

1 Does insect herbivory suppress ecosystem productivity? Evidence from a temperate
2 woodland

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4 Kristiina Visakorpi*: Department of Zoology, University of Oxford, Oxford, UK,
5 kristiina.matilda@gmail.com.

6 Sofia Gripenberg: School of Biological Sciences, University of Reading, Reading, UK,
7 s.gripenberg@reading.ac.uk

8 Yadvinder Malhi: Environmental Change Institute, School of Geography and the
9 Environment, University of Oxford, Oxford, UK, yadvidner.malhi@ouce.ox.ac.uk

10 Terhi Riutta: Environmental Change Institute, School of Geography and the Environment,
11 University of Oxford, Oxford, UK; Imperial College London, Department of Life Sciences,
12 Silwood Park Campus, Ascot, UK, terhi.riutta@ouce.ox.ac.uk

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14 *Corresponding author

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22 Author contributions: Conceived and designed study: KV, SG, TR; Performed research: KV;

23 Analyzed data: KV; Wrote the paper: KV, SG, TR, YM

24 **Abstract**

25 Our current understanding of the relationship between insect herbivory and ecosystem
26 productivity is limited. Previous studies have typically quantified only leaf area loss, or have
27 been conducted during outbreak years. These set-ups often ignore the physiological changes
28 taking place in the remaining plant tissue after insect attack, or may not represent typical,
29 non-outbreak herbivore densities. Here, we estimate the amount of carbon lost to insect
30 herbivory in a temperate deciduous woodland both through leaf area loss and, notably,
31 through changes in leaf gas exchange in non-consumed leaves under non-outbreak densities
32 of insects. We calculate how net primary productivity changes with decreasing and increasing
33 levels of herbivory, and estimate what proportion of the carbon involved in the leaf area loss
34 is transferred further in the food web. We estimate that the net primary productivity of an oak
35 stand under ambient levels of herbivory is 54 - 69% lower than that of a completely intact
36 stand. The effect of herbivory quantified only as leaf area loss ($0.1 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$) is
37 considerably smaller than when the effects of herbivory on leaf physiology are included (8.5
38 $\text{Mg C ha}^{-1} \text{ yr}^{-1}$). We propose that the effect of herbivory on primary productivity is non-linear
39 and mainly determined by changes in leaf gas exchange. We call for replicated studies in
40 other systems to validate the relationship between insect herbivory and ecosystem
41 productivity described here.

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46 **Keywords:** insect herbivory, carbon cycle, net primary productivity, gross primary
47 productivity, respiration, *Quercus robur*, *Operophtera brumata*, Wytham Woods

48

49 **Introduction**

50 By affecting plant abundance, distribution and physiology, herbivores can have large impacts
51 on ecosystem carbon storage and cycling (Chapin 1997, Kurz et al. 2008, Clark et al. 2010,
52 Schäfer et al. 2010, Heliasz et al. 2011, Estes et al. 2011, Schmitz et al. 2014, Flower and
53 Gonzalez-Meler 2015, Lund et al. 2017). To date, many studies have demonstrated the role
54 of large grazers and their predators in controlling primary productivity (e.g. Zimov et al.
55 2009, Estes et al. 2011, Schmitz et al. 2014, Wilmers and Schmitz 2016) or insect outbreaks
56 in causing defoliation and tree mortality (Kurz et al. 2008, Clark et al. 2010, Amiro et al.
57 2010, Edburg et al. 2012, Flower et al. 2013, Flower and Gonzalez-Meler 2015). Under
58 outbreak densities, the effects of insect herbivores on forest carbon cycling can be large
59 enough to shift the ecosystem from being a carbon sink into a carbon source (Kurz et al.
60 2008, Heliasz et al. 2011, Lund et al. 2017).

61 However, the role of non-outbreak, low-density populations of insect herbivores on
62 carbon cycling has received less attention. The ubiquity of insect herbivory in terrestrial
63 ecosystems (Strong et al. 1984, Schoonhoven et al. 2005, Forister et al. 2015), and its
64 potential effects on the rates of photosynthesis and respiration of the remaining plant tissue
65 (Nykänen and Koricheva 2004, Nabity et al. 2009, Bilgin et al. 2010) suggest that even low
66 densities of insect herbivores could have a large impact on ecosystem carbon sequestration
67 and loss (Strickland et al. 2013, Visakorpi et al. 2018).

68 Although insect herbivory has been shown to affect rates of photosynthesis and plant
69 respiration beyond leaf area loss (“indirect effect of herbivory”, as opposed to “direct effect”
70 of leaf area loss; Oleksyn et al. 1998, Zangerl et al. 2002, Nykänen and Koricheva 2004,
71 Nabity et al. 2009, Bilgin et al. 2010, Meza-Canales et al. 2017), these physiological plant
72 responses to herbivory have generally been neglected when estimating changes in ecosystem
73 CO₂ exchange. Consequently, we currently do not have a clear picture how the most typical

74 levels of insect herbivory affect ecosystem CO₂ exchange. Ignoring the effects of insect
75 herbivory could lead to biased estimations of ecosystem productivity, or of the role of forests
76 as carbon sinks (Kurz et al. 2008, Campioli et al. 2016).

77 In this study, we quantify the effects of insect herbivory on forest-level net primary
78 productivity in a temperate maritime woodland in southern England, UK. In a previous study
79 in this system (Visakorpi et al. 2018), we found that photosynthesis of oak (*Quercus robur*,
80 L.) was substantially lower in leaves subjected to herbivory by winter moth (*Operophtera*
81 *brumata*, L.) caterpillars than in intact leaves surrounded only by other intact leaves.
82 Moreover, a similar reduction in photosynthetic rate was seen in intact leaves on the same
83 shoots as the damaged leaves, resulting in an estimated 50% reduction in canopy-level
84 photosynthesis. How these changes in carbon assimilation affect tree and stand level
85 productivity remains unknown. Here, we combine our previous measurements of herbivory-
86 inflicted leaf area loss and indirect changes in photosynthetic rate (Visakorpi et al. 2018) with
87 measurements on canopy and woody respiration, hourly meteorological data and tree survey
88 data from the study site to estimate the effects of herbivory on oak primary production over a
89 growing season (Figure 1). We ask: 1) what is the potential effect of insect herbivory on net
90 primary production (NPP) of an oak stand, estimated separately through leaf area loss and
91 through changes in canopy gas exchange and 2) how does the effect of herbivory on forest
92 productivity change with changing herbivory pressure?

93

94 **Methods**

95 *Study site and system*

96 All data were collected in Wytham Woods (51°47' N, 1° 20' W, 160 m.a.s.l), located in
97 Oxfordshire, UK. Wytham Woods is an ancient semi-natural woodland of 390 ha. Most parts
98 of the woodland have experienced long-standing management practices (e.g. coppicing,

99 selective logging) until 50 year ago (Savill 2011). Recruitment is low, and established
100 vegetation accounts for most of the carbon uptake (Thomas et al. 2011). The area within
101 Wytham Woods in which our study took place has been a woodland at least since the 18th
102 century, and most likely since the last ice age (Savill 2011).

103 Our focal study area is an 18-ha forest dynamics monitoring plot, part of the
104 Smithsonian Global Earth Observatory network (www.forestgeo.si.edu). The plot is
105 dominated by sycamore (*Acer pseudoplatanus*, ca. 50% of the basal area), pedunculate oak
106 (*Quercus robur*, ca. 20% of the basal area) and ash (*Fraxinus excelsior*, ca. 20% of the basal
107 area; Butt et al. 2009, Savill 2011). The plot was surveyed for tree growth, recruitment and
108 mortality in 2008, 2010 and 2016. The carbon cycle of the plot has been measured using the
109 eddy covariance technique (Thomas et al. 2011) and biometric quantification of leaf and
110 woody biomass in a 1 ha subplot (Fenn et al. 2015, Table 1). Previous work at the site has
111 revealed seasonal dynamics in oak photosynthesis, which peaks on average 63 (\pm 6) days
112 after budburst (Morecroft et al. 2003).

113 In Wytham Woods, lepidopterous caterpillars are the first herbivores to attack the
114 newly flushed leaves of most tree species (Feeny 1970). They emerge in synchrony with the
115 budburst, and feed until early June (Hunter 1992). Relatively few herbivore species feed on
116 the mature leaves later in the season (Feeny 1970). Of the early-spring herbivores, the winter
117 moth (*Operophtera brumata*) is one of the most common species (Feeny 1970), feeding on
118 most of the trees in the area. The winter moth is native to the area, and its population reaches
119 outbreak densities approximately every 10 years. The last high abundance year prior to our
120 study was in 2010 (285 caterpillars per m² of oak canopy, Lionel Cole; unpublished data).
121 Since 2013, the population size has been small (e.g. 5 caterpillars per m² in 2014; Lionel
122 Cole, unpublished data).

123

124 *Quantifying leaf area loss and the effect of insect herbivory on leaf-level photosynthesis*

125 Data on leaf area loss were collected from leaves in the upper canopy of five mature oak trees
126 located in the 18-ha plot, accessible from a canopy platform. To estimate the level of insect
127 herbivory on the five focal oaks throughout the growing season, we used estimates of the
128 proportion of leaf area loss and the frequency distributions of three different leaf types per
129 tree: completely intact leaves on shoots with only intact leaves (“completely intact”), intact
130 leaves on shoots with at least one herbivore-damaged leaf (“systemically affected”), and
131 leaves damaged by herbivores (“damaged”) (Visakorpi et al. 2018). Data on the effect of
132 winter moth caterpillars on leaf-level photosynthesis were obtained from the manipulative
133 experiment reported in Visakorpi et al. (2018). In brief, we introduced winter moth
134 caterpillars on selected oak shoots, and subsequently measured light-photosynthesis response
135 curves on three leaf types (intact, systemically affected, damaged). To estimate the amount of
136 carbon lost through the consumed leaf tissue, we used estimates for leaf mass per area
137 (“LMA”, gm^{-2}) and leaf carbon content (% of dry mass) for the same leaf types from the
138 same experiment (Visakorpi et al. 2020; Appendix 2, Table S3).

