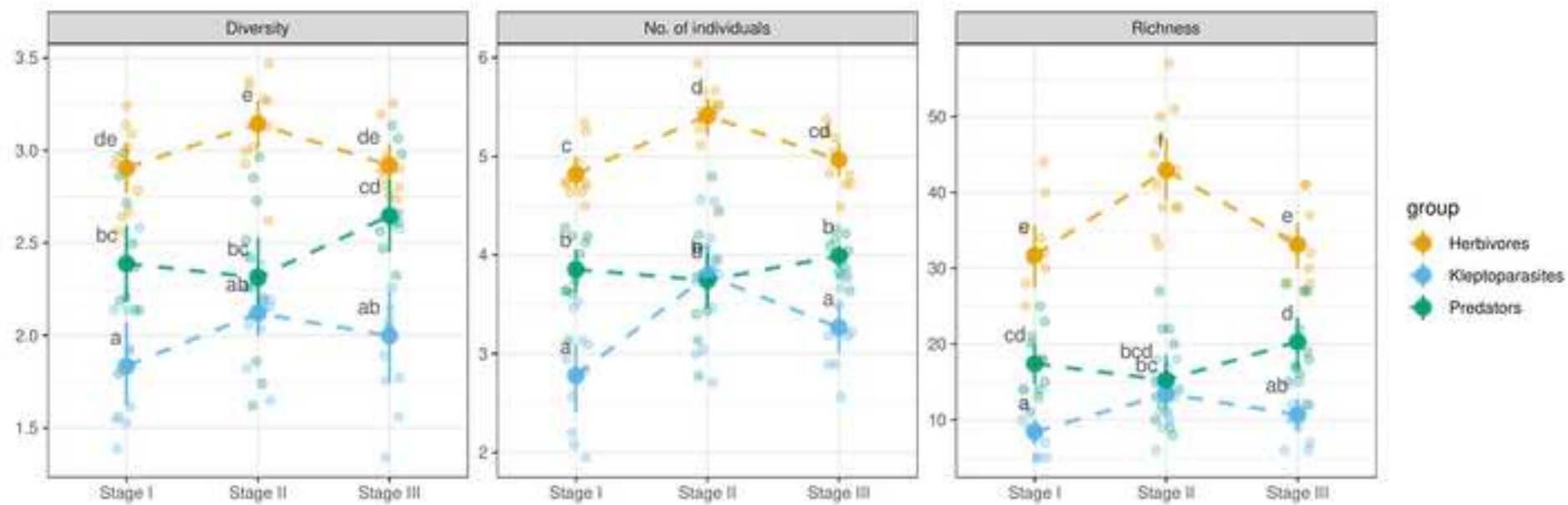


Figure 4

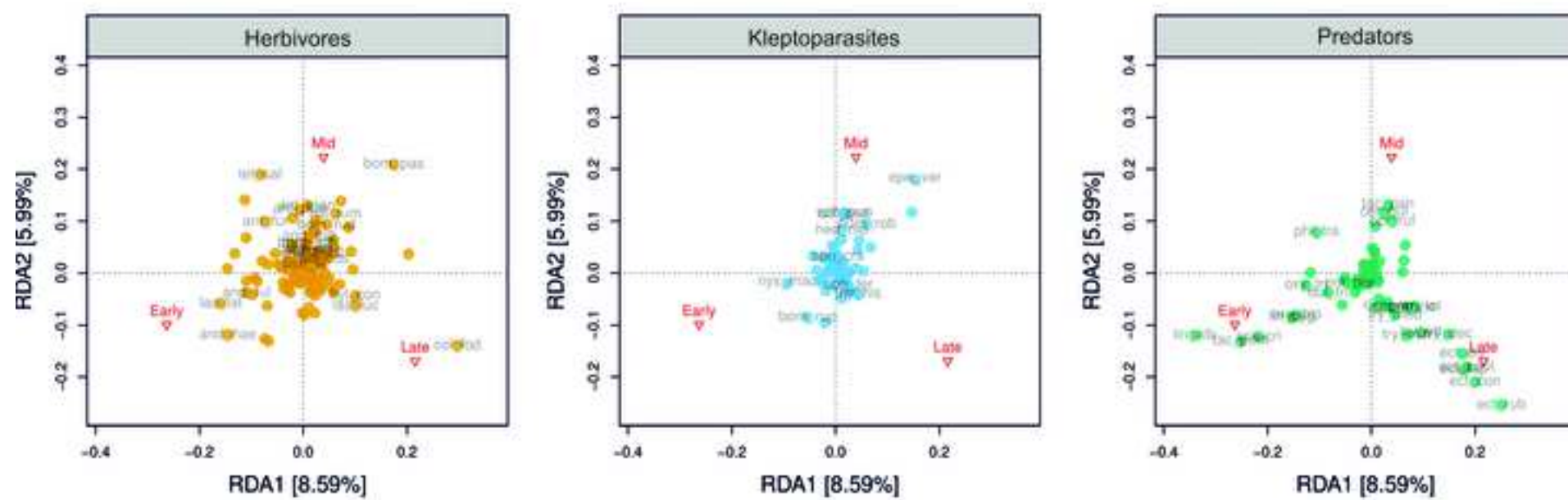


