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Running title: Insect outbreaks, herbivory and climate change

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Abstract

With warming climate many species are predicted to shift their distributions toward the poles. However, climate change models developed to predict species distributions do not always incorporate interactions between them. The northerly shift of the boreal forest and associated dwarf shrub communities will be directly affected by warming. But warming will also indirectly affect plant communities via impacts on the intensity and frequency of associated insect outbreaks. We present a general model exploring plant host herbivory in response to the balance between insect crowding, host consumption and climate. We examined how these factors dictate the feeding preference of *Epirrita autumnata* larvae during an outbreak on dwarf shrub vegetation in Sub-arctic Fennoscandia. Data were collected from an outdoor experiment investigating future climate change scenarios (elevated CO_2 and temperature) on the dwarf shrub community that included deciduous (*Vaccinium myrtillus*) and evergreen species (*V. vitis-idaea* and *Empetrum nigrum*). We observed that larval crowding was independent of treatment under outbreak conditions. We also tested and confirmed model predictions that larvae would prefer monospecific stands of either deciduous shrubs or its evergreen competitors. For current climate conditions, larvae had a preference to consume more deciduous shrubs in mixed stands. However, at elevated temperature bilberry consumption and herbivore pressure was lower, particularly in mixed stands. Our results show that during future warming, *E. autumnata* herbivory could promote the success of thermophile deciduous species and possible northward migration. Insect behaviour and preferences should therefore be considered when predicting future vegetation movements responding to warming.

1. Keywords: Climate change; Gompertz; herbivore pressure; host plant preference; insect outbreaks; Sub-arctic.Introduction

Spatial bioclimatic models predict and some studies already demonstrate range expansion towards the poles and higher elevations of thermophile vegetation under climate change scenarios (Lewis, 2006; Post *et al.*, 2009; Callaghan *et al.*, 2013). However, this depends on whether the ability of species to disperse matches the displacement of corresponding climate envelopes. At the same time these models are constrained by the absence of attention to ecological interactions (Araújo & Luoto, 2007; Berg *et al.*, 2010; Van der Putten *et al.*, 2010. In northern latitude forests, the success of a plant species may be strongly coupled to herbivory, particularly during outbreaks of forest defoliating insects and bark beetles (Karlsen *et al.*, 2013). These, together with the direct effects of climate on plants will be highly relevant to consider when predicting effects of a changing climate on boreal forest ecosystems (Niemelä *et al.*, 2001; Hicke *et al.*, 2012). Responses to herbivory and climate may include changes in plant community structure and biomass (Olofsson et al., 2009) and range (Van Bogaert *et al.*, 2009).

Host plant preference by herbivores is particularly important at vegetation boundaries (Janz & Nylin, 1997). Climate change factors (including temperature and CO_2) and herbivory itself directly influence plant chemistry and defences, dictating subsequent host preference of the herbivore (Wilf *et al.*, 2001; Haukioja, 2005). A host plant species targeted by a particular herbivore can be competitively disadvantaged and must balance resources between herbivore and plant competition (Agrawal *et al.*, 2006). However, this balance will be influenced by the intensity of herbivory, which will also be modulated by climate (Andrew & Hughes, 2007; Post *et al.*, 2009).

It is generally predicted that the rate of herbivory may intensify with future warming (Tylianakis *et al.*, 2008). However, Barrio *et al.* (2016) investigated how future warming could influence herbivores and herbivory of tundra plants by the Arctic moth (*Gynaephora groenlandica*) in the Yukon, Canada. They showed that the performance of insects themselves was compromised by warming and that the insects also shifted to consuming faster growing plants high in nitrogen. Further, the insect's typically preferred host plant species (*Salix arctica*) also responded

66 negatively to warming. Hence predicting the effects of warming is in many cases a complex, far from trivial task.

67

68 During outbreak events in forested areas, it is hypothesized that herbivore-plant interactions and impacts will intensify with ongoing climate

69 changes, leading in some cases to more or less permanent shifts in understory communities (Tenow, 1972; Jepsen *et al.*, 2013; Karlsen *et al.*,

70 2013). This study addresses two central questions that will help us understand how the impacts of current herbivore outbreaks and outbreaks of

71 the future will affect plant communities and vegetation boundaries during climate warming and at elevated CO_2. We ask firstly, how does host

72 choice affect herbivory during an outbreak? Secondly, will future climatic changes affect herbivore pressure (i.e., as in density of larvae per

73 percent cover of a species)? To examine these questions, we investigated how future global climate change factors will affect consumption rates

74 during an outbreak of the autumnal moth *Epirrita autumnata* (Borkhausen, Lepidoptera: Geometridae) by using a general model of larval

75 herbivory validated from experimental simulations of expected future changes in temperature and atmospheric CO_2 concentrations. In Sub-arctic

76 Fennoscandia, populations of such forest defoliating insect species sometimes grow to outbreak densities and when their host trees are defoliated

77 they search for food at ground level on dwarf shrubs communities (Tenow, 1972). Here we introduce a simple and general mechanistic mixed

78 model combining climate-dependent host plant choice and consumption. This model can be applied to any insect that shows outbreak dynamics

79 with larval herbivory and limited larval dispersal. Using unique field collected data we are able to test its validity and predict shifts in herbivory

80 among species. Data were collected on *E. autumnata* larval densities during an outbreak, and by assessing the impacts on plants in experimental

81 plots subjected to ambient and expected future elevated CO_2 and temperature treatments in Sub-arctic Sweden. The host preference model would

82 predict shifts in feeding choice in mixed shrub plots. The herbivory (consumption) component defines a nonlinear decreasing function defining a

83 balance between individual consumption and larval crowding.

84

2. Material and methods

85

86 We developed a model based on the hypothesis that future climate change scenarios (including elevated CO_2 and temperature) will influence host

87 preference of an insect herbivore at high densities through intraspecific competition (i.e., larval crowding and consumption).

