

1 **Taxonomic, temporal, and spatial variation in the dynamics of High-Arctic arthropod**  
2 **populations**

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24

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27

28 **Significance statement:** Terrestrial arthropods, including insects and spiders, serve critical  
29 ecosystem functions and are excellent indicators of environmental change due to their physiology,  
30 short generation time, and abundance. The Arctic, with its rapid climate change and limited direct  
31 anthropogenic impact, is ideal for examining arthropod population dynamics. We use the most  
32 comprehensive, standardized dataset available on Arctic arthropods to evaluate the variability in  
33 population dynamics for the most common arthropod groups at various taxonomic levels across 24  
34 years. Our results highlight that temporal trends of arthropod populations seem less directional in  
35 the Arctic than in temperate regions. Although abundances of some arthropod taxa are declining,  
36 particularly in recent decades, population trends still display high variation among time periods,  
37 taxa, and habitats.

38

39 **ABSTRACT**

40 Time-series data on arthropod populations are critical for understanding the magnitude, direction,  
41 and drivers of abundance changes. However, most arthropod monitoring programs are short-lived  
42 and limited in taxonomic resolution and spatial extent. Consequently, variation in population  
43 dynamics among taxa and habitats remains poorly understood. Monitoring data from the Arctic are  
44 particularly underrepresented, yet important to assessments of species abundance changes because  
45 many anthropogenic drivers of change that are present in other regions are absent in polar regions.  
46 Here, we utilise 24 years of abundance data from Zackenberg in High-Arctic Greenland, which is  
47 the longest running Arctic arthropod monitoring program, to study temporal trends in abundance.  
48 Despite a strong warming signal in air temperature, we only find evidence of weak temporal trends  
49 in arthropod abundances across most taxa. These trends are more pronounced in the most recent  
50 decade, with change point analyses suggesting distinct non-linear dynamics within some functional  
51 groups such as predators and detritivores. Although the abundances of many taxa were correlated,  
52 we detected both positive and negative correlations, suggesting that multiple processes are affecting  
53 arthropod populations even in this relatively simple Arctic food web. Finally, we found clear  
54 differences among species within single families of arthropods, indicating that an apparent lack of  
55 change in abundance at broader taxonomic or functional levels could mask substantial species-  
56 specific trends. Our results reiterate the need for more basic research into the life-history, ecology,  
57 and adaptation of arthropod species to better understand their sensitivity to global changes.

58

59 **INTRODUCTION**

60 The abundance and diversity of terrestrial arthropods are under threat from several anthropogenic  
61 pressures (e.g. 1, 2-8). Long-term monitoring data indicate that abundances of many arthropod  
62 species are declining, as shown in a meta-analysis study that documented declines in abundances of

63 >450 invertebrate species globally (9). However, each assessment of a decline has its various  
64 strengths and weaknesses. Some are based on biological records requiring corrections for sampling  
65 effort (1, 4, 6, 7), while others only provide a comparison of discrete points in time (4, 10). These,  
66 and other shortfalls have strengthened calls for more standardized, long-term biological monitoring  
67 (11-14), including in areas less dominated by humans where drivers other than agricultural intensity  
68 can be investigated (15-17).

69           Previous work on species declines has suggested that the primary pressures on  
70 arthropod populations and communities in recent decades include habitat fragmentation, habitat  
71 loss, and land-use intensification (2, 18), though climate change will likely increase in importance  
72 as warming continues, even at low latitudes (19). Teasing apart the effects of land-use change and  
73 climate on arthropods, however, remains a major challenge (17). For example, while Hallmann, *et*  
74 *al.* (3) found a mid-summer decline in flying insect biomass of 82% over 27 years in protected areas  
75 in Germany, this pattern could not be attributed to landscape or climatic factors. Similarly, the most  
76 apparent and recent evidence of declines in arthropod biomass, abundance, and richness from  
77 standardized sampling could not confirm hypotheses about the impact of local land-use intensity  
78 (2). The impacts of individual drivers associated with land-use intensity, such as pesticide use, are  
79 particularly difficult to separate without a careful experimental design incorporated into monitoring  
80 systems (17, 20), and particularly so over the long-term.

81           Arctic regions are useful to study the impacts of climate change because many direct  
82 anthropogenic disturbances are absent (21), and because these regions are warming rapidly (22).  
83 While long term data are generally scarce in the Arctic (15), the arthropod monitoring program at  
84 Zackenberg, North-East Greenland, has been collecting standardised data since 1996, representing  
85 the longest running program in the Arctic (23). These data offer a rare opportunity to detect  
86 empirical change in a broad array of taxa, not least because of the availability of samples across

87 taxonomic groups in different habitats. Many long-term monitoring programs that include  
88 arthropods often only report trends at coarse taxonomic resolution or focus on single habitat types  
89 (3, 8, 24, 25). This can mask important variation, which can be teased apart only with analyses of  
90 long-term population dynamics of arthropods from different habitats and taxa (e.g. 26, 27, 28). Our  
91 previous work on spiders (Araneae) and a single family of flies (Diptera) has shown that habitat  
92 type can play an important role in the strength of species abundance trends (16, 28, 29). Previously,  
93 we also found evidence of differential long-term changes across invertebrate orders, altering the  
94 entire community composition (30). Therefore, there is an urgent need for an improved  
95 understanding of the spatial and taxonomic variation in population dynamics of arthropods. The  
96 Zackenberg dataset is unique in addressing these issues by including sampling across taxonomic  
97 groups, in different habitat types, and across multiple decades.

