

1 **Climate warming leads to decline in frequencies of melanic individuals in subarctic leaf**
2 **beetle populations**

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12

13 **Abstract**

14

15 Intraspecific diversity buffers populations from deleterious impacts of environmental change.
16 Nevertheless, the consequences of climate warming for phenotypic and genetic diversity
17 within populations and species remain poorly understood. The goal of our study was to
18 explore among-year variations in the phenotypic structure of populations and their
19 relationships with climate variability and population dynamics. We analysed multiyear
20 (1992–2018) data on colour morph frequencies within populations of the leaf beetle,
21 *Chrysomela lapponica*, from multiple sites in the Kola Peninsula (northwestern Russia). We
22 observed a strong decline in the proportion of dark (melanic) morphs among overwintered
23 beetles during the study period; this decline was consistent across all study sites. Using model
24 selection procedures, we explained declines in the dark morph of overwintered beetles by
25 increases in minimum spring (May–June) daily temperatures. Other climatic characteristics,
26 pollution load, and beetle population density were unrelated to variation in colour morph
27 frequencies. Among newly emerged beetles (August), dark morph frequencies also decreased
28 with an increase in average spring temperatures, but were unrelated to mean temperatures
29 during the larval development period (July). These results suggest that the two-fold decline in
30 dark morph frequencies during the past 26 years has been driven by the 2.5°C increase in
31 spring temperatures, most likely because dark males lose the mating advantages over light
32 males that they obtain during cold springs. The continued loss of dark morphs and related
33 decrease in within-population diversity may render leaf beetle populations more vulnerable to
34 future environmental changes, in particular to those expressed in extreme weather
35 fluctuations. Our study demonstrates that declines in within-population diversity are already
36 underway in subarctic areas, and that these declines are likely driven by climate warming.

37

38 Keywords: polymorphism, population density, spring temperatures, *Chrysomela lapponica*,
39 Kola Peninsula, within-population diversity.

40

41 **1. Introduction**

42

43 Global environmental change is a complex phenomenon imposing a wide range of impacts on
44 biota (Scheffers et al., 2016). Among these, changes in the distribution ranges of plants and
45 animals, and shifts in their phenology, are particularly well documented (Parmesan and
46 Hanley, 2015; Boggs, 2016). Much less is known about the impacts of climate warming on
47 species' abundance, which relates closely to extinction risk and ecosystem functions (Bellard
48 et al., 2012; Martay et al., 2017). Finally, the consequences of global change for the genetic
49 structure of populations, including levels of genetic diversity, have not been assessed across
50 taxa (Pauls et al., 2013). Among the ways in which global climate change may affect
51 intraspecific genetic diversity (Hoffmann and Sgrò, 2011), evolutionary adaptations under
52 changing selection pressures from the abiotic and biotic environment remain relatively
53 unexplored.

54

55 Polymorphism, in particular colour polymorphism, can provide considerable benefits for
56 species and populations (Forsman, 2016). Several driving forces have been proposed to
57 explain the evolution and maintenance of colour polymorphism in different groups of animals
58 (Ford, 1945; Roulin, 2004; Forsman et al., 2008; Wellenreuther et al., 2014). In particular, the
59 maintenance of colour polymorphism in a population is possible if co-existing colour morphs
60 gain selective advantages in either spatially or temporally heterogeneous environments (Gray
61 and McKinnon, 2007; Svardal et al., 2015). When conditions are unpredictably variable,
62 polymorphic populations may be able to cope better with temporally variable environments

63 than are monomorphic ones (Wennersten and Forsman, 2012; Valverde and Schielzeth,
64 2015). For example, a recent review of 45 studies provided strong evidence that variable
65 (polymorphic) populations and species are less vulnerable to environmental changes and
66 therefore less extinction prone, than are less variable populations and species (Forsman and
67 Wennersten, 2016).

68

69 Climate variability is is one of the most important sources of environmental variation
70 affecting organisms. Importantly, global climate models predict not only general climate
71 warming, but stronger climate fluctuations, and the signature of an increase in the occurrence
72 and severity of climatic extremes is already apparent (IPPC, 2007). From an ecological
73 perspective, the unprecedented severity of such events highlights the pressing need to better
74 understand the role that climate extremes will play in the future (Smith, 2011). Therefore,
75 studies of within-population polymorphism, which potentially reflects relative resistance of
76 populations to environmental changes, and factors affecting this polymorphism in the course
77 of climate change, are of particular importance.

78

79 Heritable colour polymorphism, which usually reflects genetic diversity, renders rich, albeit
80 underutilized, opportunities to investigate and understand evolutionary processes (Svensson,
81 2017), including those associated with global environmental change. In particular, melanin-
82 based colour polymorphism is predicted to be affected by climate change (Roulin, 2014). In
83 ectotherms, dark (melanic) individuals gain advantages over light (pale) individuals in cold
84 climates due to more efficient conversion of radiation to body heat, and this thermal melanism
85 hypothesis has obtained support from numerous latitudinal and altitudinal studies (reviewed
86 by Clusella-Trullas et al., 2007). Therefore, it has been predicted that warming may decrease
87 the advantages of darker, melanic species over light ones and thus lead to decreases in the

88 abundance of dark species as the climate warms (Zeuss et al., 2014). However, studies that
89 have directly explored effects of past climate changes on within-species or within-population
90 polymorphism, in particular by studying temporal trends in melanism in ectothermic
91 organisms, remain scarce (but see Brakefield and de Jong, 2011; Bishop et al., 2016;
92 MacLean et al., 2018).

