Dear Editor,

We thank you and the referees for all comments that have helped us to improve the manuscript. We have updated the manuscript according to your last comment:

5 We have changed unbiased to (P. 14, L. 3-4): "The intercept is -0.11 and the slope is 1.01 indicating that the LUE model performs well for years without outbreaks." We have also changed to two significant digits in all results. In this document we include detailed responses to Referee 1 (P. 2-11) and Referee 2 (P. 12-16) followed by a marked-up version of the manuscript (P. 17-51).

10 Sincerely,

Per-Ola Olsson

Dear Referee one. We thank you for the constructive and detailed comments and suggestions. We agree with most of the comments and have made some further analysis to improve the study. We have made most of the required updates to the manuscript.

Major comments:

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1. Using the mean GPP over no-outbreak years as the basis to estimate GPP reduction caused by outbreaks seems inadequate for two different reasons. First, differences in weather may affect both GPP and outbreak occurrence/severity. If the two variables are indeed correlated across years, the approach likely causes a bias. This should be checked; no need for fancy statistical tests, just compare, based on the GPP lue model, the mean GPP and its standard deviation for outbreak vs. no-outbreak years over pixels that have never been 10 defoliated. Second. GPP in pixels previously defoliated is unlikely equal to what it would have been if no outbreak had occurred. For example, canopy trees might have not fully recovered yet (hence underestimating the nooutbreak GPP) or total tree+understory productivity might increase for a few years due to the defoliation-caused arowth release of the understory (hence overestimating the no-outbreak GPP). The authors should rather have estimated the no-outbreak GPP in pixels that have been defoliated up to X years before (with X to be defined; 15 maybe 3-5 years?) based on the NDVI DL values of neighbouring pixels that have never been defoliated. (More precisely: for each defoliated pixel, define a window large enough to include never-defoliated pixels, but small enough to have similar conditions. Then, compute the mean NDVI DL difference between the defoliated pixel and the never defoliated pixels over all years prior to the (first) defoliation event in the defoliated pixel; let's say NDVI DL was on average 10% higher in the defoliated pixel. Finally, for the X years after the defoliation event 20 (excluding the defoliation year itself), estimate the annual no-outbreak GPP in the defoliated pixel with the GPP_lue model, but with a value of NDVI_DL 10% higher than the mean annual NDVI_DL value over the neighbouring never-defoliated pixels [instead of using the annual MODIS NDVI DL value in the defoliated pixel].) Ideally, the authors should re-do their analyses using this new approach. At a minimum, the authors must use

25 this new approach for >100 randomly-selected defoliated pixels and see to which extent it affects their results.

Response: We agree that these are import points. We first respond to the issue with recovery after an outbreak and thank you for the good suggestion about how to handle this limitation. We did explore the possibility to perform the suggested analysis but decided not to go ahead with the analysis. The main motivation is the difficulty to find pixels without any defoliation.

- 30 Even though there are pixels that are not detected as defoliated during outbreak years we cannot know that these pixels are not influenced by lower defoliation levels. Slightly lower NDVI values may be due to meteorological conditions, but also due to minor defoliation by small larvae populations. Since it is not possible to distinguish between the two causes in remote sensing data such an analysis would increase uncertainties. Instead we modeled GPP based on PAR for the five years for which we have data from the EC-tower and compared to measured GPP. A comparison between measured GPP and PAR-
- 35 modeled GPP suggests that the birch forests were slightly defoliated by growing larvae populations the two years prior to the outbreak in 2012. In 2007 and 2009 measured and PAR-modeled GPP agreed well. In 2007, measured GPP was slightly lower than PAR-modeled GPP and in 2009 measured GPP was slightly larger than PAR-modeled GPP. We have also observed lower NDVI values in the years prior to an outbreak in time-series of NDVI over the study area. One important note here is that the annual GPP values in Table 1 (p. 15 in manuscript) were not displayed in the correct order for the years
- 40 2009, 2010, 2011 and 2014. The correct numbers in Table 1 are given below and agree with the lower annual GPP values in 2010 and 2011 (Note that we also changed to two significant digits):

		Outbreak				
Year	2007	2009	2010	2011	2014	2012
$\mathbf{GPP} (g C m^{-2} yr^{-1})$	450	530	370	400	450	180

For the outbreak year 2012 the difference between EC derived GPP and PAR-modeled GPP was 290 g C m⁻² yr⁻¹, which is close to the decrease of 260 g C m⁻² yr⁻¹ estimated in the study. In addition, we ran the LUE model with meteorological data from the scientific research station in Abisko (ANS) for the year 2008 to fill the gap in the time-series with measured GPP and to study how well it agreed with the years 2007 and 2009. According to the LUE model the annual GPP at the EC tower was 440 g C m⁻² yr⁻¹ in 2008, which indicates that the GPP for undisturbed years of 440 g C m⁻² yr⁻¹ that we use is a reasonable value. We have added a discussion about these uncertainties and the challenge to find baseline conditions for GPP in areas with reoccurring insect outbreaks (P. 20, L. 7-19). In addition, a figure showing EC-derived and PAR-modeled GPP was added to the supplementary material. We have also added references that have found that the birch forests appear 10 to reach pre-outbreak LAI and GPP 2-3 years after an outbreak (P. 20, L. 3-5).

As a response to the first part of the comment above we studied correlations between NDVI and meteorological data available from ANS, where we used the mean of the highest seasonal $NDVI_{DL}$ value derived from 200 MODIS pixels with birch forest. To minimize the influence of insect induced defoliation we excluded the outbreak years and years immediately

- prior to and after outbreaks. No linear correlations between PAR and GPP were found. There were, however, negative 15 correlations between temperature and $NDVI_{DL}$, with the strongest correlation between $NDVI_{DL}$ and the mean temperature in May-June. The influence of temperature on NDVI_{DL} was however, weak. Due to the low influence on NDVI and the large estimated uncertainty of the LUE model (30%) we did not adjust for these correlations in the analysis. We do, however, mention these results in the discussion (P. 20, L. 21-32) but due to the limited amount of data we do not further elaborate on
- 20 the results as that would be speculations.

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There are studies related to insect outbreaks and climate but results are partly contradicting and only weak correlations between climate variables and outbreaks are found (se e.g. Young et al. 2014 and references within). Hence, we did not include this in the manuscript.

2. In the Discussion, the authors must at least explicitly acknowledge four major methodological weaknesses; when possible, explain the likely impact of each weakness (i.e., under- or overestimating defoliation-caused GPP 25 losses) and propose a way to address the weakness. (1) fAPAR was based on measurements for the upper canopy only, so it is unclear to which extent the fAPAR vs. NDVI DL relationship applies to the entire forest. This is particularly critical due to the (possible) growth release of the understory highlighted by the authors. (2) The fAPAR vs. NDVI DL relationship was derived for undefoliated years (2010-2011) only, yet was also used in the GPP_lue, defoliated model. Why not developing a fAPAR vs. NDVI_DL for defoliated conditions (no defoliation 30

event at the spectral tower over the entire study)? (3) The defoliation detection algorithm missed 26% of defoliated areas and misclassified 39% of undefoliated areas. (4) How representative was the EC tower footprint of the entire

study area, both during outbreak and no-outbreak years? This is critical, as EC tower data provided the basis for all GPP estimates through the values of nepsilon_max, epsilon_max,def, and the GPP reduction factor.

Response: We agree that these weaknesses need to be discussed and have added them as limitations in the discussion: (1)

- 5 This limitation is not easily handled since considerably more data are required to derive fAPAR and NDVI relationships depending on understory responses. We have, however, clarified the limitation in the discussion mentioning that a model including different relationships between fAPAR and NDVI depending on understory responses will be complex (P. 21. L. 1-8). (2) Unfortunately, the larvae were disrupting the PAR-sensors during the outbreak; hence, we have no reliable fAPAR data for defoliated conditions. We have added a section about this limitation in the discussion (P. 20, L. 31-34). (3) We have
- 10 added a section about the accuracy of the defoliation detection method in the discussion (P. 21, L. 21-26) (4) We agree that this could be an important limitation but according to Heliasz (2012) GPP is relatively stable over the study area. We have clarified this in the discussion (P. 21, L. 17-20): "There are also uncertainties in how well the EC tower footprint represents the study area. Heliasz (2012) utilized a permanent EC tower as reference and a mobile EC tower to study variability in carbon exchange in the birch forests around Abisko and concluded that there were only minor differences in GPP at seven
- 15 sites during the peak growing season in 2008 and 2009. Hence, we consider the EC-tower footprint to be representative for the study area."

3. I object to providing the 3-year *total* GPP reduction caused by defoliation, as this inadequately inflate numbers. Please provide the 3-year *mean* reduction instead throughout the text, making it clear the reduction is for outbreak years only (not the mean values over all years since 2000): Abstract; P16, L15 to P17, L1; P17, L7-8; P19, L5-7; P19, L15; P21, L18-20.

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Response: We agree that the total reduction in GPP may inflate the numbers. Hence, we have updated the manuscript accordingly except for in the discussion where we want to keep the comparison between the total decrease in GPP for the three outbreak years with the mean annual GPP for years without defoliation. We did, however, clarify that the total reduction was for the three years (P. 19, L. 8-10): "The total decrease in regional GPP, due to the three insect defoliation events studied here was estimated to be 45 ± 14 Gg C, which is of the same magnitude as the average annual regional GPP of 41 ± 12 Gg C yr⁻¹ for single years with no disturbances.

4. P3, L15-26. I have various issues with the text from "Since near-linear" to "(Liljedahl

- 30 et al. 2011)". First, it should be in the Methods; I suggest merging at the beginning of Section 2.3. Second, units are not provided for the variables and the equation is not numbered; please number *all* equations and provide units for *all* variables throughout the text (even when unitless; e.g., NDVI). Third, the sentence starting on L20 is cumbersome; if kept in Section 2.3, I suggest re-writing along the following lines: "The light use efficiency coefficient varies between vegetation types and the influence of meteorological conditions is accounted for
- 35 through reduction factors for temperature and vapour pressure deficit [...]". Fourth, the sentence starting on L23 is an overstatement because: 1) temperature is not always the main limiting factor in cold climates (Nemani et al. 2003; Beer et al. 2010); and 2) neither Bergh et al. (1998) nor Lagergren et al. (2005) really tested for the impact of factors other than temperature in their studies that covered only two sites in Sweden. The authors should acknowledge that they assumed accounting for temperature only was sufficient in their study region, an
- 40 assumption supported (but not demonstrated) by Bergh et al. (1998) and Lagergren et al. (2005). Fifth, delete the

sentence starting on L25: water stress is a major limiting factor in some boreal and other forests, not just for "ecosystems dominated by non-vascular plants".

Response: We have moved most of the section to Methods as suggested and re-written or removed some parts of the text.

- 5 What remains in the Introduction is (P. 3, L. 21-23): "Since near-linear relationships between satellite derived vegetation indices and the fraction absorbed PAR (fAPAR) have been established (e.g. Asrar et al. 1984; Sellers 1987; Goward & Huemmrich 1992; Myneni & Williams 1994; Olofsson and Eklundh 2007), it is possible to create a LUE model driven by remote sensing data. Such a LUE model could be applied for...". Consequently, Section 2.3 is updated according to the suggestions. The equation and the sentence "ecosystems dominated by non-vascular plants" are removed. We have also
- 10 added to the methods (Section 2.3) that (P. 9, L. 12-13): "We assumed that accounting for temperature only is sufficient in our study region, which is supported by Bergh et al. (1998) and Lagergren et al. (2005)."

5. P6, L12. Why wasn't fAPAR_canopy also smoothed with TIMESAT before the regression?

Response: fAPAR_{canopy} used in the regression is the mean of daily fAPAR_{canopy} over eight day periods, coinciding with the
MODIS eight day periods. Hence, the fAPAR_{canopy} values in the regression are already smooth and we did not want to risk introducing further artefacts by applying more smoothing. However, we have clarified in section 2.2.2 that we are working with eight day mean values (P. 6, L. 11-12): "Average *fAPAR_{canopy}* over eight day periods, coinciding with the MODIS eight day periods, were computed and an ordinary least squares (OLS) regression was performed...."

6. P7, Figure 3. The TIMESAT smoothing removed a second NDVI 'peak' each year. Please explain what was the origin of this (wintertime?) second annual peak and why removing it was OK.