98           In this study, we use the Zackenberg dataset consisting of > 1 million individuals  
99 collected and counted over the last 24 years to address some of the above issues with long-term data  
100 reporting, while also improving our understanding of long-term change in a community of  
101 terrestrial and semi-aquatic arthropods under rapid climate change. Our specific objectives are 1) to  
102 assess and compare the temporal dynamics in climate and arthropod abundance across taxa,  
103 habitats, and time periods by estimating linear trends as well as non-linear dynamics, 2) to quantify  
104 shared and opposing population dynamics among arthropod taxa using cross-correlations, and  
105 finally, 3) to assess the credibility of using trends in broader taxonomic groups as indicators of  
106 single species by comparing species-level and family-level trends in abundance using available data  
107 from a subset of 18 years. Since no direct anthropogenic pressures occur at this site, our baseline  
108 assumption is that significant changes in arthropod abundances are a result of direct (e.g., of  
109 temperature on physiology) and indirect (e.g., via species interactions) effects of climate change.  
110

## 111 **RESULTS**

112 We found only limited evidence for long-term abundance trends in insect, spider, and micro-  
113 arthropod populations at Zackenberg from a total of 1,006,848 individuals collected across the  
114 entire 24-year time period (Figure 1a). An explanation of the taxonomic affiliation and broad  
115 functional group of the taxa included is presented in Table S1. When the study period was broken  
116 up into shorter decadal time-windows, we still found few significant trends (n=3) in the first decade  
117 (Figure 1b), but more significant trends in the central (n=9; Figure 1c), and last (n=13) decades  
118 (Figure 1d). Trends in abundance were generally a mix of positive and negative, although in the last  
119 decade more than two thirds of the significant trends were negative (Figure 1).

120 We used principal component analysis (PCA) to summarize several climate variables  
121 from Zackenberg of relevance to the terrestrial arthropod community. The PCA with varimax  
122 rotation revealed that 69% of the variation in our climatic variables was explained by the first three  
123 axes of the PCA (see Table S2 for relative contributions of each of the climatic variables to the  
124 derived PCs). Higher values of PC1 indicate warmer previous fall temperatures and higher summer  
125 precipitation, of PC2 indicate warmer previous summer and shorter winter duration, and of PC3  
126 warmer winter and spring temperatures (Figure 2). We then applied change point analysis to these  
127 PCs to detect whether there was evidence of abrupt and linear climatic change over the study  
128 period, and to visually assess whether these changes corresponded to changes in arthropod  
129 abundances. We found significant change points in all three PCs (Figure 2, Table S3) as well as in  
130 several individual climate variables (Figure S1). The change point analysis of arthropod abundance  
131 also revealed distinct commonalities in the dynamics of functionally related taxa. Specifically, the  
132 highest abundances of predators and parasitoids were detected during the central part of the study  
133 period. Conversely, decomposers experienced reduced abundances in the central part of the study  
134 period and relatively high abundances in the earlier and more recent years. Within the Diptera,

135 which are diverse in their ecosystem function, we found contrasting and complex dynamics between  
136 groups. Herbivores and pollinators were stable throughout the study period in arid heath and  
137 generally rare in the fen. In mesic heath, they were generally declining with a distinct drop halfway  
138 through the study period. Detailed results from the change point analyses of individual taxa from  
139 each habitat are presented in Table S4 and analysis of linear trends for those cases where no break  
140 points were identified are presented in Table S5.

141 Shared population dynamics among arthropod taxa would indicate that they are driven  
142 by similar environmental factors or biotic feedbacks. Without knowing the exact regulating factors  
143 for the species belonging to each taxa grouping in our study, we conducted cross-correlations  
144 among taxa to guide further study. Clusters of functionally-related taxa that exhibit correlated  
145 population dynamics could be directly influenced by specific climatic conditions or affected by the  
146 same biological feed-backs. In contrast, a negative correlation among taxa could indicate species  
147 interactions or opposing responses to external factors such as climate. Cross-correlation analysis  
148 across habitats revealed frequent significant correlations among taxa (Figure 3). Significant  
149 negative correlations (n=13) were almost as common as significant positive correlations (n=15).  
150 Collembola, parasitoids (Chalcidoidea) and Culicidae were typically negatively correlated to other  
151 taxa, while Collembola, Muscidae, and linyphiid spiders were positively correlated to each other.  
152 Lycosid spiders were positively correlated to other predators and parasitoids, but negatively to  
153 Collembola and Culicidae (Figure 3). Cross-correlation analyses within each individual habitat are  
154 shown in Figure S2.

155 Finally, in order to gain insight into how trends for broader taxonomic groups relate to  
156 dynamics at the species level, we compared species-specific trends with their corresponding family-  
157 level trends. Specifically, using species-level data for all species in the spider family Linyphiidae  
158 and the fly family Muscidae, we estimated the temporal trends in abundance through time at both

159 taxonomic levels (Figure 4). We found that there were more pronounced and contrasting abundance  
160 trends among the individual species of muscid flies as compared to the overall trend for the family  
161 (Figure S3). By contrast, the family-level trend for linyphiids largely resembled the trends of  
162 individual species (Figure S4). Generally, trends were most variable among species in the arid  
163 habitats (Figure 4).