93

94 Populations of the eruptive leaf beetle, *Chrysomela lapponica*, from the Kola Peninsula,
95 include dark and light colour morphs. This melanism-based polymorphism, like in other
96 beetles (Michie et al., 2011; Brakefield and de Jong 2011), is at least partly heritable: the
97 proportion of dark morphs in the progenies of pairs with one dark parent is twice as high as
98 that from pairs in which both parents are light (Zverev et al., 2018). However, low
99 temperatures during larval development may also lead to an increase in dark morph
100 frequencies due to developmental plasticity (Zverev et al., 2018). This system fits the thermal
101 melanism hypothesis: dark males have a mating advantage over light males, but only when
102 temperatures are low during the mating period in spring (Zverev et al., 2018). Therefore, we
103 suggested that among-year variation in colour morph frequencies, observed in Kola
104 populations of *C. lapponica* (Zvereva et al., 2002), may be driven by among-year variation in
105 weather conditions. Climate warming in this area during the past decades has been especially
106 strong, mostly through increases in mean spring and autumn temperatures (Zvereva et al.,
107 2016; Marshall et al., 2016), and this warming led us to predict gradual temporal declines in
108 dark morph frequencies in *C. lapponica* populations.

109

110 However, factors other than weather conditions can also contribute to among-year variation in
111 morph frequencies. In particular, the intensity and direction of natural selection driving this
112 variation may depend on both morph frequencies in the population and on population density.

113 For example, bird predation on polymorphic prey often depends on colour morph frequencies,
114 because birds learn to find (in the case of cryptic prey) or to avoid (in the case of aposematic
115 prey) the morph which is more frequent in the population, due to faster memorization of
116 frequently encountered colour patterns (Ruxton et al., 2004). In *C. lapponica*, beetles of the
117 two colour morphs are differentially preyed upon by birds at high and low beetle densities
118 (Doktorovová et al., 2019). Density-dependent selective pressure may be also imposed by
119 bottom-up factors due to differential sensitivity of colour morphs to plant defences induced by
120 severe leaf damage at high *C. lapponica* population densities (Zvereva et al., 2002).

121
122 Variation in morph frequencies may be causally linked with population dynamics when there
123 is feedback between the differential survival of morphs and population density. Specifically,
124 selective survival of phenotypes with different fitness traits during different stages of
125 population change may result in self-induced cycles (Chitty, 1960; Krebs, 1978). If a
126 population is polymorphic in terms of coloration, colour may be linked with life-history traits
127 (for example, fecundity), potentially influencing population dynamics (Svensson and Abbott,
128 2005; Ducrest et al., 2008; McKinnon and Pierotti, 2010). The first evidence for Chitty's
129 cycles was found in study of a lizard, *Uta stansburiana* (Sinervo et al., 2000), in which colour
130 morphs are associated with different female reproductive strategies.

131
132 Colour morphs of *C. lapponica* differ in important life history traits. Light females are larger
133 (Zvereva et al., 2002), and have two-fold higher lifetime fecundity than dark females (Zverev
134 et al., 2018). Dark beetles are more susceptible to plant defences induced by previous
135 defoliation than are light beetles (Zvereva et al., 2002). Therefore, we suggested previously
136 that the decrease in frequency of low-fitness (dark) individuals in post-outbreak populations
137 and the accumulation of low-fitness phenotypes at the population peak may create feedbacks

138 contributing to regulation of density fluctuations in *C. lapponica* through changes in
139 population quality (Zvereva et al., 2002). However, these feedbacks explained only a part of
140 the among-year variation in morph frequencies that we observed, and we therefore concluded
141 that effects of colour morph frequencies on density fluctuations in *C. lapponica* likely occur
142 through interactions between intrinsic and extrinsic factors (Zvereva et al., 2002), climate in
143 particular.

144

145 The goal of our current study was to explore the interplay between the phenotypic structure of
146 *C. lapponica* populations, reflected by the percentage of dark (melanic) beetles, changes in
147 environmental conditions (temperature in particular), and leaf beetle population dynamics.
148 Using multiyear (1992–2018) data on multiple populations of *C. lapponica* from the Kola
149 Peninsula, we assessed (1) effects of among-year variation in weather conditions and of
150 gradual climate warming on colour morph frequencies and (2) links between colour morph
151 frequencies and density fluctuations in leaf beetle populations. We predicted that (i) lower
152 spring temperatures would increase dark morph frequencies through the mating advantages of
153 dark males over light males; (ii) climate warming observed during the past 26 years would
154 lead to decreases in dark morph frequencies in leaf beetle populations, (iii) the frequencies of
155 dark morphs would increase in cold summers due to developmental plasticity; and (iv)
156 variations in morph frequencies would be linked with density fluctuations in a feedback
157 fashion due to selective survival of colour morphs on different stages of population
158 fluctuations.

159

160 **2. Materials and methods**

161

162 *2.1. Study area and climate data*

163

164 The study was conducted near the town of Monchegorsk (67°56' N, 32°49' E), located about
165 150 km south of the tree line, which is home to a large nickel–copper smelter. The 12 sites
166 used in this study were in Norway spruce (*Picea abies* (L.) Karst.) forests, 1 to 31 km from
167 the smelter. For location and detailed characteristics of the study sites, consult Zvereva et al.
168 (2016).

169

170 Daily values of temperature (average, minimum and maximum) and precipitation recorded at
171 the meteorological station in Monchegorsk were obtained from the Lapland Biosphere
172 Reserve (1991–2004) and from the web-based archive (www.rp5.ru; 2005–2018). The data
173 were averaged to four values for each climate variable (Table S1) as follows: summer of the
174 preceding year (July and August), autumn of the preceding year (September and October),
175 winter (November of the preceding year to April of current year) and spring of the current
176 year (May and June). These periods each correspond to a specific part of the leaf beetle life
177 cycle (see below). Available pollution data included annual emissions of sulphur dioxide,
178 nickel and copper (Zvereva et al., 2016; and unpublished).

179

180 2.2. Leaf beetle species and host plants

181

182 Our study species, the medium-sized (5–8 mm length) polymorphic leaf beetle *C. lapponica*,
183 is widely distributed in the Palaearctic region and capable of occasionally causing severe
184 defoliation of its host plants, primarily willows and birches. In Fennoscandia, *C. lapponica*
185 feeds on willows, strongly preferring *Salix myrsinifolia*. Beetles have one generation per year.
186 Adults hibernate in soil and start feeding and copulating on host plants soon after leaf flush
187 (from mid May to the first days of June in our study area). Females lay clutches of 35–40

188 eggs on host plant leaves. Larvae feed for about 1 month and pupate on leaves of their host
189 plants at the end of July. Beetles of the next generation emerge in early or mid-August, feed
190 for a couple of weeks, and then dig into the soil for overwintering. Both larvae and adults are
191 chemically defended against natural enemies.