2.1. Host preference in relation to larval crowding rates

88

89 57% of Lepidoptera, among them *E. autumnata*, are polyphagous (Zalucki *et al.*, 2002) and hence, potentially able to feed on different plant

90 species. Late instar larvae of many forest Lepidoptera have been shown to demonstrate host preference of an insect herbivore to be strongly

91 linked to limited, free-moving late instar larval dispersal, as opposed to passive ballooning in neonate larvae (Ward *et al.*, 1990; Carrière, 1992;

92 Robinson & Raffa, 1997). For *E. autumnata*, there is evidence of limited dispersal in late instars (Tanhuanpää *et al.*, 2000). Here our definition of

93 limited dispersal is of the order of 5 meters given the small temporal and spatial scales associated with starving late instar larval movement in the

94 experimental system. Hence, in the model, larvae aggregate within or avoid patches with a certain cover of a plant species. Preference for a host

95 plant is defined as the rate at which larvae move to forage (i.e., crowd) or away from a specific location with a certain host plant composition.

96 We surveyed vegetation at two consecutive survey times. L_1 and L_2 represent counts of larvae at times 1 (initial time) and 2 respectively

97 (immediately before pupation, see below for data collection). As larval population movement takes place in continuous time, larvae at the site

98 were expected to crowd (i.e., aggregate in a patch) according to an exponential expression with an intrinsic growth rate (Lombaert *et al.*, 2006)

99 $r=a+bR$.

100

101 Accordingly, $\lambda=e^r=L_2/L_1$ is the finite crowding rate of larvae at the site. R is the host percent cover in the site. a is a parameter describing natural

102 crowding rate in the absence of the host, and b is the rate at which crowding changes with host cover, although other coefficients can be added to

103   account for the dependence on environmental variables (see *Statistical analysis* below). Thus, *r>0* and *r<0* denote crowding or avoidance of

104   other larvae, respectively, while *b>0* and *b<0* point towards preference for, or rejection of the host, respectively.

105

106   If two plant host species *x* and *y* coexist, the crowding rates of their consumers will be $r_x=a_x+b_xR_x$ and $r_y=a_y+b_yR_y$, respectively. If their

107   percentage covers are complementary (that is, $R_y=100-R_x$), several preference responses are possible:

108   1. If there is preference towards one plant species and rejection towards the other ($b_x<0<b_y$ or $b_x>0>b_y$), preference is given to the host

109   providing the higher *r*, independently of its cover. In an illustration depicting crowding rate *r* as a function of the resource R_x, the crowding rates

110   for both hosts will not cross.

111   2. If any of the two scenarios, $b_x,b_y>0$ or $b_x,b_y<0$, is true, then host preference is defined by the point where both crowding rate responses

112   cross in that graph. Crowding will avoid mixed stands and overall preference will be described by a *v*-shaped relationship. In the first scenario,

113   host preference will shift from *y* to *x* as *x* cover increases (Fig. 1a). In the second scenario preference will shift from *x* to *y*. Equating both

114   crowding rates, we obtain the critical breakpoint defining shifting preference between species *x* and *y*:

115        $$p_{xc} = \frac{a_y + 100b_y - a_x}{b_x + b_y}$$

116   However, if *r<0* at any range of host densities, larvae will move towards other sites which present a cover that satisfies crowding conditions.

117   If $b_x,b_y>0$, the constraint *r>0* will determine that susceptible sites will be those with $R_x>-a_x/b_x$ and $R_x>-a_y/b_y-100$.

118

119   **2.2.A Gompertz model of herbivory**

120   Many biological interactions have been described by density-dependent, Gompertz growth dynamics. In population ecology, studies with a

121   mechanistic basis are rare (Geritz & Kisdy, 2004), but Gompertz growth has also been used to describe the dynamics of insect outbreaks (Dennis

122   & Taper, 1994; Karban & de Valpine, 2010), and only once as a model of resource depletion in insect outbreak systems (Økland & Bjørnstad,

123   2006). In both cases Gompertz dynamics are derived and tested from statistical rather than mechanistic assumptions.

124

125   Gompertz growth is generally defined by a double-exponential equation. Specifically, for Gompertz decay, the equation takes the form

126        $$X_t = X_1 exp\big(g(1 - e^{ht})\big) \qquad (1)$$

127   where X_i is a state variable at time *i, t* is the time lapse starting from time *1,* and *g<0; h>0* or *g>0;h<0* are parameters of the equation.

128

129   In this section, to discern the role of consumption versus larval crowding on the defoliation of host plants during an outbreak, we derive a

130   mechanistic model of herbivory for Gompertz decay in resources that accounts for the observed patterns in resource consumption by *E.*

131   *autumnata* larvae, but can be generalized to other herbivorous insects. The model is a 2D (resource and larvae) differential equation autonomous

132   system:

133        $$\frac{dR_t}{dt} = -kL_tR_t; \frac{dL_t}{dt} = rL_t \qquad (2)$$

134   where *k>0* represents the consumption rate per larva (see *Calculating consumption rates* for further development). *R* and *L* are resource and

135   larval abundance (as defined in the previous subsection), *r* stands for the crowding rate which indicates host preference and depends on the initial

136   plant cover, as calculated in the previous section, and environmental factors (see *Statistical analysis* below). Integrating the second equation in

137   system (2) and separating variables, the system is integrated into:

138        $$R_t = R_1 exp(-k(e^{rt} - 1)L_1/r) \qquad (3)$$

139   Therefore, we recover Eq. 1 (*aka* the Gompertz equation) for the resource dynamics.

140

2.3. Calculating consumption rates

To calculate consumption rates, we first consider herbivore pressure at a certain time as $P_t=L_t/R_t$, measured in this study as insects per percent

host cover at time t. Using Eqs. 1 and 3, and taking logarithms, the resulting growth rate in herbivore pressure over the sampling interval time is:

$$ln(P_t/P_1) = k(e^{rt} - 1)\,L_1/r - rt \qquad (4)$$

Using an arbitrary time scale corresponding to the sampling lapse, $t=1$, the realized consumption rates are calculated as:

$$k = \frac{r(ln(P_2/P_1)+r)}{L_1(e^r-1)} \qquad (5)$$

Three specific scenarios arise from these equations:

(1) In the absence of larval movement, $r=0$, $lim_{r\to 0}\,k = ln(P_2/P_1)/L_1$, and Eq. 4 becomes $ln(P_2/P_1) =kL_1$.

