

1 **Climate-warming alters the structure of farmland tri-trophic ecological networks and**
2 **reduces crop yield**

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18 **Running title:** Climate-warming alters ecological networks

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Abstract. It is unclear how sustained increases in temperature and changes in precipitation, as a result of climate-change, will affect crops and their interactions with agricultural weeds, insect pests and predators, due to the difficulties in quantifying changes in such complex relationships. We simulated the combined effects of increasing temperature (by an average of 1.4°C over a growing season) and applying additional rainwater (target of 10% extra per week) using a replicated, randomized block experiment within a wheat crop. We examined how this affected the structure of 24 quantitative replicate plant-aphid-parasitoid networks constructed using DNA-based methods. Simulated climate-warming affected species richness, significantly altered consumer-resource asymmetries and reduced network complexity. Increased temperature induced an aphid outbreak but the parasitism rates of aphids by parasitoid wasps remained unchanged. It also drove changes in the crop, altering in particular the phenology of the wheat as well as its quality (*i.e.* fewer, lighter seeds). We discuss the importance of considering the wider impacts of climate change on interacting-species across trophic levels in agro-ecosystems.

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50 Introduction

51 Climate change is expected to have profound impacts on food production systems over the coming
52 decades (Lobell *et al.* 2008). Crops will be adversely affected by a combination of both abiotic
53 (e.g. heat, drought, salinity and submergence in water) and biotic (e.g. pests and pathogens)
54 stresses (Baulcombe *et al.* 2009; Maxmen 2013; Bebber *et al.* 2014; Lesk *et al.* 2016), posing
55 significant threats to food security (Godfray *et al.* 2010). Despite the growing research
56 demonstrating the impacts of climate change on species abundances and distributions, community
57 composition and organismal physiology (Sala *et al.* 2000; Parmesan 2006; Garcia *et al.* 2014),
58 climate change effects on the networks of interactions among species are poorly understood
59 (Tylianakis *et al.*, 2008), particularly in agro-ecosystems. This is largely due to the difficulties in
60 quantifying changes in interactions compared with changes in biodiversity (McCann 2007). Yet,
61 complex networks of biotic interactions, such as insect pollination and parasitism, play an
62 important role in the maintenance of biodiversity (Bascompte *et al.* 2006), provide valuable
63 ecosystem services (Pocock *et al.*, 2012), and can mediate ecosystem responses to environmental
64 change (Sydes & Miller 1988; Brooker 2006). Species-interactions may, however, be more
65 susceptible to climate change, as they are sensitive to the phenology, behaviour, physiology and
66 relative abundances of multiple species (Memmott *et al.* 2007; Suttle *et al.* 2007; Tylianakis *et al.*
67 2007).

68

69 Combining advances in both network theory and molecular ecology offers unprecedented
70 opportunities to describe interactions between species, the structure of communities and the
71 function and stability of ecosystems (Evans *et al.* 2016). Ecological networks provide a
72 quantitative framework to unify the study of biodiversity and ecosystem function (Thompson *et*
73 *al.* 2012) and have been successfully used to quantify the ecosystem-level consequences of global
74 environmental change (Tylianakis *et al.* 2010). There is growing interest in developing these
75 approaches to provide a more holistic, systems-based understanding of agro-ecosystems that could
76 be used to maximise the ecosystem services provided by farmland biodiversity, as well as for
77 anticipating and mitigating future scenarios (Bohan *et al.* 2013). For example, Macfadyen *et al.*
78 (2009) constructed quantitative plant-herbivore-parasitoid networks on paired organic and
79 conventional farms and showed that the organic farms had more species across the three trophic
80 levels and significantly different network structure. However, such networks take considerable
81 effort to construct and can be subject to bias because of the limitations of taxonomically selective
82 rearing success as well as the reliance on accurate morphological identification (Evans *et al.* 2016).
83 Advances in DNA sequencing technologies provide enormous potential to determine hitherto
84 difficult to observe species interactions and thus to produce highly-resolved ecological networks
85 (Wirta *et al.* 2014; Derocles *et al.* 2018; Evans *et al.* 2016). An accurate and cost-effective PCR
86 diagnostics approach has recently been developed to allow the rapid construction of quantitative
87 ecological networks of farmland aphid-parasitoid interactions (Derocles *et al.* 2012a, 2014)
88 providing new opportunities to examine the impacts of environmental change on network structure
89 and complexity.

90

91 In northern Europe, climate models predict significant warming and an increase in both

92 precipitation (mainly in winter) and the frequency of extreme weather events (IPCC 2014), which
93 are likely to cause significant damage to agro-ecosystems (Olesen *et al.* 2011). With increasing
94 evidence that present climate change is altering geographical ranges, population dynamics and
95 phenologies of some insects (Altermatt 2010; Morris *et al.* 2015), there is growing concern that
96 global food security is threatened by the emergence and spread of crop pests and pathogens
97 (Maxmen 2013). Given the ecological and economic importance of phytophagous insects and their
98 natural enemies, a greater understanding of their direct and indirect interactions and how these
99 respond to experimental manipulation is needed (van Veen *et al.* 2006), particularly in the context
100 of climate-warming.

101
102 Experimental manipulations of temperature and precipitation have provided important insights
103 into the responses of terrestrial ecosystems, with climate-warming generally stimulating total net
104 primary productivity, increasing ecosystem photosynthesis and respiration (see Wu *et al.* 2011 for
105 a review). Real-world experimental climate manipulations can help to fill the knowledge gap
106 between highly controlled, closed-system laboratory studies (e.g. Le Lann *et al.* 2014) that tend to
107 focus on a small number of species, and large scale open-field experiments that rely on variations
108 in temperature along environmental gradients (see de Sassi & Tylianakis 2012; Romo & Tylianakis
109 2013). To date, most field-based simulated-warming experiments have used infrared heating
110 devices (see de Sassi *et al.* (2012) who used underground heating cables) but have mainly focused
111 on plant responses to elevated temperatures. To our knowledge, none have examined the impacts
112 on networks of interacting species across multiple trophic levels. Within grasslands, de Sassi &
113 Tylianakis (2012) demonstrated that in a tri-trophic system of plants, herbivores and parasitoids,
114 each trophic level responded differently to warming and overall the community was increasingly

115 dominated by herbivores. Within arable crops, a small number of individual simulated climate-
116 warming studies have demonstrated a reduction in wheat yield (Fang *et al.* 2013) and increases in
117 aphid pests (Dong *et al.* 2013) and insect predators (Berthe *et al.* 2015). Thus it is unlikely that
118 climate-warming will affect species richness within arable crops, rather it will alter network
119 structure and complexity, in particular consumer-resource asymmetries (e.g. network ‘generality’
120 - the mean effective number of lower trophic level species per higher trophic level species) and
121 interaction evenness, driven by changes in the abundances and frequency of interactions between
122 plants, aphids and parasitoids. However, predicting the specific impacts on the complex pattern of
123 interactions among species in a community remains a pressing challenge (Staniczenko *et al.* 2017).

124
125 Here, we experimentally increase temperature and rainwater within farmland plots consisting of
126 spring-sown wheat and common uncultivated plant (weed) species. The study is framed in the
127 context of understanding climate change implications as it relates to policy targets (e.g., limiting
128 warming to 2°C) within North European agriculture (Olesen *et al.* 2011). We examine the
129 responses of quantitative plant-aphid-parasitoid networks, constructed using DNA-based methods,
130 as well as the impacts on crop yield. Although predicting the direct and indirect responses of plants,
131 phytophagous insects and their natural enemies to perturbation is a major challenge, quantitative
132 ecological networks are particularly well suited for assessing direct and indirect interactions in the
133 first instance (van Veen *et al.*, 2006). Our objectives are threefold. (1) To construct replicated,
134 quantitative tri-partite food-webs describing the interactions between crop and non-crop plants,
135 aphids and parasitoids. We apply a DNA-barcoding approach to accurately and cost-effectively
136 quantify the interactions of Aphidiinae endoparasitoids with their aphid hosts. (2) To examine the
137 combined effects of a 1.4°C temperature elevation and increase in rainwater on measures of

138 network structure and complexity. We use suspended infrared heaters, which have been effectively
139 applied in other habitats for climate change simulation experiments (Price & Waser 2000; Wan *et*
140 *al.* 2002; Harte *et al.* 2015) to warm farmland plots *in situ*, and apply extra rainwater following
141 established protocols (Rollinson & Kaye 2012). We predict no impacts on total species richness,
142 but significant increases in aphid abundances in warmed plots due to a positive direct effect on
143 population growth rate (Barton & Ives 2014) and a corresponding increase in the frequency of
144 parasitoid interactions, potentially leading to changes in network consumer-resource asymmetries
145 and interaction evenness. As aphids and parasitoids are highly specialized in agro-ecosystems (Le
146 Ralec *et al.* 2011; Derocles *et al.* 2014), we do not expect an increase in network connectance (a
147 measure involving the number of interactions) in the short-term, as this would indicate an
148 expansion of generalism of the species involved. We test this for both bipartite and tripartite
149 networks. (3) To investigate the overall effects of warming on crop yield and whether any changes
150 can be mediated by an increase in rainwater (either as precipitation or as added irrigation).