192

193 We sampled beetles for measurements of morph frequencies from different subsets of our
194 study sites during 1992–2005 and again during 2014–2018 (see Table S2 for sample-specific
195 data). In some years we sampled both overwintered beetles and beetles of the next (summer)
196 generation. Overwintered beetles were surveyed in early-mid June when all beetles had left
197 their overwintering sites and started feeding on their host plants (exact sampling dates
198 depended on phenology in a particular year). During the sampling, all bushes of the primary
199 host plant (*S. myrsinifolia*) growing in the study site were searched and all beetles found were
200 either collected or visually assigned to colour morph *in situ* during 1–2 hour sessions.
201 Summer beetles (progenies of overwintered beetles) were collected in late July as pupae from
202 5–10 bushes of *S. myrsinifolia* per site, allowed to hatch, and were assigned to colour morphs
203 in the laboratory. For this study, we did not use any beetles reared under laboratory
204 conditions, and therefore only natural agents of selection could have influenced morph
205 frequencies in our samples.

206

207 *C. lapponica* beetles are aposematically coloured and have an extremely variable pattern,
208 ranging from completely black or metallic to light yellow (Mikhailov, 2001). However, all
209 beetles which we classified by colour morph in the course of this study (6481 individuals)
210 belonged to black-and-red patterned morphs. The shape and size of the black bands and spots
211 on the red elytra of this morph vary considerably, and, as in our previous studies (Zvereva et
212 al., 2002; Zverev et al., 2018; Doktorovová et al., 2019), we divided the beetles into two

213 categories, which we hereafter refer to as the light morph (less than 80% of the elytra area is
214 black) and the dark morph (80% or more of elytra area is black; Fig. 1). For this purpose, we
215 selected 100 individuals of *C. lapponica*, representing all patterns found in our population,
216 photographed them and used Adobe Photoshop CC to measure the proportion of the black
217 area on the elytra, which varied from 50% to 90%. We then created a template showing the
218 most typical colour patterns assigned to either the dark or the light morph according to our
219 threshold (80% black); the template was then used throughout the study to assign beetles to
220 either light or dark morph.

221

222 Beetle densities were estimated in early summer (11 June–5 July; median date 19 June) from
223 1993 to 2018, by 10-min counts of beetles on bushes of all willow species growing in our
224 study sites (Table S2). Each year, we conducted three counts per study site. The counts were
225 performed on days with good weather (no rain, clear sky, slight or no wind), when beetles
226 were active. During these counts, observers walked along a pre-defined path (the same during
227 all observation years) and counted individuals of all leaf beetle species observed along the
228 path on all species of willows. For more details, consult Zvereva et al. (2016).

229

230 2.3. Data analysis

231

232 We identified overall sources of variation in dark morph frequencies (arcsine-square root
233 transformed) by mixed model ANOVA (SAS GLIMMIX procedure; SAS Institute, 2009).

234 This analysis was limited to samples in which morph frequencies were recorded for males and
235 females separately and which contained at least 5 beetles of each sex. In this analysis, sex and
236 time of sampling (spring or summer, i. e. before or after overwintering) were considered as
237 fixed effects, whereas study site and year were treated as random effects. To facilitate

238 accurate F tests of the fixed effects, we adjusted the standard errors and denominator degrees
239 of freedom in this analysis, as well as in all subsequent analyses, by the latest version of the
240 method described by Kenward and Roger (2009). The significance of the random factors in
241 these analyses was evaluated by calculating the likelihood ratio and testing it against the chi-
242 squared distribution (as described in Littell et al., 2006).

243

244 Our analyses of temporal variation took three forms. First, we asked whether the proportion of
245 dark morphs demonstrated systematic change during the observation period. This analysis
246 was restricted to the overwintered beetles, because the data on newly emerged beetles were
247 insufficient for the planned analysis (Table S2). As in the previous analysis, we included
248 samples in which morph frequencies were calculated from at least 5 beetles. The site-specific
249 proportions of dark morphs (pooled by sex and arcsine-square root transformed) for all
250 available years were analyzed using the SAS GLIMMIX procedure. In this analysis, the study
251 site was considered as a random effect and year was considered as a covariate.

252

253 Second, to uncover potential mechanisms underlying the observed trends, we used the
254 GLMSELECT procedure (SAS Institute, 2009) to choose the model with the lowest small-
255 sample-size corrected version of Akaike's information criterion (AICc) associating yearly
256 variation in the frequency of the dark morph with climate and pollution data. Because there is
257 only a single value of climate and pollution variables per year, we used the average frequency
258 of the dark morph among sites (pooled across sexes) as the dependent variable (arsine square-
259 root transformed prior the analysis). Independent variables that could enter the model
260 included previous-year beetle density (N_{t-1}), 16 climate variables (four per each season), and
261 the amounts of aerial emissions in the current or previous year.

262

263 Third, we asked whether the proportions of dark morphs in male and female beetles showed
264 similar responses to climate. We ran a general linear model (SAS GLM) with the average
265 frequency of the dark morph (pooled among sites) as the dependent variable, beetle sex as a
266 fixed effect, and minimum spring temperature as a covariate. Minimum spring temperature
267 was identified by the GLMSELECT analysis (above) as the strongest (and only significant)
268 predictor of temporal change in dark morph frequencies.