Response: The second peak occurs during the winter when there is no vegetation in the area. We have not studied the origin of the second peak which could be due to e.g. snow or darkness (no light in the winter season). Hence, we do not discuss the second peak, but we have added a clarification to the figure caption explaining that removing the second peak is OK (Fig. 3,

25 P. 7): "There is a small peak in raw NDVI (a) appearing each year. This peak appears during the winter when there is no vegetation in the study area and is hence, removed from the smoothed data (b).

7. P12, L4-6. I do not understand why Method 1 should not also capture the effect of refoliation: the EC tower data should account for the post-refoliation increase in GPP, no? Unless no refoliation occurred within the EC tower footprint after the 2012 outbreak?

Response: To our knowledge there was no refoliation around the EC tower in 2012, hence, the reduction factor represents an outbreak year without refoliation. We have clarified this (P. 11, L. 23-24): "derived from the EC data from 2012 when the birch forest in the footprint of the tower was severely defoliated, and no refoliation occurred."

- 8. P14, Figure 6. Many readers will likely expect defoliation to substantially decrease NDVI (due to a much lower leaf area index (LAI)) and leave LUE barely affected, so they will question the defoliation results (small NDVI decrease, large LUE decrease). It would thus be helpful to explain that small reductions in NDVI are associated with large reductions in LAI (e.g., Wulder et al. 1998), while LUE can substantially decrease for lower LAI because more leaves operate in the light-saturated portion of the photosynthesis curve (e.g., Medlyn 1998). Also,
- 40 please indicate the weeks during which defoliation occurred.

Response: We agree with this reasoning and have added a section to the discussion (P. 21, L. 13-16): "It may also seem surprising that the difference in *NDVI_{DL}* was comparably low in relation to the difference in light use efficiency. It is, however, known that NDVI saturates for high LAI and that small changes in NDVI can be associated with large changes in LAI (e.g. Myneni et al. 2002). The light use efficiency on the other hand can decrease substantially with lower LAI since

more leaves will operate in the light-saturated portion of the photosynthesis (e.g. Medlyn 1998)."

9. P15, Figure 7 and P16, Figure 8. Give the equations for the regression lines on Figures 7 and 8. The line seems pretty close to 1:1 with zero intercept in Figure 7 (hence no bias for no-outbreak years), but the GPP_lue, defoliation model in Figure 8 seems to underestimate GPP over most of the range of actual values (i.e., up to _2 gC m^-2 day^-1); this should be added to the list of weaknesses in the Discussion (see comment #2).

Response: We have added the equations for the regressions line in the figure captions (Fig. 7, P. 15; Fig. 16, P. 8). We also added the following to the text (P. 14, L. 3-4): "The intercept is -0.11 and the slope is 1.01 indicate that the LUE model performs well for years without outbreaks." and (P. 16, L. 2-3) "The figure, with an intercept of -0.54 and a slope of 1.25

- 15 indicates that the LUE model underestimates GPP for lower values. Furthermore, we elaborate on the topic as a weakness in the discussion (P. 21, L. 8-12): "Another potential limitation is that the LUE model developed for years with defoliation seems to underestimate GPP for values lower than about 1.5 g C m⁻² day⁻¹ (Figure 8). However, for the outbreak year with available EC data (2012) the underestimated values from the LUE model are mainly due to a cold spring that resulted in a large reduction factor (f_{8day}). During the main growing season LUE modelled and EC derived GPP agrees well, which
- 20 increases confidence in the modelling."

10. P18, L7-10. Unless I am mistaken, the authors do not correctly interpret these results. If Method 2 captured the effect of refoliation whereas Method 1 did not, then Table 3 results should have a higher absolute value for refoliated than non-refoliated pixels *regardless* of the actual sign. This is what was obtained, suggesting that Method 2 did better capture refoliation's effect; however, the differences between refoliated and non-refoliated pixels are always within the error margin, so this better performance is marginal. (The sign of Table 3 values (negative for 2004 and 2012, positive for 2013) is not directly related to the effect of refoliation, but to the bias

between the two methods.)

- Response: It is true that we made a mistake for 2013 when there is little difference between the two methods. Thanks for 30 noting this. We have updated the manuscript accordingly (P. 18, L. 7-11): "We compared the differences in GPP decrease between Method 1 (GPP reduction factor) and Method 2 (two LUE models) to study if Method 2 performed better for MODIS pixels where the birch trees recovered later in the growing season. For all years the mean differences in GPP loss (g C m⁻² yr⁻¹) between the methods were lower for pixels that recovered later in the growing season. These results suggest that Method 2 captured some of the refoliation, though the differences are small and within the error margin.
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11. P19, L26 to P20, L3. I do not think these explanations for Table 3 results (i.e, the difference

in GPP loss between Method 1 and Method 2) are appropriate. The refoliation argument does not hold because, as noted by the authors, both 2004 and 2013 had high refoliation yet had opposite signs for Method 1 minus Method 2. Furthermore, the lower GPP losses in 2013 for Method 2 were basically the same for non-refoliated and refoliated pixels (Table 3). The argument of "uncertainties in nepsilon max.def" does not seem appropriate either, because the same value was used for all years (so why a sign change in 2013 for Method 1 minus Method 2?). The argument of higher NDVI due to understory growth would work if this growth was stronger in 2013 compared to 2004 and 2012; are there reasons to believe this was the case? Here is another hypothesis that could account for the much lower mean GPP reduction in 2013 under Method 2 compared to all other values

5 (and hence account for the sign change in 2013): could it be that growing conditions were better in 2013, thereby leading to higher f_8day and/or PAR_8day used in GPP_lue, defoliated compared to the mean f_8day/PAR_8day no-outbreak values used in GPP_lue?

Response: We do agree that the discussion in this paragraph was a bit weak. We have removed the part about refoliation and

- 10 uncertainties in $\varepsilon_{max, def}$ We studied meteorological data and compared the seasonal development in NDVI for the years 2004 and 2013. The seasonal trajectories of NDVI suggest that the growing season was shorter and that refoliation started earlier in 2013, which is one possible explanation for the smaller decrease in annual GPP for Method 2. We have added this to the discussion (P. 22, L. 26-30): "For the years 2004 and 2012, the two methods resulted in similar estimates of the GPP loss with slightly larger decrease in GPP for Method 2. In 2013, the difference between the methods was larger with the highest
- 15 decrease in annual GPP for method 1. One possible explanation for the smaller decrease in annual GPP according to Method 2 for the year 2013 is that the growing season seems to have been shorter and that refoliation started earlier and was stronger in 2013 compared to 2004; this is indicated by the seasonal developments of NDVI."

Minor comments:

12. Throughout the text: when possible replace the vague "carbon uptake" expression by the more accurate term

- 20 applicable (GPP, NEE, etc.). Therefore, the title should be: "Mapping the reduction in gross primary productivity due to insect defoliation in subarctic birch forests". In the Discussion, the authors should stress that their results are not for the net carbon balance, but for GPP only; based on Heliasz et al. (2011), would it be possible to speculate whether, on a percentage basis, NEP losses should be higher or lower than GPP losses?
- 25 Response: We have changed to either GPP or NEE and accordingly also changed the title as suggested and we have stressed that the results are for GPP only and we also mention in the discussion that (P. 19, L. 12-13): "during the outbreak in 2012 the decrease in R_{eco} was larger than the decrease in GPP during the growing season around the EC tower."

13. Throughout the text: please use the "regional GPP" expression when applicable, to make it clearer the values are for the total GPP over the study region.

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Response: We have updated the manuscript accordingly.

14. P1, L18-20. I have various issues with this sentence; I suggest re-writing along the following lines: "In the study area of 100 km², the results suggested a mean regional GPP decrease of XX +/- YY Gg C yr⁻¹ for the three outbreak years (2004, 2012, and

35 GPP decrease of XX +/- YY Gg C yr^-1 for the three outbreak years (2004, 2012, and 2013), compared to a mean regional GPP of 41.1 +/- 12 Gg C yr^-1 for the five years without defoliation".

Response: We have updated the manuscript (P. 19, L. 18-20): "In the study area of 100 km² the results suggested an average

40 decrease in regional GPP over the three outbreak years (2004, 2012, and 2013) of 15 ± 5 Gg C yr⁻¹, compared to the mean regional GPP of 40 ± 12 Gg C yr⁻¹ for the five years without defoliation."

15. P2, L1. Reference(s) should support the "a warmer climate is likely to increase forest productivity" part of the sentence. Here are some suggestions: Pastor and Post (1988), Nemani et al. (2003), or Boisvenue and Running (2006).

5 Response: We have added (Nemani et al. 2003; Boisvenue & Running 2006) as suggested (P. 2, L. 6).

16. P2, L21. Since Brown et al. (2012) is already cited later on, I suggest mentioning it here too. Response: We have added (Brown et al. 2012) as suggested (P. 2, L. 26).

17. P3, L3. Please give the temporal coverage of Landsat.

10 Response: We have added the temporal coverage of Landsat (P. 3, L. 9):
18. P3, L13. It is Monteith and Moss (1977).

Response: We have updated the manuscript accordingly (P. 3, L. 19):

19. P3, L27-28. Bright et al. (2013) already used remote sensing (Landsat to identify
trees killed by the mountain pine beetle) and a LUE model (MODIS GPP results, which are based on LUE) to quantify the impact of an insect outbreak on carbon uptake. To my knowledge, the authors can still claim being the first ones to do it for defoliators.

Response: We have updated the manuscript accordingly and added Bright et al. (2013) as a reference (P. 3, L. 25-28).

20 20. P3, L30-34. Delete the "This combination of [...]" sentence or merge it with the previous one (it is repetitive). Delete the "The method was developed [...]" sentence (it is repetitive with "Our main study objective [...]").

Response: We have rewritten the section and the sentences are removed.

25 21. P3, L34 to P4, L2. Delete or merge with the Methods.

Response: The section is removed.

22. P4, L2-4. The sentence is confusing, as it seems to imply that results will be provided for every year "between 2000 and 2015". I suggest re-writing along the following

30 lines: "Our main study objective was to compare GPP for years with (2004, 2012, and 2013) and without (2007, 2009, 2010, 2011, and 2014) insect outbreak in the birch forest of a subarctic valley of northern Sweden".

Response: We have updated the manuscript accordingly (P. 3, L. 30-32): "Our main study objective was to compare GPP for

35 years with (2004, 2012 and 2013) and without (2007, 2009, 2010, 2011 and 2014) insect outbreak in the birch forest of a subarctic valley of northern Sweden."

23. P5, L18 to P6, L1. The purpose of "quality classes based on QA data" is not clear: how where these classes used in the analysis?

40 Response: We agree that mentioning the quality classes was confusing, hence, we have changed the text (P. 15, L. 17-18): "Double logistic functions were used to smooth the raw NDVI data and QA data from both MOD09Q1 and the more comprehensive QA-flags in MOD09A1 were utilized to estimate the quality of the NDVI observations."

24. P6, L4. Replace "fraction canopy absorbed PAR" by "fraction of absorbed PAR by

the canopy". Similar comment for "canopy absorbed PAR" in Figure 4 caption.

Response: We have updated the manuscript accordingly (P. 6, L. 6-7; Fig. 4, P. 14).

25. P6, L8. Is the "pure canopy absorbed PAR" different from fAPAR_canopy? If yes, quickly explain what is the difference and why it matters. If not, replace the expression by "fAPAR_canopy".

Response: Pure canopy absorbed PAR is the same as fAPAR_{canopy}. We have updated the manuscript accordingly (P. 6, L. 8).

26. P6, L11. I would provide here (after "NDVI_DL") — instead of on P3, L20 — the reference to Myneni & Williams (1994) that supports the linear relationship.

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Response: We have updated the manuscript accordingly (P. 6, L. 12).

27. P7. I suggest combining Figure 2 with Figure 1. For all multi-panel Figures, please add letters to each panel and refer to the appropriate panel in the text (e.g., Fig. 5a).

15 Response: We do agree that it could be a good idea to merge the figures so that the orthophoto over the area around the ECtower is shown together with the location of the tower. However, we decided to keep them as separate figures with the main motivation that we want to keep the size of Figure 2 large to make the photo easy to interpret. Letters have been added to all multi-panel figures.

28. P8, L28. Please put here (instead of on P11, L8-10) the sentence about the value of the temperature lapse rate.

Response: We have updated the manuscript accordingly (P. 8, L. 31-33).

29. P9, L2. The units for PAR_8day should be MJ m⁻² day-1.

25 Response: We have updated the manuscript accordingly (P. 9, L. 6).

30. P9, L5. Add something like "(see Section 2.3.3)" so that readers know the value of epsilon_max will be discussed later. Similar comments for GDD_thresh (P9, L16) and T_thresh (P10, L2).