151

152 MATERIALS AND METHODS

153 *Experimental layout*

154 The study was conducted in 2013 at Stockbridge Technology Centre (STC), North Yorkshire, UK
155 (53°49' N -1°9' W), a conventional farm consisting of meadows and cereal crops used for field
156 experiments. The climate is temperate oceanic, with a mean minimum and maximum annual
157 temperature and precipitation of 5.5–14°C (8.6–19.1 °C during the experiment) and 537.7 mm
158 (156.6 mm during the experiment) respectively. We established a replicated, randomized block
159 open-field experiment consisting of six replicates of four simulated climate change treatments in
160 a field of spring wheat (*Triticum aestivum* cultivar Tybalt) (see Berthe *et al.* 2015, Figure S1,

161 Supporting information). The four treatments consisted of: (W) 1.4°C increase in temperature; (P)
162 10% increase in precipitation/rainwater per week, based on historic records; (WP) warming and
163 precipitation treatments combined; and (C) control (ambient conditions). We refer to “climate-
164 warming” when reporting the effect of warmed treatments and “precipitation” when reporting the
165 effect of additional rainwater treatments. Treatments were randomly allocated to 2×2 m
166 experimental plots that were each separated by 2 m of wheat to provide a buffer and allow the free
167 movement of insects. The W and WP treatments involved suspending 240 V infrared heaters 1.5
168 m above each plot (following Rollinson & Kaye 2012), consistently heating throughout the day
169 and night: this primarily drives plant phenology rather than heating the column of air (Kimball
170 2005; White *et al.* 2011). A ‘dummy’ heater of the same size and shape was suspended in the non-
171 heated plots to account for any possible effects of shading/shelter.

172
173 A real-time proportional-integrative-derivative feedback system ensured constant temperature plot
174 warming through infrared radiometer (IRR) monitoring of surface temperatures in warmed plots.
175 Soil-surface temperatures were monitored by 6 Infrared Remote Temperature Sensors (IR120;
176 Campbell Scientific; Loughborough, UK), positioned 1.10 m above the plots and directed to the
177 middle of the plot and connected to a data logger (Campbell Scientific; Loughborough, UK) to
178 record the temperatures every 10s and to control the constant output of the infrared heaters. Their
179 positions were selected randomly, three within a heated plot (W, WP) and three within an unheated
180 plot (C, P). Our original aim was for the system to increase the temperature in the warmed plots
181 by 2°C. Over the course of the experiment, temperatures were raised, on average, by 2.2°C
182 (standard deviation 0.6) in block 1; 1.1°C in block 2 (standard deviation 0.6) and 1.1°C in block 3
183 (standard deviation 0.8) that most likely reflected subtle microclimate differences within the field.

184 This provided a mean temperature increase of 1.4°C (standard deviation 0.9) across all the plots.
185 Increased rainwater was simulated in the P and WP plots by manually adding 10% extra collected
186 rainwater each week based on STC mean monthly rainfall data collected between 2002 and 2012.
187 This can either be interpreted as representing weather conditions in a warm and wet summer, or a
188 farmer increasing irrigation to mitigate the effects of a warm and drier summer. We added the
189 following water each week: 13 L in April; 19 L in May; 24 L in June; 26 L in July and 30 L in
190 August, amounting to 407 L in total for each plot. During the course of the experiment, just 156.6
191 mm of rainfall was measured at Stockbridge Technology Centre, well below the annual average.
192 Thus we actually increased precipitation/rainwater by 40% that year. The experimental area in
193 which the plots were located received herbicide applications on 2nd April and 13th May
194 (pendimethalin; metsulfuron-methyl and thifensulfuron-methyl); our aim was to allow some weed
195 growth without out-competing the wheat. Experimental treatments commenced immediately after
196 the sowing of spring wheat on 13th April and stopped with the harvest of the crop on 16th August.

197

198 *Plant surveys and crop yield*

199 Plants were identified to the species level, with a small proportion to the genus or family, and the
200 percentage cover of each was recorded weekly (18 surveys) in each plot. The date of emergence
201 of the first leaf and the date of emergence of the first ear for *T. aestivum* was recorded in each plot
202 and converted into Julian date for statistical analysis. At harvest, a 0.5×0.5m quadrat was placed
203 in the area directly below the heaters/dummy heaters (we selected this area because the heating
204 pattern is likely to be more consistent; Kimball 2005) and the number of *T. aestivum* ears counted.
205 The density of wheat (number of wheat ears m⁻²) was then calculated for each plot. We also
206 harvested five ears randomly from each plot, which were dried in an oven at 80°C for 48 hours in

207 the laboratory. The seeds were counted and the total seed weight was measured for each ear. For
208 each plot, crop yield (g/m^2) was calculated as: (total seed weight / ear) x density of wheat.

209

210 *Insect surveys*

211 Plant-aphid interactions were recorded by systematically searching each plot and counting the total
212 number of aphids and visibly parasitized aphids ('mummies') on each plant species every week
213 (18 surveys) throughout the sampling period. We collected up to 30 aphid individuals per colony
214 and placed them in a 1.5ml tube filled with 95% ethanol and then stored at $-20\text{ }^\circ\text{C}$ in the laboratory
215 for later identification (see below). All aphid mummies were collected and stored in 1.5ml tubes,
216 but without 95% ethanol. Instead, these were stored under laboratory conditions and observed for
217 10 days for the emergence of adult parasitoids. Adult parasitoids and aphid mummies where
218 parasitoids did not emerge were then stored individually in a 1.5ml tube filled with 95% ethanol
219 at $-20\text{ }^\circ\text{C}$.

220

221 *Insect identification*

222 Aphids were first identified morphologically following Blackman & Eastop (1994, 2000, 2006).
223 We extracted the DNA of all the aphids collected using a hotshot DNA extraction (Montero-Pau
224 *et al.*, 2008). Aphid identification was confirmed with DNA barcoding: a fragment 658 bp from
225 Cytochrome C oxidase subunit I [COI] was amplified and sequenced with the PCR conditions
226 described by Derocles *et al.* (2012b) and the following primer pairs: LCO1490 (5'-
227 GGTCAACAAATCATAAAGATATTGG-3'; Folmer *et al.* 1994) and the degenerate reverse
228 primer HCO2198-puc (5'-TAAACTTCWGGRTGWCCAAARAATC-3'; Cruaud *et al.* 2010).
229 Adult parasitoids and non-emerged parasitoids from the mummies ($n = 181$) were identified using

230 the DNA barcoding tool described by Derocles *et al.* (2012b): a fragment 658 bp from COI was
231 amplified and sequenced to identify these parasitoids. Aphid-parasitoid interactions and parasitism
232 rates were determined using two different molecular methods based on the extracted DNA of
233 aphids. First, we used a multiplex PCR approach developed by Traugott *et al.* (2008) on the aphid
234 species collected on *T. aestivum* (*Sitobion avenae* and *Metopolophium dirhodum*) to detect both
235 primary and secondary parasitoids. We used nine primary parasitoid and two hyperparasitoid
236 species-specific primer pairs to detect and identify immature primary and secondary parasitoids
237 within cereal aphid hosts. Second, for all the other aphid species, we used the approach developed
238 by Derocles *et al.* (2012a) that uses the sequences of a 210 bp fragment from the 16S gene to
239 identify to species-level (in most cases) the immature Aphidiinae parasitoids within an aphid host.
240 To improve the reliability, we added an ‘in tube control’ to determine if an absence of parasitoid
241 detection is due to either a true absence of parasitism or a technical problem during DNA extraction
242 or PCR amplification. For this, we followed the PCR protocol for parasitoid detection described
243 by Derocles *et al.* (2012a) and we added in the PCR-mix the aphid COI barcode assay described
244 above. A detection of a parasitoid within an aphid host is characterized by two bands on a 1.5%
245 agarose electrophoresis gel: a band of 658 bp (COI, aphid and parasitoid) and a band of 210 bp (16S
246 parasitoid); an unparasitized aphid is characterised only by the band of 658 bp, from the aphid
247 DNA. An absence of band indicates a failure from either the DNA extraction or the PCR
248 amplification. In this case, the PCR amplification is performed a second time. If after a second
249 PCR amplification a failure is observed, the individual is removed from the analysis. Sixteen
250 aphids were removed from the analysis following two PCR failures. We used two hyperparasitoid
251 species-specific primer pairs (Traugott *et al.* 2008) to detect the secondary parasitoids in non-crop
252 aphid species. We compared parasitism rate determined using this method versus the conventional

253 approach (i.e. the number of aphid mummies collected) / (number of aphid counted).