139

140 *Estimating oak NPP.* Figure 1 summarizes our approach and Appendix 1 provides more
141 detail on the methodology. In brief, we used three methods to estimate oak NPP. First, NPP
142 was estimated as the difference between canopy net photosynthesis and woody (stem + root)
143 respiration (“*NPP through canopy upscaling*”). Second, we used census data on woody
144 growth and combined these data with allometric equations to estimate leaf production and
145 belowground production (“*NPP through tree growth census*”). Third, we used earlier
146 estimates of oak above- and belowground NPP at the site obtained from biometric
147 measurements (“*NPP through biometric measurements*”) (Fenn 2010, Fenn et al. 2015). For
148 each of the three methods, we estimate oak NPP for a hypothetical stand comprising only of

149 mature oak trees, assigning the total basal area ($33 \text{ m}^2 \text{ ha}^{-1}$) of trees at the site to oaks only,
150 and for the actual per ha of oak of the site (oak basal area $6.7 \text{ m}^2 \text{ ha}^{-1}$). For each case, we
151 estimate oak NPP for two scenarios: 1) for an intact canopy (hereafter “*Intact canopy*”) and
152 2) for a canopy under the observed level of herbivory (“*Normal herbivory*”). The effect of
153 insect herbivory on NPP is the difference in NPP between the *Intact canopy* and the *Normal*
154 *canopy* scenarios.

155 *NPP through canopy upscaling:* We used photosynthesis-light response curves
156 measured from completely intact, systemically affected and damaged leaves from the five
157 focal oak trees (one per leaf per leaf type per tree, Table 1). The leaf-level measures were
158 scaled up with the Big Leaf approach of The Joint UK Land Environment Simulator
159 (“JULES”, Clark et al. 2011). The canopy assimilation model included estimates for
160 photosynthetic rate and daytime respiration rate (i.e. net photosynthesis) scaled to changes in
161 LAI through the canopy, while taking into account leaf area loss to herbivory and the
162 frequency distributions of the three different leaf types. Light was assumed to be reduced
163 through the canopy layers (Monsi and Saeki 1953), photosynthesis to respond to light
164 according to the light-photosynthesis response curves, and increased light to inhibit
165 respiration (Mercado et al. 2007). To estimate night-time respiration, we measured respiration
166 rates on the three leaf types on each of our five focal trees during two nights in July 2015. To
167 scale night respiration to canopy level, we accounted for the frequency distributions of
168 different leaf types and corrected for differences in respiration rates between different canopy
169 layers (Griffin et al. 2001). Canopy gas exchange (daytime net photosynthesis – night
170 respiration) was scaled to hourly light (daytime net photosynthesis) and temperature (night
171 respiration) data, to seasonal changes in LAI (Stokes 2000, Fenn 2010) and to seasonal
172 changes in photosynthetic rate of oak (Morecroft et al. 2003). The canopy night respiration
173 rate was further scaled with the daytime photosynthetic rate of the previous day (Whitehead

174 et al. 2004). To estimate woody respiration, we used data from previous measurements of oak
175 stem respiration at the site (Walker 2017). We assumed that stem respiration followed the
176 same pattern as leaf respiration in response to herbivory, since both leaf and stem respiration
177 rates have a similar, positive relationship with photosynthesis (Wertin and Teskey 2008).
178 Stem respiration was scaled to hourly temperature data. Root respiration was assumed to be
179 13% of stem respiration, based on earlier measurements at the site (Fenn et al. 2015). Canopy
180 gas exchange and woody respiration were scaled to plot level by assuming leaf area index
181 (“LAI”) of $6.5 \text{ m}^2/\text{m}^2$ and stem area index (“SAI”) of $1.5 \text{ m}^2/\text{m}^2$, both previously estimated
182 for the site (Fenn 2010, Nils Rutjes 2016, unpublished data; Fenn and others 2015, Table 1).
183 For all meteorological data, we used hourly data recorded at an open site in Wytham Woods
184 during years 2014 and 2015 (Figure 2, Rennie et al. 2017).

185 *NPP through tree growth census:* We used dbh measurements from all oak trees (355
186 stems, >10 cm dbh) within the 18 ha forest dynamics plot obtained from censuses in 2010
187 and 2016 (Y. Malhi, unpublished analysis). We estimated the yearly growth as an increase in
188 aboveground woody biomass divided by the length of the census interval. To estimate woody
189 NPP we multiplied the estimated change in woody biomass by the carbon content of oak
190 wood (0.47; Butt et al. 2009). We then used oak-specific NPP allocation patterns obtained
191 from (Fenn 2010) to estimate oak leaf NPP and belowground NPP (Appendix 1, Table S2).
192 To estimate the effect of herbivory on oak NPP, we estimated NPP in the absence of
193 herbivory assuming that the total NPP under normal herbivory situation was reduced to the
194 same extent (ca. 56%, Appendix 1, Table S2) as canopy gas exchange in the canopy
195 upscaling calculations described above. We then extrapolated the values per tree to estimates
196 per hectare of a plot with only oak trees, and per hectare of the actual study site.

197 *NPP through biometric measurements:* We combined data on aboveground oak NPP
198 collected in a one hectare subplot of the 18 ha forest dynamics plot with information on the

199 oak-specific ratios of wood NPP to leaf NPP and aboveground biomass to belowground
200 biomass (Fenn 2010; Fenn et al. 2015; see Appendix 1, Table S2). The biometric estimates
201 were based on dendrometer measurements (woody production), measures of leaf production
202 (litter traps) and of root production (soil respiration and inputs). We combined these
203 relationships for an estimate of whole oak NPP as Mg C yr⁻¹ per ha of the actual study site.
204 To estimate the effect of herbivory on oak NPP, we again assumed that the total NPP was
205 reduced to the same extent as canopy gas exchange in the canopy upscaling calculations
206 above.

207

208 *Predicting the effects of herbivory on canopy assimilation under varying levels of herbivory*

209 To predict the effect of herbivory on oak assimilation under different levels of caterpillar
210 herbivory, we first simulated changes in the proportions of the three different leaf types
211 (intact, systemically affected, damaged) in the oak canopy. We assumed that the ratio of
212 damaged leaves to systemically affected leaves (1:2.3) and leaf area loss per damaged leaf
213 (8.53%) stay at the same levels as observed in our herbivory surveys until all shoots have at
214 least one damaged leaf. After this, the proportion of damaged leaves was set to increase until
215 all leaves were damaged. Finally, we set the proportion of leaf area loss per leaf to increase,
216 until the tree was completely defoliated. In other words, we assumed that the herbivory first
217 spreads evenly to all shoots, then to all leaves, and then increases per leaf. LAI was assumed
218 to decrease as leaf area loss increased, increasing the amount of light reaching lower canopy
219 levels (Figure S7, Appendix 2). We assumed a linear relationship between winter moth
220 caterpillar density and leaf area loss, with 5 individuals m⁻² in 2015 (Lionel Cole,
221 unpublished data) corresponding to 5.9% leaf area loss (across the canopy) and to peak-
222 season LAI of 6.5, and maximum reported density of 1200 individuals m⁻² corresponding to
223 complete defoliation (Feeny 1970). We then estimated daytime canopy net photosynthesis

224 with herbivory levels ranging from 0% to 100% leaf area loss. To test how sensitive the
225 estimated relationship between the level of herbivory and its effect on canopy assimilation
226 was to the assumptions of our models, we estimated the same relationship under four
227 alternative scenarios: 1) the difference in photosynthetic rate between intact and damaged
228 leaves is smaller than our field measurements suggest, 2) the photosynthetic rate of intact
229 leaves increases with increasing level of herbivory in the canopy, 3) herbivory spreads
230 through the canopy following a different spatial pattern than in our initial assumptions and 4)
231 a second leaf flush compensates for some of the leaf area loss. For details, see Appendix 3.

232

233 **Results and discussion**

234 We estimate that insect herbivores remove on average $0.12 (\pm 0.02)$ Mg C ha yr⁻¹ in an oak
235 stand through leaf area loss. Through reducing photosynthesizing leaf area and the
236 photosynthetic rate of intact leaf tissue, insect herbivores prevent between $8.5 (\pm 5.1, \text{canopy}$
237 $\text{upscaling})$ and $4.1 (\pm 2.1, \text{tree census})$ Mg C ha⁻¹ yr⁻¹ of carbon from being assimilated
238 (Figure 2 and 3; Appendix 2, Figure S5). Depending on the method, we estimate the NPP of a
239 forest consisting of only mature oak trees to be between $3.4 (\pm 0.6; \text{biometric measurements})$
240 and $4.6 (\pm 1.1; \text{tree census})$ Mg C ha⁻¹ yr⁻¹ under the observed level of herbivory (5.9% leaf
241 area loss, Table 2, Figure 3). This is between $54 \pm 21\%$ to $69 \pm 42\%$ lower than the NPP of a
242 completely intact canopy (Table 2). While previous studies (Kurz et al. 2008, Clark et al.
243 2010, Schäfer et al. 2010, Heliasz et al. 2011, Metcalfe et al. 2014, Lund et al. 2017) have
244 shown that herbivore outbreaks can result in a considerable loss of carbon from the
245 ecosystem, our study suggests that insect herbivores can have a large impact on the forest
246 primary productivity even at a low density.

247 We suggest that the relationship between the intensity of herbivory and its effect on
248 ecosystem productivity is non-linear and described by two stages: first, a rapid, linear

249 increase in the effect of herbivory due to the spread of systemic effects in the canopy
250 (suppression of photosynthesis), and second, a slower non-linear increase with increasing leaf
251 area loss (Figure 4). Starting with a completely intact canopy, as the level of herbivory
252 increases, the proportion of intact, unaffected leaves decreases until the level of ca. 5%
253 herbivory (Appendix 2, Figure S6a). At this point, all shoots are likely to have at least one
254 damaged leaf, and consequently all leaves would be affected by herbivory (either directly or
255 through systemic effects). After this point, further changes in canopy photosynthesis are
256 caused entirely by the direct effects of leaf area loss (Appendix 2, Figure S6cd). Assuming
257 that the photosynthetic rate of intact leaves increases with herbivory for example as a
258 compensatory response (Thomson et al. 2003, Retuerto et al. 2004), or that part of the
259 missing leaf area is compensated through a second leaf flush reduces the magnitude of these
260 estimates, but not the shape of the relationship (Appendix 3).