Response: We have updated the manuscript accordingly (P. 9, L. 11; P. 9, L. 25; P. 10, L8).

30 **31**. *P*9, Equation (7). Replace the current condition on the middle line by "-8_T_min8 < -3".

Response: We have updated the manuscript accordingly (Eq. 7, P. 10).

32. P10, L3. T_mean8 was never negative for such a northern site at the end of September? If negative values occurred, explain how they were dealt with (Equation (8) suggests a negative value for f_8day, which would make no sense).

Response: There were no negative values for T_{mean8} in the period studied (coldest value was 3°C). There were eight day periods with temperatures below zero, but no eight day period with a mean value < 0°C.

40 33. P10, L6. Here and in Figure 5, replace "RMS" by "RMSE".

Response: We have updated the manuscript accordingly (P. 10, L. 12; Fig. 5, P. 13).

34. P10, Equation (9). Replace "nepsilon" by "nepsilon_max".

Response: We have updated the manuscript accordingly (Eq. 9, P. 10).

35. P11, L8. Delete the first sentence (repetitive with the previous paragraph).

Response: We have removed the sentence.

5 36. P11, L15-16. The text should be expanded, because at this point the reader is still unaware that an outbreak occurred in 2012 within the EC tower footprint: please state this explicitly here and add what was the percentage of defoliation within the tower footprint.

Response: We have clarified according to the comment (P. 11, L. 21-23): "Two methods were applied to study the reduction in annual GPP due to the insect outbreaks: (1) a method based on a reduction factor derived from the EC data from 2012

10 when the birch forest in the footprint of the tower was severely defoliated, and no refoliation occurred."

37. P12, L1-2. The sentence is cumbersome; I suggest re-writing along the following lines: "For each year with insect outbreak, the regional reduction in GPP was computed by summing, over all pixels identified as defoliated, the difference between the mean GPP for no-outbreak years and the GPP for this specific outbreak year".

15 Response: We have updated according to the suggestion (P. 11, L. 10-11).

38. P13, L6. For consistency, replace "GDD threshold" by "GDD_thresh", and "temperature factor" by "T_thresh".

20 Response: We have updated according to the suggestion (P. 13, L. 6).

39. P14, Figure 6 legend. For consistency, replace "f_MOD8" by "f_8day".

Response: We have updated according to the suggestion (Fig. 6, P. 14).

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40. P15, L8. Here and throughout the text (including Figures): provide full units for local, mean, and regional GPP (i.e., with yr^-1) even when writing "annual".

Response: We have updated the manuscript according to the comment.

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41. P16, L14-15. This sentence is repetitive with P11, L4-6.

Response: We have removed the sentence.

35 42. P17, L1-2. Make it clearer that the 41.1 value was computed as the mean over nooutbreak years, based on the GPP_lue equation (add a number) given on P14. Please also add this information as a footnote to Table 2.

Response: We have clarified according to the comment (P. 17, L. 6): "The average annual regional GPP in the study area, derived with the LUE model (Eq. 12) and the five years without insect outbreak..." and added a footnote to Table 2.

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43. P18, Figure 9 caption. Replace "birch moth outbreaks" by "outbreaks of autumnal moth and winter moth".

Response: The figue caption is updated according to the comment.

45 44. P19, L2. The word "demonstrated" seems too strong; similar comment for P21, L17.

Response: We have changed to shown (P. 19, L. 5) and (P.23, L. 31).

45. P19, L3. Replace "decreased with 260 g C m⁻2" by "decreased by 261 g C m⁻2 yr⁻1" (based on Table 1, the difference is 261). Similar comment for P20, L25.

Response: We have changed all values to two significant digits; hence, this comment is no longer relevant.

46. P19, L5. According to Table 2, the highest value is 265 +/- 93 (not 244 +/- 73).

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Response: Thanks for noting. We have updated the manuscript accordingly (P. 19, L. 4).

47. P20, L31. Replace "turned a forest into a carbon sink" by "turned a forest into a carbon source". Stands were carbon sinks only during the growing season; the main point here is that insect-caused mortality led to negative annual NEP... although these stands seem to be recovering quickly, as correctly noted by the authors in the second part of the sentence!

Response: Thanks for noting. This was a mistake that has been corrected now.

20 48. P21, L1-2. For (partially) contrasting modeling results about the effect of insect outbreaks on the carbon balance, see Seidl et al. (2008), Albani et al. (2010), and Landry et al. (2016) (the last one is not the same reference as already cited in the manuscript).

Response: Thanks for these interesting references. We did not include them though as they mainly discuss longer term

25 impacts.

49. P21, L10-11. Delete the whole "since it has been suggested [...] (Medvigy et al. 2012)" part of the sentence. The "spatial distribution of defoliation" issue addressed by Medvigy et al. (2012) dealt with tree-level defoliation within a stand (e.g., 100% defoliation of 40% of trees vs. 40% defoliation of 100% of trees). This is not something addressed here, nor is MODIS-like remote sensing appropriate for this.

30

Response: We have removed the part of the sentence as suggested.

50. P21, L13-14. Delete the sentence: there is no firm basis for such an extrapolation, and the number would then likely end up being cited by future studies...

35

Response: Since these insect infestations occur frequently across very large areas in the region we think that it is relevant to include some information about the potential effect on the carbon uptake. However, we agree that it is an uncertain estimation and reformulated the text accordingly (P. 23, L. 27-29): "Assuming that the conditions were similar over northern Fennoscandia, the insect defoliation over these vast areas would result in a potential total regional GPP loss for the time

40 period of the magnitude 2–3 Tg C. Models not accounting for such recurring disturbance events would seriously overestimate the ability of these forests to absorb atmospheric CO₂."

References:

Heliasz (2012). PhD thesis, Dep. of Geography and Ecosystem Science, Lund Univ., Lund, Sweden.

45 Young et al. (2014). Arctic, Antarctic, and Alpine Research, 46, 659-668, 10.1657/1938-4246-46.3.659.

Dear Referee two. We thank you for the constructive and detailed comments and suggestions. We agree with most of the comments and have made some further analysis to improve the study. We have made most of the required updates to the manuscript.

Specific comments:

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In several places the approach seems to take too simplistic a view, without properly discussing the assumptions or their impact. For example, a key result presented is the difference between GPP derived from EC measurements in an outbreak year (2012) compared to five other years without insect utbreaks. Unfortunately, it seems EC data were only available for one outbreak year, but there is no analysis of differences between years due to factors other than insect damage. Inter-annual variability in meteorological conditions (rainfall/soil moisture, solar radiation and temperature in particular) can result in different annual total GPP. The values given in Table 1 should therefore be analysed with respect to meteorological conditions. This should also allow the 2012 value to be given some context – if the insect outbreak had not occurred, would the 2012 total be lower/higher/similar to the average based on meteorological conditions alone? Furthermore, is it possible that the 15 outbreaks in 2012 and 2013 contributed to the lower GPP obtained in 2014, or is this attributable to meteorological conditions?

Response: We agree that these important considerations need to be discussed, and we have consequently studied relationships between meteorological conditions and GPP as well as $NDVI_{DL}$. One important note here is that the annual GPP values given in Table 1 (p. 15 in manuscript) were not displayed in the correct order for the years 2009, 2010, 2011 and 2014. The correct figures in Table 1 are (Note that we also changed to two significant digits):

-		Outbreak				
Year	2007	2009	2010	2011	2014	2012
$\mathbf{GPP} (g C m^{-2} yr^{-1})$	450	530	370	400	450	180

where annual GPP was largest in 2007 and 2009, and the lower annual GPP in 2010 and 2011 indicates that there were minor defoliation already in these years.

- 25 Due to the limited number of years with EC derived GPP we did not consider it reliable to study correlations between annual GPP measured at the EC tower and meteorological variables. Instead we modeled GPP for the birch forest around the tower with PAR, and compared EC derived and PAR-modeled GPP. The comparison suggests that in the two years (2010 and 2011) prior to the outbreak, measured GPP was lower than PAR-modeled GPP, indicating that there were signs of defoliation by growing larval densities. Also in 2014 when the birch forest most likely was recovering from the outbreak,
- 30 measured GPP was lower than PAR-modeled GPP. For the earlier years (2007 and 2009) when the birch forest was likely closer to undisturbed conditions, EC derived GPP and GPP modeled with PAR data agreed well; measured GPP was slightly lower compared to PAR-modeled in 2007 and slightly larger in 2009. For the outbreak year 2012 the difference between EC derived GPP and PAR-modeled GPP was 290 g C m⁻² yr⁻¹, which is similar to the decrease of 260 g C m⁻² yr⁻¹ we found in our study. In addition, we ran the LUE model with meteorological data from the scientific research station in Abisko (ANS)
- 35 for the year 2008 to fill the gap in the time-series with measured GPP and to study how well it agreed with the years 2007

and 2009. According to the LUE model the annual GPP at the EC tower was 440 g C m⁻² yr⁻¹ in 2008. This indicates that the GPP for undisturbed years of 440 g C m⁻² yr⁻¹ that we used is reasonable. However, with data from the EC tower available for more years it would be a potentially important improvement to include meteorological data when estimating the decrease in annual GPP. We have added a section about these results in the discussion (P. 20, L. 7-20) and the figure showing EC derived and PAR-modeled GPP was added to the supplementary material.

- We also studied correlations between NDVI and meteorological data available from ANS, where we used mean of the highest seasonal $NDVI_{DL}$ value derived from 200 MODIS pixels with birch forest. To minimize the influence of insect induced defoliation we excluded the outbreak years and years immediately prior to and after outbreaks. No linear relationships between PAR and GPP were found. There were, however, negative correlations between temperature and
- 10 NDVI_{DL}, with the strongest correlation between NDVI_{DL} and the mean temperature in May-June. The influence of the temperature on NDVI was however, weak and due the large estimated uncertainties of the LUE model (30%) we did not include these correlations in the analysis. We do, however, mention these results in the discussion (P. 20, L. 21-32) but due to the limited amount of data we do not further elaborate on the results as that would be speculation.
- The comparison with the 2004 results of Heliasz et al. (2011) on page 20 is useful and indicates that closer analysis of the temporal evolution of the EC data may be beneficial. Currently data are separated into years with and without insect outbreaks. During those years with outbreaks, does the reduction in GPP over the course of the growing season agree with the timing of insect population growth/insect damage? Is this also supported by the NDVI data? In the years classified as being without insect outbreaks, are there any effects of (albeit smaller) insect populations on the GPP or NDVI values?
- 20 Perhaps such analyses could offer further insight into the refoliation effect; it is currently hard to draw meaningful conclusions on this subject from the information given in the article. Some evidence to support the assumption that NDVIDL captures refoliation would also be useful; Fig 3 is not very convincing in this respect.

Response: For the year 2004, when we had EC data for the later part of the insect defoliation and the following refoliation at

25 the EC tower, we can see that GPP is low during the defoliation events and increasing later in the growing season with the new leaves appearing. We have clarified this in the discussion (P. 22, L. 5-17).

As mentioned in our previous comment we found influence on GPP at the EC tower the two years prior to the outbreak that are likely due to increasing insect population before reaching outbreak levels. This pattern is suggested in time-series of NDVI where there seems to be weak signs of defoliation 1-2 years prior to the outbreak.

- 30 P15, L6-10: Section 2.2.3 states that EC data were available from 1 May to 30 Sep, covering most of the growing season. Do the EC observations and values given in Table 1 agree with this timeframe, or is it possible GPP in Table 1 is underestimated if the growing season extended beyond these dates? This study focuses on GPP, but could the authors comment on other potential impacts of the insect outbreak on the carbon balance? For example, how might respiration rates be affected, and might this impact the partitioning into Reco and GPP?
- 35

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Response: Budburst usually occurs early in June or very late in May so including data from first of May means that we capture the start of the growing season. For the years included in this study GPP was approaching zero by the last week of September implying that there were no underestimates of annual GPP. We have clarified this (P. 8, L. 5-10).

We have also added a discussion about respiration (P. 19, L. 11-18): " In this study we have estimated the impact on GPP only but we noted that during the outbreak in 2012 the decrease in R_{eco} was larger than the decrease in GPP during the growing season around the EC tower. Respiration is affected by insect outbreak in two ways: (1) Autotrophic respiration is reduced as defoliated trees cannot photosynthesize, and (2) heterotrophic respiration increases when dead larvae decompose.

5 The amount of carbon respired by larvae is likely to be the same as the amount of carbon in eaten leaves, so we should only observe a shift of respiration in time. In addition, larvae transport nutrients from trees to fungi and bacteria living in soil, which further increase respiration. The increase in heterotrophic respiration did not offset decrease in autotrophic respiration, and R_{sco} for outbreak year was decreased in comparison to non-disturbed years."