164

## 165 **DISCUSSION**

166 Recent commentaries of insect declines have called for standardised methodology, well-designed  
167 syntheses of insect demography (31), balanced analysis (14), and realistic interpretation of results  
168 given the limitations of available data (32). In this study, we attempt to meet these challenges by  
169 presenting all relevant data from a long-term, standardised monitoring programme in the Arctic  
170 whereby arthropods were sampled weekly across the entire growing season. As a result of this  
171 effort, we identify substantial gaps in our knowledge of arthropod abundance trends. For example,  
172 based upon previous work from Zackenberg documenting effects of climate on body size (33, 34),  
173 phenology (35-37), abundance (16, 38), community composition (28, 30) and species interactions  
174 (39, 40), we expected there to be clear links between trends in climate and arthropod abundances,  
175 but we actually found much more complex dynamics, even at a broad taxonomic resolution of  
176 functional groups. While we did find some negative trends in arthropod abundance and even  
177 evidence that they are becoming more common, the abundances of most taxa show few directional  
178 changes and display substantial inter-annual variability. We note that climatic parameters also  
179 exhibit substantial inter-annual variability. Furthermore, our results from the cross-correlation  
180 analysis highlight the inherent challenges in attempting to understand complex interactions among  
181 taxa from long-term monitoring data. We also caution that species-level abundance trends may not  
182 be reflected in trends of broader taxonomic groups. Together, our findings suggest that we may not



183 have successfully captured the relevant climate drivers, that species interactions and density  
184 dependent feedbacks could play stronger roles than have been previously acknowledged, that broad  
185 taxonomic groups are often comprised of species that do not fluctuate in synchrony or a  
186 combination of the above. Still, the empirical findings that we present here could have only  
187 emerged from long-term, standardized data, and we argue that it is by integrating such data with  
188 experiments and modelling that we will be best prepared to advance our mechanistic understanding  
189 of arthropod population dynamics (41).

190

### 191 **Long-term dynamics across taxa and habitats**

192 The rapid climatic changes and the absence of many of the other human-mediated disturbances  
193 should make it easier to attribute long-term changes in Arctic arthropod population dynamics to  
194 shifts in environmental conditions, compared to temperate regions. However, it is also clear that  
195 arthropod population dynamics typically exhibit substantial idiosyncratic inter-annual variation,  
196 even in ecosystems primarily driven by climate (16, 28, 29). In addition, differences between short-  
197 term and long-term trends (42), as well as the occurrence of extreme events (43) are important to  
198 keep in mind as we develop a more synthetic understanding of the global phenomenon of insect  
199 declines (17).

200         Despite the range of temporal patterns we found here, the change point analysis provides  
201 insight into the nature of the trends. Change in local climate is not linear and the different climate  
202 factors do not change in synchrony. Most notably, in 2014 the change point for the climate PC1  
203 (warmer falls and higher summer precipitation; Figure 2), coincides with significant change points  
204 for most taxa. The recent mix of positive and negative changes are congruent with the trends found  
205 in the most recent short term time series (Figure 1d), and thereby suggests that there are winners  
206 and losers under certain changing climate conditions. However, many of the earlier change points in

207 arthropod abundance are more difficult to summarise, because they do not coincide with climate  
208 changes, indicating that long-term trends can be complicated by inter-annual and multi-annual  
209 variability. We note that individual species within taxa could be responding differently, and that  
210 although rare taxa were omitted, the likelihood of detecting change points is possibly lower for the  
211 less abundant taxa included in our analyses.

212         A number of challenges remain in linking temporal variation in environmental conditions to  
213 arthropod populations. The first and arguably most important is a better understanding of which  
214 climate metrics are the most relevant for predicting responses to change in individual arthropod  
215 species and even life stages. Here, the choice of location for temperature measurements (air,  
216 surface, or soil), the spatial resolution, and the choice of metric (mean, extreme, or variability) need  
217 to be further explored. Water stress is another known factor of importance to arthropods in cold  
218 environments (44), which may interact with temperature stress (45). Although soil moisture varies  
219 over small spatial scales (46), and thus can be challenging to measure, such variation has been  
220 shown to influence arthropod communities (47, 48). We are also only beginning to understand how  
221 thermal tolerance of Arctic arthropods varies across life stages (e.g. 49) and in response to past  
222 exposure to extreme conditions (e.g. 50). Variation in climate-abundance relationships may be  
223 further affected by the predictability of the thermal and hydrological environment (51), and flexible  
224 life stage lengths and generation times could buffer unfavourable conditions. Such complexities are  
225 likely to be even greater further south, where anthropogenic pressures are more pronounced. New  
226 efforts to compile and model microclimate data may help in our understanding of relevant scales  
227 (52, 53), but much more data from cold biomes are highly needed and called for (e.g., by the  
228 SoilTemp initiative 54).