261 Our study illustrates the potential magnitude of the effect of insect herbivores on
262 forest carbon cycling. Nevertheless, our estimates are based on the upscaling of leaf-level
263 measurements and on allometric relationships, rather than on direct measurements of
264 canopies and forest stands with and without herbivory. Below, we compare our results to
265 previous estimates of the effects of herbivores on forest NPP. We discuss the limitations of
266 our models and the discrepancies between our simulation and the real-world effects of
267 herbivores on ecosystem productivity.

268

269 *Previous estimates of the effects of insect herbivores on carbon cycling.* The estimates of oak
270 forest NPP under ambient herbivory levels derived through the three different methods
271 (canopy upscaling, tree census and biometric measurements; Table 2) were similar to one
272 another, and agree with previous estimates of NPP at the site (Fenn et al. 2015) and at other
273 oak-dominated temperate forests (e.g. Whitehead et al. 2004; Schäfer et al. 2010). The

274 observed leaf area loss was 5.9 %, which is close to the reported global average for forests
275 (5%; Cebrian 1999, 2004). We estimated that canopy gas exchange was reduced by 54%, and
276 whole tree NPP by 54-69% due to herbivory, depending on the estimation method. These
277 values are similar to previously published results: based on observed changes in sap flow and
278 canopy modelling, Schäfer et al. (2010) estimated that a gypsy moth outbreak reduced
279 canopy assimilation of an oak/pine forest by 24%. Focusing on the same outbreak, Clark et
280 al. (2010) estimated on average 55% reduction in net ecosystem CO₂ exchange using eddy
281 covariance and biometric measurements (Table 3). In line with our simulations, (Flower and
282 Gonzalez-Meler 2015) showed in a meta-analysis how the relationship between pest outbreak
283 intensity and its effect on forest NPP was sigmoidal rather than linear, though the effects of
284 pests were evident only after at least 30% of the basal area was affected. Comparing an
285 outbreak year to a typical (non-outbreak) level of herbivory is likely to yield different results
286 from the kind of comparison made in our study: even in years of low herbivore density, forest
287 canopies experience some herbivory (Cebrian 1999, 2004). Since the indirect suppression of
288 photosynthesis in intact plant tissue was the biggest driver of the effect of herbivory on NPP,
289 comparing a plant experiencing a low level of herbivory to a completely intact plant might
290 reveal a larger effect of herbivory than comparing a normal level of herbivory to an outbreak
291 level (Figure 4).

292 In our study, the largest effect of herbivory on NPP (69%) was estimated through the
293 canopy upscaling approach. This is most likely because stem and root respiration were
294 assumed to respond to herbivory similarly to leaf respiration, and because the difference
295 between the two scenarios (intact and with herbivory) was smaller for leaf respiration than for
296 photosynthesis. One of the biggest uncertainties in our calculations is how woody respiration
297 responds to leaf herbivory. This is a clear knowledge gap that needs to be addressed in future
298 studies. Had we assumed that a change in photosynthesis would not result in a change in stem

299 respiration, or that stem respiration would increase after herbivory, our estimate for the effect
300 of herbivory on oak NPP would have been even larger. Thus, our current assumptions on the
301 response of woody respiration to herbivory provide a more conservative estimate on the
302 effect of herbivory on forest NPP than if we had assumed constant stem respiration or an
303 increased respiration after herbivory.

304

305 *The effect of increasing herbivory pressure on forest productivity.* Our estimate of the effect
306 of herbivores on oak NPP is based on data from a year with a low winter moth population
307 density. Previous reports of winter moth outbreaks in Wytham Woods include records of
308 complete defoliation of trees (Feeny 1970). Intuitively, we might expect increasing herbivory
309 pressure to have a linearly increasing effect on ecosystem productivity. Nevertheless, the
310 herbivore-induced changes in leaf gas exchange per unit leaf area of the remaining leaf tissue
311 appear not to depend on the amount of damage per leaf (Visakorpi et al. 2018), and the vast
312 majority of leaves show some signs of feeding damage even under low herbivore densities.
313 Thus, increased herbivore densities would likely not further affect the leaf gas exchange in
314 the remaining tissue. Consequently, we predict that increases in herbivore densities above
315 those observed in our study are unlikely to result in large changes in the magnitude of the
316 effect of herbivory on ecosystem NPP, except in outbreak years with very high proportion of
317 leaf area loss (e.g. 75% or more, Figure 4). If the systemic plant responses observed in our
318 system are widespread, many forests could be at a stage where a large part of the
319 photosynthesizing plant tissue is already indirectly affected by herbivory. Consequently,
320 observing large-scale herbivore-induced changes in ecosystem productivity in natural
321 conditions might be restricted to situations with insect outbreaks.

322 The predicted magnitude of reduction in productivity caused by reduced
323 photosynthesis is large, and we recognise that this prediction needs explicit testing. There are

324 several additional factors that might change how herbivory affects ecosystem productivity
325 which have not been considered in our predictions. First, the reduced leaf area caused by
326 herbivory could increase light penetration to lower canopy layers (Anten and Ackerly 2001)
327 and increase canopy light use efficiency (Gough et al. 2013). The effect of increased light
328 penetration might compensate for some of the loss of leaf tissue (e.g. 5-30% according to
329 Anten and Ackerly, 2001). Even though our assimilation model accounts for light diffusion
330 through the canopy, and our simulations assume that LAI changes with herbivory (Appendix
331 2, Figure S7), a more detailed canopy model taking into account sunlit and shaded areas
332 could simulate the effects of increased light more accurately (Clark et al. 2011). Our model
333 also assumes that efficiency at which canopy intercepts light (i.e. the light extinction
334 coefficient, see Equation 1 in Appendix 1) is constant, which is most likely unrealistic.
335 Furthermore, how herbivory is distributed between canopy layers is currently unknown, but
336 could affect how much light reaches the lower leaves. Estimating light interception in relation
337 to herbivory-induced changes in LAI and patterns of herbivory within canopies would allow
338 better quantification of the effects of increased light at lower canopy layers.

339 Second, increased herbivory is likely to result in increased deposits of frass, insect
340 tissue, leaf fragments ('greenfall') and nutrient leaching from damaged leaves
341 ("throughfall"). Herbivore-induced reduction in tree growth could also reduce competition
342 experienced by the surrounding vegetation. The increased nutrient cycling and competitive
343 release could increase forest productivity and compensate for the loss of carbon to herbivory
344 (Gough et al. 2013, Lund et al. 2017, Costilow et al. 2017). Third, increased leaf herbivory
345 might increase carbon allocation to roots (Dyer et al. 1991), which might increase root
346 productivity and root and soil respiration (Holland et al. 1996). Fourth, the total litterfall
347 might remain unchanged even after severe defoliation due to compensating second leaf
348 flushes (Grace 1986, Clark et al. 2010). If the second leaf flush ("lammas shoots" on oak)

349 produces more leaves as a response to early-season herbivory, or if these new leaves
350 photosynthesize at a higher rate, they might compensate for the effects of herbivory on the
351 canopy gas exchange. Lastly, insect feeding can increase transport of photosynthetic end-
352 products away from certain leaves, and thereby reduce the negative effects of herbivory on
353 photosynthesis (Retuerto et al. 2004, Schwachtje and Baldwin 2008). These types of sink-
354 source dynamics might change the distribution of photosynthetic efficiency within the
355 canopy. The higher photosynthetic rate of intact leaves could thus be a compensatory
356 response to herbivory (see e.g. Thomson et al. 2003, Retuerto et al. 2004).

357 We simulated the relationship between the effect of herbivory on canopy assimilation
358 and the intensity of herbivory assuming compensatory photosynthesis and a second leaf flush.
359 If photosynthesis of intact leaves increases with increasing level of herbivory (which could be
360 assumed if the response was compensatory) the effect of herbivory on canopy assimilation
361 would be lower than without the compensatory response, especially at low herbivore
362 densities (e.g. 23% compared to 49% with 6% herbivory, Figure S8b in Appendix 3). A
363 second leaf flush occurring 1st of August, compensating 50% of the leaf area loss, would on
364 the other hand lower the estimate on the effect of herbivory at high herbivore densities: the
365 effect of herbivory would never exceed 75% (Figure S8d in Appendix 3). Compensatory
366 plant responses are likely to be important in reducing the impact of herbivory on forest
367 productivity, but their exact effect depends on the compensating mechanism. Quantifying the
368 compensatory plant responses to herbivory and the photosynthetic rate of lammas leaves
369 would be important topics for future studies in this system.

370

371 *The effect of decreasing herbivory pressure on forest productivity.* Our results indicate that
372 the lower the herbivory rate, the more important the indirect effects of herbivory on
373 photosynthesis. When only a small part of the canopy is affected by herbivores, even small

374 increases in herbivory could cause a large change in the canopy photosynthesis through the
375 disproportionate decrease in the number of intact leaves (herbivory on a single leaf will
376 trigger systemic effects on all leaves within that shoot). For example, in a study by (Zvereva
377 et al. 2012), a small increase in low intensity herbivory (from 1% to 3% leaf area loss) in
378 mountain birch (*Betula pubescens* subsp. *czerepanovii*) resulted in a much larger (30%)
379 reduction in plant growth. Nevertheless, since our study represents a year with a relatively
380 low herbivore density, situations of even lower levels of herbivory and the rapid changes in
381 productivity might be rare in natural conditions.

382 Predicting the effects of reduced levels of early-season herbivory on forest carbon
383 cycling is not straightforward. Reduced densities of herbivores early in the season could
384 result in altered investments in plant defences and change the level of herbivory experienced
385 by the host plant at a later point (Agrawal 2000, Poelman et al. 2008). Changes in the
386 frequency of insect herbivory could also change the susceptibility to plant pathogens (Felton
387 and Korth 2000, De Vos et al. 2006), which could decrease leaf photosynthesis (Copolovici
388 et al. 2014). How the interplay between different plant enemies affects carbon sequestration
389 and cycling is currently unknown.

390 The seasonal changes in oak photosynthesis in our study system (Morecroft et al.
391 2003) might depend on early-season herbivore densities. The slow onset and the late peak of
392 oak photosynthesis could be a strategy to avoid losing photosynthesised sugars to early-
393 season caterpillars and could be driven by phenotypic plasticity in the responses to the
394 intensity of early-season herbivores. The oak photosynthesis could develop faster when the
395 spring-feeding caterpillars occur at low density compared to a high-density year, changing
396 the amount of carbon sequestered over the season.