(2) In the absence of consumption, $k=0$, therefore Eq. 4 becomes $ln(P_2/P_1) = -r$.

(3) In conditions of optimal behaviour, larval populations migrate to minimize competition and maximize resource availability ($A=1/P$) along

time. In that case, no resource reduction takes place (i.e. $ln(P_2/P_1) =0$). Hence, optimal consumption is given by:

$$k_c = \frac{r^2}{L_1(e^r-1)} \qquad (6)$$

where k_c is an optimal consumption rate in that migration and consumption balance each other and resource availability is kept constant through

time (Fig. 1b). Negative differences between the realized consumption rates and optimal ones due to crowding or feeding preference indicate

whether overall larval consumption in the patch is suboptimal (i.e., below that necessary to balance crowding, so $k-k_c<0$) or superoptimal ($k-$

$k_c>0$), pointing towards reductions, and increases in herbivore pressure, respectively. Therefore, Eq. 5 shows that variations in herbivore pressure

can be ascribed to crowding, which in turn reflects differences in host composition and environmental factors, such as temperature and CO_2.

158

The Gompertz model can be used to calculate consumption and immigration (crowding) rates based on the host preference r by herbivore larval

populations derived from the previous model. In communities composed of different potential hosts, the combined host preference-Gompertz

model predicts: 1) shifts in crowding rates according to the relative cover of each host, and 2) calculation of realized consumption rates following

Eq. 5. However, the model itself can encompass situations in all the three specific scenarios above (i.e., no preference and/or no consumption).

Hence, its generality makes it suitable for any situation in which a short-dispersal herbivore can feed on one or two competing species, including

lack of interaction between the plants and the insect or lack of limited larval dispersal.

165

2.4. Study site and data collection

Data were collected during an outbreak of *Epirrita autumnata* in 2004 at Abisko, Sweden (68.35° N, 18.82° E, 360 m a.s.l., well below the

treeline of 500-600 m a.s.l.). The larvae hatch in spring at the time of *Betula pubescens* var. *pumila* (L.) Govaerts (mountain birch, their main

host) bud burst and forage for approximately one month on the mountain birch (Tenow, 1972). When the birch leaves have been depleted in

outbreak years, larvae search for other food sources by descending to the ground to feed on shrub vegetation before pupating (Tenow *et al.*,

2004). The site, with a Sub-arctic montane climate, was based in a mountain birch forest with a ground layer dominated by a dwarf shrub

community composed mostly by the deciduous *Vaccinium myrtillus* (bilberry) and two evergreen shrubs, *Vaccinium vitis-idaea* (lingonberry) and

Empetrum nigrum (black crowberry) plus other deciduous shrubs (*Betula nana*), grasses and herbs (e.g. *Deschampsia flexuosa*, *Cornus suecica).*

Both *Vaccinium* species and *E. nigrum* compete for space in the regeneration process after disturbance (Phoenix *et al.*, 2000). We investigated

larval numbers and percentage (%) cover of vegetation in an experimental system (established in June 2000) that was entering its fifth growing

season of treatment during the insect outbreak of June 2004. The experimental system employed 1.5m^2 Open Top Chambers (OTCs) to elevate

177 CO_2 to 730± 25 ppm (versus 377 ppm ambient) using a fan sourced air supply injected with pure CO_2. Warming was controlled with soil heating

178 cables and above canopy infrared lamps that elevated temperature by 5°C (see Olsrud et al., 2004, Svensson *et al*., 2018). In this study we used

179 six replicate plots per treatment, based around fully randomized experimental setup where the response of the dwarf shrub plant community was

180 investigated to the following treatments i) Ambient conditions; ii) Elevated CO_2; iii) Elevated temperature; iv) Elevated CO_2 in combination with

181 elevated temperature.

182

183 Larval numbers and vegetation cover of plant species were assessed within a 0.34 m^2 area within each chamber. Larvae were free to move

184 between plots via the space between the chamber and ground or they could climb the chamber walls. They entered the plots post birch defoliation

185 in surrounding areas and were counted (22nd June and 1st July 2004) from three 15 × 15 cm quadrats per plot (total plot size investigated 0.34 m

186 with chamber footprint of 1.5 m^2). All larvae were returned to their respective collection areas upon completion of counts. For each quadrat, we

187 also estimated reductions in the percentage cover of dwarf shrubs (bilberry, lingonberry and black crowberry). This was done visually to the

188 nearest 5% on both dates as a surrogate of biomass removal for all treatments.

189

190 In this study, we focused on herbivory and food preference related to the three dominant shrub species with all other vegetation types including

191 grass, herbs, lichens and mosses classified as "Other species". The mountain birch trees in the experimental area had almost totally been

192 defoliated (95-100 %) both above and around the sites by the time measurements began with larvae searching for food in the understorey shrub

193 area.