On a similar note, many of the decisions taken in the presentation of results and development of the model rely on data collected during non-outbreak years. Is the gap-filling approach also suitable in defoliated years?

Response: The gap-filling approach is suitable also for defoliated years. We have clarified this in the manuscript (P. 8, L. 15-17): "We considered the gap-filling approach suitable also for defoliated years since the gap-filling function is created based on data from short time windows, usually seven days, and hence, do adjust the fitting parameters for changing ecosystem

15 conditions."

P8, L10-11: More detail is needed about the quality control. Under which 'bad' weather/measuring conditions were data removed? How much data remained after quality control and what proportion was gap-filled?

Response: Data were removed mainly due to precipitation since an open path gas analyzer was used, or if the atmosphere

- 20 was not fulfilling the turbulent conditions required for eddy covariance measurements. Available data after cleaning: 2007 61%; 2009 71%; 2010 66%; 2011 65%; 2012 58%; 2014 65%. We have clarified this in the manuscript (P. 8, L. 13-15): "The main reasons for removing data were precipitation as we used an open path gas analyser, and atmospheric conditions that did not fulfill turbulent the conditions required."
- P10, L11-2: Here, it is not clear which years have been used or why. The years for which the EC data are
 available should be stated in Section 2.2.3. Why was 2012 the only year used to calculate "max with insect defoliation? Why were data from 2008 and 2013 not included/not available?

Response: We have clarified this in Section 2.3.3 (P. 10, L. 18-21): "Two ε_{max} values were computed: one including data from the five years (2007, 2009, 2010, 2011 and 2014) with undisturbed birch forest, and one ($\varepsilon_{max, def}$) for the year 2012

30 with insect defoliation. No data were available from 2008 due to equipment failure, and in 2013 the measurements were disturbed by larvae climbing the equipment."

P12, L13: It is not clear how these statistics were calculated and they don't seem to follow from Fig 4. Please provide more details/clarification

35 Response: We do agree that these statistics were not well described. Previously the statistics were based on the entire study area. We have changed the statistics to include only the pixels around the EC tower to correspond to the figure and clarified this (P. 12, L. 22-24): "The influence of observations with $NDVI_{DL}$ values < 0.4 and with f_{8day} > 0 was small. For the years with data available from the EC tower 8% of the eight day periods had $NDVI_{DL} < 0.4$ and $f_{\partial day} > 0$ in the MODIS pixels surrounding the tower. For these time periods average $f_{\partial day}$ was 0.068.

P14, Fig 6: The two green lines for NDVIDL show higher NDVI values early in the growing season for the defoliated year. Possible reasons for this should be investigated and the impact on the results commented on.

5

Response: Thanks for pointing this out. This is due to a weak fitting of the double logistic functions in TIMESAT. In a currently developed version of TIMESAT the fitting of the functions will be more robust. We have added a clarification in Section 3.3.1 (P. 16, L. 7-10): "In Figure 6, $NDVI_{DL}$ has higher values in the year with defoliation compared to undisturbed years in May (period 16-18). These high $NDVI_{DL}$ values are due to poor fitting of the double logistic function during winter

and early spring in 2012 (see Figure 3, where $NDVI_{DL}$ increases earlier in 2012 compared to the other years). The impact on the result is however small since these eight periods are in the early part of the growing season when f_{8day} is zero.

Minor comments:

P2, L22: Change 'difference' to 'differences'

15 Response: We have updated the manuscript accordingly.

P2, L26: Would be useful to give the land cover type for the southern France site

Response: We have added that the defoliation occurred in holm oak (Quercus ilex L.) (P. 2, L. 31).

P3, L17: Change to read 'of the form'
 P3, L18: Number this equation and update the others accordingly
 P3, L20-1: Change to read 'and with variability in meteorology'

Response: The section is updated and these comments are no longer relevant.

25 P4, L24-6: It is not clear that these recent outbreaks are for the study site – please state the area they apply to. Also give some information about the EC tower in that study (i.e. location, and mention the flux measurements were also for the birch forest)

Response: We have clarified that the outbreaks mentioned were in the study area, and that the EC tower mentioned was

30 located in birch forest (P. 4, L. 17-19): "The latest outbreaks in the study are occurred in 2004, with a documented reduction in carbon sink strength of 89% at an EC tower located in birch forest...."

P5, L10: Change 'derived' to 'derive'

Response: We have updated the manuscript accordingly.

35

P6, L16-7: Change to read 'to be about'

Response: We have updated the manuscript accordingly.

40 P6, L18: Keep the order of 'east/west' the same as previously (L17). When the wind is from the west, the footprint is located to the west of the tower

Response: We have updated the manuscript accordingly (P. 6, L. 18-20): "The prevailing wind directions are from the west and from the east, hence the main footprint of the EC tower is to the west and east from the tower where vegetation is most homogenous."

5 P6, L24: Change 'wind speeds' to 'stability', as wind direction and stability tend to be the major controls on EC footprints

Response: We have updated the manuscript accordingly.

10 P7, Fig 3: Change y-axis of RH plot to 'NDVIDL'

Response: We have updated the manuscript accordingly.

P8, L16: Change 'measured the' to 'the measured'

15

Response: We have updated the manuscript accordingly.

P9, Eq3: Units on LHS do not equate to units on RHS

20 Response: We have updated the manuscript accordingly.

P11, L22-23 Suggest choosing alternative notation for GPPreduction, as it is a ratio of GPPs, rather than GPP itself

Response: We have changed the notation of the reduction factor to GPPredfact.

25 P12, L6: Change 'accurate' to 'accurately'

Response: We have updated the manuscript accordingly.

P13, Fig 5: Add units for RMS

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Response: We have updated the manuscript accordingly and also changed RMS to RMSE (Fig. 5, P. 13).

P14 L5-6 and Fig 7: The text mentions 'low GPP observations' but in Fig 7 it looks as though the modelled GPP values are lower than the EC observed values, with several zero values. Please clarify

Response: We have calrified (P. 14, L. 4-6): "The low GPP observations with several zero values for LUE modelled GPP are from May, before budburst for the birch forest. These low GPP values have little influence on annual GPP."

Mapping the reduction in carbon uptakegross primary productivity in subarctic birch forests due to insect outbreaks

Per-Ola Olsson, Michal Heliasz, Hongxiao Jin, Lars Eklundh

5 Department of Physical Geography and Ecosystem Science, Lund University, Sölvegatan 12, S-223 62 Lund, Sweden. *Correspondence to*: Per-Ola Olsson (per-ola.olsson@nateko.lu.se)

Abstract. It is projected that forest disturbances, such as insect outbreaks, will have an increasingly negative impact on forests with a warmer climate. These disturbance events can have a substantial impact on forests' ability to absorb atmospheric CO_2 , and may even turn forests from carbon sinks into carbon sources; hence, it is important to develop methods to both monitor forest disturbances and to quantify the impact of these disturbance events on the carbon balance. In this study we present a method to monitor insect induced defoliation in a subarctic birch forest in northern Sweden, and to quantify the impact of these outbreaks on gross primary productivity (GPP). Since frequent cloud cover in the study area requires data with high temporal resolution and limits the use of finer spatial resolution sensors such as Landsat, defoliation was mapped with remote sensing data from the MODIS sensor with 250×250 m spatial resolution. The impact on GPP was

- 15 estimated with a light use efficiency (LUE) model that was calibrated with GPP data obtained from eddy covariance (EC) measurements for-from five years with undisturbed birch forest and for one years with insect induced defoliation. Two methods were applied to estimate the impact on GPP: (1) A GPP reduction factor derived from EC measured GPP was applied to estimate GPP loss, and (2) a LUE model was run both for undisturbed and defoliated forest and the differences in modelled GPP were derived. In the study area of 100 km² the results showed suggested an average total decrease in carbon
- ²⁰ uptakeregional GPP over the three outbreak years (2004, 2012, and 2013) of 15 ± 5 Gg C yr⁻¹, 44.6 ±13 Gg C, which is of the same magnitude as compared to the estimated mean annual regional GPP of 401.1 ±12 Gg C yr⁻¹ for the five years without defoliation, a year without disturbance. In the most severe outbreak year (2012), 76% of the birch forests were defoliated and annual regional GPP was merely 50% of GPP for years without disturbances. The study has generated valuable data that improve previous studies on impact estimates and demonstrates a potential for mapping insect disturbance impact over
- extended areas.

10

Keywords: Insect defoliation, subarctic mountain birch, MODIS, GPP, LUE

1 Introduction

It is estimated that forests account for half of the global terrestrial net primary productivity and act as important sinks of atmospheric CO_2 (Bonan 2008). Forests in the northern hemisphere contribute significantly to this sink, with the mid- and high latitude ecosystems as major contributors (Goodale et al. 2002; Kurz et al. 2008b). The high latitude forests are,

- 5 however, predicted to be among the ecosystems that are most strongly influenced by climate change (Kurz et al. 2008b); a warmer climate is likely to increase forest productivity (e.g. Nemani et al. 2003; Boisvenue & Running 2006), and result in higher uptake of CO_2 from the atmosphere. On the other hand, it is projected that the impact of forest disturbances will increase with a warmer climate (Seidl et al. 2014), and there are indications that disturbances such as wind, fires, and insect outbreaks have lead to saturation of the carbon sinks in European forests (Nabuurs et al. 2013). One important forest
- 10 disturbance agent is insects; it is projected that the temporal and spatial dynamics, as well as the intensities and ranges of insect herbivore outbreaks will be influenced by global warming (Vanhanen et al. 2007; Battisti 2008; Jepsen et al. 2008; Netherer & Schopf 2010). These insect outbreaks can severly disturb forest ecosystems and have a strong impact on carbon dynamics (Kurz et al. 2008a; Jepsen et al. 2009; Heliasz et al. 2011). Quantitative effects of insect outbreaks on the carbon balance are, however, not well known (Clark et al. 2010; Schäfer et al. 2010; Hicke et al. 2012), and insect outbreaks are
- 15 generally excluded in large scale carbon modelling, which may result in overestimation of forests' ability to act as carbon sinks (Kurz et al. 2008b; Hicke et al. 2012). Consequently, it is important to develop methods both to monitor the spatial extent of insect outbreaks and to quantify the impact of these outbreaks on the carbon balance.
- One alternative to estimate the impact on forest productivity is modelling: The impact of a large-scale outbreak of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) in British Columbia, Canada, was studied with a forest ecosystem
- 20 model by Kurz et al. (2008a). The impact on the carbon balance of gypsy moth (*Lymantria dispar* L.) defoliation in New Jersey, USA, was modelled with both a canopy assimilation model (Schäfer et al. 2010) and a terrestrial biosphere model (Medvigy et al. 2012). Dymond et al. (2010) was applied to model the impact of Spruce Budworm (*Choristoneura fumiferana* Clem.) outbreaks in eastern Canada, and Landry et al. (2016) developed a Marauding Insect Module (MIM) in the Integrated Biosphere Simulator (IBIS) that enables simulation of insect outbreak for three insect functional types.
- Another alternative to quantify the influence of an insect outbreak on the carbon balance is to apply eddy covariance (EC) measurements: Brown et al. (2010, 2012) studied how a mountain pine beetle outbreak influenced net ecosystem productivity (NEP) in British Columbia, Canada; Clark et al. (2010, 2014) studied differences in NEE between undisturbed years and years with severe defoliation by the gypsy moth in New Jersey, USA; and Heliasz et al. (2011) estimated the reduction in net ecosystem exchange (NEE) during the growing season due to an autumnal moth (*Epirrita autumnata*)
- 30 Borkhausen) and winter moth (*Operophtera brumata* L.) outbreak in northern Sweden in 2004. Even though not explicitly studied, there was gypsy moth defoliation of holm oak (*Quercus ilex* L.) present in a time-series of EC measurement in southern France (Allard et al. 2008). These methods generate valuable data on the impact of insect defoliation on the carbon balance; however, to quantify the total regional impact, data on the extent of defoliation events are required.