397

398 *The fate of carbon contained in the leaf area lost to herbivory.* Previous studies on the
399 patterns of leaf area loss and insect energetics allows us to estimate the pathways of carbon
400 once it is removed from the canopy. Based on previous studies on the amounts of greenfall
401 (falling leaf fragments due to herbivore feeding), roughly 75% of the lost leaf area is ingested
402 by the caterpillars (Russell et al. 2004). Of the ingested carbon, approximately 15% will be
403 respired, 60% will be turned into frass and transported into the soil, and the rest will turn into
404 insect tissue (of lepidopteran caterpillars; Wiegert and Petersen 1983). Based on estimated
405 predation rates of winter moth caterpillars and cadavers, most of this insect tissue will be
406 eaten by predators (East 1974). Thus, we estimate that 18% of the carbon contained in the
407 observed leaf area lost to herbivory ($0.02 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$) is likely to be transferred to higher
408 trophic levels in this system, and 70% of the leaf area loss ($0.08 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$) is directly
409 deposited in the soil, partly as greenfall and partly as frass (Figure 5). Data on the amount of
410 plant biomass consumed by herbivores have been collected for several ecosystems (Cebrian
411 2004). By using similar calculations here, it could be possible to estimate herbivore-mediated
412 carbon fluxes to soil or higher trophic levels for a wide variety of ecosystems (see e.g.
413 Metcalfe and others 2014).

414

415 *Conclusions*

416 We propose that insect herbivores can, even at low densities, have a large effect on
417 ecosystem NPP in a temperate deciduous forest, mainly through indirect changes in the rates
418 of canopy gas exchange. Most forest ecosystems might naturally be in a state where
419 photosynthesis is substantially reduced by the effects of herbivory, in particular by the
420 indirect effects. The relationship between the intensity of herbivory and its effects on the host
421 plant is most likely non-linear. At low herbivore densities, the effect of herbivory on NPP is
422 primarily driven by changes in leaf gas exchange in the remaining leaf tissue, while the

423 contribution of leaf area loss increases with increasing herbivore abundances. We predict that
424 comparisons of productivity between completely intact plants and plants with even a small
425 amount of herbivory-inflicted damage are likely to yield large estimates on the effects of
426 herbivory on plant productivity. On the other hand, comparisons between plants experiencing
427 low (but non-zero) and high levels of herbivory are likely to result in lower estimates on the
428 effect of herbivory. The presence of compensatory plant responses, like increased
429 photosynthesis or additional leaf flushes will likely reduce the impact of herbivory, the exact
430 effect depending on the compensating mechanism. Further and more detailed studies
431 including different study systems and species are needed to validate whether the proposed
432 relationship between intensity of herbivory and its effect on plant productivity holds. Where
433 there is strong interannual variability in herbivory, ecosystem measurements of productivity,
434 such as eddy covariance approaches (Thomas et al. 2011) or detailed estimates on tree growth
435 (Varley and Gradwell 1962, Whittaker and Warrington 1985, Zvereva et al. 2012) could be
436 coupled with herbivory measurements to test this relationship. The distributions and
437 abundances of insect herbivores are likely to change in the future (Ayres and Lombardero
438 2000, Jepsen et al. 2008, Kurz et al. 2008), with increasing temperature (Bale et al. 2002),
439 CO₂ concentration (Stiling et al. 2009), drought (Gaylord et al. 2013) and advancing
440 phenology (Charmantier et al. 2008) affecting the intensity of herbivory differently.
441 Quantifying the effect of insect herbivores carbon cycling is therefore an intriguing and
442 important avenue of research.

443

444 **Acknowledgements**

445 We thank Lionel Cole for providing data on winter moth abundances, Alexander Shenkin and
446 Kieran Walker for the stem respiration data and the Journal Club of the Ecosystems lab and
447 three anonymous reviewers for helpful comments on the text. KV was funded by Osk.

448 Huttunen Foundation and Finnish Cultural Foundation. SG is a Royal Society University
449 Research Fellow. YM was supported by the Jackson Foundation and by a European Research
450 Council Advanced Investigator Grant (GEM-TRAIT: 321131).

451

452 **References**

- 453 Agrawal, A. A. 2000. Specificity of induced resistance in wild radish: causes and
454 consequences for two specialist and two generalist caterpillars. *Oikos* 89:493–500.
- 455 Amiro, B. D., A. G. Barr, J. G. Barr, T. A. Black, R. Bracho, M. Brown, J. Chen, K. L. Clark,
456 K. J. Davis, A. R. Desai, S. Dore, V. Engel, J. D. Fuentes, A. H. Goldstein, M. L.
457 Goulden, T. E. Kolb, M. B. Lavigne, B. E. Law, H. A. Margolis, T. Martin, J. H.
458 McCaughey, L. Misson, M. Montes-Helu, A. Noormets, J. T. Randerson, G. Starr,
459 and J. Xiao. 2010. Ecosystem carbon dioxide fluxes after disturbance in forests of
460 North America. *Journal of Geophysical Research* 115:G00K02.
- 461 Anten, N. P. R., and D. D. Ackerly. 2001. Canopy-level photosynthetic compensation after
462 defoliation in a tropical understorey palm. *Functional Ecology* 15.
- 463 Ayres, M. P., and M. J. Lombardero. 2000. Assessing the consequences of global change for
464 forest disturbance from herbivores and pathogens. *Science of The Total Environment*
465 262:263–286.
- 466 Bale, J. S., G. J. Masters, I. D. Hodkinson, C. Awmack, T. M. Bezemer, V. K. Brown, J.
467 Butterfield, A. Buse, J. C. Coulson, J. Farrar, J. E. G. Good, R. Harrington, S. Hartley,
468 T. H. Jones, R. L. Lindroth, M. C. Press, I. Symrnioudis, A. D. Watt, and J. B.
469 Whittaker. 2002. Herbivory in global climate change research: direct effects of rising
470 temperature on insect herbivores. *Global Change Biology* 8:1–16.

- 471 Bilgin, D. D., J. A. Zavala, J. Zhu, S. J. Clough, D. R. Ort, and E. H. DeLucia. 2010. Biotic
472 stress globally downregulates photosynthesis genes. *Plant, Cell & Environment*
473 33:1597–1613.
- 474 Butt, N., G. Campbell, Y. Malhi, M. Morecroft, K. Fenn, and M. Thomas. 2009. Initial
475 results from establishment of a long-term broadleaf monitoring plot at Wytham
476 Woods, Oxford, UK. University of Oxford, Oxford.
- 477 Campioli, M., Y. Malhi, S. Vicca, S. Luysaert, D. Papale, J. Peñuelas, M. Reichstein, M.
478 Migliavacca, M. A. Arain, and I. A. Janssens. 2016. Evaluating the convergence
479 between eddy-covariance and biometric methods for assessing carbon budgets of
480 forests. *Nature Communications* 7:13717.
- 481 Cebrian, J. 1999. Patterns in the fate of production in plant communities. *The American*
482 *Naturalist* 154:449–468.
- 483 Cebrian, J. 2004. Role of first-order consumers in ecosystem carbon flow. *Ecology Letters*
484 7:232–240.
- 485 Chapin, F. S. 1997. Biotic Control over the Functioning of Ecosystems. *Science* 277:500–
486 504.
- 487 Charmantier, A., R. H. McCleery, L. R. Cole, C. Perrins, L. E. B. Kruuk, and B. C. Sheldon.
488 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird
489 population. *Science* 320:800–803.
- 490 Clark, D. B., L. M. Mercado, S. Sitch, C. D. Jones, N. Gedney, M. J. Best, M. Pryor, G. G.
491 Rooney, R. L. H. Essery, E. Blyth, O. Boucher, R. J. Harding, C. Huntingford, and P.
492 M. Cox. 2011. The Joint UK Land Environment Simulator (JULES), model
493 description – Part 2: Carbon fluxes and vegetation dynamics. *Geoscientific Model*
494 *Development* 4:701–722.

- 495 Clark, K. L., N. Skowronski, and J. Hom. 2010. Invasive insects impact forest carbon
496 dynamics: defoliation and forest carbon dynamics. *Global Change Biology* 16:88–
497 101.
- 498 Copolovici, L., F. Vaartnou, M. P. Estrada, and U. Niinemets. 2014. Oak powdery mildew
499 (*Erysiphe alphitoides*)-induced volatile emissions scale with the degree of infection in
500 *Quercus robur*. *Tree Physiology* 34:1399–1410.
- 501 Costilow, K. C., K. S. Knight, and C. E. Flower. 2017. Disturbance severity and canopy
502 position control the radial growth response of maple trees (*Acer* spp.) in forests of
503 northwest Ohio impacted by emerald ash borer (*Agrilus planipennis*). *Annals of*
504 *Forest Science* 74:10.
- 505 De Vos, M., W. van Zaalen, A. Koornneef, J. P. Korzelius, M. Dicke, L. C. Van Loon, and C.
506 M. J. Pieterse. 2006. Herbivore-induced resistance against microbial pathogens in
507 *Arabidopsis*. *Plant Physiology* 142:352–363.
- 508 Dyer, M. I., M. A. Acra, G. M. Wang, D. C. Coleman, D. W. Freckman, S. J. McNaughton,
509 and B. R. Strain. 1991. Source-sink carbon relations in two *Panicum coloratum*
510 ecotypes in response to herbivory. *Ecology* 72:1472–1483.
- 511 East, R. 1974. Predation on the soil-dwelling stages of the winter moth at Wytham Woods,
512 Berkshire. *The Journal of Animal Ecology* 43:611.
- 513 Edburg, S. L., J. A. Hicke, P. D. Brooks, E. G. Pendall, B. E. Ewers, U. Norton, D. Gochis, E.
514 D. Gutmann, and A. J. Meddens. 2012. Cascading impacts of bark beetle-caused tree
515 mortality on coupled biogeophysical and biogeochemical processes. *Frontiers in*
516 *Ecology and the Environment* 10:416–424.
- 517 Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter,
518 T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen,
519 R. T. Paine, E. K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J.