194
195 ## 2.5. Statistical analysis

196 To detect shifts in host preference, segmented linear regression models (Toms & Lesperance 2003) were performed. The models relate host cover

197 and the environmental variables temperature and CO_2 to intrinsic crowding rates with the use of the R statistical package (R Development Core

198 Team 2011). Since the cover abundances of all species suffer from multicollinearity, we performed a "detection of breakpoints" test on host

199 preference by reducing the dimensionality of the system into two groups: evergreen shrubs and a group with the rest of the species, which include

200 both bilberry and "other species". Due to the presence of some plots with zero larvae, we used the crowding rate of larval abundance as

201 $r=(L_2+1)/(L_1+1)$. This modification did not significantly alter the assumptions of normality and homoscedasticity, and allowed us to use the

202 linear model with a full factorial design. Crowding rates may, however, depend not only on host cover, but may also be related to the initial

203 number of larvae L_1 due to density-dependence, in which case our assumption for the exponential model for crowding, which depends only on

204 host cover, would be invalidated. Post-hoc analysis on all 72 sampled quadrats (from 24 plots) showed similar initial larval densities ($ln(L_1+1)$)

205 and density variability at the beginning of the survey (Tables S1 and S2 and Fig. S1) in all plots regardless of treatment or species cover. There

206 was also an absence of collinearity between initial evergreen species cover at the beginning of sampling in 2004 and either temperature

207 (polyserial correlation Ω=0.39, P=0.37) or CO_2 (Ω=0.22, P=0.66) treatments, indicating, again, that initial host densities had not been affected by

208 previous history in the environmental signature of the plots.

209

210 Thus, the full factorial segmented linear model, dependent on host composition (Kuussaari *et al.,* 2000), and environmental factors, takes the

211 form (Toms & Lesperance, 2003):

212
$$r = b_0+b_{11}R_x+b_2T + b_3C + b_4TC + \varepsilon \qquad \forall R_x \leq p_{xc}$$
$$r = b_0+b_{11}R_x+b_{12}(R_x - R_{xc})+b_2T + b_3C + b_4TC + \varepsilon \quad \forall R_x > p_{xc} \qquad (7)$$

213 where r is the response variable (crowding rate), and R_x, T, and C define the covariates evergreen cover, temperature and CO_2, respectively. b_{11}

214 describes the first and $b_{11}+b_{12}$ the second slope (in the *v*-shaped relationship) for the evergreen cover. $b_i \forall i \geq 2$ represent the coefficients for the

6

215 environmental main effects and second and third order interactions, and ε stands for the independent, additive error with zero mean and constant

216 variance. Model fits were developed using the package "segmented" (Muggeo, 2009). We performed stepwise model selection to select the most

217 parsimonious model through AIC values.

218

219 We tested the accuracy of the previous segmented regressions by implementing thin plate splines for the crowding rates using the package "fields"

220 (Nychka *et al.*, 2014) over two selected groups: evergreen shrubs and bilberry. They were performed over a Cartesian coordinate system with the

221 two shrub groups (bilberry versus evergreen) as covariates to test for potential multicollinearity, and converted back into a barycentric coordinate

222 system with bilberry, evergreen and other species as covariates.

223

224 Consumption rates were calculated following Eq. 5 for bilberry and evergreen species. Since consumption rates followed quasi-Poisson

225 distributions (Fig. S2), we used generalized linear models with quasi-Poisson error structure to determine the effect of crowding rate, temperature

226 and CO_2 on the consumption rates of both shrub groups and the logarithmic growth rates of herbivore pressure (insects per % species cover). The

227 initial larval densities were pooled for each significant treatment scenario using their geometric mean.

228

229 When resource saturation takes place, larval populations following Gompertz dynamics are expected to balance movement with consumption,

230 defined by the optimal consumption k_c in Eq. 6. We tested deviations from optimal behaviour, and hence, realized reductions in herbivore

231 pressure, by calculation of $k-k_c$ (see *Calculating consumption rates*). Finally, thin plate splines were also used to map those scenarios of host

232 cover and treatment where consumption was lower than expected under an optimal, balanced model of herbivory (i.e., $k-k_c<0$). All thin plate

233 splines were performed over polynomials of degree 3.

234

4. Results

236 As opposed to a case when non-dominant crowding rate responses exist and crowding is independent of plant cover (c Fig. 1a), plant cover did

237 dictate larval crowding rate, which determined host choice. Our results show a strong larval affinity towards mono-specific stands, especially

238 towards those covered by bilberry, and avoidance of mixed stands (i.e., those where bilberry and evergreen shrubs coexist in similar proportions),

239 following a *v*-shaped pattern for host preference (i.e., dominant crowding rate response, bold line in Fig. 1a). Evergreen species were preferred

240 when their cover represented >40% of the community (Fig. S3, F=7.07, P<0.001) and, against our initial hypothesis, this was independent of the

241 climate change factors tested (temperature (F=0.72, P=0.40) and CO_2 (F=1.10, P=0.30), Table S1-S2). Larval crowding manifested when

242 evergreen cover was less than 26% or more than 70%. In between, larvae left the plots (Figs. 2a, S3). The presence of a critical shifting

243 breakpoint in larval preference at 40% of evergreen species cover was confirmed by the thin-plate smoothing spline, indicating that species other

244 than evergreen shrubs or bilberry play no perceptible role in larval preference (Figs. 2a, S3)

245

246 Temperature was the only significant environmental variable tested that had any effects on consumption: there was lower consumption of the

247 deciduous species *V. myrtillus* (bilberries, P<0.05) at elevated temperature (Table 1). The consumption level under this treatment reached values

248 similar to those found for evergreen species under ambient temperature (Fig. 2b, Table 1). However, for evergreen species, temperature

249 interacted with CO_2: the consumption of evergreen species was reduced when the community was exposed to future temperature and CO_2 alone

250 but there was no effect when both these factors were applied together (Fig. 2b).