254

255 *Insect abundance, species richness and parasitism rates*

256 For each plot, we pooled data across the sampling period to calculate:

257 1) percentage of aphids sampled: number of aphids sampled / number of aphids counted

258 2) aphid abundance: total number of aphids counted on each plant species throughout the
259 sampling period

260 3) total species richness

261 4) species richness per trophic level (i.e. plants, aphids, parasitoids)

262 5) parasitism rate using the DNA-based method: (the number of aphid mummies collected +
263 number of parasitised aphids detected) / (number of aphid mummies collected + number
264 of aphids collected);

265 6) parasitism rate using the conventional method (no DNA-based method): (the number of
266 aphid mummies collected) / (number of aphid counted);

267 7) multiparasitism rate using the DNA-based method: (number of aphids parasitised by at
268 least two detected primary parasitoid species / number of aphids collected + number of
269 mummies collected)

270 8) hyperparasitism rate using the DNA-based method: (number of aphids parasitised by a
271 secondary parasitoid + number of secondary parasitoids identified in mummies / number
272 of aphids collected + number of mummies collected).

273

274 *Ecological network construction, visualisation and description*

275 Plant-aphid-parasitoid quantitative networks were constructed for each plot by pooling data

276 collected during the course of the experiment. We visualised the tripartite interactions for each of
277 the four treatments (by pooling replicate data from replicate plot) using the “HiveR” package
278 (Krzywinski *et al.* 2011) in R 3.3.1 (R Core Team, 2016). We were particularly interested in how
279 the experimental treatments affects consumer-resource asymmetries, classically described in
280 network ecology as vulnerability and generality (i.e. the mean number of consumers per prey, and
281 the mean number of prey per consumer, respectively), as well as standard measures of complexity
282 (Bersier *et al.* 2002). They are well suited for describing antagonistic interactions and the extent
283 to which consumers are specialized to the resource and how the resource is attacked by the higher
284 trophic level (Wirta *et al.* 2014). For each of the 24 tripartite networks, we calculated the following
285 qualitative, unweighted quantitative and weighted quantitative network descriptors described by
286 Bersier *et al.* (2002) using ‘cheddar’ (Hudson *et al.* 2013) and ‘bipartite’ packages in R 3.3.1
287 (Dormann *et al.* 2009): Link density (average number of links per species: LD, LD’q, LDq);
288 Connectance (proportion of possible links between species that are realized: C, C’q, Cq);
289 Vulnerability (mean effective number of higher trophic level species per lower level species: V,
290 V’q, Vq) and Generality (mean effective number of lower trophic level species per higher trophic
291 level species: G, G’q, Gq). We based our analysis on weighted quantitative network descriptors
292 (LDq, Cq, Vq and Gq) to specifically examine changes in network complexity and consumer-
293 resource asymmetries as they are commonly used in ecological network studies and less prone to
294 sampling biases (Tylianakis *et al.* 2007; Macfadyen *et al.*, 2009; Wirta *et al.* 2014). As interaction
295 evenness may be ecologically important, and that these network descriptors are relatively
296 insensitive to differences in the evenness of the distribution of link magnitude, we calculated the
297 quantitative tri-partite interaction evenness (IEq) following Albrecht *et al.* (2007). To examine
298 whether plant-herbivore and herbivore-parasitoid interactions react differently to climate change,

299 we also calculated network descriptors for the plant-aphid and aphid-parasitoid bipartite networks
300 separately.

301

302 *Statistical analysis*

303 Statistical analysis was performed in R 3.3.1 (R Core Team, 2016). The effects of treatment on the
304 plants (including yield), insects, parasitism rates and network descriptor response variables were
305 examined using Generalized Linear Models (GLM) with a Gaussian family (except for aphid
306 abundance data, where a Poisson family was used). To account for the intercorrelation between
307 the network descriptors, and to reduce the probability of a type I error, we used a Bonferroni-
308 corrected α of 0.01 to assess the level of significance for the five network descriptors (*i.e.* LDq,
309 Cq, Vq, Gq and IEq, following Tylianakis *et al.* 2007). This correction was used when assessing
310 the effect of treatments on tri-partite network descriptors and on bipartite (plant-aphid and aphid-
311 parasitoid) network descriptors.

312

313 The effects of treatment on the crop phenology (Julian dates of emergences of first leaf and first
314 ear) were examined with Mann-Whitney tests. The effects of treatment on the crop (*i.e.* number of
315 seeds / ear, the seed weight / ear, the density of wheat and yield) were examined using GLM with
316 a Gaussian family. In addition to the climatic treatments, biological interactions may also affect
317 the crop yield (see Gagic *et al.* 2016). Non-crop plants are competitors for space and resources
318 with the crop (Fahad *et al.* 2015). *Sitobion avenae* and *Metopolophium dirhodum* are aphid species
319 feeding on the wheat which may alter the yield (van Emden & Harrington 2007). In order to
320 examine the potential impact of uncultivated plants on the density of the wheat, a second GLM
321 was performed with the percent cover of non-crop plants included as a covariate. Similarly, when

322 analysing the yield data, we included the abundance of wheat aphids *S. avenae* and *M. dirhodum*
323 as a covariate in a separate model and compared the model fit with and without the covariates
324 using Akaike Information Criteria (AIC). In summary, we compared the AIC of the following
325 models:

- 326 a) the effect of precipitation and increased temperatures on the density of the wheat versus
327 the effect of precipitation, increased temperatures and percent cover of non-crop plants on
328 the density of the wheat;
- 329 b) the effect of precipitation and increased temperatures on the crop yield versus the effect of
330 precipitation, increased temperatures and the abundance of wheat aphids on the crop yield.

331 In addition, ANOVA was performed on these two model comparisons to test whether the inclusion
332 of covariates provided a significantly better fit to the model.

333

334 **Results**

335 We quantified 2836 interactions between eight plant species (6 plants identified to species level, 1
336 to the genus level and 1 to the family level), 1946 aphids (1765 living aphids and 181 aphid
337 mummies) belonging to six species, 761 primary parasitoids from 13 species and 129 secondary
338 parasitoids from two species. Of the 129 secondary parasitoids identified, only 41 primary
339 parasitoid – secondary parasitoid interactions were recovered. Consequently, primary and
340 secondary parasitoids were considered as belonging to the same trophic level and separate primary
341 parasitoid – secondary parasitoid interactions were not examined (Figure 1). Overall, the 1946
342 aphids included in the ecological network analysis represented 56.3% of the total aphids counted
343 in the experimental plots.

344

345 *Plant cover and richness*

346 We found no effect of treatment on plant species richness (GLM, warming: $F = 1.577$, $df = 1$, $p =$
347 0.223 ; precipitation: $F = 3.09$, $df = 1$, $p = 0.093$; Table 1), but climate-warming significantly
348 reduced crop percentage cover (GLM, warming: $F = 11.746$, $df = 1$, $p = 0.003$; precipitation: $F =$
349 1.043 , $df = 1$, $p = 0.319$). The overall non-crop species cover was significantly increased in the
350 warmed plots (GLM, warming: $F = 4.78$, $df = 1$, $p = 0.04$; precipitation: $F = 1.519$, $df = 1$, $p =$
351 0.231).

352

353 *Aphid abundance and parasitism rates*

354 We found no effect of treatment on aphid species richness, but climate-warming resulted in
355 significant aphid outbreaks (GLM, $df = 1$, $p < 0.001$; Table 1), with four times as many aphids in
356 the warmed plots compared to control plots. The abundance of the wheat aphids *S. avenae* and *M.*
357 *dirhodum* doubled as a result of warming (GLM, $df = 1$, $p = 0.009$; Figure 1, Table 1). Molecular
358 analyses revealed high rates of parasitism (based on parasitoid detection within aphids and
359 mummies sampled; mean $36 \pm 1.7\%$) compared to the conventional ‘mummy’ collection/rearing
360 method (based solely only on mummies sampled; mean $9.9 \pm 1.8\%$). Climate-warming did not
361 significantly change parasitoid species richness, although we did detect a trend (GLM, $df = 1$, $F =$
362 4.247 , $p = 0.052$). There were no significant effects of treatment on parasitism rates nor
363 multiparasitism (two primary parasitoids within a single aphid) and hyperparasitism rates (aphids
364 parasitised by secondary parasitoids), which were relatively low across the treatments ($3.77 \pm$
365 0.01% and $7.38 \pm 0.01\%$ respectively; Table 1).