229

230 **Climate effects vs. biotic feed-back mechanisms**

231 Strong relationships with climate drivers have been identified for life history variation in individual  
232 species in the past (33, 34, 36). However, the results from our cross-correlation analyses clearly  
233 demonstrate that many taxa do not fluctuate in synchrony or even exhibit strong negatively  
234 correlated dynamics. For example, the negative correlation and the opposing change point patterns  
235 between Lycosidae and Collembola could arise from their trophic link to each other, but indirect  
236 climate impacts may also independently impact these groups. For example, Collembola abundances  
237 may decline as has been found in warming experiments (55), with concurrent increases in  
238 Lycosidae due to activity-related improved hunting ability (56) or via more complex indirect  
239 interactions (57, 58). Similarly, positive correlations among taxa with related diets (Lycosidae and  
240 Thomsidae) could indicate co-existence via niche diversity, mutualisms or independent responses to  
241 biotic or abiotic drivers (59). The cause of negative correlations with parasitoids and Culicidae  
242 remains unclear but could be related to their distinct life cycles which do not resemble those of the  
243 majority of other taxa. We also note that correlations or lack thereof, may mask substantial variation  
244 in correlations among individual species. In any case, taxa that are correlated in abundance provide  
245 interesting focal points for future work. To advance the field of insect population dynamics, we  
246 need to support more basic work on the resource requirements, climatic constraints, and biological  
247 feed-backs of tundra arthropod species and their interactions (15, 40, 60).

248

249 **Abundance changes at the species-level**

250 Trait-based approaches allow for broader functional inference about species-environment  
251 relationships (55, 61). However, such approaches rely on accurate and complete information about  
252 functionally important traits, which is severely lacking for most arthropods (62). For practical  
253 reasons, species are often lumped together in broad taxonomic groups, which may not be

254 functionally similar. In some cases, higher taxonomic resolution can be sufficient to understand  
255 overall trends in community structure, or biomass (30, 63), but our study suggests that this is often  
256 not the case for variation in abundance. There is clearly also a problem with feasibility in running  
257 long-term arthropod monitoring programs and resolving time series to the species level, which  
258 explains why there are very few long-term arthropod monitoring programs worldwide. However,  
259 our study demonstrates that when we aggregate species to broader taxonomic levels, our ability to  
260 understand the drivers of abundance change are constrained, as even closely related species may  
261 differ in their response to environmental drivers (28, 29).

262

### 263 **Recommendations for future work**

264 Arthropod monitoring in remote regions such as the Arctic is rare, yet critical to our understanding  
265 of the role of climate in arthropod population dynamics. New monitoring initiatives should align  
266 with established programs to ensure inter-site comparability with respect to sampling methodology,  
267 spatio-temporal coverage, curation of samples and specimens, and digitization of collections (15,  
268 31, 64). More efforts should also be made to address the common problems with monitoring and  
269 analysing arthropod trends described at length by Didham, *et al.* (32). Complementary to this, large-  
270 scale programs utilizing standardized sampling protocols and covering vast gradients in  
271 environmental conditions should be implemented (15). However, both approaches are hampered by  
272 our current lack of sufficient taxonomic resolution, our limited knowledge about which life-history  
273 stages, populations, and species are the most sensitive to environmental change, as well as how  
274 species interact. One solution to this is to focus on a few taxa that may serve as indicators.  
275 However, given that species respond differently to environmental drivers (15, 28), we need better  
276 data on species-specific trends before selecting potential indicator species. Arthropod trait databases  
277 could contribute to a better understanding of which species are likely to exhibit correlated responses

278 to climatic factors (61, 62). We acknowledge that it is often not feasible to obtain all this  
279 information due to lack of expertise and funding. However, current technological developments  
280 offer promising outlooks. For instance, molecular tools can provide high taxonomic resolution, and  
281 although abundance thought to be difficult to derive, new analytical tools are emerging (e.g. 65).  
282 Image-based solutions employing deep learning models form a powerful tool for automated insect  
283 identification and biomass estimation as well as for monitoring of species and species interactions  
284 in their natural environment (66, 67). In addition to improved taxonomic resolution and trait  
285 information, a current and major challenge is that there is limited data collection of relevant  
286 environmental conditions that are likely driving arthropod abundance changes. Such data should be  
287 collected at the localized scale of arthropod sampling, including at established monitoring stations  
288 where such data have thus far been missing. From there, relevant modelling tools can be further  
289 developed to scale-up paired arthropod and micro-climatic data. Together such future advances to  
290 our understanding of arthropod population dynamics require interdisciplinary efforts such as those  
291 stimulated by the Network for Arthropods of the Tundra (60).

292

## 293 **Conclusions**

294 This study is the product of a relatively simple monitoring program in the High Arctic, and  
295 demonstrates that data from such a site can provide invaluable insights into arthropod population  
296 trends when collected over long time periods. We find that even in a species-poor ecosystem subject  
297 to rapid climate change but few other direct human disturbances, arthropod population dynamics are  
298 no less challenging to comprehend. Unlike recent high profile findings further south, we have not  
299 found evidence of an impending “insectageddon” (*sensu* 14), although some taxa and individual  
300 species exhibit strong and increasing negative trends in abundance. Nevertheless, the complexities  
301 we have shown highlight the need for detailed long-term data and thoughtful analysis. For example,

302 we require even longer term data to establish whether our change point patterns are random, are  
303 biological records of extreme events, or whether they represent longer cyclic patterns in abundance  
304 (e.g., via density dependent mechanisms or interspecific interactions). We need more such insights  
305 from a wider range of locations around the Arctic region, which could form the basis of comparable  
306 datasets. We suggest that biome-wide coordination of monitoring efforts, species-level population  
307 and trait data improvements, the continual development of efficient monitoring technologies, and  
308 the collection of relevant climate variables are equally important in the pursuit of a fuller  
309 understanding of biotic and abiotic impacts on such a pivotal group of organisms.