Figure 5

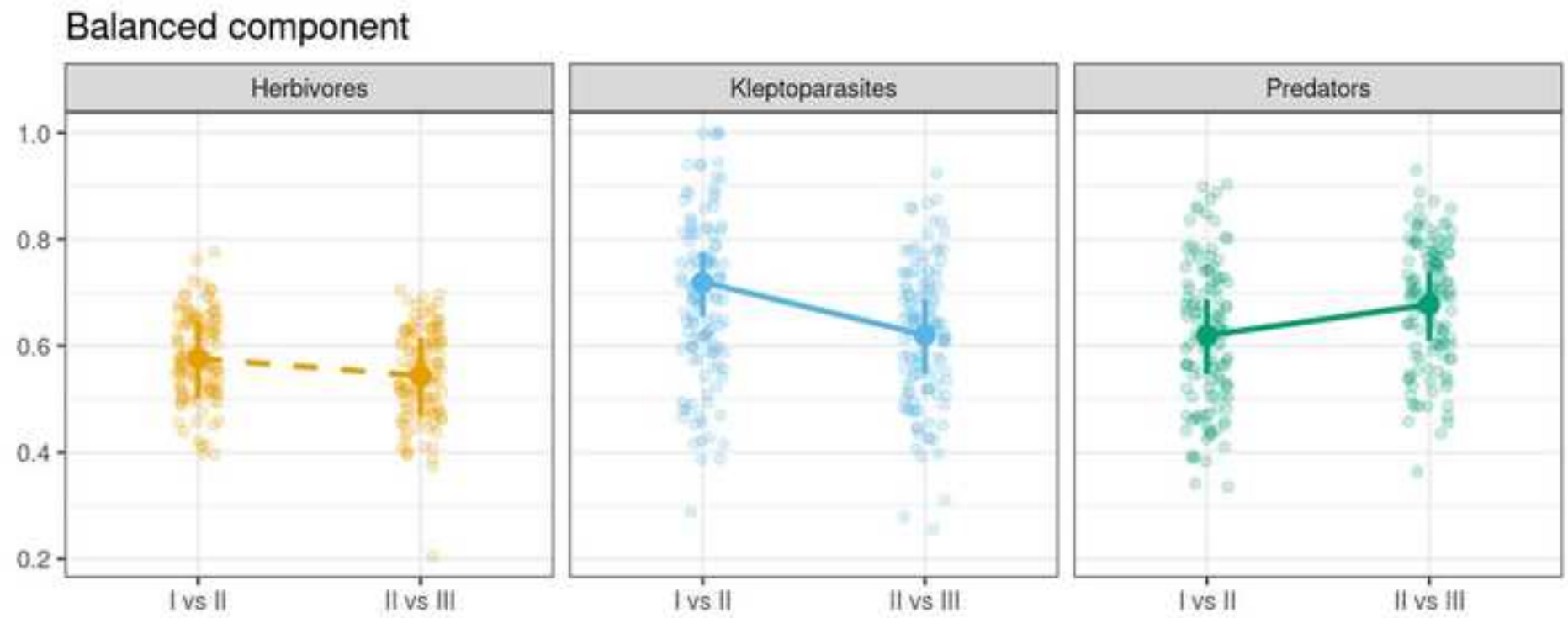
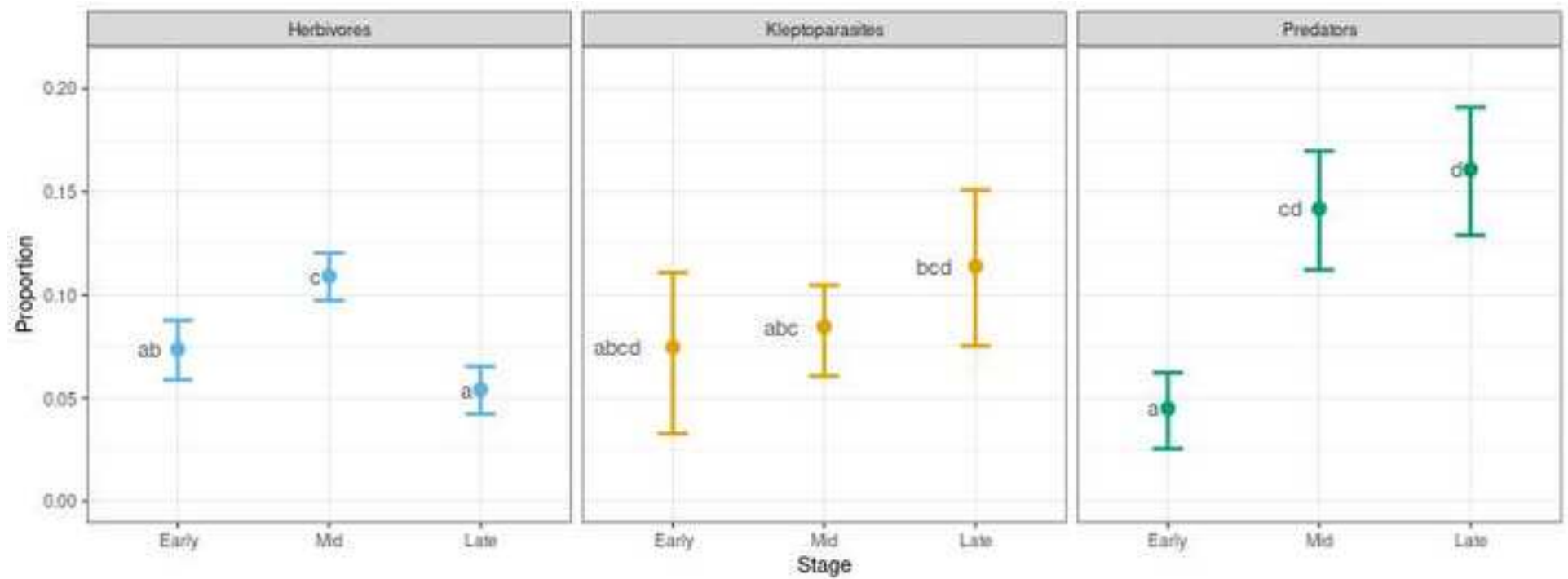