366

367 *Tripartite ecological network structure*

368 We found a significant effect of climate-warming on total species richness across trophic levels
369 (Table 1, Figure 1). Precipitation did not affect quantitative tripartite network descriptors V_q
370 (GLM, $F = 0.003$, $df = 1$, $p = 0.959$), IE_q (GLM, $F = 0.274$, $df = 1$, $p = 0.606$; Figure 2), LD_q , C_q
371 and G_q (Table 2). Simulated climate-warming did not affect qualitative network descriptors (Table
372 S1), however it did significantly decrease quantitative tripartite V_q (GLM, $F = 10.063$, $df = 1$, $p =$
373 0.005 ; Figure 2) and LD_q , but did not affect C_q , G_q (Table 2) and IE_q (GLM, $F = 0.362$, $df = 1$, $p =$
374 0.554 ; Figure 2). Within the 24 networks, both aphids and parasitoids never consumed more than
375 three different species from the lower trophic level (Figure 1).

376

377 *Plant-aphid bipartite network structure*

378 Precipitation did not affect plant-aphid quantitative network descriptors V_q (GLM, $F = 0.425$, df
379 $= 1$, $p = 0.522$), IE_q (GLM, $F = 0.0001$, $df = 1$, $p = 0.991$; Figure 2), LD_q , C_q and G_q (Table 2).
380 Likewise, climate-warming did not affect plant-aphid quantitative network descriptors V_q (GLM,
381 $F = 0.753$, $df = 1$, $p = 0.395$), IE_q (GLM, $F = 5.574$, $df = 1$, $p < 0.029$; Figure 2), LD_q , C_q and G_q
382 (Table 2)

383

384 *Aphid-parasitoid ecological network structure*

385 Precipitation did not affect aphid-parasitoid quantitative network descriptors V_q (GLM, $F = 0.005$,
386 $df = 1$, $p = 0.944$), IE_q (GLM, $F = 1.091$, $df = 1$, $p = 0.308$; Figure 2), LD_q , C_q and G_q (Table 2).
387 However, climate-warming significantly decreased aphid-parasitoid quantitative network
388 descriptors V_q (GLM, $F = 18.456$, $df = 1$, $p < 0.001$) and LD_q , but did not affect C_q and G_q .
389 Climate-warming negatively affected aphid-parasitoid IE_q (GLM, $F = 37.599$, $df = 1$, $p < 0.0001$).
390 This suggests that higher trophic interactions are more sensitive in our system and was likely

391 caused by an increase in the frequency of interactions between wheat aphids and two primary
392 parasitoid species: *Aphidius rhopalosiphi* and *Aphidius ervi*.

393

394 *Wheat phenology*

395 First leaves emerged three days earlier in the warmed plots (Mann-Whitney, $W = 118$, $p = 0.002$).

396 First ears emerged eleven days earlier on average in the warmed plots (Mann-Whitney $W = 144$,

397 $p < 0.001$). Precipitation affected neither the emergence of the first leaves (Mann-Whitney, $W =$

398 63.5 , $p = 0.586$) nor the first ears (Mann-Whitney, $W = 72$, $p = 1$).

399

400 *Crop yield*

401 Climate-warming significantly reduced the seed number (GLM, $F = 4.272$, $df = 1$, $p = 0.041$, Table

402 3), the seed weight (GLM, $F = 3.049$, $df = 1$, $p = 0.012$; Table 3) but not the density of the wheat

403 (GLM, $F = 2.109$ $df = 1$; $p = 0.161$; Table 3), resulting in no overall reduction in crop yield (GLM,

404 $F = 3.835$, $df = 1$, $p = 0.064$; Table 3). However, when including the detrimental effect of non-crop

405 plants or wheat aphid abundance in the models, we found a significant decrease in wheat density

406 (GLM, $F = 11.606$, $df = 1$, $p = 0.003$; Table 4) and crop yield (GLM, $F = 6.33$, $p = 0.021$, $df = 1$;

407 Figure 3; Table 4). Yield loss was not compensated by increased rainfall (GLM, $F = 0.066$, $df = 1$;

408 $p = 0.8$; Table 4). These models, which including wheat aphid abundances and non-crop cover,

409 provided a significantly better fit to the data than the models considering experimental treatment

410 alone (ANOVA; wheat density: $F = 95.582$, $p < 0.001$; crop yield: $F = 14.663$, $df = 1$, $p = 0.001$)

411 Table 5).

412

413

414 **Discussion**

415 We provide the first experimental evidence, to our knowledge, of the impacts of climate-warming
416 on the structure of tripartite ecological networks, constructed using a DNA-barcoding approach.
417 Experimental warming altered total species richness across trophic levels (but not plant and aphid
418 species richness respectively), it significantly reduced crop percentage cover and substantially
419 increased aphid abundance (the abundance of the economically important aphids *S. avenae* and *M.*
420 *dirhodum* doubled as a result of warming). This affected quantitative network structure and
421 complexity, including aphid-parasitoid interaction evenness. Molecular analyses revealed much
422 higher rates of parasitism compared to traditional rearing/identification methods, with generally
423 fewer natural predator species in the warmed plots. However there were no significant effects of
424 treatment on parasitism rates, nor multiparasitism and hyperparasitism. Thus, in the short-term at
425 least, natural pest control (assessed here using a molecular approach to determine parasitism rate)
426 provided by parasitoids appears unaffected, although studies of aphid and parasitoid population
427 dynamics over the long-term are needed. Overall, we show that wheat grown 1.4°C above ambient
428 temperature produced significantly fewer and lighter seeds resulting in a reduction in crop yield,
429 with the best fitting model including aphid abundance and non-crop cover as covariates. We found
430 no statistically significant effect of increased rainwater on any of our response variables, despite
431 it being a very low rainfall season.

432

433 *Study limitations*

434 Despite the advances made by our study, there are important limitations to our experiment. First,
435 the 4 m² plots sampled are not directly comparable to a large cereal crop field. Our results may
436 instead reflect how agricultural communities at field edges respond to climate change. However,

437 because insect herbivory and parasitism rate are edge-dependent (Maron & Crone 2006; Reeve &
438 Cronin 2010), our results might nevertheless be indicative of the direction of change for plant and
439 animal populations and communities at larger spatial scales as a result of climate-warming,
440 although more research is necessary. Although all simulated climate-warming methods have
441 limitations (Sassi *et al.* 2012), they are nevertheless one of the few tools available in empirically
442 testing how ecosystems response to climate change and provide much-needed data for predictive
443 network models (Staniczenko *et al.* 2017). In the future, complementary approaches including
444 large-scale field experiments and small-scale mesocosms or laboratory experiments (see Romo &
445 Tylianakis 2013) might give a more comprehensive view of the ecosystem response to climate
446 change. Second, we did not control non-crop plant or insect communities as we wished to quantify
447 how they interact. Thus, conventionally managed cereal crops are likely to have responded
448 differently to the experimental treatments. Third, we only examined the effects of treatment over
449 a single growing season. Further temporal replicates would determine whether the response
450 observed is year-dependent and the extent of interaction turnover (Kemp *et al.* 2017). Fourth, we
451 did not consider other organisms potentially affecting the plant-aphid-parasitoid networks, such as
452 ants interacting with aphids or predators consuming both aphids and parasitoids (Traugott *et al.*
453 2011; Barton & Ives 2014; Raso *et al.* 2014). Future studies should examine a more exhaustive
454 range of species interactions (e.g. following Pocock *et al.* 2012; Evans *et al.* 2013), which are
455 increasingly possible using the molecular approaches described here and/or Next Generation
456 Sequencing technologies (Kitson *et al.* 2018). Fifth, we could not disentangle whether the insect
457 responses were mainly due to foraging decisions of organisms (*i.e.* dispersal between the plots) or
458 their demographic response to climatic manipulation (*i.e.* treatments affecting population growth
459 rates), although it is likely that the observed aphid species responses were demographic. Further

460 experimental manipulations at larger-spatial scales (and including other important factors such as
461 elevated CO₂) are urgently required as well as more detailed observations of host-parasitoid and
462 other predator-prey interactions, although this would need to involve much larger controlled
463 enclosures than are currently available. Finally, we conducted a relatively exhausting sampling
464 where all aphid mummies and more than 50% of aphids were collected for further molecular
465 analyses. Such intensive sampling may certainly affect the aphid and parasitoid population
466 dynamics at the plot-level and could have potentially affected our results. However, adequate
467 network analysis is very dependent on sampling completeness (Blüthgen et al. 2006; Rivera-
468 Hutinel et al. 2012; Jordano 2016). Consequently, such intensive sampling is well established in
469 studying host-parasitoid interactions (see Traugott et al. 2008) and ecological networks more
470 generally (e.g. Macfadyen *et al.* 2009) and was therefore necessary for the purposes of this study.
471 Assessing the effect of climate change on aphid and parasitoid dynamics, while also a major issue,
472 would then require a different experimental design.