251

252 Under current ambient climatic conditions, higher *V. myrtillus* consumption rates were linked to a preference towards mono-specific stands,

253 which was reflected in an increased herbivore pressure on pure bilberry stands. However, in a warmer climate scenario herbivore pressure was

254 partially eased (Figs. 3, 4, Table 1). The importance of both crowding and consumption mechanisms is reflected by the statistical fit of our

255 Gompertz model (Fig 3, Table 1). The Gompertz model predicts that the balance between crowding and consumption will determine herbivore

256 pressure, and follows a log-log linear relationship with crowding rates in the absence of consumption (see *Calculating consumption rates)*. Our

257 statistical fit validates both mechanisms as contributors to herbivore pressure, providing a faster than linear increase for herbivore pressure in

258 log-log axes (Fig. 3). A future warmer climate scenario clearly shows suboptimal consumption, and thus, released herbivory pressure on bilberry

259 in mixed vegetation areas (Fig. 4),

260

5. Discussion

262 Overall, the statistical fit of the data based on the mixed model predicts that: 1. shifts (i.e., increases and decreases) in herbivore pressure on the

263 potential hosts in monocultures following increasing temperatures; 2. decreased herbivore pressure on the host in mixed stands is most likely to

264 occur as a result of climate warming.

265

266 We initiated this study to assess the importance of host preference during an outbreak of *E. autumnata* and whether future climatic changes

267 (elevated CO_2 and temperature) will affect herbivore pressure. Regarding CO_2 the only observed effect was that consumption of evergreen

268 species was reduced when the community was exposed to elevated CO_2 alone but there was no significant effect when in combination with

269 elevated temperature.

270

271 Pooling all plots together, our study found that consumption rates on bilberry were not significantly affected either by warming or CO_2, agreeing

272 with recently reported results during the 2003-2004 outbreak in Abisko (Svensson et al., 2018). CO_2 has been previously hypothesized to alter

273 palatability on a per-species basis by changing foliar C:N ratios or its production of consumption-inhibiting secondary compounds (Lindroth,

274 1996) Our analysis, showing that CO_2 effects on consumption rates in different shrubs are present, but not significantly different, hence, we can

275 not confirm this hypothesis. A possible balance between both increases in carbon storage compounds and secondary metabolites (the well-known

276 carbon nutrient balance hypothesis, *sensu* Bryant *et al*., 1983) precludes a clear response, added to further complexities due to interactions with

277 temperature, as reflected in the apparent distinctive consumption patterns of evergreen shrub consumptions in regard to both CO_2 and

278 temperature.

279

280 Regarding temperature, we detected significant reductions of bilberry consumption in mixed evergreen-deciduous shrub plots under warming

281 (Fig. 4), but not significant increases in bilberry-dominated plots. This result does explain the overall reduction in bilberry consumption when all

282 plots are pooled in the analysis. Yet, in ambient conditions, herbivory on bilberry was higher than on the evergreen shrubs, confirming previous

283 observations regarding the higher palatability of the first (Svensson *et al*., 2018).

284

285 Our study also differs from that of Barrio *et al.* (2016) who studied the effects of elevated temperature on non-outbreak insect activity, yet some

286 common findings were observed. In both studies, larvae shift their food preference, described by the *v*-shaped host choice function. For Barrio *et*

287 *al.*, herbivory shifted towards higher consumption of more nutritious hosts with warming. In contrast, in the current study and under outbreak

288 conditions the opposite effect was observed. The v-shaped function indicates that, during an outbreak, larvae choose food according to quantity,

289 rather than tissue quality (Ruohomäki *et al.*, 2000), and the effect can be dependent on larval densities and the herbivore species (Birkemoe *et al.*,

290 2016). Although larvae preferred to feed on bilberry in current temperature conditions (as in Svensson *et al.,* 2018), there were substantial

291 crowding levels also observed on plots largely dominated by evergreen shrubs. However, mixed vegetation stands were generally avoided.

292 Although not measured in this study, switching between host plants has been previously shown to indicate a capacity to overcome host-induced

293 resistance (Kaitaniemi *et al.*, 1999).

294

295 Hence, our model also shows that herbivore pressure during outbreaks depends both on the host-dependent larval movement (or preference

296 towards a host) and the actual temperature-driven consumption. The Gompertz model confirms that preference translates into higher

297 consumption per larva in bilberry for the current climate scenario. Although larvae are still attracted to bilberry under warmer temperatures, their

298 individual consumption rates are halved to suboptimal levels, reducing overall herbivore pressure on this host in mixed deciduous-evergreen

299 areas. This result partly contradicts previous findings that warmer temperatures accelerate insect growth and consumption (Bale *et al.*, 2002,

300 Birkemoe *et al.*, 2016), but agrees with Barrio *et al.*'s (2016) findings that the performance of invertebrate herbivores is reduced under warmer

301 conditions. The difference here in the current study is that measurements were undertaken during an insect outbreak.

302

303 Two main assumptions govern our model: first, crowding is affected by environmental conditions (temperature and CO_2) and resource

304 availability; two, this dependence on resource availability is general in that it does not need to be either linear or monotonic (which would in

305 fact be two extra specific assumptions) and can shift preference between different host species. As shown in Fig. 3, failure to comply with

306 these assumptions (either lack of larval crowding, or zero consumption) would have generated herbivore pressure models unable to fit the

307 field data. These assumptions entail that consumption is mostly dependent on the local awareness or information that larvae have on their

308 surrounding resources (Gamarra, 2005). Consequently, the model resource and herbivore dynamics are limited at the small spatial and within-

309 seasonal temporal scales, where birth and death processes of both resource and herbivore, typically used for among-year population dynamics,

310 are not considered.

311

312 Several studies have observed vegetation changes in the north (e.g. Callaghan *et al.*, 2013; Post *et al.*, 2009; Tömmervik *et al.*, 2004) and others

313 suggest increased dwarf shrub growth and success in response to future warming in the Arctic (Van Wijk *et al.*, 2003; Elmendorf *et al.*, 2012),

314 including bilberry growth (Richardson *et al.*, 2002). Furthermore, envelope bioclimatic models confirm that more thermophile plant species

315 including bilberry will expand their ranges as the climate warms (Tömmervik *et al.*, 2004; Milbau *et al.*, 2009). Although, contrary to Barrio *et*

316 *al*'s (2016) study, we found a release of herbivory on the preferred shrub host plant *V. myrtillus* in mixed stands under predicted future climate

317 conditions. However, for the first time, we show that under warming herbivory could potentially promote expansion of this plant species via a

318 reduction in its selection by the autumnal moth in areas with mixed deciduous/evergreen shrub composition. This of course depends on the

319 severity and the distribution of outbreaks as during very intensive outbreaks the insects can consume all available vegetation within a given area.