269

270 To explore potential effects of current morph frequencies on subsequent population dynamics
271 (Chitty's cycles), we investigated whether the density of overwintered beetles in the following
272 year was a function of current-year morph frequency. We restricted this analysis to the period
273 1993–2003, when strong density fluctuations were recorded in several sites and this effect
274 could therefore be expected. During the later period of the study (2014–2018), beetle
275 densities were generally low and did not vary substantially either in space or in time. For this
276 analysis, we calculated per capita rates of increase as $\ln(N_{t+1}/N_t)$ for each pair of years in the
277 site-specific time series and asked (SAS GLIMMIX procedure) whether dark morph
278 frequency in year t (covariate) influenced per capita rate of change between years t and $t+1$;
279 site and year were treated as random effects. Additionally, we calculated Pearson linear
280 correlation coefficients between dark morph frequency, study year, temperature and per capita
281 rate of density change between years, and compared dark morph frequencies between the
282 subsequent leaf beetle generations, as well as between beetles collected before and after
283 overwintering, with a paired t -test.

284

285 **3. Results**

286

287 *3.1. Sources of variation in dark morph frequencies*

288

289 Beetle sex, generation and study year significantly affected dark morph frequencies, whereas
290 morph frequency did not vary among study sites (Table 1). The proportion of dark morphs
291 was 2.7 times higher among males than among females (estimated marginal means \pm S.E.:
292 $38.2 \pm 5.5\%$ and $14.4 \pm 3.9\%$, respectively) and 3.6 times higher among overwintered beetles
293 (collected in spring) than among beetles of the next (summer) generation ($42.2 \pm 5.7\%$ and
294 $11.7 \pm 3.6\%$, respectively; Fig. 2). Overwintering had similar effect on dark morph
295 frequencies in males and females (Table 1).

296

297 The frequencies of dark morphs in overwintered beetles declined significantly over the course
298 of the study (Fig. 3; $F_{1,52} = 15.1$, $P = 0.0003$), and this decline was consistent across study sites
299 (interaction term: $\chi^2 = 0.00$, $df = 1$, $P = 0.99$). Like in the previous analysis (Table 1), we
300 found no variation among study sites ($\chi^2 = 0.10$, $df = 1$, $P = 0.75$).

301

302 *3.2. Effects of climate on dark morph frequencies*

303

304 Model selection procedures identified the daily minimum spring (May–June) temperature as
305 the single best predictor for yearly variation in the frequency of the dark morph in
306 overwintered beetles ($AICc = -28.3$, $R^2 = 0.28$). Other climatic characteristics, annual
307 emissions of pollutants and previous-year population density did not enter the model. Further
308 analysis demonstrated that the decrease in dark morph frequencies with an increase in
309 minimum spring temperature (Fig. 4) was significant and similar for both males and females
310 (Table 2).

311

312 In beetles from the summer generation, dark morph frequencies decreased with an increase in
313 average spring temperatures ($r = -0.73$, $n = 7$ years, $P = 0.06$; Fig. 5a), but were not related to

314 mean mid-summer temperatures during the larval development, i.e. in July ($r = 0.31$, $n = 7$
315 years, $P = 0.49$; Fig. 5b).

316

317 *3.3. Dark morph frequencies and density fluctuations*

318

319 The per capita rate of change in leaf beetle population densities between years t and $t+1$ in the
320 monitored study sites was not explained by dark morph frequency in year t (Fig. 6; $F_{1,25} =$
321 0.47 , $P = 0.50$). Addition of the quadratic term did not improve the explanatory power of the
322 model (data not shown).

323

324 **4. Discussion**

325

326 *4.1. Climate effects on morph frequencies*

327

328 We observed a nearly two-fold decrease in dark morph frequencies of *C. lapponica* in the
329 Kola populations between 1992 and 2018. Analyses of potential drivers of this change
330 supported our prediction of the role of climate warming, in particular the 2.5°C increase in
331 spring temperatures in the study area during the observation period, in dark morph declines.
332 This finding is consistent with the differential effects of spring ambient temperatures on dark
333 and light colour morphs of *C. lapponica* reported previously. Dark males gain mating
334 advantages on cold days (6–14°C) during the mating period (from late May to mid-June) over
335 light males, mostly due to differences in locomotory activity; however, these advantages are
336 lost on warmer days (Zverev et al., 2018). The differences in beetle activity were explained by
337 higher heating rates in dark morph beetles than in light morph beetles, in line with the thermal
338 melanism hypothesis (Crusella-Trullas et al., 2007). Thus, the negative correlation between

339 frequencies of dark morphs in the summer generation and spring temperatures may be
340 explained by mating advantages that males of the parental generation gained during cold
341 springs, because dark coloration is at least partly heritable (Zverev et al., 2018) and therefore
342 higher mating success of dark morph males would increase the frequency of this morph in the
343 next generation. When spring temperatures increase, dark males lose their mating advantage
344 over light males, which leads to decrease in the proportion of dark beetles in the next
345 generation. However, we cannot rule out a role for phenotypic plasticity in explaining the
346 declines in dark morph frequency (see below).

347

348 Mating advantage is not the only mechanism by which dark morphs of ectotherms can be
349 favoured in cold conditions. In some systems, melanic individuals better survive the winter
350 than their light conspecifics (Su et al., 2009; Michie et al., 2011). The substantial increase in
351 the proportion of dark morphs in the populations of *C. lapponica* after overwintering,
352 compared to the same populations in the previous autumn (Fig. 2) provides indirect support
353 for this suggestion. However, our model selection provided no evidence that the proportion of
354 dark morphs among overwintered beetles is related to winter temperatures. On the other hand,
355 dark beetles may obtain survival advantages in spring, when they become active and therefore
356 more sensitive to changing temperatures. In our study area, the minimum temperatures in
357 May, when beetles leave their overwintering habitats, may occasionally drop as low as -10°C.
358 Under these conditions, dark beetles may have a survival advantage over light beetles due to
359 better absorption of irradiation from the sun during periods of frost. The latter suggestion is
360 supported by a negative correlation between dark morph frequencies and minimum spring
361 temperatures.