To generate wall-to-wall estimates of the disturbance effect on the carbon balance, remotely sensed data from satellites can be used. Several studies have demonstrated that satellite based remote sensing techniques can be applied to detect insect disturbances with high accuracy; see e.g. Wulder et al (2006); Adelabu et al. (2012) and Rullan-Silva et al. (2013) for reviews. In this paper we study outbreaks of autumnal moth and winter moth in subarctic mountain birch (*Betula pubescens*)

- 5 ssp. Czerepanovii N.I. Orlova) forests in northern Sweden. These outbreaks are often followed by within-season recovery of the foliage in parts of the outbreak areas, which in combination with cloudy conditions can limit the possibility to map the outbreaks with remote sensing methods. Nevertheless, outbreaks of autumnal and winter moth have been mapped in northern Fennoscandia with high accuracy with Landsat data (Tømmervik et al. 2001; Babst et al. 2010). The low temporal resolution of Landsat (16 days revisit time) can, however, be a limitation; as an example, only fractions of the area included in this
- 10 study were visible in Landsat data during the peak of a severe outbreak in 2013. An alternative to Landsat data is coarse spatial resolution data from e.g. the moderate resolution imaging spectroradiometer (MODIS) sensor, which provides data with high (daily) temporal resolution and a spatial resolution of 250×250 m or coarser. MODIS derived Normalized Difference Vegetation Index (NDVI) have been used to map autumnal and winter moth outbreaks with high accuracy in northern Fennoscandia (Jepsen et al. 2009); and Olsson et al. (2016b) developed a method for near real-time monitoring of insect induced defoliation that also facilitates monitoring of refoliation later in the growing season.
- Furthermore, there is a large body of research demonstrating that vegetation primary productivity can be estimated with remotely sensed data and a light use efficiency (LUE) approach (e.g. Prince 1991; Ruimy et al. 1994; Running et al. 2004; Xiao et al. 2004; Wu et al. 2010; McCallum et al. 2013; Gamon 2015). The LUE concept was introduced by Monteith (1972); Monteith & Moss (1977), suggesting that the primary productivity of plants has a strong linear relationship to the
- absorbed amount of photosynthetically active radiation (APAR), i.e. solar radiation in the spectral range 400–700 nm that is absorbed by the plant canopy. Since near-linear relationships between satellite derived vegetation indices and the fraction absorbed PAR (fAPAR) have been established (e.g. Asrar et al. 1984; Sellers 1987; Goward & Huemmrich 1992; Myneni & Williams 1994; Olofsson and Eklundh 2007), it is possible to create a LUE model on the formdriven by remote sensing data. (Prince 1991; Running et al. 2004):

25 $GPP = \varepsilon \times fAPAR \times PAR$

where *GPP* is gross primary productivity, ε is the light use efficiency coefficient and *fAPAR* is estimated as: *fAPAR* = a + b × NDVI (Myneni & Williams 1994). The light use efficiency coefficient varies between vegetation types and variability in meteorology, hence, it is common to model ε with a maximum efficiency depending on vegetation type, and reduction factors based on temperature and vapour pressure deficit (e.g. Field et al. 1995; Prince & Goward 1995; Potter et

- 30
 - al. 1999; Turner et al. 2003). In cold climates, temperature is the main limiting factor for photosynthetic capacity (Bergh et al. 1998), and it has been shown that the variability in *c* can be modelled with temperature data only (Lagergren et al. 2005). For ecosystems dominated by non vascular plants it should, however, be noted that water stress is a major limiting factor (Liljedahl et al. 2011). This type of Such a LUE model could be suitable applied for large-area estimates of the impact of forest disturbance on the uptake component of the carbon balance, GPP. Bright et al. (2013) utilized Landsat data to map

bark beetle damage in northern Colorado, USA, and MODIS GPP data, which are based on a LUE model, to quantify the impact of the outbreak on GPP. However, to the knowledge of the authors, no previous study has utilized remote sensing data and <u>developed</u> a LUE model to monitor and quantify the impact of <u>defoliatingan</u> insects' outbreak on <u>earbon</u> uptake<u>GPP</u>.

- 5 In this study we utilized EC measured GPP to develop a LUE model, <u>driven by MODIS derived NDVI</u>, and <u>satellite based</u> remote sensing data to map insect induced defoliation, as well as to <u>upscale quantify</u> the <u>regional</u> impact on GPP of this <u>insect induced</u> defoliation, and to map the spatial extent of the defoliation. with the aid of the LUE model. This combination of EC data to calibrate a LUE model, and remote sensing data to map and quantify the impact of insect disturbances on the earbon balance is a major advantage compared to methods that lack spatial observations. The method was developed in
- 10 insect defoliated subarctic mountain birch forests in northern Sweden. The fractional absorbed photosynthetically active radiation was derived from NDVI obtained from the MODIS sensor with a temporal resolution of eight days. Temperature data, used to model variability in *c*, and PAR was obtained from an EC tower. Our main study objective was to quantify the reduction in-compare GPP for years with (2004, 2012 and 2013) and without (2007, 2009, 2010, 2011 and 2014) insect outbreak -due to insect defoliation-in the birch forest of a subarctic valley of northern Sweden-between 2000 and 2015, a
- 15 period during which three significant insect outbreak events have occurred. The analysis was achieved with two methods: (1) finding GPP for undisturbed forest and estimate the impact of an insect outbreak with a common reduction factor derived from EC data; and (2) by applying a LUE model for both undisturbed and defoliated pixels and computing the differences.

2 Materials and methods

2.1 Study area

- 20 The study area was the mountain birch (*Betula pubescens ssp. Czerepanovii* N.I. Orlova) forests in a valley south-west of Abisko village (68.35N, 18.82E), and along the lake Torneträsk, as illustrated in Fig. 1 (green). The area is located in the subarctic zone in northern Sweden with lake Torneträsk at an altitude of 345 m.a.s.l. and with the highest mountains reaching 1 700 m.a.s.l. (Interact, 2016). These birch forests are infested by the autumnal moth (*Epirrita autumnata* Borkhausen) and the winter moth (*Operophtera brumata* L.) in time intervals of 9–10 years (Bylund 1995; Tenow et al. 2007). The first reported outbreaks by the autumnal moth in northern Fennoscandia are from mid-1800, and the winter moth has been reported in the northern parts of Fennoscandia since late 1800 (Tenow 1972). These insect outbreaks strongly influence the birch forests (Ammunét et al. 2015); severe defoliation events may result in stem mortality, requiring decades of recovery (e.g. Tenow 1996; Tenow & Bylund 2000; Jepsen et al. 2013), and understorey vegetation can shift into more grass dominated communities (Karlsen et al. 2013; Jepsen et al. 2013). Root-associated fungal communities can change
- 30 (Saravesi et al. 2015) as well as chemical and physical properties of the soil (Kaukonen et al. 2013). A warmer climate, especially a lower frequency of years with extremely cold winters, as reported by Callaghan et al. (2010), strongly influences birch moth populations (Babst et al. 2010). The autumnal moth outbreaks have expanded into colder, more continental

regions, and the winter moth has reached further to the north-east into areas where the autumnal moth previously dominated (Jepsen et al. 2008). The latest outbreaks <u>in the study are</u> occurred in 2004, with a documented reduction in carbon <u>uptakesink strength</u> of 89% at an EC tower <u>located in birch forest</u> (Heliasz et al. 2011), and in 2012 and 2013 (Bengt Landström, County administrative board of Norrbotten, pers. comm. 31.10.2013). These outbreak events were included in this study.



Source: Lantmäteriet, Dnr: I2014/00579

Figure 1. The studied birch forest (green) along the south-west part of lake Torneträsk and in the valley to the south-west of Abisko village. The locations of the eddy covariance (EC) tower used to obtain GPP, and the spectral tower used to obtain fAPAR
 data are also shown. Reference system is SWEREF99 TM and latitude and longitude are in WGS84. Source of background map: Lantmäteriet (Dnr: I2014/00579).

2.2 Data

5

2.2.1 Remote sensing data and smoothing of time-series

We used two Terra/MODIS satellite data products with eight days temporal resolution: (1) MOD09Q1 version 5, surface
reflectance in the red and near infrared (NIR) bands, including quality assurance (QA) information, with 250×250 m spatial
resolution, used mainly to derive NDVI (LPDAAC 2016a); and (2) MOD09A1 version 5, surface reflectance, as well as QA
data, with 500×500 m spatial resolution (LPDAAC 2016b), utilized due to the product's more comprehensive QA data.
NDVI was computed from the MODIS data as (Rouse et al. 1973; Tucker 1979):

$$NDVI = (NIR - red)/(NIR + red)$$
(1)

where *red* is reflectance in the red wavelength band, and *NIR* is reflectance in the near infrared wavelength band. We created time-series for the period 2000–2014 for all pixels in the study area and processed in TIMESAT ver. 3.2. TIMESAT is a software package used to reduce the influence of noise by fitting smoothed functions to time-series of data (Jönsson & Eklundh 2002, 2004). In this study we applied the same fittings and weights as in Olsson et al. (2016b): Double logistic functions were used to smooth the <u>raw NDVI</u> data and <u>the NDVI observations were classified into quality classes based on</u> QA data from both MOD09Q1 and the more comprehensive QA-flags in MOD09A1 were utilized to estimate the quality of the NDVI observations. In this study we use the term *NDVI_{DI}* to refer to the smoothed time-series of NDVI.

2.2.2 Fraction of canopy absorbed PAR and relationships with NDVI

The fraction of canopy absorbed PAR by the canopy (fAPAR canopy) was measured at a spectral tower located in birch forest

- north-west from Abisko village (Fig. 1, black star). *fAPAR_{canopy}* was obtained using the four-component method, i.e. measurements of incoming PAR above canopy, the total reflected PAR above the canopy, the transmitted PAR below the canopy, and the reflected PAR by the understorey vegetation and ground below the canopy. See Eklundh et al. (2011) for detailed information about the estimation of *fAPAR_{canopy}* the pure canopy absorbed PAR. All PAR sensors were calibrated at the field site following the procedure by Jin & Eklundh (2015), and *fAPAR_{canopy}* at solar noon time was calculated and used
 - in the final analysis. *fAPAR_{canopy}* data were available for the years 2010 and 2011.
 Average *fAPAR_{canopy}* over eight day periods, coinciding with the MODIS eight day periods, were computed and an ordinary least squares (OLS) regression was performed to find the relationship between *fAPAR_{canopy}* and *NDVI_{DL}* (Myneni & Williams 1994)., and tThe linear equation derived was used in the LUE model to obtain fAPAR from the double logistic fitted NDVI.

2.2.3 Eddy covariance and meteorological data

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- The EC tower is situated in the eastern part of the study area (Fig. 1, black triangle), and located near the crossing point of four nominal MODIS pixels with 250×250 m spatial resolution (Fig. 2). Vegetation in the four pixels is similar with some open mires in the northeast pixel and a paved road crossing the two southernmost pixels. The tower's footprint is estimated to <u>be</u> about 200 m which is slightly smaller than a MODIS pixel. The prevailing wind directions are from the west and from the east, hence the main footprint of the EC tower is to the <u>east-west</u> and <u>west-east</u> from the tower where vegetation is most
- 25 homogenous. Time-series of NDVI were extracted and mean values and standard deviations were computed for the four MODIS pixels to study if there were any larger deviations in the pixels' NDVI signals. In Figure 3, mean NDVI and standard deviation for the four pixels in the period 2010–2014 are shown. The low standard deviations indicate that there are minor differences in the NDVI signal between the pixels during the main growing season for both raw NDVI and *NDVI_{DL}* both for years without disturbance and for outbreak years. Hence, we assume that a varying footprint of the EC tower due to
- 30 varying wind directions and wind speeds stability will have a limited influence on the EC measurements.



Source: Lantmäteriet Dnr: I2014/00579.

Figure 2. The location of the eddy covariance (EC) tower (yellow triangle) near the crossing point of four nominal MODIS pixels with 250×250 m spatial resolution (white lines). Reference system: SWEREF99 TM. Lantmäteriet (Dnr: I2014/00579).



Figure 3. Mean (black) and standard deviation (gray) of NDVI 2010–2014 for the four pixels around the eddy covariance (EC) tower. (a) is raw NDVI and (b) is NDVI fitted with double logistic functions in TIMESAT (NDVI_{DL}). 2012 and 2013 are years with insect outbreak. In 2013 the birch forest was refoliating later in the growing season. There is a small peak in raw NDVI (a) appearing each year. This peak appears during the winter when there is no vegetation in the study area and is hence, removed from the smoothed data (b).

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The EC measurements were made 8 m above ground, 3.3 m above canopy, using a 3-dimensional sonic anemometer (Metek USA-1; METEK Gmbh., Germany) and an open path infrared gas analyzer (Licor 7500, LI-COR Inc., USA). The system was operated with a frequency of 20 Hz and data were recorded by a data logger (CR1000; Campbell Scientific, Inc., USA). Additional measurements of air temperature (Vaisala WXT510; Vaisala, Finland) and incoming photosynthetic flux density (PPFD; JYP 1000, SDEC, France), used for flux partitioning and gap filling, were made at the tower. Data were obtained each year during the period May 1 to September 30, which is from before the start of the growing season (Karlsson et al.