- 520 B. Shurin, A. R. E. Sinclair, M. E. Soulé, R. Virtanen, and D. A. Wardle. 2011.
521 Trophic downgrading of planet Earth. *Science* 333:301–306.
- 522 Feeny, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring
523 feeding by Winter moth caterpillars. *Ecology* 51:565–581.
- 524 Felton, G. W., and K. L. Korth. 2000. Trade-offs between pathogen and herbivore resistance.
525 *Current Opinion in Plant Biology* 3:309–314.
- 526 Fenn, K. M. 2010. Carbon cycling in British deciduous woodland: processes, budgets,
527 climate & phenology. DPhil, University of Oxford.
- 528 Fenn, K., Y. Malhi, M. Morecroft, C. Lloyd, and M. Thomas. 2015. The carbon cycle of a
529 maritime ancient temperate broadleaved woodland at seasonal and annual scales.
530 *Ecosystems* 18:1–15.
- 531 Flower, C. E., and M. A. Gonzalez-Meler. 2015. Responses of Temperate Forest Productivity
532 to Insect and Pathogen Disturbances. *Annual Review of Plant Biology* 66:547–569.
- 533 Flower, C. E., K. S. Knight, and M. A. Gonzalez-Meler. 2013. Impacts of the emerald ash
534 borer (*Agrilus planipennis* Fairmaire) induced ash (*Fraxinus* spp.) mortality on forest
535 carbon cycling and successional dynamics in the eastern United States. *Biological*
536 *Invasions* 15:931–944.
- 537 Forister, M. L., V. Novotny, A. K. Panorska, L. Baje, Y. Basset, P. T. Butterill, L. Cizek, P.
538 D. Coley, F. Dem, I. R. Diniz, P. Drozd, M. Fox, A. E. Glassmire, R. Hazen, J. Hreck,
539 J. P. Jahner, O. Kaman, T. J. Kozubowski, T. A. Kursar, O. T. Lewis, J. Lill, R. J.
540 Marquis, S. E. Miller, H. C. Morais, M. Murakami, H. Nickel, N. A. Pardikes, R. E.
541 Ricklefs, M. S. Singer, A. M. Smilanich, J. O. Stireman, S. Villamarín-Cortez, S.
542 Vodka, M. Volf, D. L. Wagner, T. Walla, G. D. Weiblen, and L. A. Dyer. 2015. The
543 global distribution of diet breadth in insect herbivores. *Proceedings of the National*
544 *Academy of Sciences* 112:442–447.

- 545 Gaylord, M. L., T. E. Kolb, W. T. Pockman, J. A. Plaut, E. A. Yepez, A. K. Macalady, R. E.
546 Pangle, and N. G. McDowell. 2013. Drought predisposes piñon-juniper woodlands to
547 insect attacks and mortality. *New Phytologist* 198:567–578.
- 548 Gough, C. M., B. S. Hardiman, L. E. Nave, G. Bohrer, K. D. Maurer, C. S. Vogel, K. J.
549 Nadelhoffer, and P. S. Curtis. 2013. Sustained carbon uptake and storage following
550 moderate disturbance in a Great Lakes forest. *Ecological Applications* 23:1202–1215.
- 551 Grace, J. R. 1986. The influence of gypsy moth on the composition and nutrient content of
552 litter fall in a pennsylvania oak forest. *Forest Science* 32:855–870.
- 553 Griffin, K. L., D. T. Tissue, M. H. Turnbull, W. Schuster, and D. Whitehead. 2001. Leaf dark
554 respiration as a function of canopy position in *Nothofagus fusca* trees grown at
555 ambient and elevated CO₂ partial pressures for 5 years. *Functional Ecology* 15:497–
556 505.
- 557 Heliasz, M., T. Johansson, A. Lindroth, M. Mölder, M. Mastepanov, T. Friborg, T. V.
558 Callaghan, and T. R. Christensen. 2011. Quantification of C uptake in subarctic birch
559 forest after setback by an extreme insect outbreak: carbon uptake setback by insect
560 outbreak. *Geophysical Research Letters* 38.
- 561 Holland, J. N., W. Cheng, and D. A. Crossley. 1996. Herbivore-induced changes in plant
562 carbon allocation: assessment of below-ground C fluxes using carbon-14. *Oecologia*
563 107:87–94.
- 564 Hunter, M. D. 1992. Interactions within herbivore communities mediated by the host plant:
565 the keystone herbivore concept. Pages 287–325 *in* M. D. Hunter, T. Ohgushi, and P.
566 W. Price, editors. *Effects of resource distribution on animal–plant interactions*.
567 Academic Press, Inc., San Diego, California, USA.
- 568 Jepsen, J. U., S. B. Hagen, R. A. Ims, and N. G. Yoccoz. 2008. Climate change and outbreaks
569 of the geometrids *Operophtera brumata* and *Epirrita autumnata* in subarctic birch

- 570 forest: evidence of a recent outbreak range expansion. *Journal of Animal Ecology*
571 77:257–264.
- 572 Kurz, W. A., C. C. Dymond, G. Stinson, G. J. Rampley, E. T. Neilson, A. L. Carroll, T.
573 Ebata, and L. Safranyik. 2008. Mountain pine beetle and forest carbon feedback to
574 climate change. *Nature* 452:987–990.
- 575 Lund, M., K. Raundrup, A. Westergaard-Nielsen, E. López-Blanco, J. Nymand, and P.
576 Aastrup. 2017. Larval outbreaks in West Greenland: Instant and subsequent effects on
577 tundra ecosystem productivity and CO₂ exchange. *Ambio* 46:26–38.
- 578 Mercado, L. M., C. Huntingford, J. H. C. Gash, P. M. Cox, and V. Jogleddy. 2007.
579 Improving the representation of radiation interception and photosynthesis for climate
580 model applications. *Tellus B: Chemical and Physical Meteorology* 59:553–565.
- 581 Metcalfe, D. B., G. P. Asner, R. E. Martin, J. E. Silva Espejo, W. H. Huasco, F. F. Farfán
582 Amézquita, L. Carranza-Jimenez, D. F. Galiano Cabrera, L. D. Baca, F. Sinca, L. P.
583 Huaraca Quispe, I. A. Taype, L. E. Mora, A. R. Dávila, M. M. Solórzano, B. L. Puma
584 Vilca, J. M. Laupa Román, P. C. Guerra Bustios, N. S. Revilla, R. Tupayachi, C. A. J.
585 Girardin, C. E. Doughty, and Y. Malhi. 2014. Herbivory makes major contributions to
586 ecosystem carbon and nutrient cycling in tropical forests. *Ecology Letters* 17:324–
587 332.
- 588 Meza-Canales, I. D., S. Meldau, J. A. Zavala, and I. T. Baldwin. 2017. Herbivore perception
589 decreases photosynthetic carbon assimilation and reduces stomatal conductance by
590 engaging 12-oxo-phytodienoic acid, mitogen-activated protein kinase 4 and cytokinin
591 perception. *Plant, Cell & Environment* 40:1039–1056.
- 592 Monsi, M., and T. Saeki. 1953. Ueber den Lichtfaktor in den Pflanzengesellschaften und seine
593 Bedeutung fuer die Stoffproduktion. *Journal of Japanese Botany*:22–52.

- 594 Morecroft, M. D., V. J. Stokes, and J. I. L. Morison. 2003. Seasonal changes in the
595 photosynthetic capacity of canopy oak (*Quercus robur*) leaves: the impact of slow
596 development on annual carbon uptake. *International Journal of Biometeorology*
597 47:221–226.
- 598 Nability, P. D., J. A. Zavala, and E. H. DeLucia. 2009. Indirect suppression of photosynthesis
599 on individual leaves by arthropod herbivory. *Annals of Botany* 103:655–663.
- 600 Nykänen, H., and J. Koricheva. 2004. Damage-induced changes in woody plants and their
601 effects on insect herbivore performance: a meta-analysis. *Oikos* 104:247–268.
- 602 Oleksyn, J., P. Karolewski, M. J. Giertych, R. Zytowskiak, P. B. Reich, and M. G. Tjoelker.
603 1998. Primary and secondary host plants differ in leaf-level photosynthetic response
604 to herbivory: evidence from *Alnus* and *Betula* grazed by the alder beetle, *Agelastica*
605 *alni*. *New Phytologist* 140:239–249.
- 606 Poelman, E. H., C. Broekgaarden, J. J. A. Van Loon, and M. Dicke. 2008. Early season
607 herbivore differentially affects plant defence responses to subsequently colonizing
608 herbivores and their abundance in the field. *Molecular Ecology* 17:3352–3365.
- 609 Rennie, S., J. Adamson, R. Anderson, C. Andrews, J. Bater, N. Bayfield, K. Beaton, D.
610 Beaumont, S. Benham, V. Bowmaker, C. Britt, R. Brooker, D. Brooks, J. Brunt, G.
611 Common, R. Cooper, S. Corbett, N. Critchley, P. Dennis, J. Dick, B. Dodd, N. Dodd,
612 N. Donovan, J. Easter, E. Eaton, M. Flexen, A. Gardiner, D. Hamilton, P. Hargreaves,
613 M. Hatton-Ellis, M. Howe, J. Kahl, M. Lane, S. Langan, D. Lloyd, B. McCarney, Y.
614 McElarney, C. McKenna, S. McMillan, F. Milne, L. Milne, M. Morecroft, M.
615 Murphy, A. Nelson, H. Nicholson, D. Pallett, D. Parry, I. Pearce, G. Pozsgai, R. Rose,
616 S. Schafer, T. Scott, L. Sherrin, C. Shortall, R. Smith, P. Smith, R. Tait, C. Taylor, M.
617 Taylor, M. Thurlow, A. Turner, K. Tyson, H. Watson, M. Whittaker, M. Wilkinson,

- 618 and C. Wood. 2017. UK Environmental Change Network (ECN) meteorology data:
619 1991-2015. NERC Environmental Information Data Centre.
- 620 Retuerto, R., B. Fernandez-Lema, Rodriguez-Roiloa, and J. R. Obeso. 2004. Increased
621 photosynthetic performance in holly trees infested by scale insects. *Functional*
622 *Ecology* 18:664–669.
- 623 Russell, C. A., K. R. Kosola, E. A. Paul, and G. P. Robertson. 2004. Nitrogen cycling in
624 poplar stands defoliated by insects. *Biogeochemistry* 68:365–381.
- 625 Savill, P. S., editor. 2011. *Wytham woods: Oxford's ecological laboratory*. Oxford Univ.
626 Press, Oxford.
- 627 Schäfer, K. V. R., K. L. Clark, N. Skowronski, and E. P. Hamerlynck. 2010. Impact of insect
628 defoliation on forest carbon balance as assessed with a canopy assimilation model.
629 *Global Change Biology* 16:546–560.
- 630 Schmitz, O. J., P. A. Raymond, J. A. Estes, W. A. Kurz, G. W. Holtgrieve, M. E. Ritchie, D.
631 E. Schindler, A. C. Spivak, R. W. Wilson, M. A. Bradford, V. Christensen, L.
632 Deegan, V. Smetacek, M. J. Vanni, and C. C. Wilmers. 2014. Animating the carbon
633 cycle. *Ecosystems* 17:344–359.
- 634 Schoonhoven, L. M., J. J. A. van Loon, and M. Dicke. 2005. *Insect-plant biology*. 2nd ed.
635 Oxford University Press, Oxford, UK.
- 636 Schwachtje, J., and I. T. Baldwin. 2008. Why does herbivore attack reconfigure primary
637 metabolism? *Plant Physiology* 146:845–851.
- 638 Stiling, P., D. Moon, A. Rossi, B. A. Hungate, and B. Drake. 2009. Seeing the forest for the
639 trees: long-term exposure to elevated CO₂ increases some herbivore densities. *Global*
640 *Change Biology* 15:1895–1902.