362

363 Interestingly, the proportion of dark morphs decreased during summers (Fig. 2), indicating
364 that thermal melanism may be disadvantageous at that time, as suggested for other beetle
365 species (Su et al., 2009; Michie et al., 2011). In our study, selection against dark morphs
366 could have occurred only during larval development or during reproduction of the parental
367 generation, because we recorded morph frequencies in summer beetles immediately after
368 hatching. Temperature during development can influence colour morph frequencies due to
369 phenotypic plasticity (Kingsolver and Wiernasz, 1991; West-Eberhard, 2003), and rearing
370 larvae of *C. lapponica* in climatic chambers at temperatures below 15°C considerably
371 increases the proportion of dark morphs among hatching beetles (Zverev et al., 2018).
372 However, analysis of field-collected beetles of the summer beetles did not find any effect of
373 temperatures during larval development on morph frequencies. Temperatures during larval
374 development in our study area (mean multiyear temperature in July is 12.8°C:
375 <https://en.climate-data.org>) may be too high to induce this phenotypic effect, which is
376 expressed most strongly at 10 °C (Zverev et al., 2018). Importantly, dark morph frequencies
377 in beetles that emerged in late summer was much lower than those of their parental generation
378 (Fig. 2), and we suggest that this decrease was due to the two-fold higher fecundity of light
379 morph females across temperature ranges from 10 to 25 °C (Zverev et al., 2018).
380
381 In line with our previous studies of *C. lapponica* (Zvereva et al., 2002; Zverev et al., 2018),
382 the proportion of dark morphs was significantly higher in males than in females. The greater
383 proportion of dark morphs in males may be adaptive because they become active earlier in the
384 season, run faster, and mate more frequently in cold days when compared to the light males.
385 In contrast, dark and light morph females show similar movement and mating activities on
386 both cold and warm days (Zverev et al., 2018). These differences between sexes may be at
387 least partly explained by their mating strategies. In leaf beetles, females do not search for

388 mates but spend most of their time feeding, whereas males actively search for receptive
389 females (Nahrung and Allen, 2004; Dick et al., 2013). Therefore, dark females do not obtain
390 any mating advantages at low temperatures, whereas males may be largely responsible for
391 maintenance of dark morph frequencies in populations due to thermal melanism.

392

393 The production of melanin is energetically costly, which results in trade-offs between
394 melanisation rate and fitness-related traits (Roff and Fairbairn, 2013, and references therein).
395 In *C. lapponica*, light females are larger and twice as fecund as dark females (Zverev et al.,
396 2018), suggesting that there may be a physiological cost of melanin production and deposition
397 paid by dark morphs. Such a physiological cost may also explain why dark morph beetles are
398 more susceptible to plant chemical defences (Zvereva et al., 2002). Due to these costs, loss of
399 advantages by dark morphs would lead to disadvantage and consequently decline in dark
400 morph frequencies under warming conditions. VAR: There costs may explain [OR: may be
401 responsible for] the observed decline in dark morph frequencies, because advantages of dark
402 morphs decrease with climate warming.

403

404 Overall, we conclude that the decline in melanic morph frequencies in subarctic populations
405 of *C. lapponica* during the past 26 years is best explained by the increase in spring
406 temperatures observed during this period, and the concomitant loss of thermoregulatory
407 advantages by melanic individuals. While some other animal populations have shown similar
408 temporal shifts in coloration during past decades (Brakefield and de Jong, 2011; Özgo and
409 Schilthuizen, 2012; MacLean et al., 2018), our study is the first to directly link shifts in
410 phenotypic population structure with local patterns of climate warming and to provide a
411 mechanistic explanation for the effect.

412

413 4.2. Factors co-occurring with climate change

414

415 It remains possible that other factors may have contributed to the observed declines in dark
416 morph frequencies. In particular, our study area has experienced a five-fold decrease in aerial
417 pollution emissions from the nickel-copper smelter in Monchegorsk. This emission decline
418 has resulted in declines in population densities of *C. lapponica* associated with a nearly three-
419 fold increase in leaf beetle mortality from natural enemies during the past two decades
420 (Zvereva et al., 2016). Pollution favours melanic morphs of some insects, and declines in
421 pollution may explain the observed decreases in frequencies of dark morphs, most famously
422 the decrease in melanism in peppered moths, *Biston betularia* (Majerus, 1998; Saccheri et al.,
423 2008). However, among-site variation in dark morph frequency in *C. lapponica* populations
424 was not associated with variation in pollution levels, which would be expected if pollution
425 favours melanic individuals of our leaf beetle. Furthermore, annual amounts of emissions did
426 not enter our model explaining temporal trends in morph frequencies. Taken together, these
427 two results suggest that pollution decline was unlikely to contribute directly to the observed
428 decrease in dark morph frequencies in *C. lapponica* populations.

429

430 Different morphs of polymorphic species may obtain selective advantages at either high or
431 low population densities (Sinervo et al., 2000; Zvereva et al., 2002; Doctorovová et al., 2019).
432 The question then arises whether the overall declines in *C. lapponica* population densities
433 observed in our study area (Zvereva et al., 2016) may have caused the temporal declines in
434 dark morph frequencies during the observation period. However, our analysis revealed no
435 relationship between previous-year leaf beetle population density and current-year dark
436 morph frequency, suggesting that density declines are not driving declines in the dark morphs.
437 Furthermore, dark morphs of *C. lapponica* are more sensitive to host plant defences induced

438 at high population densities than are light morphs (Zvereva et al., 2002). Therefore, declines
439 in leaf beetle density should have actually favoured dark morphs because of higher host plant
440 quality, the opposite of the pattern that we observed. Similarly, under bird predation pressure,
441 dark morphs of *C. lapponica* have survival advantages over light morphs, but only at low
442 population densities (Doctorovová et al., 2019); this should result in an increase in dark
443 morph frequencies as densities decline, the opposite of our observations. Thus, the density-
444 dependent factors of plant quality and bird predation seem unlikely to have contributed to the
445 observed decline in the proportion of dark morphs in leaf beetle populations. We conclude
446 that the temporal trend in morph frequencies is independent of the overall decline in *C.*
447 *lapponica* population densities, and that these two co-occurring processes are explained by
448 different factors: leaf beetle densities declined due to increases in natural enemy pressure
449 resulting from decreases in pollution (Zvereva et al., 2016), while dark morph frequencies
450 decreased due to climate warming.