2003) until late growing season; during the years included in this study GPP was approaching zero by the last week of <u>September</u>. For the years 2004 and 2013, temperature and PAR were obtained from Abisko scientific research station (ANS); comparisons between data from ANS and the EC tower showed small differences for the years when data were available from both sources.

- 5 EC flux calculations were done with the EddyPro software ver. 5.2.1 (LI-COR Inc., USA). Gaps caused by bad weather conditions, bad EC measuring conditions, or short breaks in instrument functioning were filled with the online model: Eddy covariance gap-filling & flux-partitioning tool (http://www.bgc-jena.mpg.de/~MDIwork/eddyproc). The main reasons for removing data were precipitation as we used an open path gas analyser, and atmospheric conditions that did not fulfill turbulent the conditions required. We considered the gap-filling approach suitable also for defoliated years since the gap-
- filling function is created based on data from short time windows, usually seven days, and hence, do adjust the fitting parameters for changing ecosystem conditions. A model from the same website was used to partition NEE into GPP and ecosystem respiration (R_{eco}). It was assumed that night time NEE is equal to night time R_{eco}. Accordingly, the accepted night-time data were fitted to the Lloyd and Taylor (1994) model based on air temperature. This model was also used to estimate R_{eco} during daytime conditions. GPP was estimated as the residual after subtracting R_{eco} from the measured the NEE. Details about gap filling and flux partitioning are described in Reichstein et al. (2005).

2.2.4 Land cover and elevation data

Land cover data were obtained from the Swedish mapping, cadastral, and land registration authority (Lantmäteriet; Dnr: I2014/00579). These land cover data are based on a classification of Landsat TM data and updated in the year 2000 as a part of the CORINE land cover project, but with a finer spatial resolution of 25×25 m (Lantmäteriet 2010). Birch forests in the

20 study area were identified by extracting all pixels with broadleaved forest. Since birch is the dominating tree species with only a few sporadic individuals of other species (Sonesson & Lundberg 1974), all forests were considered to be birch. These data were used to calculate the fraction forest cover per MODIS pixel.

Elevation data were obtained from Lantmäteriet as a digital elevation model (DEM) with 50×50 m spatial resolution (Lantmäteriet; Dnr: I2014/00579). Mean elevation for each MODIS pixel was computed as the average altitude of all DEM

25 pixels covered by a MODIS pixel. These data were used to compute altitudinal differences in temperatures when applying the LUE model. To adjust for altitudinal differences in temperatures across the study area, a mean summer temperature gradient of 0.5°C per 100 m (Josefsson 1990; Holmgren & Tjus 1996) was applied to the temperature data from the ECtower.

2.3 Light use efficiency model

30 A LUE model with mean values of daily GPP in eight day intervals (GPP_{lue}) (g C m⁻² day⁻¹), corresponding to the time interval of the MODIS data, was developed as:

$$GPP_{lue} = \varepsilon \times fAPAR_{\mathcal{B}day} \times PAR_{\mathcal{B}day}$$
(2)

where ε (g C MJ⁻¹) is the light use efficiency, *fAPAR*_{8day} is fAPAR for a MODIS eight day period derived from *NDVI*_{DL}, and *PAR*_{8day} (MJ m⁻²_day⁻¹) is mean daily PAR measured at the EC tower over the eight day period. The light use efficiency varies between vegetation types and variability in meteorological conditions are accounted for through reductions factors for temperature and vapour pressure deficit (e.g. Field et al. 1995; Prince & Goward 1995; Potter et al. 1999; Turner et al. 2003).

5 <u>In this study the The-</u>light use efficiency was computed as:

$$\varepsilon = \varepsilon_{max} \times f_{\mathcal{B}day} \tag{3}$$

where ε_{max} (g C MJ⁻¹) (see Section 2.3.3) is the maximum efficiency applied in the model and f_{Bday} is a reduction factor. introduced to model the variability in ε depending on temperature. We assumed that accounting for temperature only is sufficient in our study region, which is supported by Bergh et al. (1998) and Lagergren et al. (2005). Two models were

10 created to describe $f_{\partial day}$, as in Lagergren et al. (2005): One model for the first part of the growing season and one model for the second part of the growing season.

2.3.1 First part of the growing season

During the first part of the growing season, covering May to late June, $f_{\mathcal{B}day}$ depended on growing degree days (GDD) and frost events, where GDD was computed with a base temperature of 5°C, following Senn's et al. (1992) method applied to mountain birch development in northern Finland:

$$GDD_{t} = \begin{cases} GDD_{t-1} & , T_{mean8} \le 5\\ GDD_{t-1} + T_{mean8} - 5 & , T_{mean8} > 5 \end{cases}$$
(4)

where T_{means} (°C) is the mean temperature for a MODIS eight day period. The reduction factor was computed as:

$$f_{8day} = \begin{cases} 1 & , GDD_{thres} - S_{GDD} \\ 1 - \frac{GDD_{thres} - S_{GDD}}{GDD_{thres} + S_{GDD}} & , GDD_t \ge GDD_{thres} \end{cases}$$
(5)

where GDD_{thres} (see Section 2.3.3) is a threshold applied to decide when temperature and frost events no longer influence ε , in a similar fashion as Bergh et al. (1998) and Lagergren et al. (2005). S_{GGD} is a reduction factor influenced by GDD and frost events and computed as:

$$S_{GDD} = \frac{GDD_t}{1 + P_{frost}} \tag{6}$$

where P_{frost} is a reduction factor controlled by frost events and computed as:

$$P_{frost} = \begin{cases} \frac{0.05 \times (-3 - T_{min8})}{5} & , \frac{T_{min8}}{-8} \le -3 \\ 0.05 & , -8 \le T_{min8} < -3 \\ , T_{min8} < -8 \end{cases}$$
(7)

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where $T_{min\theta}$ (°C) is the lowest temperature during a MODIS eight day period.

2.3.2 Second part of the growing season

In the second part of the growing season, covering late June to September, $f_{\mathcal{B}day}$ is controlled by mean temperature only as:

$$f_{8day} = \begin{cases} 1 & , T_{mean8} \ge T_{thres} \\ \hline T_{thres} & , T_{mean8} < T_{thres} \end{cases}$$
(8)

where T_{thres} (°C) (see Section 2.3.3) is a temperature factor for controlling the influence of the eight day mean temperature 5 during the second part of the growing season.

2.3.3 LUE model optimization

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The LUE model was optimized to find three factors: (1) the GDD threshold (GDD_{thres}), (2) the temperature factor (T_{thres}), and (3) the period to change from the first to the second seasonal model, by minimizing the root mean square error (RMSE) and maximizing R², based on GPP_{lue} and daily mean values of GPP from the EC tower over MODIS eight day periods (GPP_{EC}). To compute ε_{max} , the mean value of the light use efficiency for all MODIS periods with maximum efficiency i.e. $f_{Bday} = 1$

$$\varepsilon_{max} = \frac{GPP_{EC}}{fAPAR_{8day} \times PAR_{8day}} \tag{9}$$

where GPP_{EC} was derived from the EC tower. Two ε_{max} values were computed: one including data from the five years (2007, 2009, 2010, 2011 and 2014) with undisturbed birch forest, and one ($\varepsilon_{max, def}$) for the year 2012 with insect defoliation. No data were available from 2008 due to equipment failure, and in 2013 the measurements were disturbed by larvae climbing the equipment.

2.3.4 LUE model uncertainty

A Monte Carlo approach was applied to evaluate the uncertainty of the LUE model by creating sets with 100 parameter values each for ε_{max} and slope and intercept derived from the OLS regression between *fAPAR_{canopy}* and *NDVI_{DL}*. The standard deviation of ε_{max} was estimated from all MODIS periods with maximum efficiency, as described in 2.3.3, and a 95% confidence interval for the regression line was estimated. The different sets of parameters were created randomly from a uniform distribution, and the Monte Carlo simulation was run for all possible combinations of parameter values for the five years with undisturbed forests and over 15 sets of 100 MODIS pixels with birch forest. Mean and standard deviation of LUE modelled GPP were estimated from these simulations.

25 2.4 Identifying MODIS pixels with defoliated birch forest

was calculated, where the efficiency was computed as:

Defoliated MODIS pixels were identified for the three years with insect outbreaks with a near real-time monitoring method based on Kalman filtering and cumulative sums (Olsson et al. 2016b). The method identifies a seasonal trajectory of NDVI

representing birch forest during a year without disturbances, called *stable season*. A Kalman filter (Kalman 1960) is applied to the raw NDVI observations from the year of study and deviations from the stable season are computed. A cumulative sum (CUSUM) filter (Page 1954) is applied to these deviations, and a pixel is classified as defoliated when the cumulative sum of deviations reaches a given threshold. In a near real-time application the stable season can only be derived from years prior to

- 5 the year of study. In this study we modified the method so that the stable season was derived from all years with available data. For high detection accuracy, the method requires that a MODIS pixel is covered by at least 50% forest. Hence, based on the land cover data from Lantmäteriet, forest in pixels with lower forest cover were excluded, resulting in 100 km² of the totally 125 km² birch forest in the study area being included; the mean forest cover was 80% per MODIS pixel. The method detected 74% of the defoliated sampling areas in the study area with a misclassification of undisturbed areas of 39% (Olsson
- 10 et al. 2016<u>b</u>).

2.5 Annual GPP loss due to insect defoliation

The LUE model was applied to all MODIS pixels with a forest cover of at least 50%. To adjust for altitudinal differences in temperatures across the study area, a mean summer temperature gradient of 0.5°C per 100 m (Josefsson 1990; Holmgren & Tius 1996) was applied to the temperature data from the EC tower. We considered the eight day average of incoming PAR

- 15 (*PAR*_{8day}), measured at the EC tower, to be valid for all pixels in the study area; comparisons between PAR measured at the EC-tower and Abisko scientific research station also showed that average PAR is similar. GPP for a-years without insect defoliation was estimated for all pixels by applying the LUE model and computing the mean value for the five years without insect outbreak, and with data available from the EC tower. We considered the eight day average of incoming PAR (*PAR*_{8day}), measured at the EC-tower, was assumed to be valid for all pixels in the study area; comparisons between PAR
- 20 <u>measured at the EC-</u> tower and Abisko scientific research station also showed that average PAR is similar. and computing the mean value for the five years without insect outbreak, and with data available from the EC tower.

Two methods were applied to study the reduction in annual GPP due to the insect outbreaks: (1) a method based on a reduction factor derived from the EC data from 2012 when the birch forest in the footprint of the tower was severely defoliated, and no refoliation occurred. and This reduction factor was applied to all pixels in the study area, and (2) a method

where the LUE model was applied to all defoliated pixels with $\varepsilon_{max, def}$ computed for defoliated growing seasons, and where the loss in GPP was computed as the difference between undisturbed and defoliated years.

2.5.1 Method 1 - GPP reduction factor

The fraction of the measured annual GPP at the EC tower that was lost due to the insect outbreak in 2012 (GPP_{reduction})-was computed as:

30 <u>*GPP_{redfact}* = 1 - *GPP_{defoliated}/GPP_{undisturbed}* (10) Where <u>*GPP_{redfact}* is the reduction factor and</u> *GPP_{defoliated}* is annual GPP from the EC tower in 2012. *GPP_{undisturbed}* is GPP from the tower representing a year without disturbances and computed as the mean of annual GPP for the five years without disturbances.</u> The reduction in annual GPP was computed for each pixel by applying the reduction factor to GPP for undisturbed years and multiplying with the area forest cover in the pixel. The same reduction factor was applied to all years with insect defoliation. The total impact <u>on of the defoliation</u> uptake was computed as the sum of GPP loss for all defoliated pixels in the study area, and for each year with insect outbreak.

5 2.5.2 Method 2 - LUE model for defoliated pixels

The LUE model, modified to model growing season with defoliation, was applied to all defoliated pixels in the study area to estimate annual GPP for each year with defoliation. Derivation of $\varepsilon_{max, def}$ was done with the same method as ε_{max} , but only data from the one year with insect outbreak (in-2012) were available to estimate $\varepsilon_{max, def}$, and to evaluate the performance of the defoliation LUE model. For each year with insect outbreak, the regional reduction in GPP was computed by summing,

10 over all pixels identified as defoliated, the difference between GPP for years without outbreak and GPP for this specific outbreak year. The total reduction in GPP was computed by summing the differences between GPP for healthy years and GPP for defoliated years for all pixels identified as defoliated.