- 641 Stokes, V. 2000. Effects of microenvironment and leaf developmental characteristics on
642 annual carbon gain and water use in two deciduous tree species. DPhil, University of
643 Oxford.
- 644 Strickland, M. S., D. Hawlena, A. Reese, M. A. Bradford, and O. J. Schmitz. 2013. Trophic
645 cascade alters ecosystem carbon exchange. *Proceedings of the National Academy of*
646 *Sciences* 110:11035–11038.
- 647 Strong, D. R., J. H. Lawton, and R. Southwood. 1984. *Insects on Plants*. First edition.
648 Blackwells Scientific Publications, Southampton, United Kingdom.
- 649 Thomas, M. V., Y. Malhi, K. M. Fenn, J. B. Fisher, M. D. Morecroft, C. R. Lloyd, M. E.
650 Taylor, and D. D. McNeil. 2011. Carbon dioxide fluxes over an ancient broadleaved
651 deciduous woodland in southern England. *Biogeosciences* 8:1595–1613.
- 652 Thomson, V., S. Cunningham, M. Ball, and A. Nicotra. 2003. Compensation for herbivory by
653 *Cucumis sativus* through increased photosynthetic capacity and efficiency. *Oecologia*
654 134:167–175.
- 655 Varley, G. C., and G. R. Gradwell. 1962. The effect of partial defoliation by caterpillars on
656 the timber production by oak trees in England. *Proceedings of the XIth International*
657 *Congress of Entomology (Vienna 1960)* 2:211–214.
- 658 Visakorpi, K., S. Gripenberg, Y. Malhi, C. Bolas, I. Oliveras, N. Harris, S. Rifai, and T.
659 Riutta. 2018. Small-scale indirect plant responses to insect herbivory could have
660 major impacts on canopy photosynthesis and isoprene emission. *New Phytologist* 220.
- 661 Visakorpi, K., T. Riutta, Y. Malhi, J.-P. Salminen, N. Salinas, and S. Gripenberg. 2020.
662 Changes in oak (*Quercus robur*) photosynthesis after winter moth (*Operophtera*
663 *brumata*) herbivory are not explained by changes in chemical or structural leaf traits.
664 *PLOS ONE* 15:e0228157.

- 665 Walker, K. 2017. Variation and patterns of CO₂ efflux and sapwood content of three
666 deciduous broadleaved trees. B.S. thesis, University of Oxford, Oxford, UK.
- 667 Wertin, T. M., and R. O. Teskey. 2008. Close coupling of whole-plant respiration to net
668 photosynthesis and carbohydrates. *Tree Physiology* 28:1831–1840.
- 669 Whitehead, D., K. L. Griffin, M. H. Turnbull, D. T. Tissue, V. C. Engel, K. J. Brown, W. S.
670 F. Schuster, and A. S. Walcroft. 2004. Response of total night-time respiration to
671 differences in total daily photosynthesis for leaves in a *Quercus rubra* L. canopy:
672 implications for modelling canopy CO₂ exchange. *Global Change Biology* 10:925–
673 938.
- 674 Whittaker, J. B., and S. Warrington. 1985. An Experimental Field Study of Different Levels
675 of Insect Herbivory Induced By *Formica rufa* Predation on Sycamore (*Acer*
676 *pseudoplatanus*) III. Effects on Tree Growth. *The Journal of Applied Ecology* 22:797.
- 677 Wiegert, R. G., and C. E. Petersen. 1983. Energy transfer in insects. *Annual Review of*
678 *Entomology* 28:455–486.
- 679 Wilmers, C. C., and O. J. Schmitz. 2016. Effects of gray wolf-induced trophic cascades on
680 ecosystem carbon cycling. *Ecosphere* 7:e01501.
- 681 Zangerl, A. R., J. G. Hamilton, T. J. Miller, A. R. Crofts, K. Oxborough, M. R. Berenbaum,
682 and E. H. DeLucia. 2002. Impact of folivory on photosynthesis is greater than the sum
683 of its holes. *Proceedings of the National Academy of Sciences* 99:1088–1091.
- 684 Zimov, N. S., S. A. Zimov, A. E. Zimova, G. M. Zimova, V. I. Chuprynin, and F. S. Chapin.
685 2009. Carbon storage in permafrost and soils of the mammoth tundra-steppe biome:
686 Role in the global carbon budget. *Geophysical Research Letters* 36.
- 687 Zvereva, E. L., V. Zverev, and M. V. Kozlov. 2012. Little strokes fell great oaks: minor but
688 chronic herbivory substantially reduces birch growth. *Oikos* 121:2036–2043.
- 689

690 **Table 1.** Characteristics of the study site, and the five oak trees used for the gas exchange measurements and
 691 herbivory manipulations. Errors are ± 1 SEM.

Plot-level measures	Value	Year	Reference
Annual rainfall	637 mm	2015	Rennie et al. 2017
Mean annual temperature	10.2 °C	2015	Rennie et al. 2017
Mean daytime summer temperature	13.8 °C	2015	Rennie et al. 2017
Mean night-time summer temperature	10.7 °C	2015	Rennie et al. 2017
Total stem density (>1 cm dbh)	1128.2 ha ⁻¹	2008	Butt et al. 2009
Total basal area (>10 cm dbh)	33.3 m ² ha ⁻¹	2008	Butt et al. 2009
Peak LAI	7.8 m ² m ⁻²	2008	Thomas et al. 2011
	6.5 m ² m ⁻²	2007	Fenn 2010
	ca. 6.5 m ² m ⁻²		Nils Rutjes 2016, unpublished data
Stem area index	1.5 m ² m ⁻²	2008	Fenn et al. 2015
Average oak budburst	19 th April	1996, 1999, 2000	Morecroft et al. 2003
100% oak leaf fall	22 nd November	2007	Fenn 2010
Peak oak photosynthesis	4 th July	1999	Morecroft et al. 2003
Percentage of oak of total LAI	11 \pm 3 %	2007	Fenn 2010
Oak basal area	6.7 m ² ha ⁻¹	2008	Butt et al. 2009
Biometric GPP	21.9 Mg C ha ⁻¹ yr ⁻¹	2008	Fenn et al. 2015
Eddy flux GPP	21.1 Mg C ha ⁻¹ yr ⁻¹	2008	Thomas et al. 2011
Biometric NPP	7.0 Mg C ha ⁻¹ yr ⁻¹	2008	Fenn et al. 2015
Eddy flux NEP	1.2 Mg C ha ⁻¹ yr ⁻¹	2008	Thomas et al. 2011
Biometric R _{eco}	20.3 Mg C ha ⁻¹ yr ⁻¹	2008	Fenn et al. 2015
Eddy flux R _{eco}	19.8 Mg C ha ⁻¹ yr ⁻¹	2008	Thomas et al. 2011
The five intensively studied oak trees			
Age	150 - 200 years		Morecroft et al. 2003
Mean dbh	67.2 cm \pm 5.4 cm	2017	Y. Malhi, unpublished analysis
Mean height	21.6 m \pm 0.6 m	2017	this study
Mean % of herbivory	5.9 % \pm 0.4 %	2015	Visakorpi et al. 2018
Mean A _{sat}	16.1 \pm 1.2 μ mol m ⁻² s ⁻¹	2015	Visakorpi et al. 2018
Mean leaf mass per area	64.6 \pm 0.9 gm ⁻²	2015	Visakorpi et al. 2020
Mean C % in leaf tissue	47.8 \pm 0.8 %	2016	Visakorpi et al. 2020

692
 693 **dbh – diameter at breast height (1.3 m), LAI – leaf area index, GPP – gross primary**
 694 **productivity, NPP – net primary productivity, NEP – net ecosystem productivity, R_{eco} –**
 695 **ecosystem respiration, A_{sat} – light saturated photosynthesis**
 696

697

698 **Table 2.** Oak net primary productivity (NPP) for intact canopy and canopy under normal level of herbivory and
 699 the effect of herbivory on the NPP estimated with different methods (canopy upscaling, biometric
 700 measurements, and tree census) and at different scales: a hypothetical plot consisting only of oak trees (basal
 701 area of 33.3 m² ha⁻¹), and the measured site (basal area of oaks 6.7 m² ha⁻¹, 20% of the total basal area). The
 702 errors are propagated measuring errors and uncertainties related to the different scaling functions. The unit in the
 703 table is Mg C ha⁻¹ year⁻¹.