310

## 311 **MATERIALS AND METHODS**

### 312 **Sampling and specimens**

313 The Greenland Ecosystem Monitoring Programme has been in operation at Zackenberg in Northeast  
314 Greenland (74°28'N, 20°34'W) since 1996, and includes standardized pitfall trapping in five plots:  
315 one fen, two mesic heaths, and two arid heath plots (see 23 for further details). Each plot consisted  
316 of eight yellow pitfall traps (1997 – 2006) or four pitfall traps (1996 & 2007 – 2018; each trap 5m  
317 from nearest neighbour). The traps were in operation during the growing season starting at  
318 snowmelt in late May-early June and ending by late August-early September, and emptied once a  
319 week. To compare across the years of sampling (1996–2018), we truncated our arthropod data to  
320 June, July, and August. Arthropods were then sorted to the family level for spiders and most  
321 insects, superfamily level for Aphidoidea, Chalcidoidea, and Coccoidea, and subclass level for other  
322 arthropods and counted as part of the monitoring programme. We note that juveniles were included  
323 in the family level abundances for spiders.

324 For the years 1996–2014, all spiders, as well as the muscid flies from selected traps,  
325 were identified to the species. For species-level data, only adults were used in analyses as juvenile

326 spiders and fly larvae could have different dynamics, and are difficult to identify with confidence.  
327 For spiders, we included individuals sampled in all five plots, whereas for muscid flies, only a  
328 subset of traps from the wet fen plot, one mesic and one arid heath plot were identified (see 28 for  
329 details). For some early years of the programme, certain families of Diptera were not sorted, but one  
330 family strongly dominated samples from later years (35), hence we pooled the Chironomidae and  
331 Ceratopogonidae (hereafter called Chironomidae), Anthomyiidae and Muscidae (hereafter called  
332 Muscidae) and Mycetophilidae and Sciaridae (hereafter called Sciaridae), respectively.

333           The wet fen plot is primarily composed of mosses, grasses (e.g., *Eriophorum* sp.), and  
334 sedges with scattered Arctic willow (*Salix arctica*). The mesic plots primarily consist of Arctic bell-  
335 heather (*Cassiope tetragona*) and Arctic willow, grasses/sedges, and berry plants (*Vaccinium*),  
336 while the arid plots have a greater dominance of mountain avens (*Dryas octopetala*) (35). All plots  
337 are located within an area less than one km<sup>2</sup>. The wet fen and arid plots typically have snowmelt  
338 two weeks earlier than the mesic plots and soil moisture is highest in the wet fen and lowest in the  
339 arid plots. Air temperature (2 m above the surface), soil temperature (at 0cm, 5cm and 10cm depth)  
340 in mesic heath dominated by *Cassiope tetragona*, and precipitation (mm) was measured hourly by a  
341 meteorological station located centrally to all the arthropod sampling plots (68).

342

### 343 **Data and analyses**

344 We standardized weekly abundance counts for each arthropod group by calculating the abundance  
345 per trap per day for each plot in each season. In subsequent analyses, we focused on taxonomic  
346 groups for which total abundance in each habitat across the time series was higher than 500  
347 individuals to ensure robust estimates of trends even for taxa that do not occur in all years. We  
348 derived a range of climate variables of relevance to arthropod populations from the temperature and  
349 precipitation data. Summer precipitation was calculated from the sum of June, July, and August

350 measurements. Average summer temperature was calculated from air temperature measured during  
351 the same period (June, July, and August). Most Arctic arthropods overwinter beneath the snow in  
352 leaf litter and the upper portion of the soil profile. Thus, in order to estimate average seasonal  
353 temperatures experienced by arthropods for the previous fall ( $\text{October}_{t-1}$  and  $\text{November}_{t-1}$ ), winter  
354 ( $\text{December}_{t-1}$  through  $\text{March}_t$ ), and spring ( $\text{April}_t$  and  $\text{May}_t$ ), we calculated the mean hourly  
355 temperature across the data collected at 0 cm, 5 cm, and 10 cm depth within the soil profile. We  
356 defined the length of winter as the number of days from the first day in the fall with an average  
357 temperature below  $2^\circ\text{C}$  to the last day in spring with an average temperature below  $2^\circ\text{C}$ . The  
358 number of freeze-thaw cycles over the previous winter were calculated from the soil temperature  
359 data by counting the number of days with a maximum temperature above  $0^\circ\text{C}$  and a minimum  
360 temperature below  $0^\circ\text{C}$ . To avoid statistical artefacts associated with multicollinearity (69), we  
361 reduced the various climatic variables in our time series to a smaller number of composite  
362 predictors by doing a principal components analysis (PCA) using the *factoMineR* package (70). In  
363 our PCA, we also included lagged variables for summer precipitation ( $\text{precipitation}_{t-1}$ ) and summer  
364 temperature ( $\text{summer}_{t-1}$ ), as conditions during the previous growing season could influence  
365 arthropod abundance in  $\text{summer}_t$ . Precipitation data were log-transformed and all climate variables  
366 were centred and scaled prior to PCA.