320 At the landscape level, effects will likely operate most strongly where evergreen and deciduous plant species are mixed, such as range boundaries.

321 Thus, any realistic attempt to predict changes in these locations will require the inclusion of these effects in large-scale envelope models of

322 species distributions. At smaller scales, if Gompertz trends in resource depletion occur in evenly mixed plant communities, billberries will be

323 exposed to less herbivory. Consequently, as stated by Lindroth (1996) as a general CO_2 influence on host plants, and Haukioja (2005) for the

324 mountain birch community, bilberry may reduce allocation to defensive secondary compounds in favour of growth. This will likely favour the

325 establishment and faster expansion of the bilberry in those areas that currently have mixed vegetation. In turn, larvae will increasingly shift back

326 towards more consumption as it becomes dominant and exposed to further outbreaks. Yet, competitive processes between shrubs may distort this

327 patterns during the time lapse between successive outbreaks. In the end, inferring community-level projections from such experiments is

328 challenging and larger-scale studies are required (Lindroth, 1996; Birkemoe *et al.*, 2016).

329

330   The parameterization of our model is based on the specific scenarios under which *E. autumnata* herbivory occurs in the field, and is founded on a

331   small set of plots. Validation of the model parameters for this particular system can be challenging, due to the 9-10 year typical frequency of *E.*

332   *autumnata* outbreaks in Fennoscandia (Tenow, 1972) and the complexity of factors and logistics regarding the use of OTCs for environmental

333   manipulation. A practical approach will depend on the long-term continuation of the Abisko research station and objectives, combined with

334   emergency protocols to sample larval herbivory when the outbreak arrives, and possibly an increase in the sampling size (including additional

335   OTCs).

336

337   Notwithstanding the challenges of validation, the model is general in its formulation. First, it can be applied to the forest-tundra transition in

338   Fennoscandia, where *E. autumnata* outbreaks show dramatic effects. Second, it includes situations where larval switching preferences are absent,

339   in which case Gompertz decay would be absent. Thus, the generality of the model allows its application to other herbivore insects undergoing

340   large population fluctuations, either with limited mature larval movement driven by host preference, like *Lymantria dispar* (Mauffette &

341   Lechowicz, 1984), *Chroristoneura rosaceana* (Carrière, 1992*), Thyridopteryx ephemeraeformis* (Ward *et al.*, 1990) and Malacosoma *disstria*

342   (Robison & Raffa, 1997) – or without it. Although the model needs to be tested in other areas, it is a warning against the lack of both movement

343   and consumption dynamics in any large-scale species composition modelling study, particularly ecosystems exposed to insect outbreaks or any

344   other significant biotic interactions.

Acknowledgments

Conflict of interest

357   The authors are not aware of any conflict of interest.

358

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477

Supporting Information Legends

479   This information contains:

13

485   # Figures
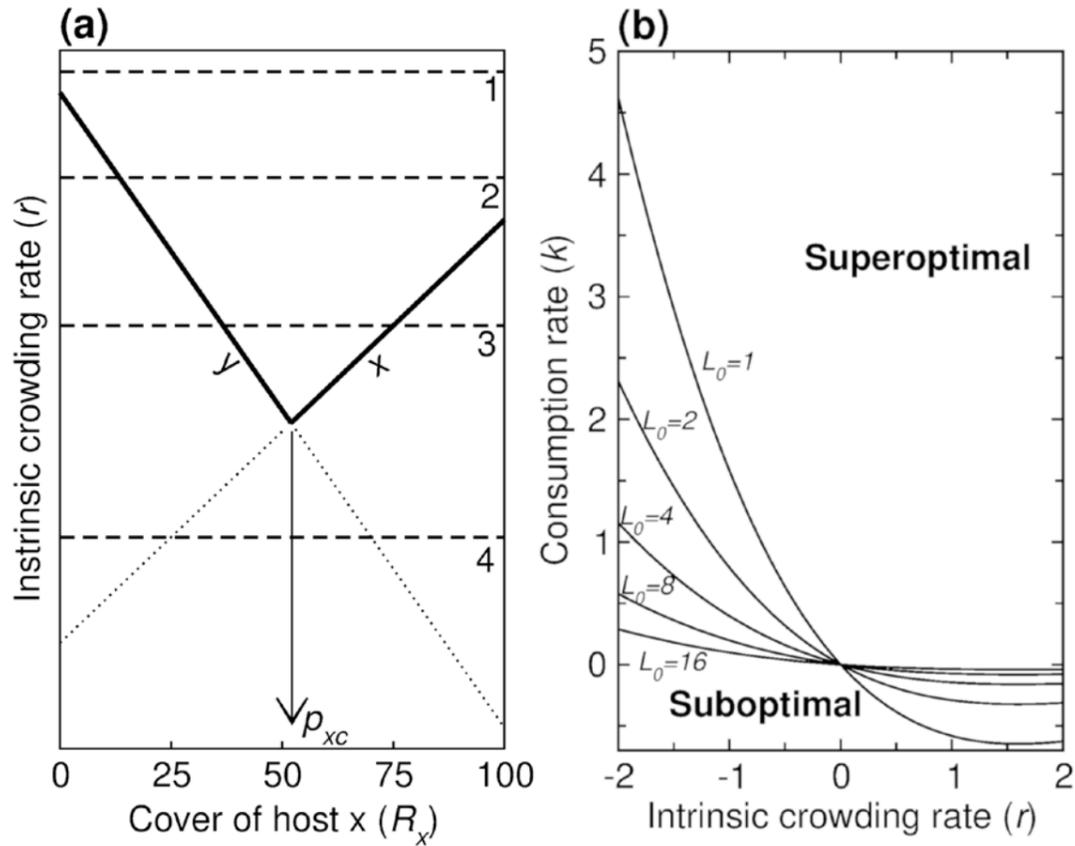
486

487   **Fig. 1.** Model for host preference and herbivory. (a) Host preference model, describing the relationship between host plant cover and larval