	NPP	±	NPP	±	Herbivory	±	Herbivory	±
	Normal	error	Intact	error	effect, C	error	effect %	error
	herbivory		canopy					
Per plot of only oak								
Canopy upscaling	3.8	4.9	12.3	8.2	8.5	5.1	69.4	41.6
Biometric measurements	4.6	1.1	10.0	1.8	5.4	2.1	54.3	20.9
Tree census	3.5	0.6	7.5	2.2	4.1	2.3	54.3	30.4
Per real plot (counting only oak trees)								
Canopy upscaling	0.8	1.0	2.5	1.7	1.7	1.0	69.4	41.6
Biometric measurements	0.9	0.2	2.0	0.4	1.1	0.4	54.3	20.9
Tree census	0.6	0.1	1.2	0.4	0.7	0.4	54.3	30.4

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706 **Table 3.** Previous estimates on the effects of insect herbivores on ecosystem carbon cycling. The baseline estimate represents productivity under normal level of herbivory
 707 (e.g. before an insect outbreak), or in the absence of herbivores (this study and Dungan et al. 2007). Herbivory level is percentage of leaf area loss, unless otherwise stated.

Reference	Baseline Mg C ha ⁻¹ yr ⁻¹	Baseline measure	Herbivore effect Mg C ha ⁻¹ yr ⁻¹	Herbivore effect %	Method	Study system	Herbivore species	Herbivory level
Nardini et al. 2004	5	NPP	-4.3	-85%	Gas exchange and canopy model	Horse chestnut (<i>Aesculus hippocastanum</i>)	Leafminer (<i>Cameraria ohridella</i>)	25-60% of LAI
Dungan et al. 2007	17.2	Canopy photosynthesis	0.7	4%	Canopy model	Beech (<i>Nothofagus solandri</i>)	Scale insect (<i>Ultracoelostoma assimile</i>)	0 (phloem feeding)
Cook a et al. 2008	3.7	NEP	-3.0	-79%	Model and eddy covariance	Temperate deciduous forest	Tent caterpillar (<i>Malacosoma disstria</i>)	34%
Kurz et al. 2008	-	NBP	-0.4	-	Forest ecosystem model	Pine /spruce	Pine beetle (<i>Dendroctonus ponderosae</i>)	-
Clark et al. 2010	1.9	NEP	-0.7-4.8	[-34%, -57%]	Eddy covariance and biometric measurements	Oak /pine	Gypsy moth (<i>Lymantria dispar</i>)	> 75%
Schäfer et al. 2010	12.4	Canopy photosynthesis	-3	-24%	Sap-flow based canopy modelling	Oak /pine	Gypsy moth (<i>Lymantria dispar</i>)	> 75%
Heliasz et al. 2011	1.1	NEP	-0.9	-89%	Eddy covariance	Mountain birch (<i>Betula pubescens</i>)	Autumnal moth (<i>Epirrita autumnata</i>)	100%
Malhi et al. 2014	14.2-15	NPP	-1.5	-11%	Estimation of leaf area loss	Tropical forest	Several	18.80%
Flower et al. 2012	3.4	NPP	-1.5	-43%	Biometric measurements	Ash (<i>Fraxinus americana</i>)	Emerald ash borer	-

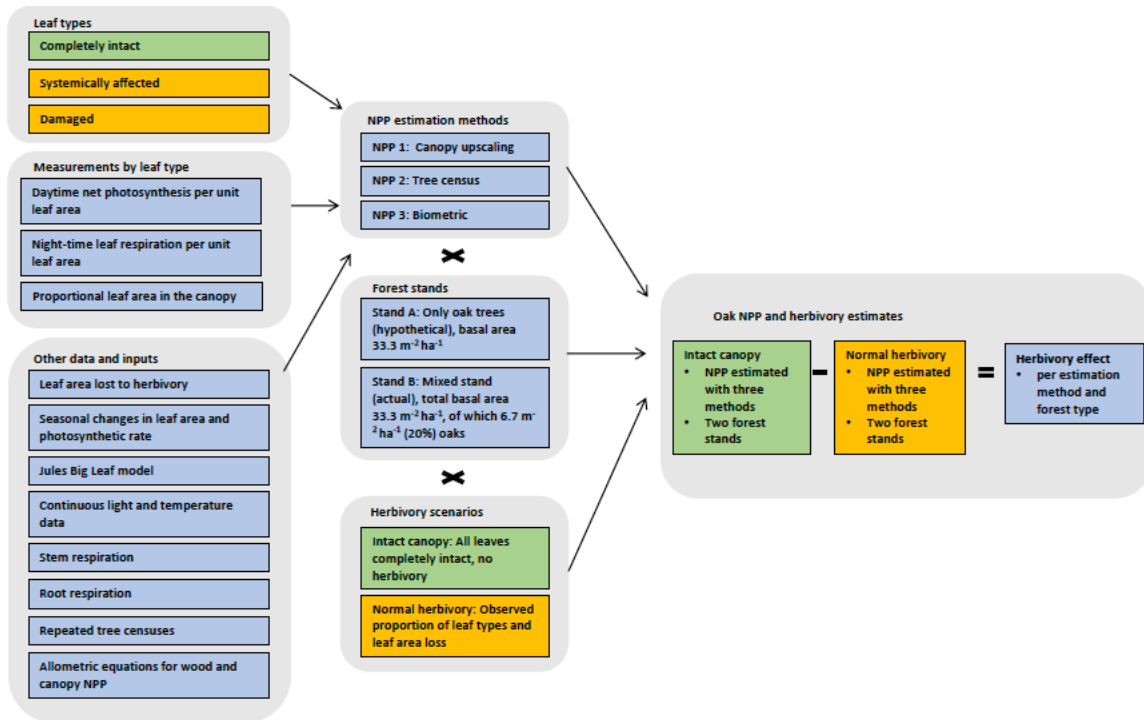
Metcalfe et al. 2013	2-5	Foliar production	-0.3-0.9	[-12%, -19%]	Estimation of leaf area loss	Tropical forest	Several	19-20%
Strickland et al. 2013	-	-	-	-33%	¹³ C pulse chace experiment	Meadow	Grasshopper (<i>Melanoplus femurrubrum</i>)	32gm ⁻² of biomass
Lund et al. 2017	4.5	NEP	-2.6	-58%	Chamber-based CO ₂ exchange	Tundra	Moth (<i>Eurois occulta</i>)	100%
this study	11.1	Oak NPP	-8.5	-69%	Leaf gas exchange	Oak (<i>Quercus robur</i>)	Early-season moth caterpillars	6%
			-0.1		Leaf area loss			

NPP – net primary productivity, NEP – net ecosystem productivity, NBP – net biome productivity

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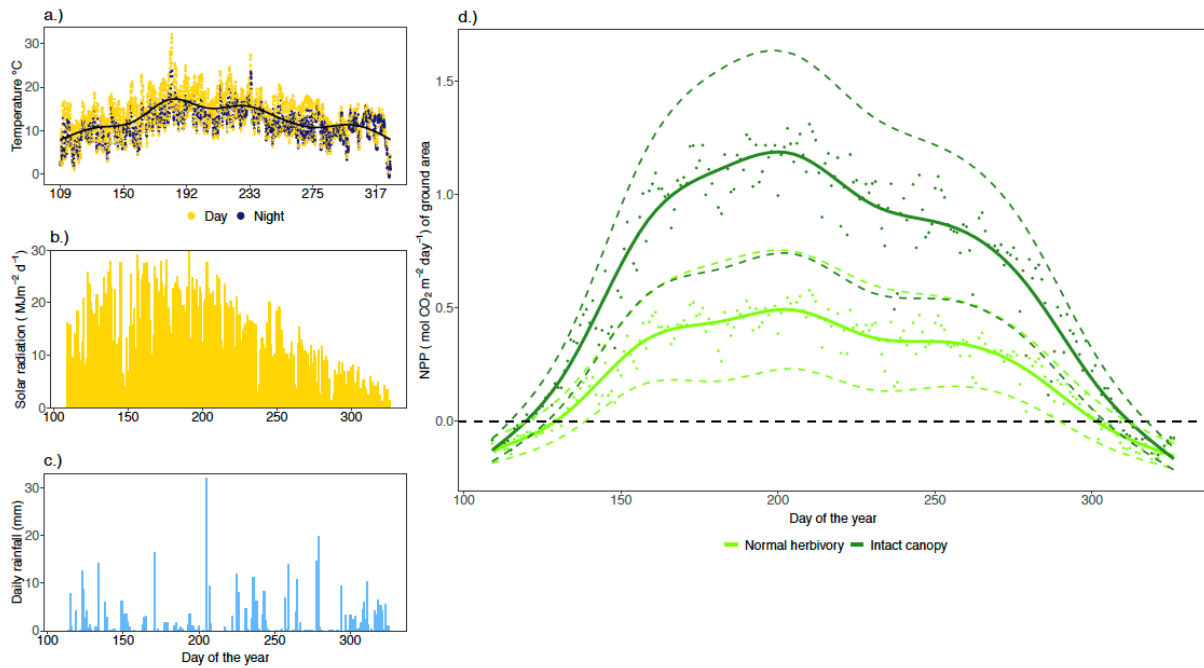


712

713 **Figure 1.** The summary of the data inputs and methods used to estimate NPP and the effect of herbivory.