367 Temporal trends in abundance were analyzed by taxa and habitat with the Mann-  
368 Kendall trend test corrected for temporal autocorrelation (71) using the *fume* package for the  
369 corrected Mann-Kendall trend test (72). We applied a change-point detection approach to each time  
370 series (climate and arthropod abundance) to identify potential shifts over time. We used the  
371 ‘breakpoints’ function of the *strucchange* package (73) to test the null hypothesis that no abrupt  
372 change has occurred over time. We compared several simple regression models with no change and  
373 with different numbers of change-points across years. The F-statistic procedure identifies the best



374 regression model with the smallest residual sum of squares based on the Bayesian Information  
375 Criterion (BIC) (74). Cross correlation in abundance among the taxonomic groups were estimated  
376 by non-parametric spearman rank correlations and visualized using the *corrplot* package (75). All  
377 statistical analyses were performed in the R 3.6.1 platform (76).

378

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385 Agency for funding over the years.

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561

562 **FIGURE LEGENDS**

563 **Figure 1**

564 Trend analysis at family or higher taxonomic level grouped according to broad functional groups as  
565 outlined in Table S1 a) across the entire study period, b) during the first decade (1996–2005), c)  
566 during the middle decade (2002–2011), and d) during the last decade (2009–2018) for each habitat.  
567 Temporal trends are estimated with the modified Mann-Kendall non-parametric trend analysis and  
568 significant trends at  $p < 0.05$  are indicated by triangles.

569

570 **Figure 2**

571 Inter-annual variation and change point analysis of key climate variables of relevance to arthropods  
572 as summarized in the three PCA axes and arthropod abundance at the family and higher taxonomic  
573 levels. Arthropod taxa are grouped into broad functional groups as outlined in Table S1. Solid lines  
574 are drawn where the change point analysis was significant (see detailed results in Tables S3, S4, and  
575 S5). Arthropod data are not available from 2010.

576

577 **Figure 3**

578 Cross-correlations of family or higher taxonomic level abundances across habitats based on non-  
579 parametric Spearman rank correlations. Ellipsoid shape indicates the strength of the spearman rank  
580 correlation, with more narrow ellipses depicting stronger cross-correlations between groups (red for  
581 negative and blue for positive correlations; the bar at the bottom of the graph depicts colour coding  
582 for the correlation coefficients). Crosses between groups depict those with non-significant  
583 correlations at the  $p < 0.05$  level. The families are organized according to broad functional groups  
584 as outlined in Table S1. Five taxa which were not significantly correlated to any other groups are

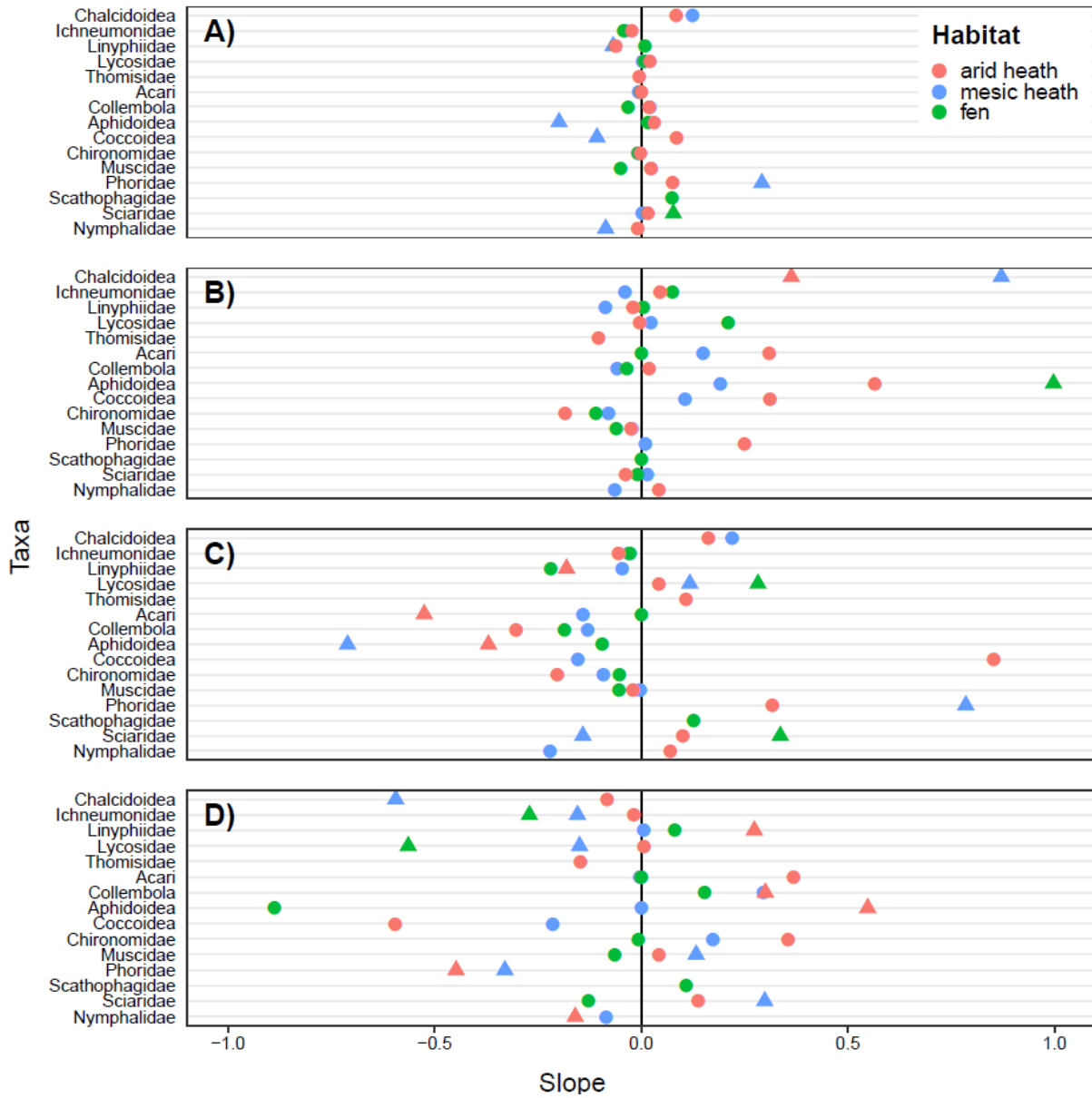
585 removed from the figure for clarity (Aphidoidea, Chironomidae, Ichneumonidae, Scatophagidae,  
586 and Sciaridae).