2.5.3 Influence of refoliation

We also studied how recovering foliage later in the growing season influenced the two methods. The assumption was that

15 recovering foliage would result in slightly higher *NDVI_{DL}* values, which would enable Method 2 to capture the refoliation and hence, estimate GPP losses more accurately. All pixels that were detected as defoliated were classified as refoliated or nonrefoliated with the defoliation monitoring method. The differences between GPP loss derived with method 1 and method 2 were computed as *GPP loss method 1 - GPP loss method 2*. Finally, the mean differences for refoliated and non-refoliated pixels were derived.

20 3 Results

3.1 Correlation between fAPAR and NDVI

There was a strong linear relationship between eight day mean values of $fAPAR_{canopy}$ and $NDVI_{DL}$ for $NDVI_{DL}$ values ≥ 0.4 (Fig. 4). The influence of observations with $NDVI_{DL}$ values < 0.4 and with $f_{Bday} > 0$ was small. For the years with data available from the EC tower 8% of the eight day periods had $NDVI_{DL} < 0.4$ and $f_{Bday} > 0$ in the MODIS pixels surrounding

25 <u>the tower. For these time periods average f_{Bday} was 0.068.</u>, including only 1.1% of the observations and with an average f_{Bday} of 0.25. Hence, an OLS regression was performed with $NDVI_{DL}$ values ≥ 0.4 to model the relationship between $fAPAR_{Bday}$ and $NDVI_{DL}$. This resulted in an R² of 0.81 and the relationship:

$$fAPAR_{\mathcal{B}day} = -0.05 + 0.60 \times NDVI_{DL} \tag{11}$$

The 95% confidence intervals for slope and intercept applied in the Monte Carlo simulation to estimate the LUE model's uncertainty were -0.05 ± 0.18 (intercept) and 0.60 ± 0.11 (slope).



5 Figure 4. Correlation between ground measured <u>fraction of absorbed PAR by the canopy</u> absorbed PAR (fAPAR_{canopy}) and MODIS derived NDVI smoothed with a double logistic function in TIMESAT (NDVI_{DL}) in eight days intervals. Only NDVI_{DL} values ≥ 0.4 were included in the OLS regression resulting in the black line. R² = 0.81 and N = 29.

3.2 Light use efficiency

Optimization resulted in a GDD_{thres} threshold of 32 growing degree days (Fig. 5, left) and a <u>*T*</u>_{thres} temperature factor of 8°C (Fig. 5, middle). The optimal period to change the model for f_{Bday} was after MODIS period 23 i.e. the last week of June (Fig. 5, right).



Figure 5. Influence on RMSE and R^2 of GDD_{thres} (lefta), T_{thres} (middleb), and the optimal period to change from the first to the second f_{8day} model (rightc). <u>RMSE is computed from mean of daily GPP over eight days periods</u>.

5 Light use efficiency for years with no disturbance and with $f_{\mathcal{B}day} = 1$ (black line with error bars in Fig. 6)) gave an ε_{max} of 1.85 ± 0.36 g C MJ⁻¹ (± 1 standard deviation), resulting in the following LUE model: $GPP_{lue} = 1.85 \times f_{\mathcal{B}day} \cdot (-0.05 + 0.60 \times NDVI_{DL}) \times PAR_{\mathcal{B}day}$ (12)

The correlation between GPP_{EC} and GPP_{lue} was strong with $R^2 = 0.90$ (Figure 7). The intercept is -0.11 and the slope is 1.01 indicate that the LUE model performs well for years without outbreaks. The low GPP observations with several zero values for LUE modelled GPP are mainly from May, before the growing season budburst for the birch forest. had started, and These low GPP values have little influence on annual GPP. The Monte Carlo simulation resulted in an estimated standard deviation of 30% of the mean annual GPP. Hence, all annual GPP values derived from the LUE model are given with a standard deviation of 30% of annual GPP.

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Figure 6. Light use efficiency (ϵ), NDVI fitted with double logistic functions (NDVI_{DL}) scaled ×2 (green), and PAR (orange) for the six years with data from the EC tower. Black lines with error bars and black circles are the light use efficiency values included when ϵ_{max} and ϵ_{max} , def were computed for undisturbed and defoliated years respectively. The error bars are symmetric and one standard deviation higher or lower than the mean values.



Figure 7. Correlation between GPP from the EC tower and LUE modelled GPP for the five years with undisturbed forests. $\frac{\text{GPP}_{\text{lue}} = -0.11 \times 1.01\text{GPP}_{\text{EC2}}}{R^2} = 0.90 \text{ and } N = 95.$

3.3 Impact of insect outbreaks on annual GPP

5 3.3.1 Reduction factor and LUE model applied to quantify loss in GPP

Method 1 - reduction factor

GPP measured from the EC tower and the five years with available data (Table 1) resulted in a mean annual GPP of 441-440 g C m⁻² yr⁻¹. During the outbreak in 2012 annual GPP was 180 g C m⁻² yr⁻¹ which resulted in a reduction in GPP compared to undisturbed conditions of 59%. Hence, a reduction factor *GPP*_{reduction} = of 0.59 was applied to quantify the impact of the insect outbreak on the carbon balance.GPP.

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Table 1. Annual GPP	P derived from the EC	tower for the five years	s without insect outbrea	ak and the vear 201	2 with insect outbreak.

		Outbreak				
Year	2007	2009	2010	2011	2014	2012
$\mathbf{GPP} (g C m^{-2} yr^{-1})$	4 <u>51450</u>	401 <u>530</u>	<u>370</u> 448	<u>400</u> 531	<u>450</u> 373	180

Method 2 - LUE model for defoliated pixels

The correlation between GPP_{EC} and GPP_{lue} for the year with defoliation (2012) and data available from the EC tower was weaker than for years without disturbances with an R² of 0.83 (Fig. 8). The figure, with an intercept of -0.54 and a slope of 1.25 indicates that the LUE model underestimates GPP for lower values. R² was 0.83 and T the light use efficiency for the MODIS eight day periods with $f_{\beta day} = 1$ (black circles in Figure 6) gave an $\varepsilon_{max, def}$ of 0.98 ± 0.25 g C MJ⁻¹ (±1 standard deviation), resulting in the following LUE model for defoliated pixels:

 $GPP_{lue, defoliated} = 0.98 \times f_{8day} \cdot (-0.05 + 0.60 \times NDVI_{DL}) \times PAR_{8day}$ (13)

In Figure 6, $NDVI_{DL}$ has higher values in the year with defoliation compared to undisturbed years in May (period 16-18). These high $NDVI_{DL}$ values are due to poor fitting of the double logistic function during winter and early spring in 2012 (see Figure 3, where $NDVI_{DL}$ increases earlier in 2012 compared to the other years). The impact on the result is however small since these eight periods are in the early part of the growing season when f_{Rdav} is zero.

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The Monte Carlo simulation resulted in an estimated standard deviation of 35% of the mean annual GPP for years with defoliation. Hence, all annual GPP losses estimated with model 2 are given with a standard deviation of 35%.



Figure 8. Correlation between GPP from the EC tower and LUE modelled GPP for the year 2012, with insect outbreak. 15 GPP_{iue defoliated} = -0.54×1.25 GPP_{EC}, R² = 0.83 and N = 19.

3.3.2 Defoliated areas and quantifying the insect outbreaks impact on annual GPP

In the year 2012, with the most widespread defoliation in this study, 76% of the 100 km² forests were defoliated (Table 2 and Fig. 9). In 2004 and 2013, 53% and 55% respectively, of the forests were defoliated. The defoliation detection method enables detection of 74% of the defoliation with a misclassification of undisturbed areas of 39% (Olsson et al. 2016). The total-mean annual reduction in carbon uptakeregional GPP due to the insect outbreaks since for the three outbreaks studied the year 2000-was 44.615 ± 13.5 Gg C yr⁻¹ according to Method 1, with the largest outbreak in 2012 with a negative impact on regional GPP of 18.4 ± 6 Gg C yr⁻¹ (Table 2). The average annual regional GPP in the study area, according derived with the LUE model (Eq. 12) and the five years without insect outbreak, was 41.1 ± 12 Gg C yr⁻¹, which gives a reduction in 2012 of 4544%. The impacts of the outbreaks in 2004 and 2013 were reduction in regional GPP of 3132% and 3334%

- 10 respectively. There were <u>only minorno</u> differences in the GPP reduction per square meter, <u>between the outbreak</u> <u>years.ranging from 240 $\pm\pm72$ g C m⁻² in 2004 to 244 $\pm\pm73$ g C m⁻² in 2013. Since a common reduction factor is used the results show that in 2013 MODIS pixels with slightly higher GPP during undisturbed conditions were defoliated. When a LUE model was applied to model GPP also during defoliation events (Method 2) the <u>total-mean annual</u> decrease in</u>
- regional GPP was 1543.7 ± 15.5 Gg C yr⁻¹ which is nearly the same estimate as with Method 1. The regional GPP loss in 2012 was 20.1 ± 7 Gg C yr⁻¹ which is slightly higher compared to Method 1. In the yYear 2004 followed the same pattern with a slightly larger decrease in GPP for Method 2the two methods resulted in similar decreases in GPP, while the year 2013 resulted in larger the GPP decrease in GPP was larger with Method 1 in 2013. Differences in GPP loss per square meter between the years were larger with Method 2: $188-190\pm 66.67$ g C m⁻² yr⁻¹ in 2013 was the lowest GPP loss, and 265 270 ± 93.95 g C m⁻² yr⁻¹ in 2012 was the largest GPP loss.
- 20 Table 2. Defoliated area (km^2) and annual reduction in GPP^a (Gg C <u>vr⁻¹</u>) for the three years with insect defoliation since the year 2000. The total area with forest cover was 100 km².

Year		2004	2012	2013		
	Defoliated area (km ²)	53	76	55		
GPP decrease ^a	Mean (g C m ⁻² yr ⁻¹)	240 <u>+</u> 72	<u>242-240</u> +±72	2 44		
				<u>240±</u> 73 <u>72</u>		
Method 1	Total (Gg C yr ⁻¹)	1 <u>32.7 ±</u> 4	18 .4 <u>+</u>5	1 <u>43.5 ±</u> 4		
(GPP reduction factor)	Total (%)	31	45	33		
GPP decrease ^a	Mean (g C m ⁻² yr ⁻¹)	<u>252-250</u> <u>±</u> 88	2 <u>7065 ±+</u> 93 <u>95</u>	1 <u>90</u> 88 ± <u>+</u> 6667		
Method 2	Total (Gg C yr ⁻¹)	13 .3 <u>+</u>5	20 .1_±_ 7	10 .3 <u>+</u>4		
(Defoliation LUE model)	Total (%)	33	49	25		
^a GPP for undisturbed conditions is derived with the LUE model (Eq. 12) and as the mean of the five years without insect						

defoliation.

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Figure 9. Reduction in annual GPP (g C m⁻² yr⁻¹) due to the birch moth outbreak <u>of autumnal moth and winter moth</u> in 2012 computed with a LUE model also for defoliation (Method 2). One standard deviation of the GPP losses is estimated to 35% of the given values. Areas with only the background map have a canopy cover less than 50% or are outside the study area shown in Fig. 1. The reference system is SWEREF99 TM and latitude and longitude are in WGS84. Source of background map: Lantmäteriet (Dnr: I2014/00579).

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We compared the differences in GPP decrease between Method 1 (GPP reduction factor) and Method 2 (two LUE models) to study if Method 2 performed better for MODIS pixels where the birch trees recovered later in the growing season. For the <u>all years-2004 and 2012</u> the mean differences in GPP loss (g C m^{-2} <u>yr⁻¹</u>) between the methods were lower for pixels that recovered later in the growing season. These results suggest that Method 2 captured some of the refoliation, though the

differences are small<u>and within the error margin</u>. For 2013, on the other hand, Method 1 resulted in higher value for refoliated pixels, but the difference was minor.

Table 3. Differences in GPP loss (g C $m^{-2} yr^{-1}$) between Method 1 and Method 2 for MODIS pixels with recovering foliage later in the season, and pixels with no refoliation according to the defoliation monitoring method. Higher GPP loss with Method 2 gives negative values.