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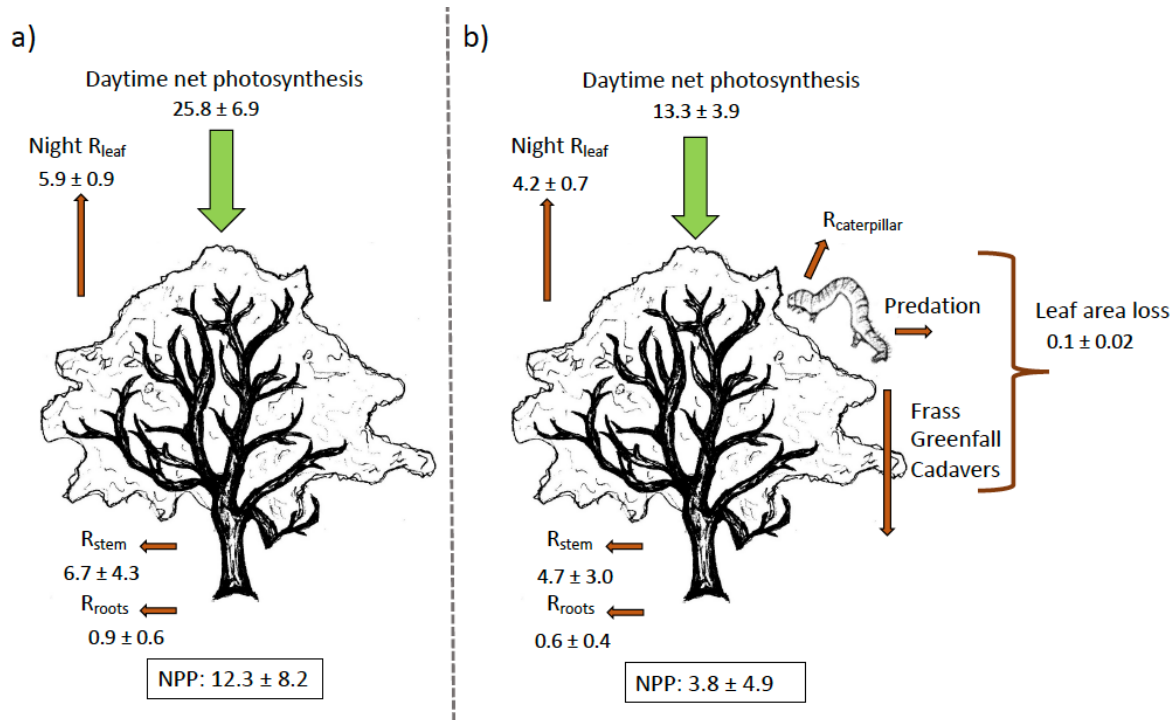


716

717 **Figure 2.** Meteorological data and net primary productivity in Wytham Woods. a) Hourly temperature for the
718 growing season 2015 (19th April – 22nd November), which were used for upscaling stem, root and night-time
719 canopy respiration. The average temperature was 13.8 °C during the day and 10.7 °C during the night. b) Solar
720 radiation per day over the season 2014, which was used to upscale the canopy photosynthesis measurements. c)
721 Amount of rainfall per day over the growing season 2015 (not used in the data analyses or upscaling). The
722 annual rainfall (637 mm) was slightly less than the 1993–2010 average of 714 mm (Fenn et al. 2015). d) Net
723 primary productivity (NPP) per m² of ground area based on data from five oak trees during the growing season
724 2015. The “intact canopy” scenario is based on measurements on intact leaves surrounded by only intact leaves,
725 whereas the estimates under “normal herbivory” are based on photosynthesis and respiration rates of three
726 different leaf types (intact, damaged, systemically affected), weighted with their observed abundance. Each data
727 point is a modelled estimate for the average rate of the five trees for one day. The dashed black line shows the
728 level of zero NPP (negative values indicate that the tree is losing carbon). The solid coloured line shows a
729 general additive model across the five trees, and the dashed coloured lines show the propagated measuring
730 uncertainty.

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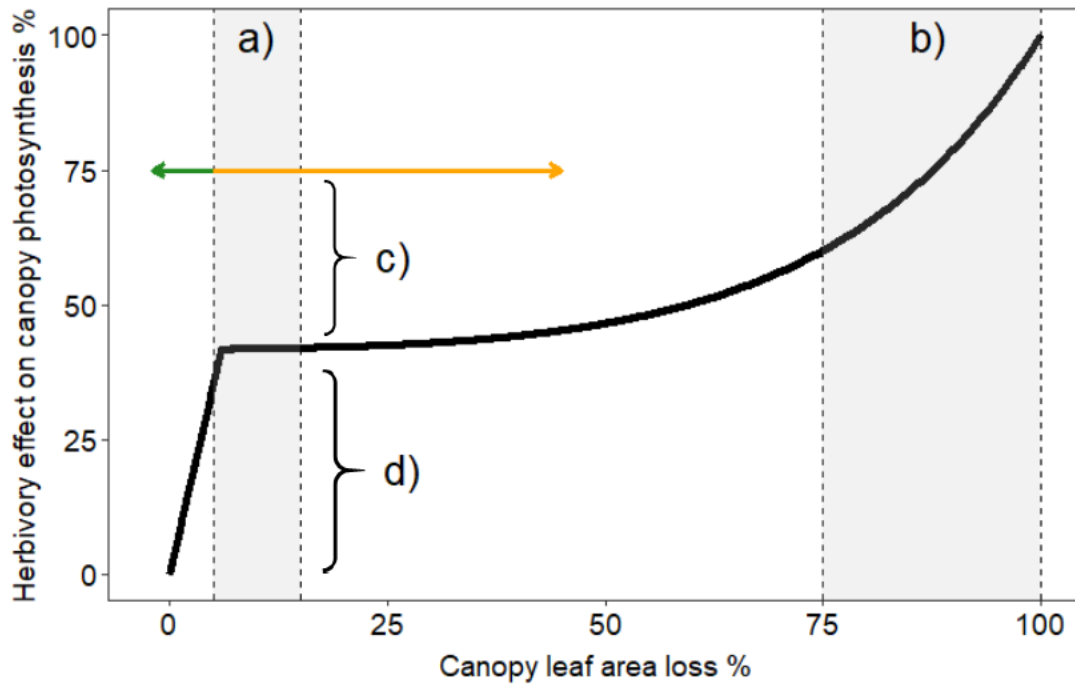


733

734 **Figure 3.** The combined carbon budget a) without and b) with herbivory for an oak forest as $\text{Mg C ha}^{-1} \text{ yr}^{-1}$
735 based on canopy upscaling. The carbon flux of leaf area loss ($0.1 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$) will continue its cycle either by
736 entering soil as frass or insect cadavers, being respired by herbivores, or being eaten by higher trophic levels
737 preying on caterpillars (see Figure 5). Errors are propagated measuring uncertainties. R - respiration, NPP – net
738 primary productivity (= Photosynthesis – ($R_{\text{leaf}} + R_{\text{stem}} + R_{\text{roots}}$)).

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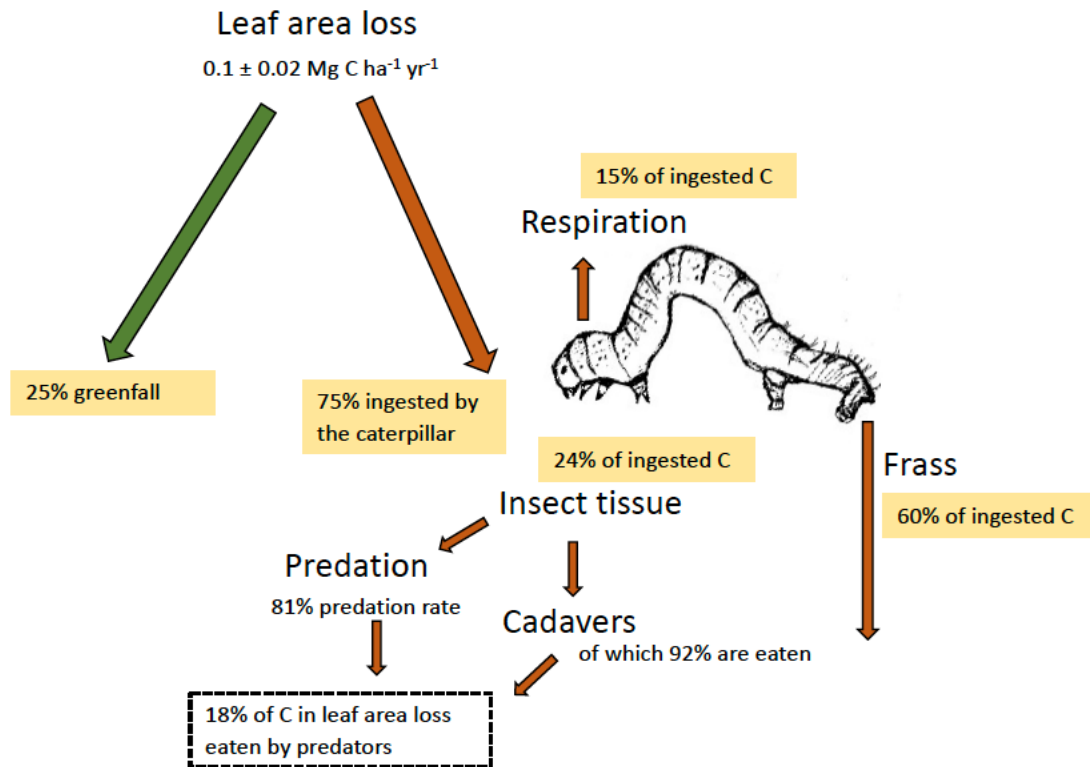


741

742 **Figure 4.** The effect of leaf area loss on daytime canopy net photosynthesis, as % reduction from the full
743 photosynthetic capacity. The first shaded area (a) represents a typical level of herbivory in temperate forests (5-
744 15% of leaf area loss; (Cebrian 1999). The second shaded area (b) shows leaf area loss during an insect
745 herbivore outbreak (75-100% leaf area loss, e.g. Clark et al. 2010, Schäfer et al. 2010). At low herbivory levels,
746 below the level at which all leaves are affected by herbivory, the herbivory effect on photosynthesis is mainly
747 driven by the spread of systemic changes in leaf gas exchange in the undamaged leaf tissue (green arrow,
748 “indirect effects”). Above this level, the changes in the effect of herbivory are driven by increasing leaf area loss
749 (orange arrow). Most previous studies on the effects of herbivory on primary productivity have compared
750 outbreak densities of herbivores to a normal level of herbivory (c). Nevertheless, we predict this effect might be
751 smaller than comparing normal levels of herbivory to a completely intact canopy (d). See Appendix 2, Figure S6
752 for description of the changes in the proportion of different leaf types and leaf area loss with changing herbivore
753 densities and Appendix 3 for relationships between insect herbivory and its effect on canopy assimilation with
754 different underlying assumptions.

755

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757

758 **Figure 5.** Estimating the fate of the carbon lost through eaten leaf area in the oak-caterpillar study system in
759 Wytham Woods. Of the observed leaf area loss, roughly 75% is expected to be ingested by the caterpillar
760 (Russell et al. 2004). Of this, 15% will be respired, 60% falls down as frass, and 24% will be used by the insect
761 to grow and reproduce, based on earlier studies of insect energetics (Wiegert and Petersen 1983). Of winter
762 moth caterpillars in Wytham Woods, 81% of live caterpillars and 92% of cadavers are preyed upon (East 1974).
763 Thus, 24% of the carbon ingested by the caterpillar (or 18% of the carbon contained in the observed leaf area
764 loss, $0.02 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$), is transferred to higher trophic levels.

765