Figure 6

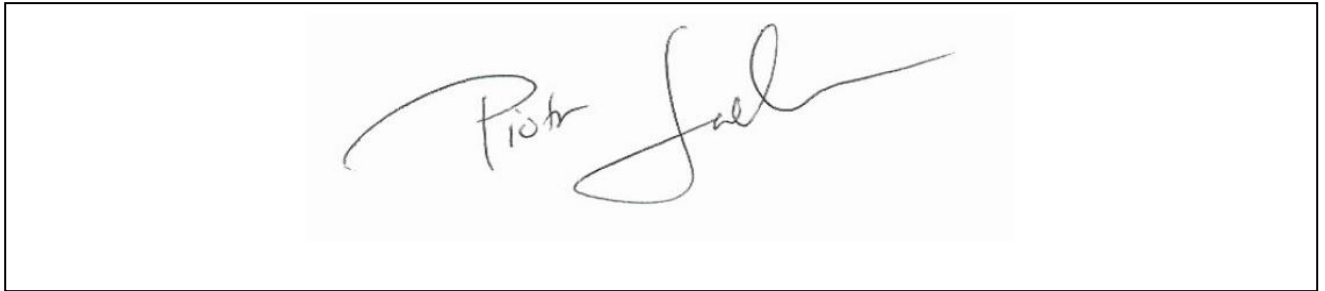




### Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:





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