488   crowding rates when two potential hosts attract larvae (b_x, $b_y > 0$) and coexist. Bold solid lines: Dominant crowding rate response. Thin solid line:

489   Non-dominant response. Dashed lines: theoretical position of the zero crowding rate isoline. The breakpoint p_{xc} indicates a shift in host

490   preference. The position of the zero crowding isoline conditions the attraction towards hosts: 1. Avoidance of both hosts. 2. Host *x* is avoided,

491   and crowding only occurs at high *y* covers. 3. Avoidance of plots where both hosts coexist. 4. No avoidance in any combination of host covers. (b)

492   Optimal herbivory. Curves represent optimal consumption rate k_c (Eq. 6) balancing crowding for different initial numbers of larvae L_1.

493   Superoptimal ($k > k_c$) and suboptimal ($k < k_c$) regions above and below the curves show areas where overall herbivore pressure in the patch

494   increases or decreases, respectively.

495
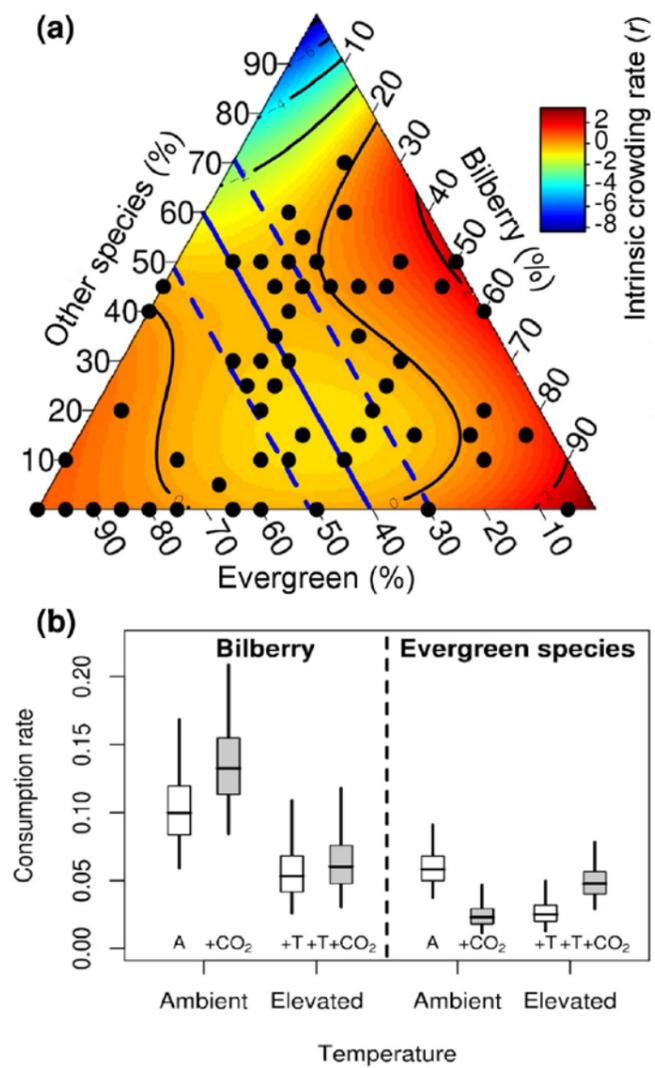
Fig. 2: Crowding and consumption rates in *E. autumnata*. (a) Triangular thin plate spline of crowding rates over the relative cover of three plant groups considered. Black dots represent the plots surveyed. The solid blue line is the position of the breakpoint in the segmented regression of crowding rate *vs.* evergreen cover (Fig. S3). Dashed blue lines are the confidence intervals of the breakpoint in the segmented regression. (b) Calculated consumption rates resulting from the quasi-Poisson generalized linear model in Eq. 5 for different temperature and CO_2 scenarios. Boxes and solid vertical lines depict 50% and 95% confidence intervals. Grey boxes depict elevated CO_2 scenarios. +T = Elevated future temperature; $+CO_2$ = Elevated CO_2; +T $+CO_2$ = Elevated temperature plus elevated CO_2.
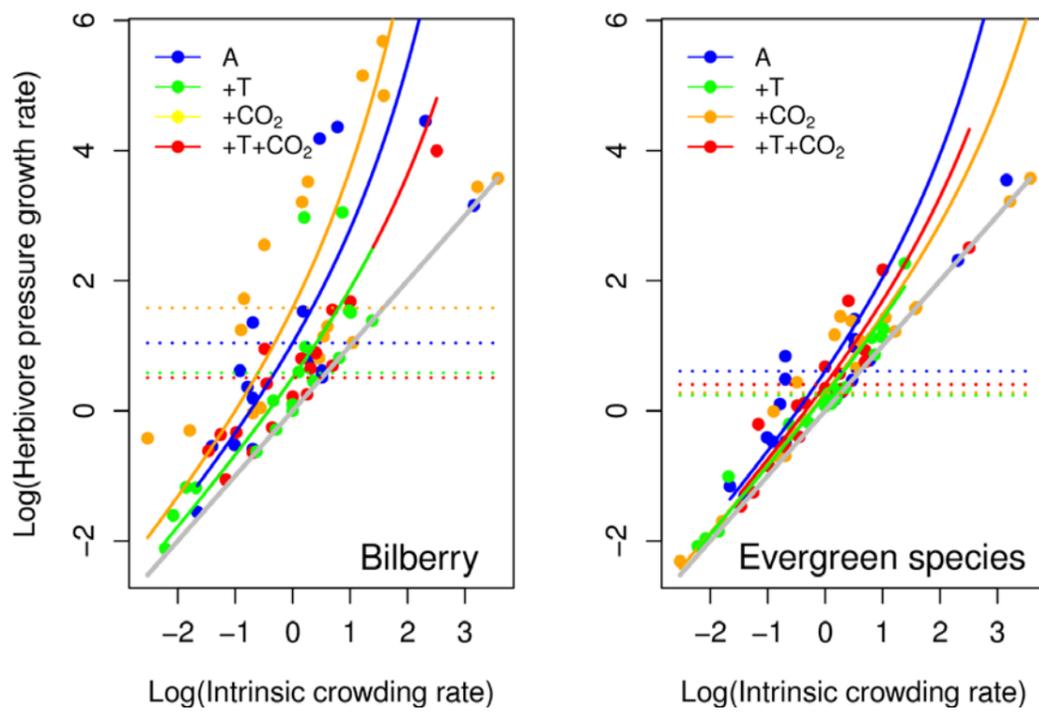
504