451

452 *4.3. Colour morph frequencies and population dynamics*

453

454 Variation in colour morph frequencies may affect population dynamics, when colour morphs
455 differ in their fitness traits and in their responses to environmental factors and thereby obtain
456 selective advantages at different stages of the population cycle (Chitty, 1960; Sinervo et al.,
457 2000). However, the hypothesis that density changes may be mediated by natural selection
458 operating on genetic composition of the population (through selective survival of phenotypes)
459 has received surprisingly little support (but see Sinervo et al., 2000; Sinclair et al., 2003).
460 Importantly, our data fit the three requirements (coined by Saccheri and Hanski, 2006) that
461 should be met in order to adequately test the Chitty hypothesis. First, we measured leaf beetle
462 densities in spatially and temporally replicated samples, because we studied several

463 asynchronously fluctuating populations. Second, we simultaneously explored multiple
464 ecological factors affecting population density (pollution, climate, past density). Third, two
465 colour morphs of *C. lapponica* differ in several life history traits important for natural
466 selection, such as mating activity, fecundity, responses to plant defences, and strength of an
467 aposematic signal for avian predators (Zvereva et al., 2002, 2016; Zverev et al., 2018;
468 Doctorovová et al., 2019).

469

470 Based on previous studies, we predicted that fluctuations in population densities in *C.*
471 *lapponica* would be linked with variations in colour morphs frequencies. For example, warm
472 springs should increase the proportion of the light morph in *C. lapponica* populations and
473 could lead to density increases due to the higher fecundity of light females (Zverev et al.,
474 2018). Conversely, accumulation of dark morphs due to low spring and summer temperatures
475 could lead to density decline due to the lower fecundity of dark females (Zverev et al., 2018)
476 and the higher mortality of dark beetles on plants with anti-herbivore defences induced by
477 severe damage associated with high *C. lapponica* densities (Zvereva et al., 2002). Our
478 previous study, based on a shorter observation period (8 years), suggested that changes in
479 frequencies of colour morphs differing in fitness may create feedbacks contributing to
480 population fluctuations in *C. lapponica* (Zvereva et al. 2002). However, our current study did
481 not confirm this suggestion. In spite of the length of the observation period (26 years) and
482 substantial changes in morph frequencies and population densities, there was no relationship
483 between these two population characteristics: morph frequencies did not influence subsequent
484 year population densities, and current population densities did not affect subsequent year
485 morph frequencies. We conclude that any potential effects of intrinsic factors on population
486 dynamics were overridden by the effects of climate on morph frequencies through the action
487 of thermal melanism.

488

489 4.4. Potential consequences of changes in morph frequencies

490

491 The two-fold decrease that we observed in dark morph frequencies during the past 26 years
492 may continue as the climate warms. This may lead to the complete elimination of dark
493 morphs from *C. lapponica* populations, not only due to the loss of their fitness advantages,
494 but also due to overheating, which can occur at high temperatures in many dark (melanic)
495 ectotherms (Crusella-Trullas et al., 2007). This suggestion is in line with the absence of dark
496 morphs in the warmer climates of Central Europe, where *C. lapponica* populations consist
497 exclusively of light-coloured beetles (Gross et al., 2004).

498

499 The persistence of dark (melanic) morphs should be advantageous for populations inhabiting
500 regions with unpredictably fluctuating cold climates, because it potentially allows a subset of
501 the population to perform successfully under low temperatures. Therefore, any continued
502 decrease in the frequency of dark morphs could make beetle populations more vulnerable to
503 low-temperature extremes, which still occur despite general climate warming (IPCC, 2007).
504 We suggest that a decrease in melanic morph frequencies with climate warming, and
505 subsequent vulnerability to climatic extremes, may occur in multiple ectothermic organisms.

506

507 Importantly, dark morph frequencies in the Kola populations of *C. lapponica* correlate
508 strongly with the Shannon diversity index for variation in colour pattern ($r = 0.82$: Zvereva et
509 al., 2002). Therefore, the decrease in dark morph frequencies reported here indicates an
510 overall decrease in within-population phenotypic diversity and, potentially, in underlying
511 genetic diversity, because colour polymorphism in *C. lapponica* is at least partly genetically
512 based (Zverev et al., 2018). As discussed above, higher levels of among-individual

513 phenotypic and genetic variation make populations and species less vulnerable to
514 environmental changes and therefore less prone to extinction, compared with less variable
515 populations and species (Forsman and Wennersten, 2016). Consequently, loss of variability
516 will result in loss of benefits provided by high among-individual diversity (Forsman et al.,
517 2008; Hughes et al., 2008). Loss of diversity is one of the major threats of global change
518 (Scheffers et al., 2016), and our study demonstrates that adverse effects of environmental
519 change on within-population diversity are already occurring in subarctic areas.

520

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522

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530

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681

682 **Table 1** Sources of variation in dark morph frequencies (SAS GLIMMIX procedure)

Effect type	Source of variation	Test statistics	<i>P</i>
Fixed	Sex	$F_{1, 96.6} = 86.64$	<0.0001
	Time of sampling (before or after overwintering)	$F_{1, 116.6} = 92.29$	<0.0001
	Sex × Time of sampling	$F_{1, 96.6} = 0.93$	0.37
Random	Site	$\chi^2_1 = 0.53$	0.23
	Year	$\chi^2_1 = 21.78$	<0.0001

683

684

685 **Table 2** Effects of minimum spring temperature on dark morph frequencies in overwintered
686 males and females of *Chrysomela lapponica* (SAS GLM procedure, type III sum of squares)

Source of variation	Test statistics	<i>P</i>
Minimum spring temperature	$F_{1,15} = 6.82$	0.020
Sex	$F_{1,15} = 9.17$	0.008
Minimum spring temperature \times Sex	$F_{1,15} = 0.84$	0.374

687

688

689 **Figure captions**

690

691 Fig. 1. Examples of colour morphs from the Kola population of *Chrysomela lapponica*
692 presented as photo of the right elytra. Upper row – light morphs, lower row – dark
693 morphs.