473

474 *Trophic level to network level responses*

475 When considering each trophic level separately, climate-warming promoted weed growth
476 (especially *Chenopodium album* and *Cirsium arvense*), which increased competition with the crop
477 and contributed to a reduction in crop percentage cover. At the second trophic level, there was a
478 fourfold increase in aphid abundance in the warmed plots, as we predicted, mostly driven by aphids
479 associated with *T. aestivum*. At the third trophic level, contrary to our predictions, parasitism rates
480 remained unchanged. However, a decrease in aphid-parasitoid interaction evenness in the warmed
481 plots suggests that climate-warming might benefit some parasitoid species at the expense of others.
482 Whilst both the reduction in crop yield and the aphid pest outbreak followed the general patterns

483 observed in other recent studies (Maxmen 2013; Dong *et al.*,2013; Bebber *et al.* 2014; Liu *et al.*
484 2016), the significant effects on network structure observed in this study provides new insights
485 into how climate-warming affects entire communities of interacting species. First, we found
486 evidence that climate-warming affects tri-partite consumer-prey asymmetries, with significantly
487 lower network vulnerability and linkage density. Second, connectance was not affected, most
488 likely due to the high trophic specialization for both aphids and associated parasitoid wasps (Le
489 Ralec *et al.* 2011; Derocles *et al.* 2014). Third, although there was no effect of treatment on
490 tripartite interaction evenness, climate-warming negatively affected bipartite aphid-parasitoid
491 interaction evenness, suggesting that higher trophic interactions might be more sensitive in our
492 system. Indeed, changes in tri-partite network structure are essentially driven by aphid-parasitoid
493 interactions: plant-aphid networks were not affected by simulated-warming while aphid-parasitoid
494 linkage density and vulnerability decreased. Overall, our results support the findings from de Sassi
495 *et al.* (2012) showing that climate-warming may have bottom-up effects (on host density and body
496 size) which can in turn affect the structure of host-parasitoid networks.

497

498 *Parasitism*

499 We found no effect of climate-warming on the parasitism rate and species richness of parasitoid
500 wasps (although precipitation and warming treatment tended to decrease parasitoid richness)
501 which are intimately linked to the ecosystem service of natural pest control (Traugott *et al.* 2008;
502 Derocles *et al.* 2014). In Northern European agricultural habitats, the most abundant parasitoid
503 species appear more specialized, with reduced attack rates on alternative hosts (Derocles *et al.*
504 2014). Macfadyen *et al.* (2009) showed significant differences in network structure between
505 organic and conventional farms with more species at three trophic levels (plant, herbivore and

506 parasitoid) on organic farms. Despite herbivores on organic farms being attacked by more
507 parasitoid species, differences in network structure did not affect parasitism rate across a variety
508 of host species. In our study, climate-warming mainly influenced two parasitoid species, *A.*
509 *rhopalosiphi* (the main natural enemy of *Sitobion avenae*) and *A. ervi*, driving a decrease in aphid-
510 parasitoid interaction evenness. These species differ in their trophic specialization: *A. rhopalosiphi*
511 is a specialist and *A. ervi* is a generalist (Kavallieratos *et al.* 2004; Starý 2006). Previous work by
512 Le Lann *et al.* (2014) under laboratory conditions showed a decrease in the attack rate of *A.*
513 *rhopalosiphi* on *S. avenae* as a result of warming, whereas aphid defense rate increased. Under
514 more realistic field-based scenarios, which include a greater range of interacting species, we found
515 the opposite effect. This not only suggests that the degree of specialization may not necessarily
516 explain which species will be more adaptable to environmental changes (as hypothesized by Rand
517 & Tschamtko 2007; Tylianakis *et al.* 2008; Jeffs & Lewis 2013) but that other factors, such as
518 changes in apparent competition (Morris *et al.* 2004), might be important considerations within a
519 food-web context. Overall, an accurate assessment of natural pest control cannot be undertaken by
520 the single measure of parasitism rate, but would require a careful examination of host and
521 parasitoid population dynamics through further study and a different experimental design. These
522 results, together with a recent study by Berthe *et al.* (2015) at the same study site that showed
523 significant increases in Coleoptera activity-densities but a reduction in community diversity as a
524 result of climate-warming, demonstrate the short-term impact of climate-warming on higher
525 trophic levels (*i.e.* predators and parasitoids) in particular. Given the potential top-down effects
526 driven by these organisms, we expect that climate-warming will result in long-term changes to the
527 structure of the ecological network and consequently in natural pest control. Thus long-term
528 climate-manipulation studies across spatial-scales are necessary to better understand the effects of

529 environmental change on agricultural plant-aphid-parasitoid interactions and the ecosystem
530 service of natural pest control (Cardinale *et al.* 2003; Tylianakis *et al.* 2006; Macfadyen *et al.*
531 2011; Peralta *et al.* 2014).

532

533 *Impacts of climate-warming on crop yields within an ecological network context*

534 We found significant effects of climate-warming not only on ecological network structure, but also
535 on crop yield. Experimental-warming has been shown to advance flowering and fruiting phenology
536 for a range of plant species (Sherry *et al.* 2007; Hovenden *et al.* 2008; Dong *et al.* 2013) and in
537 our study, first wheat leaves emerged three days earlier on average and ears emerged at least a
538 week earlier in the warmed plots. Wheat grown under experimental-warming produced fewer and
539 lighter grain, resulting in a significant impact on crop yield. There was no significant effect of
540 increased rainwater, which was perhaps surprising given the study was conducted during a very
541 low rainfall season. The yield data from the experiment is nevertheless not directly comparable
542 with commercial agricultural wheat yields. It should be emphasized that it was not our intention
543 to simulate conventional farming methods, where routine spraying would have removed most of
544 the weed species within our plots. Rather we wished to study the community wide response of
545 interacting species across trophic levels. In this context, the reduction in crop yield was primarily
546 driven by a combination of the wheat producing fewer, smaller grain as well as increased
547 competition with weed species, rather than significant insect damage (aphid load was very low:
548 0.14 ± 0.09 aphids per wheat ear across all plots). Despite this, warming did trigger a fourfold
549 increase in aphid abundance and this is likely to cause significant damage to crops in years when
550 fluctuating aphid numbers are higher. As demonstrated recently by Gagic *et al.* (2016), attacks by
551 several pests can have both positive and negative impacts on crop yield. In our study, crop yield

552 models produced a better fit when pest aphid abundance was included as a co-variate. However, it
553 still remains unclear how crop (yield in particular) and non-crop plants are affected both directly
554 and indirectly by changes in aphid-parasitoid interactions. By pioneering new molecular methods
555 to construct highly-resolved species-interaction networks, we have provided new, cost-effective
556 tools to examine the response of communities of interacting agricultural species to environmental
557 change.

558

559 *Merging DNA-based methods with ecological network analysis*

560 Merging molecular methods and ecological network analysis (ENA) provides new tools for
561 understanding ecology and evolution (Raimundo *et al.* 2018). Here we showed that the detection-
562 rate of aphid parasitism was more than three times higher using molecular assays than by
563 conventional insect-rearing approaches. Plant-aphid-parasitoid networks, constructed using
564 molecular methods, were more highly-resolved than traditional rearing methods, with significant
565 implications for host-parasitoid network-level analyses (Condon *et al.* 2014; Hrček & Godfray
566 2015). Traditional approaches based on insect rearing and morphological identification would
567 have failed to detect changes in species interactions mediated by the increase in temperature.
568 Indeed, such approaches rely on the collection of aphid mummies and rearing adults for
569 identification. In our study, only 181 aphid mummies were collected while 709 parasitoids were
570 detected and identified within their living aphid hosts. Parasitism cases using molecular methods
571 were therefore able to capture a more exhaustively range of host-parasitoid interactions. These
572 parasitism cases however still need to be considered cautiously: parasitoid eggs or larvae detected
573 do not always achieve their development to the adult stage (Starý *et al.* 1989). Consequently,
574 molecular tools could potentially overestimate parasitism (Traugott *et al.* 2008). Moreover, aphids

575 collected on the same plant were placed together in a single tube. This may lead to a potential risk
576 of contamination between aphids with parasitoid DNA. But this risk is low because in the same
577 tubes we found both unparasitised and parasitised aphids (from different parasitoid species).
578 Completely eliminating this risk would require each collected aphid to be separately stored but
579 might also result in unrealistic, time-consuming sampling protocols.