587

588 **Figure 4**

589 Species-level trends compared to family-level trends for the spider family Linyphiidae and the fly  
590 family Muscidae for which multiple species are represented in the dataset and species-level data  
591 was available. Temporal trends are estimated with the non-parametric modified Mann-Kendall trend  
592 analysis and significant trends at  $p < 0.05$  are indicated by triangles. Symbol colours are the same as  
593 in Figure 1.

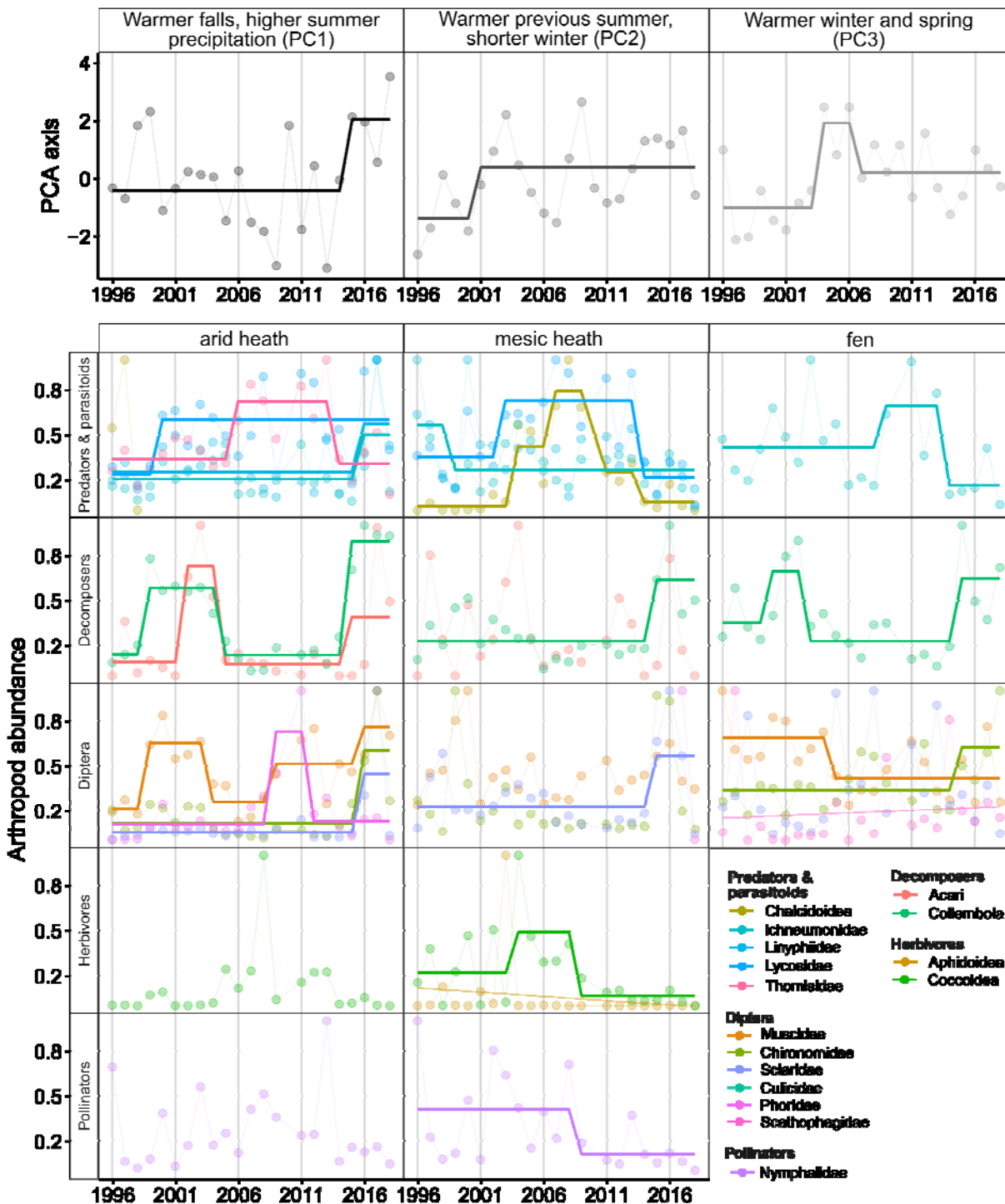
594 **FIGURE 1**



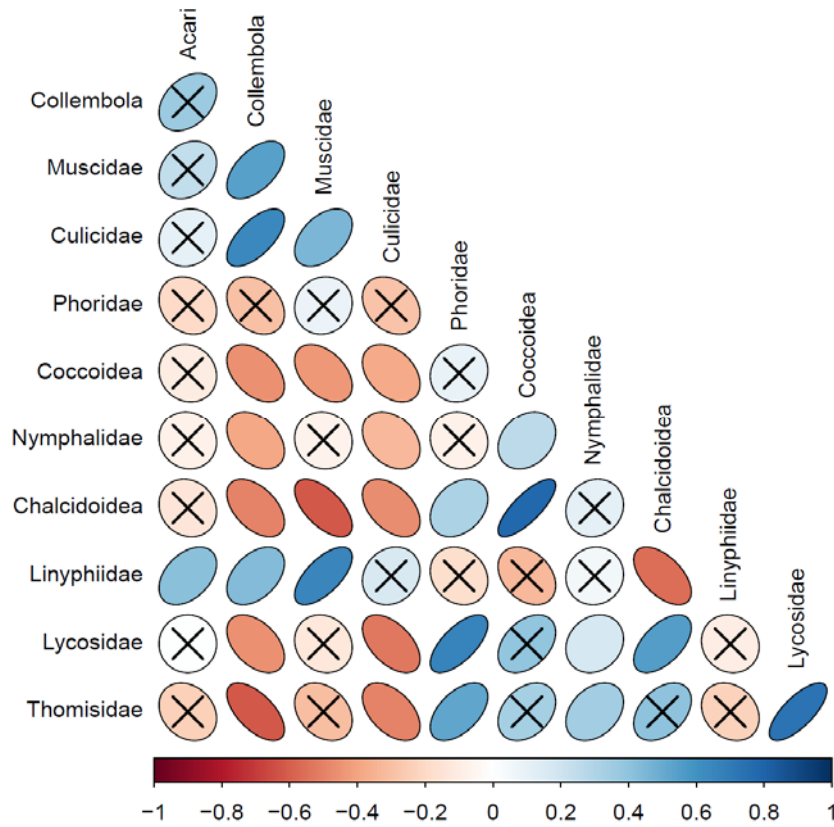
595



596 **FIGURE 2**



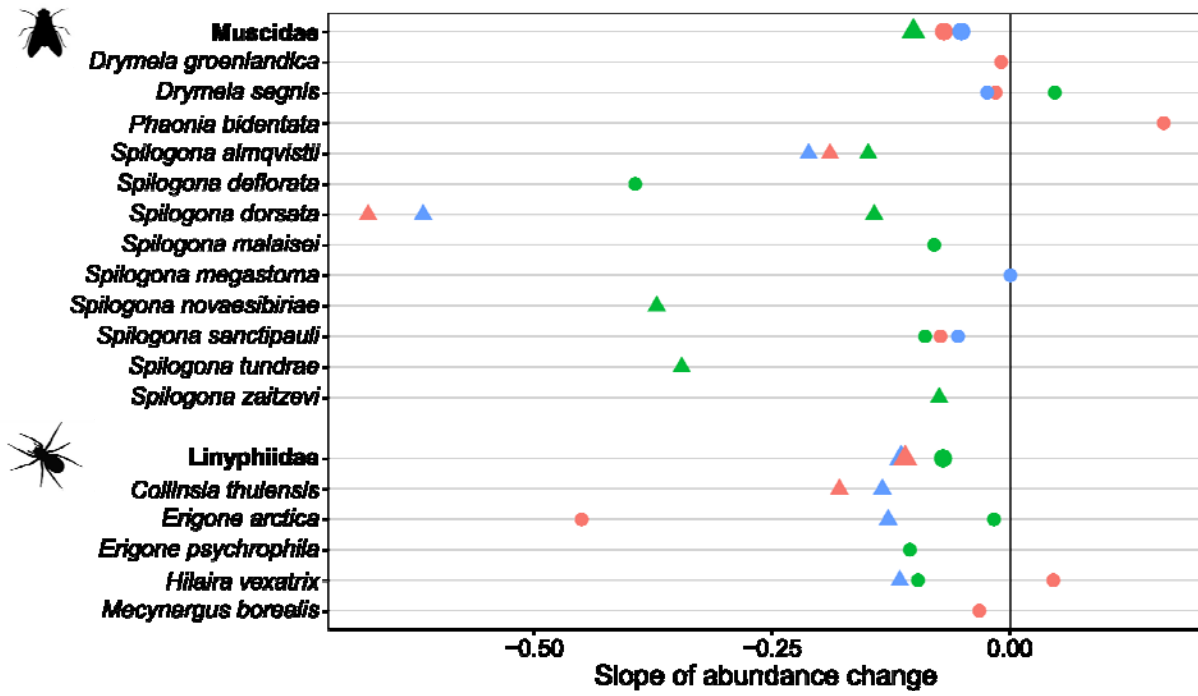
598 **FIGURE 3**



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600

601 FIGURE 4



602