694 Fig. 2. Proportions of dark morph beetles of *Chrysomela lapponica* in spring (after
695 overwintering) and in summers of the previous and current seasons (before
696 overwintering) in study years for which all three values are available. Females and
697 males are combined. Means (+SE) are each based on data from the same 6 study sites;
698 different letters indicate significant ($P < 0.05$) differences within each group (paired t -
699 test).

700 Fig. 3. Temporal trend in the frequencies of dark morphs in Kola populations of the leaf
701 beetle *Chrysomela lapponica* recorded in spring (after overwintering). Each point refers
702 to one study site by year combination; males and females are combined.

703 Fig. 4. Relationship between dark morphs frequencies in Kola populations of the leaf beetle
704 *Chrysomela lapponica* recorded in spring (after overwintering) and the average daily
705 minimum spring (May-June) temperatures. Each point refers to one study site by year
706 combination; males and females are combined.

707 Fig. 5. Relationship between dark morphs frequencies in Kola populations of the leaf beetle
708 *Chrysomela lapponica* recorded in summer (end of July) and (a) mean spring (May-
709 June) and (b) mean mid-summer (July) temperatures. Each point refers to one study site
710 by year combination; males and females are combined.

711 Fig. 6. Relationship between per capita rate of change in leaf beetle, *Chrysomela lapponica*,
712 population density between years t and $t+1$ and frequencies of dark morphs in the

713 population during year t . Data collected from 1993-2003; each point refers to one study
714 site by year combination; males and females are combined.
715

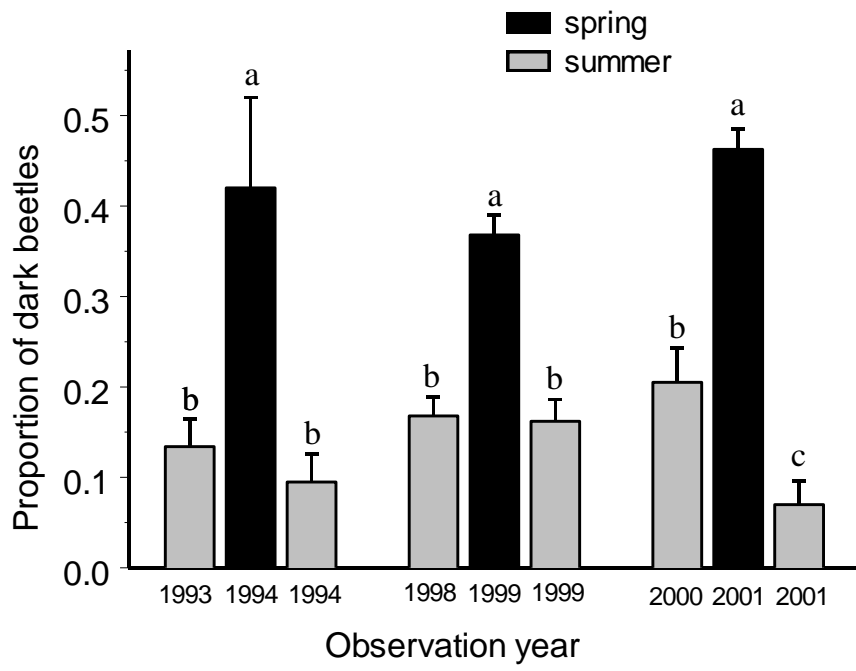


716

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718 Fig. 1

719



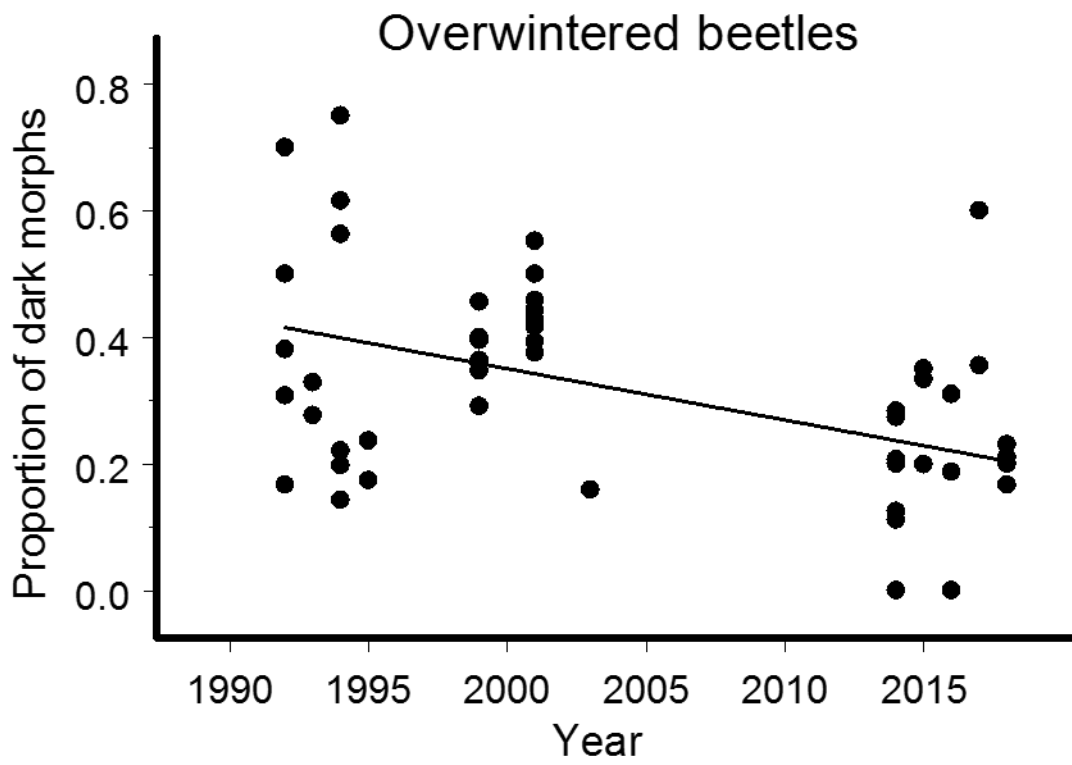
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722 Fig. 2