580

581 In summary, this study provides the first evidence, to our knowledge, of the impact of climate
582 change on farmland tri-partite ecological networks, ecosystem services and agricultural output. In
583 the short-term, we highlight the potential winners (*i.e.* pests) and losers (*i.e.* pest natural enemies)
584 of agro-ecosystems in a warmer world. Overall, our study provides insights into the potential threat
585 of global warming on both farmland biodiversity and food production. Despite limited changes to
586 biodiversity *per se*, climate-warming affects the frequency of interactions between species,
587 ultimately affecting network structure, although the long-term consequences of altered network
588 structure on ecosystem functioning warrants further study. The detrimental impact of climate-
589 warming on wheat suggests the need for adapting future agricultural methods of cropping in
590 response to a climate change (Asseng *et al.*, 2013); cropping methods which in turn can also have
591 cascading effects on agro-ecosystems and their networks of interactions. Considering the effects
592 of environmental changes on ecological networks in dynamic models rather than snapshots of
593 communities is essential (Säterberg *et al.* 2013) as well as taking into account a more complete
594 range of interactions (*i.e.* ‘networks of ecological networks’; Pocock *et al.* 2012; Evans *et al.*
595 2013). Future studies should consider the combined effects of climate-warming and elevated CO₂
596 as the latter also affects wheat growth and grain yield in particular (O’Leary *et al.* 2015). Such
597 changes in plants may also induce bottom-up effects on high trophic levels (*e.g.* pest arthropods

598 feeding on the crop). Finally, increased rainwater did not affect the ecological networks and the
599 crop yield in the present study, suggesting that extra water (either as increased precipitation or
600 irrigation) might not mitigate the effects of increased temperature. Further considerations are
601 nevertheless needed to understand the predicted changes in rainfall on agroecosystems.
602 Consequently, future climate change experiments need to simulate more realistic climate change
603 scenarios and consider increases of temperatures, precipitation and CO₂ combined. A more
604 exhaustive examination of climate change consequences on agricultural ecosystems through a
605 combined approach using ENA and DNA-based methods is the fundamental first step to predict
606 the impact of global changes on food production.

607

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617

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947 **Data accessibility**

948 DNA sequences were assigned Genbank accession numbers: MF154009 – MF154409
949 Plot level plant, insect and network data is available on Dryad: doi:10.5061/dryad.80vd7q6

950

951 **Author contributions**

952 DME designed the project. SAPD and SCFB performed the field sampling. SAPD and DHL
953 developed the molecular methodology. SAPD, SCFB and PCN performed the molecular work in
954 the laboratory. EDM processed the crop yield data. SAPD and DME analysed the data. SAPD and
955 DME wrote the first draft of the manuscript, all authors contributed substantially to revisions.

956

957 **Supporting information**

958 Additional supporting information may be found in the online version of this article.

959 Figure S1 Experimental layout of the simulated climate change experiment at Stockbridge
960 Technology Centre, North Yorkshire, UK.

961 Table S1 Qualitative network descriptors (LD, C, G, V) and unweighted quantitative network
962 descriptors (LD'q, C'q, G'q, V'q) for each treatment (mean \pm standard deviation).

963 **Tables and figure captions**

964

965 **Table 1.** Trophic-level descriptors for each treatment (mean \pm standard deviation). Descriptors
966 were calculated for each of the 24 experimental plots and then compared between treatments.
967 Effects of treatments on descriptors were tested with GLM (Family Gaussian, F-test; except for
968 Aphid abundances: family Poisson; Chi-square test). W+P: warming and precipitation; \uparrow P:
969 increase in precipitation; \uparrow T $^{\circ}$: increase in temperature. Significant effects at α of 0.05 are in bold.

970

971 **Table 2.** Weighted quantitative network descriptors (LDq, Cq, Gq) of tri-partite networks and
972 bipartite (plant-aphid and aphid-parasitoid) networks for each treatment (mean \pm standard
973 deviation). Vq and IEq are presented in Figure 2. Network descriptors were calculated for each of
974 the 24 networks and then compared to each other. Effects of treatments on network descriptors
975 were tested with GLM (Family Gaussian; F-test). W+P: warming and precipitation; \uparrow P: increase
976 in precipitation; \uparrow T $^{\circ}$: increase in temperature; sd: standard deviation. Significant effects at a
977 Bonferroni-corrected α of 0.001 are in bold.

978

979 **Table 3.** Impact of the simulated climate-change on the wheat: number of seeds / ear, total seed
980 weight per ear (g), density of wheat (number of wheat plants / m 2) and crop yield (g / m 2) for each
981 treatment (mean \pm standard error). Measurements of *T. aestivum* were calculated for each of the
982 24 experimental plots and then compared to each other. Effects of treatments were tested with
983 GLM (Family Gaussian; F-test; non-crop cover and pest aphid abundance were not included in
984 these models). Significant effects ($p < 0.05$) are in bold.

985

986 **Table 4.** Effect of treatments and covariates on the density of wheat (number of wheat plants / m 2)
987 and on the crop yield (g/m 2). Warming treatment, precipitation treatment and non-crop cover were
988 included in a single GLM (Family Gaussian; F-test) when assessing their effects on wheat density.
989 Warming treatment, precipitation treatment and pest aphid abundance were included in a single
990 GLM (Family Gaussian; F-test) when assessing their effects on crop yield. Significant effects (p
991 < 0.05) are in bold.

992

993 **Table 5.** Generalized linear models comparisons for the density of the wheat (number of wheat
994 plants / m 2) and the crop yield (g/m 2). AIC were calculated for GLMs including only the warming
995 and the precipitation treatments (GLM1, models presented in Table 3) and for GLMs including
996 warming and precipitation treatments, non-crop cover or wheat aphid abundance as covariate
997 (GLM2, models presented in Table 4).