505 **Fig. 3:** Herbivore pressure depends both on crowding and consumption. Quasi-Poisson model regressions show the dependence of the growth

506 rate of herbivore pressure on the crowding rate (Eq. 4) for both host species. A=Ambient conditions; +T =Elevated future temperature; +CO_2 =

507 Elevated CO_2; +T +CO_2 = Elevated temperature plus elevated CO_2. Initial number of larvae is included in the equation as the geometric mean.

508 Gray line: Expected herbivore pressure in the absence of larval movement. Horizontal coloured lines: Expected herbivore pressure in the absence

509 of consumption (see *Calculating consumption rates*).

510
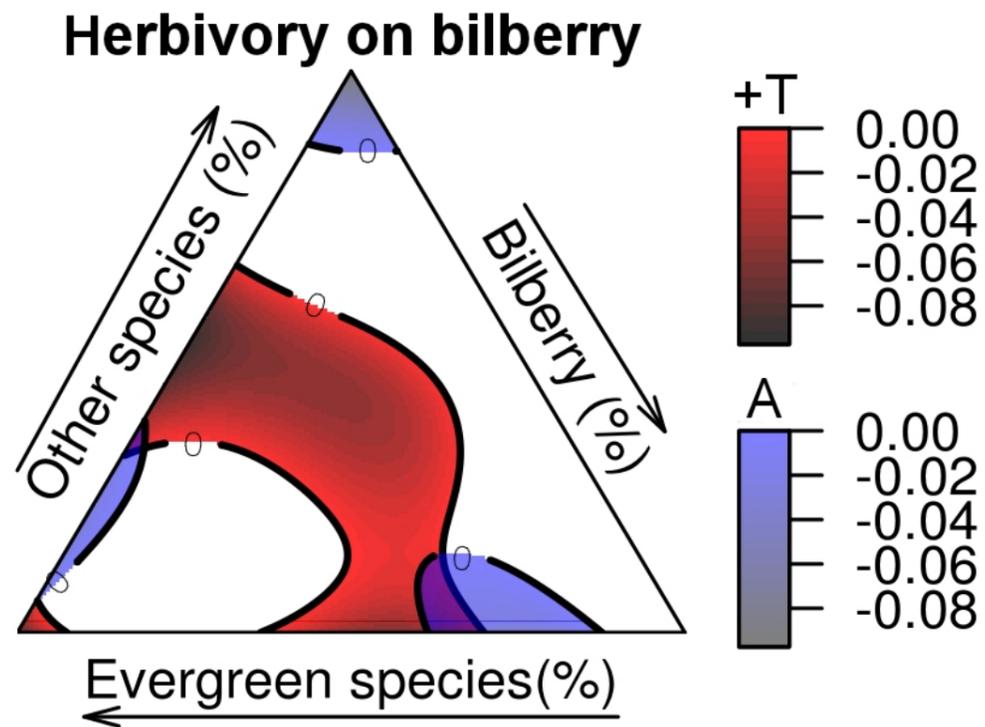
Fig. 4. Consumption on bilberry under climate change is reduced in mixed stands (coexistence of the three host species)**.** Reduction of herbivory on bilberry under current and future environmental conditions: coloured areas show suboptimal bilberry consumption (i.e., negative differences between realized and optimal consumption rates, $k-k_c<0$) (see *Calculating consumption rates*). White areas depict superoptimal consumption. Under ambient conditions, suboptimal consumption only scarcely occurs in marginal areas like some stands with large dominance of bilberry. However, under future warmer scenarios, strongly suboptimal consumption of bilberry is more prevalent in mixed stands. A=Ambient conditions; +T =Elevated future temperature.

518 **Table 1.** Summary of the quasipoisson generalized linear model (with a logarithmic link function) used to calculate consumption rates in bilberry

519 and evergreen species. Higher-order non-significant interactions were discarded. The three last columns show average deviations from optimal

520 conditions (k-k_c) where consumption balances crowding. A=Ambient conditions; +T=Elevated future temperature; +CO_2 = Elevated CO_2; +T

521 +CO_2 = Elevated temperature plus elevated CO_2. Consumption rates are shown in percentage cover per larva during a 10 days interval.

522

Species	Source	Df	Estimate	Std Error	P(>|t|)	Scenario	k-k_c	P(>|t|)
Bilberry	Intercept		-2.152	0.173	<2e-16 ***	A	0.098	0.0001***
	T effect	1	-0.718	0.302	0.02*	+T	0.021	0.036*
	Error	70						
Evergreen	Intercept		-2.842	0.228	<2e-16 ***	A	0.037	0.21
	T effect	1	-0.84	0.415	0.047*	+CO_2	0.011	0.812
	CO_2 effect	1	-0.93	0.429	0.034*	+T	0.031	0.36
	Interaction	1	1.567	0.606	0.012*	+T +CO_2	0.021	0.464
	Error	68						

523