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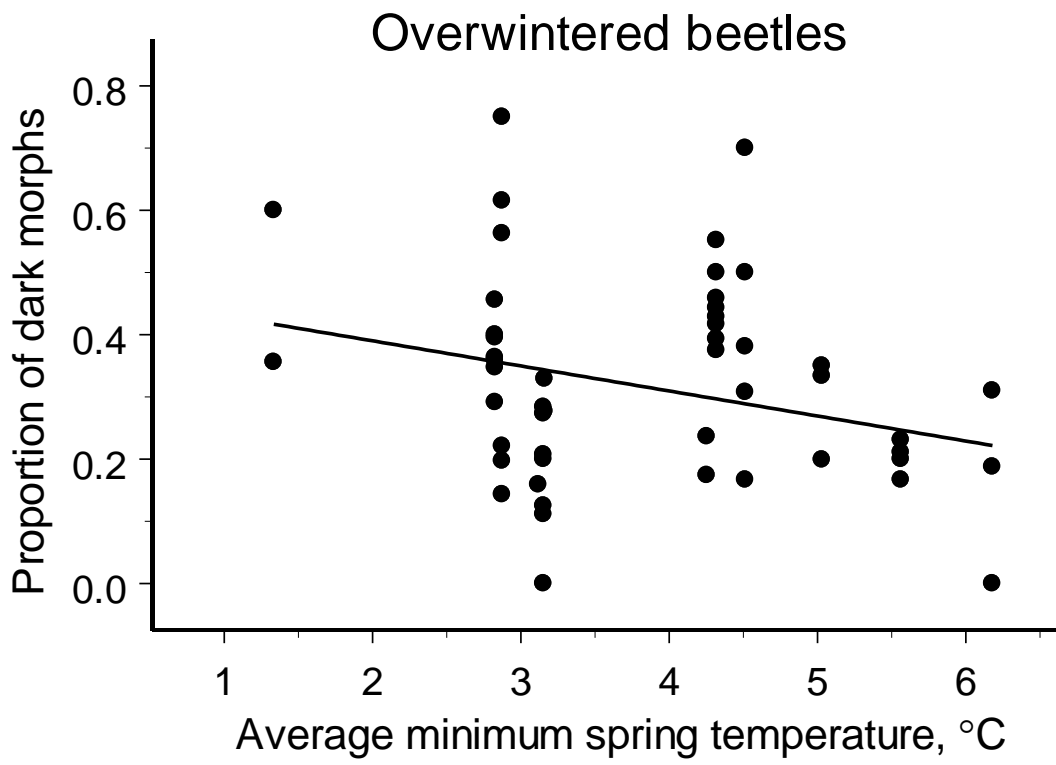
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727 Fig. 3

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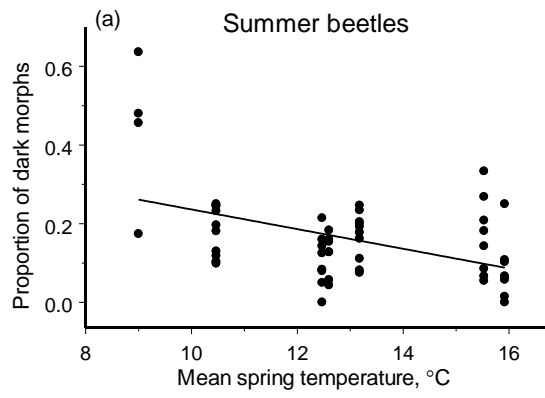
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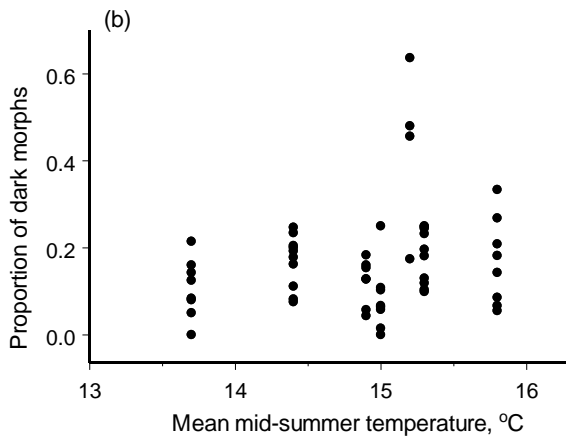
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732 Fig. 4

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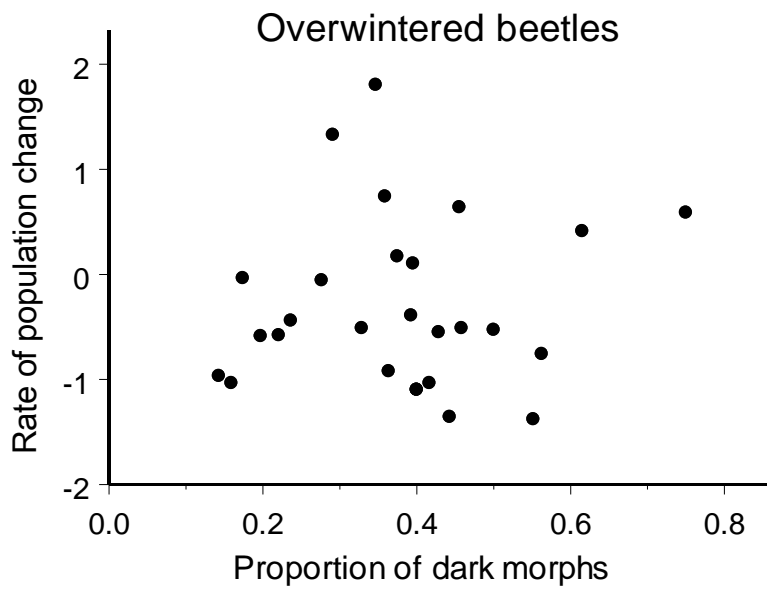
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736 Fig. 5

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738

739 Fig. 6