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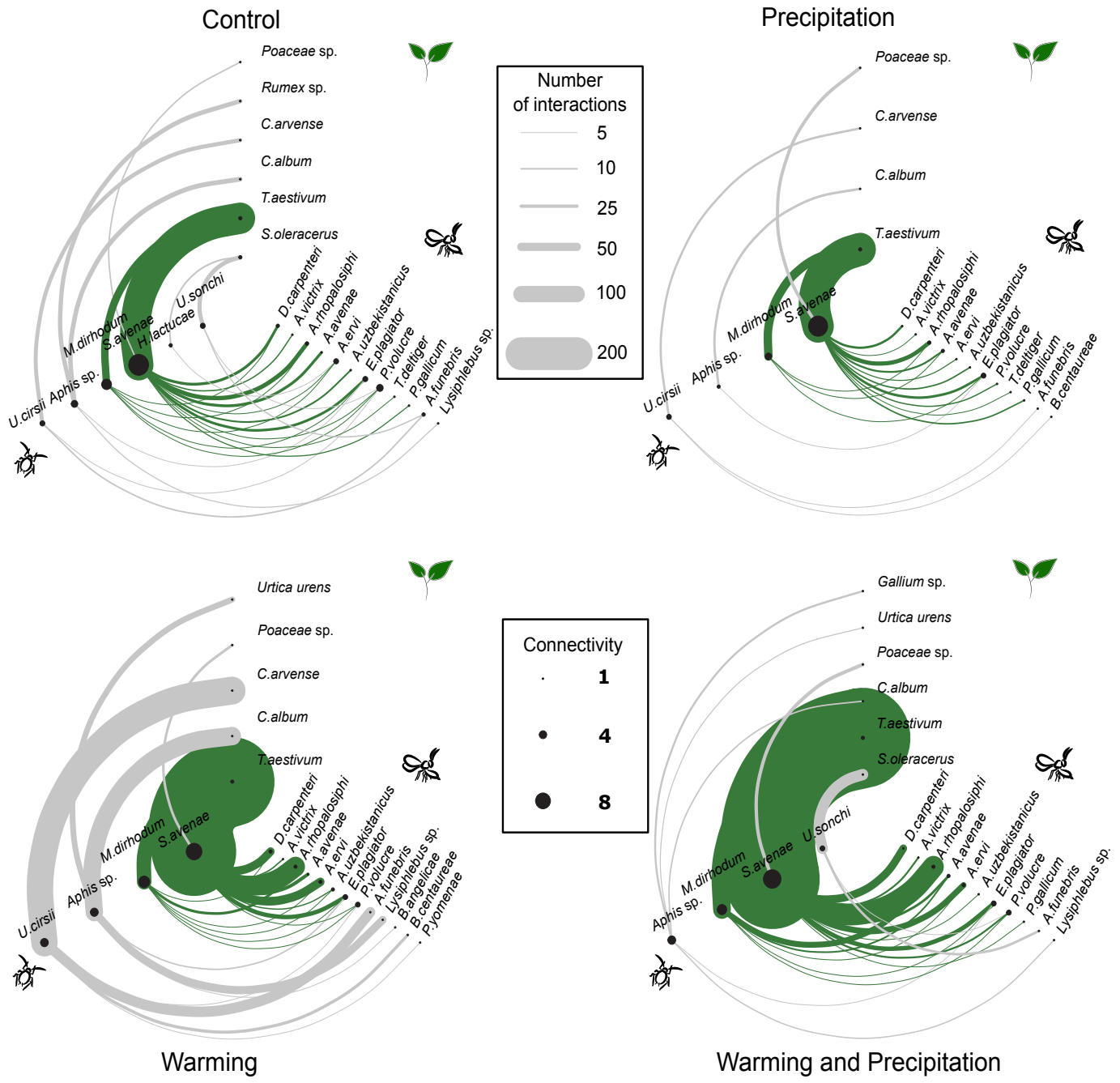
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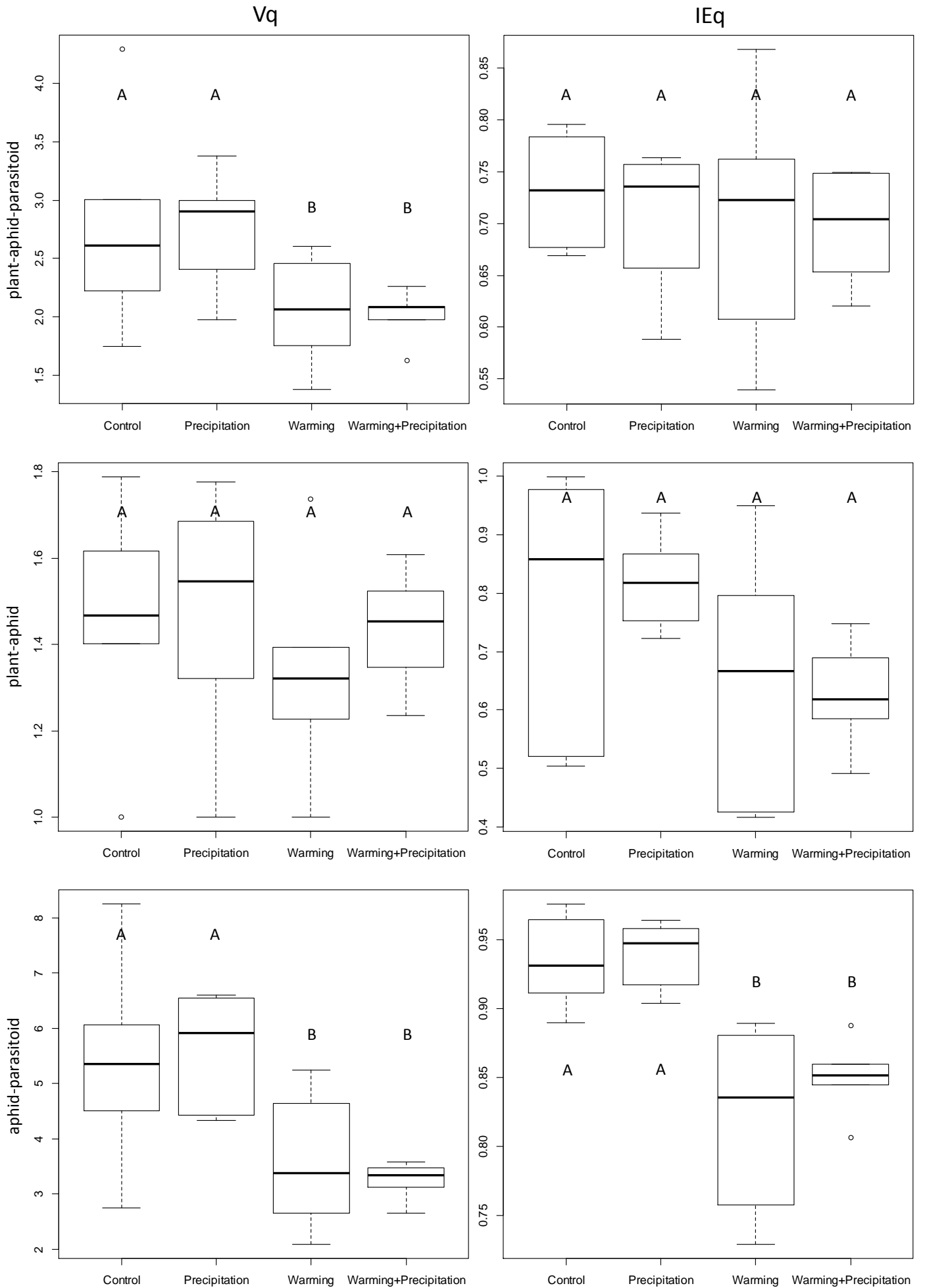
1003

1004 **Figure 1.** Impact of simulated climate-change on quantitative ecological plant–aphid–parasitoid
1005 networks. All interactions detected during the sampling season were pooled across all the plots
1006 sharing the same treatment to draw the networks. Interactions related to the crop are represented
1007 in green. Connectivity represents the number of species with which each species interacts.

1008
1009 **Figure 2.** Impact of climate-change on weighted quantitative vulnerability V_q and interaction
1010 evenness IE_q for tri-partite and bipartite networks. Different letters indicated a significant
1011 difference at a Bonferroni-corrected α of 0.01. Impact of treatments on the network descriptors
1012 was tested in distinct Generalized Linear models.

1013
1014 **Figure 3.** Impact of the simulated climate-change on the crop yield (g/m^2). The effects of the
1015 treatments on the crop yield were tested with a Generalized Linear model (pest aphid abundance
1016 included as covariate in the model).





Crop yield (g/m²)

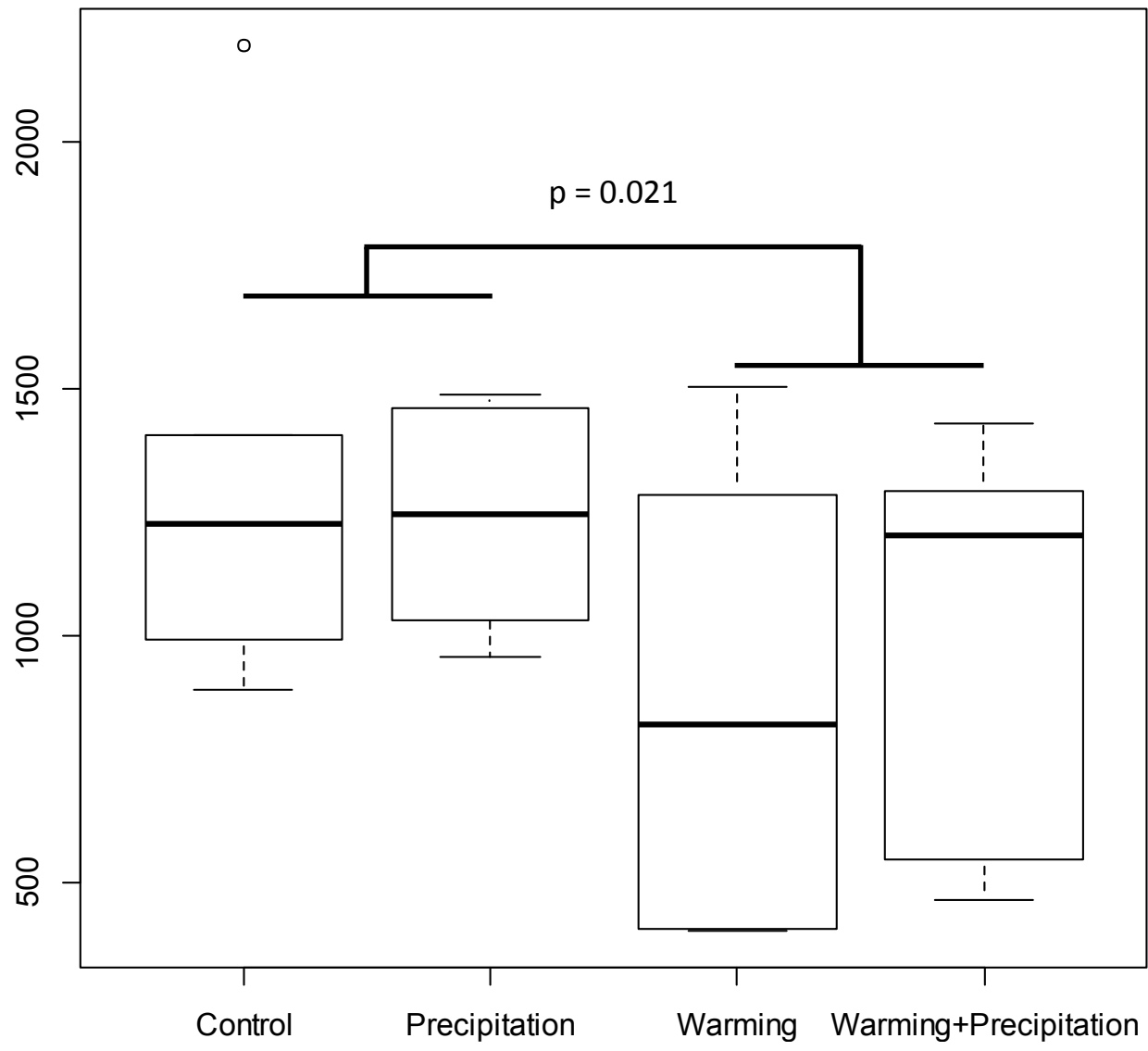


Table 1. Trophic-level descriptors for each treatment (mean \pm standard deviation). Descriptors were calculated for each of the 24 experimental plots and then compared between treatments. Effects of treatments on descriptors were tested with GLM (Family Gaussian, F-test; except for Aphid abundances: family Poisson; Chi-square test). W+P: warming and precipitation; \uparrow P: increase in precipitation; \uparrow T $^{\circ}$: increase in temperature. Significant effects at α of 0.05 are in bold.

	Plant richness	Weed Cover	Wheat Cover	Aphid richness	Aphid abundance	Wheat aphid abundance	Parasitism rate	Multiparasitism rate	Hyperparasitism rate	Parasitoid richness	Total species richness
Control	2 \pm 0.632	20.5 \pm 4.806	77.167 \pm 4.215	2.667 \pm 1.033	46.167 \pm 19.682	31.167 \pm 7.494	0.339 \pm 0.077	0.037 \pm 0.038	0.082 \pm 0.072	8.333 \pm 2.16	12.833 \pm 3.488
Precipitation	1.667 \pm 0.816	19 \pm 4.195	78.833 \pm 1.602	2.167 \pm 0.753	59.667 \pm 55.479	36 \pm 13.387	0.347 \pm 0.111	0.042 \pm 0.028	0.063 \pm 0.053	7.833 \pm 1.472	11.667 \pm 2.066
Warming	2.667 \pm 1.033	33.333 \pm 16.525	62.5 \pm 14.053	2.833 \pm 0.753	183.333 \pm 109.485	86.333 \pm 49.443	0.39 \pm 0.093	0.041 \pm 0.014	0.067 \pm 0.033	7.833 \pm 1.941	13.333 \pm 3.077
W+P	1.833 \pm 0.753	24.5 \pm 10.635	68.333 \pm 10.801	2.667 \pm 0.816	286.167 \pm 267.655	97.167 \pm 55.315	0.362 \pm 0.067	0.031 \pm 0.023	0.084 \pm 0.044	5.5 \pm 0.548	10 \pm 1.265
\uparrow P F-value	3.09	1.519	1.043	0.966			0.079	0.082	0.044	4.247	4.413
\uparrow P p-value	0.093	0.231	0.319	0.337	<0.001	0.609	0.782	0.777	0.948	0.052	0.048
\uparrow T $^{\circ}$ F-value	1.577	4.78	11.746	0.966			0.851	0.091	0.02	4.247	0.297
\uparrow T $^{\circ}$ p-value	0.223	0.04	0.003	0.337	<0.001	0.009	0.367	0.766	0.889	0.052	0.592

Table 2. Weighted quantitative network descriptors (LDq, Cq, Gq) of tri-partite networks and bipartite (plant-aphid and aphid-parasitoid) networks for each treatment (mean ± standard deviation). Vq and IEq are presented in Figure 2. Network descriptors were calculated for each of the 24 networks and then compared to each other. Effects of treatments on network descriptors were tested with GLM (Family Gaussian; F-test). W+P: warming and precipitation; ↑P: increase in precipitation; ↑T°: increase in temperature; sd: standard deviation. Significant effects at a Bonferroni-corrected α of 0.001 are in bold.

	Plant-aphid-parasitoid networks			Plant-aphid networks			Aphid-parasitoid networks		
	LDq	Cq	Gq	LDq	Cq	Gq	LDq	Cq	Gq
Control	1.945 ± 0.452	0.157 ± 0.045	1.142 ± 0.1	1.284 ± 0.175	0.297 ± 0.085	1.111 ± 0.183	3.305 ± 0.828	0.317 ± 0.095	1.231 ± 0.163
Precipitation	1.978 ± 0.22	0.175 ± 0.039	1.197 ± 0.201	1.322 ± 0.197	0.380 ± 0.104	1.164 ± 0.234	3.445 ± 0.504	0.354 ± 0.072	1.266 ± 0.174
Warming	1.593 ± 0.208	0.125 ± 0.035	1.131 ± 0.093	1.223 ± 0.116	0.245 ± 0.096	1.113 ± 0.123	2.369 ± 0.579	0.228 ± 0.056	1.170 ± 0.124
Warming+Precipitation	1.589 ± 0.136	0.162 ± 0.028	1.159 ± 0.128	1.251 ± 0.11	0.306 ± 0.094	1.066 ± 0.148	2.307 ± 0.221	0.285 ± 0.042	1.361 ± 0.185
↑P F-value	0.015	2.789	0.474	0.239	3.018	0.002	0.024	2.409	2.373
↑P p-value	0.905	0.11	0.499	0.63	0.097	0.966	0.878	0.136	0.138
↑T° F-value	9.168	1.859	0.161	0.944	2.284	0.37	16.985	6.724	0.053
↑T° p-value	0.006	0.187	0.693	0.342	0.146	0.549	< 0.001	0.017	0.821

Table 3. Impact of the simulated climate-change on the wheat: number of seeds / ear, total seed weight per ear (g), density of wheat (number of wheat plants / m²) and crop yield (g / m²) for each treatment (mean \pm standard error). Measurements of *T. aestivum* were calculated for each of the 24 experimental plots and then compared to each other. Effects of treatments were tested with GLM (Family Gaussian; F-test; non-crop cover and pest aphid abundance were not included in these models). Significant effects ($p < 0.05$) are in bold.

	Number of seeds	Seed weight / ear (g)	Density of wheat	Yield (g/m ²)
Control mean \pm se	46.67 \pm 1.72	2.46 \pm 0.11	534.7 \pm 57.5	1323.7 \pm 192.4
Precipitation mean \pm se	44.5 \pm 2.18	2.37 \pm 0.12	519.3 \pm 27.5	1239.3 \pm 97
Warming mean \pm se	40.77 \pm 1.7	2.1 \pm 0.11	401.3 \pm 82.4	872.5 \pm 209.7
W+P mean \pm se	42.7 \pm 1.81	2.14 \pm 0.12	478.7 \pm 61.5	1024.8 \pm 167.7
↑Precipitation F-value	0.0039	0.0166	0.2677	0.0399
↑Precipitation p-value	0.9502	0.8509	0.6103	0.8435
↑Warming F-value	4.2722	3.0485	2.1088	3.8351
↑Warming p-value	0.0410	0.0119	0.1612	0.0636

Table 4. Effect of treatments and covariates on the density of wheat (number of wheat plants / m²) and on the crop yield (g/m²). Warming treatment, precipitation treatment and non-crop cover were included in a single GLM (Family Gaussian; F-test) when assessing their effects on wheat density. Warming treatment, precipitation treatment and pest aphid abundance were included in a single GLM (Family Gaussian; F-test) when assessing their effects on crop yield. Significant effects ($p < 0.05$) are in bold.

	d.f.	Density of wheat		Crop yield (g/m ²)	
		F-value	P-value	F-value	p-value
Warming	1	11.6064	0.002797	6.3304	0.020518
Precipitation	1	1.4736	0.238918	0.0659	0.799986
Non-crop cover	1	95.5818	<0.0001	not included in this GLM	
Wheat aphid abundance	1	not included in this GLM		14.6634	0.001048

Table 5. Generalized linear models comparisons for the density of the wheat (number of wheat plants / m²) and the crop yield (g/m²). AIC were calculated for GLMs including only the warming and the precipitation treatments (GLM1, models presented in Table 3) and for GLMs including warming and precipitation treatments, non-crop cover or wheat aphid abundance as covariate (GLM2, models presented in Table 4).

	AIC GLM1: Treatments only	AIC GLM2: Treatments with covariate
Density of wheat	312.3637	272.2618
Crop yield (g/m ²)	362.4188	351.2199