Year	2004	2012	2013
Refoliated pixels	48%	14%	52%
Difference, refoliated (g C $m^{-2} yr^{-1}$)	-9±3	-19±7	57±20
Difference, non-refoliated (g C m ⁻² yr ⁻¹)	-15±5	-24±8	54±19

5 4 Discussion

This study has <u>showndemonstrated</u> a substantial setback to the carbon uptakein <u>GPP</u> caused by insect defoliation in a subarctic deciduous forest in northern Fennoscandia. At the EC tower, GPP decreased <u>with by 261-260 g</u> C m⁻² <u>yr⁻¹</u> (59%) during the outbreak in 2012 compared to the mean of undisturbed years. In the entire study area annual mean values of decrease in GPP ranged from <u>188-190±±66-67</u> to <u>270±95</u> <u>244 ±±73 g g</u> C m⁻² <u>yr⁻¹</u>. The total decrease in <u>earbon</u> uptakeregional <u>GPP</u>, due to the <u>three</u> insect defoliation events <u>studied heresinee the year 2000</u> was estimated to be 4<u>54.6</u> <u>±±13-14</u> Gg C, which is of the same magnitude as the average annual regional GPP of 41.<u>1 ±±</u>12 Gg C <u>yr⁻¹</u> for single years with no disturbances. These figures are likely conservative; 20% of the forests in the study area were excluded since they are located in MODIS pixels with < 50% forests cover. During the most severe outbreak year (2012), the annual regional GPP loss was nearly 50% (20 Gg C <u>yr⁻¹</u>), with 76% of the 100 km² birch forests in the study area defoliated. In this study we have estimated the impact on GPP only but we noted that during the outbreak in 2012 the decrease in R_{eco} was larger than the decrease in GPP during the growing season around the EC tower. Respiration is affected by insect outbreak in two ways: (1) Autotrophic respiration is reduced as defoliated trees cannot photosynthesize and (2) heterotrophic respiration increase when

- dead larvae decompose. The amount of carbon respired by larvae is likely to be the same as the amount of carbon in eaten leaves so we should only observe a shift of respiration in time. In addition, larvae transport nutrients from trees to fungi and
- 20 bacteria living in soil which further increase respiration. The increase in heterotrophic respiration did not offset decrease in autotrophic respiration and R_{eco} for outbreak year was decreased in comparison to non-disturbed years. This study also highlights the advantage of combining EC data and remote sensing data where data from the EC tower were applied to calibrate the LUE model, and satellite data were applied to estimate the impact on GPP over larger areas. EC measurement alone cannot be extrapolated with high accuracy if the spatial and temporal extent of an outbreak is unknown, and the LUE
- 25 model could not be developed without EC data. The combination facilitates wall-to-wall mapping of <u>forest</u> disturbances, and quantitative estimates of the impacts on primary productivity.

There are however limitations in the study that must be considered. One major challenge is to establish baseline conditions for GPP in areas with reoccurring insect outbreaks as in Abisko. As a comparison, Olsson et al. (2016a) tested a defoliation

detection method on the outbreak in Abisko in 2013 and achieved the highest detection accuracies when the baseline conditions were based on the six years with highest NDVI values in the period 2000-2012. In this study the annual GPP for years without disturbances was estimated as the mean of the five years without insect outbreak and with available EC data. It is likely that some of these five years were influenced by the insect outbreak in 2012. The two years (2010 and 2011) prior to

- 5 when the insect populations reached outbreak levels had lower annual GPP than the years 2007 and 2009 (Table 1) and it is likely that GPP in 2014 was influenced by the insect defoliation in 2012 and 2013. Michal (2012) suggests that GPP reaches pre-outbreak levels 2-3 years after an outbreak and Hoogesteger & Karlsson (1992) showed that LAI returned to predefoliation levels two years after 100% artificial defoliation even though tree ring width was lower than normal at least three years after the experiment. For the birch forests to fully recover from severe outbreaks it may take decades (Tenow &
- 10 Bylund 2000). To get an indication of the potential influence on GPP by insect defoliation for the non-outbreak years we modeled GPP based on PAR for the years with data available from the EC tower and compared with EC derived GPP (see supplementary material). The result showed that measured GPP at the EC tower, and GPP modeled with PAR data were similar in 2007 and 2009. In the two years (2010 and 2011) prior to the outbreak, measured GPP was lower than PAR modelled GPP indicating that there were signs of defoliation by growing larval population. Also in 2014 when the birch
- 15 forests were recovering, measured GPP was lower than PAR modelled GPP. During the insect outbreak in 2012 measured annual GPP was 290 g C m⁻² yr⁻¹ lower than PAR modelled GPP which is larger than the decrease of 260 g C m⁻² yr⁻¹ applied in this study. In addition, we ran the LUE model with meteorological data from ANS for the year 2008 to fill the gap in the time-series with measured GPP and to study how well it agreed with the years 2007 and 2009. According to the LUE model annual GPP at the EC tower was 440 g C m^{-2} yr⁻¹ in 2008, which agrees with the GPP value for undisturbed years of 440 g C
- m^{-2} yr⁻¹ that we are applying in the study. However, since years that are influenced by pre-outbreak defoliation as well as a 20 recovery year are included as undisturbed years it is likely that the baseline GPP applied in this study is lower than GPP for undisturbed conditions. This is also indicated by the larger difference between PAR modelled and measured GPP in 2012 and suggests that the estimated decreases in GPP due to insect outbreaks in this study are on the lower side. Another limitation is the assumption that no other factors than insect outbreaks influence annual GPP, even though it is
- 25 likely that also meteorological conditions influence GPP. The comparison between EC derived and PAR modelled GPP suggests that only two years with EC data are representing undisturbed forest; hence, the amount of data from the EC tower is too small to study correlations between EC derived GPP and meteorological variables. Instead we studied correlations between NDVI and meteorological data from ANS, where we used mean of the highest NDVI_{DL} value of each year derived from 200 MODIS pixels with birch forest. To minimize the influence of insect induced defoliation we excluded the outbreak
- 30
- years and years prior to and after outbreaks. No linear correlations between PAR and GPP were found. There were however, negative correlations between temperature and seasonal maximums of NDVIDLa with the strongest correlation between NDVI and the mean temperature in May-June. The influence of temperature on NDVI was however weak and due to the estimated uncertainties of the LUE model of 30% we did not include these correlations in the analysis. However, with data from the

EC tower available for more years it would be a potentially important improvement to include meteorological data when estimating the decrease in annual GPP.

There are also uncertainties in the LUE model. The relationship between $fAPAR_{Rday}$ and $NDVI_{DL}$ (Eq. 11) was estimated from two growing seasons without disturbances. Due to larvae disrupting the PAR-sensors there were no fAPAR data available

- 5 from the outbreak years, hence, Eq. 11 was used also for defoliation events. Furthermore, the relationship was derived from fAPAR obtained from the upper canopy which may not be representative for the entire forest, since the relationship between fAPAR_{star} and NDVI_{DI} is likely to vary with understory and forest densities in the study area. The relationship is also likely to vary with varying understory responses due to defoliation, which may influence the estimated decreases in annual GPP. Accounting for these uncertainties would require more data, both about the fAPAR and NDVI relationship and detailed land
- cover data which in turn would make the model more complex. Hence, we assume this limitation to be acceptable, and since 10 the aim of the study was to estimate the influence of defoliation of the birch trees we considered fAPAR_{canony} to be the most suitable. Another potential limitation is that the LUE model developed for years with defoliation seems to underestimate GPP for values lower than about 1.5 g C m⁻² dav⁻¹ (Figure 8). However, for the outbreak year with available EC data (2012) the underestimated values from the LUE model are mainly due to a cold spring that resulted in a large reduction factor
- 15 $(f_{\alpha\beta\alpha\nu})$. During the main growing season LUE modelled and EC derived GPP agrees well. It may also seem surprising that the difference in NDVI_{DL} was comparably low in relation to the difference in light use efficiency. Mean NDVI_{DL} for the peak of the growing season was 0.78 for the five years with EC data. In 2012 the highest value for $NDVI_{DL}$ was 0.63. The difference in maximum light use efficiency was larger with an ε_{max} of 1.85±0.36 g C MJ⁻¹ for years without disturbance, and an ε_{max} def of 0.98 ± 0.25 g C MJ⁻¹ during defoliation. It is however, known that NDVI saturates for high LAI and that small changes in
- NDVI can be associated with large changes in LAI (e.g. Myneni et al. 2002). The light use efficiency on the other hand can 20 decrease substantially with lower LAI since more leaves will operate in the light-saturated portion of the photosynthesis (e.g. Medlyn 1998). There are also uncertainties in how well the EC tower footprint represents the entire study area. Heliasz (2012) utilized a permanent EC tower as reference and a mobile EC tower to study variability in carbon exchange in the birch forests around Abisko and concluded that there were only minor differences in GPP at seven sites during the peak
- 25 growing season in 2008 and 2009. Hence, we consider the EC tower footprint to be representative for the study area. The accuracy of the defoliation detection method also influences the results of the study. The method missed 26% of the defoliated MODIS pixels and misclassified 39% of the undisturbed pixels as defoliated in the evaluation data used by Olsson et al. (2016b). This implies that the defoliated areas in 2004 and 2013 were slightly overestimated, while the defoliated area in 2012 is likely underestimated but the impact on the total numbers is likely small. It should also be considered that 20% of
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A limitation with the developed LUE model for large-area estimates is that it includes observed meteorological data (temperature and PAR). An alternative for running the model over larger areas would be to use modelled meteorological data

the forests in the study area were excluded since they are located in MODIS pixels with < 50% forests cover. The detection accuracy also influences the spatial distribution of the defoliation, but even though there is an uncertainty associated on pixel level the broader outbreak patterns are likely accurate.

(Olofsson et al. 2007; Schubert et al. 2010). There are also uncertainties related to the temperature data utilized. The gradient applied to model mean temperatures depending on altitude is likely to give accurate estimates in the study area. However, minimum temperatures are more uncertain since cold air can drain downhill and accumulate in valleys and low areas, rather than decrease with altitude. Altogether, since the EC tower is located on a small ridge in the lower, flat parts of the study

- 5 area, we anticipate that the temperatures there are not substantially lower than the area in general. We compared with lowest daily temperature from Abisko research station, which is located near the spectral tower 10 km to the west (Fig. 1), and at a slightly higher altitude than the EC tower. For all periods with frost events during the early season, i.e. when the lowest temperature influences f_{MODB} , the mean value of absolute differences, with the coldest temperatures at the research station, was only 0.4°C. With these small temperature differences and since frost events only influence GPP in the early growing
- 10 season, the impact on annual GPP was considered minor.
- The defoliation detection methods used in this study applies a Kalman filter to the raw NDVI observations which gives a time-series of smoothed NDVI that captures the timing of the defoliation event as well as potential refoliation. The LUE model on the other hand utilizes NDVI smoothed with double logistic functions. These functions do not capture the typical seasonal trajectory for years with refoliation. This is illustrated in Figure 3 where raw NDVI stays around 0.6 during the
- 15 entire growing season in 2012 when there was no refoliation around the EC tower. In 2013, when there was substantial refoliation around the EC tower, raw NDVI stays around 0.6 during June, but increase to pre-outbreak levels in early July when refoliation occurs. In 2004 the raw NDVI values have a similar pattern as in 2013 with low values (around 0.6) until early August when refoliation results in a late season peak in NDVI. This seasonal development of raw NDVI agrees well with GPP for the limited period with available EC data in the outbreak year 2004. *NDVI_{DL}* does not capture this trajectory
- 20 with sharply increasing NDVI values that levels off and starts increasing again later in the season. The higher NDVI values in the later part of the growing season in 2013 do however, result in *NDVI_{DL}* values that are higher than in 2012 but lower than for the years without defoliation even though the actual timing of the defoliation is not captured during years with refoliation. A new version of TIMESAT, currently developed and tested, will capture also more detailed seasonal trajectories with smooth fitting of curves. These new curve fitting methods have a potential to improve the performance of the LUE

25 <u>model.</u>

<u>The We applied two methods applied</u> to quantify the impacts on GPP to study which methods that performed better for refoliating birch forests. resulted in similar total GPP losses for the outbreaks, but with annual differences in GPP losses for the outbreak years. TThe assumption was that Method 2 would be more adaptive and adjust for differences in defoliation intensities between MODIS pixels. Since the level of defoliation, as well as understorey responses to the defoliation are

30 likely to influence *NDVI_{DL}*, which in turn will influence *fAPAR*, it was anticipated that a method based on a LUE model to derive GPP during defoliation events would capture variability in defoliation levels and understory responses between MODIS pixels. Method 1, on the other hand, with a common reduction factor, does not account for local differences between pixels and is similar to upscaling the local conditions at the EC tower, even though the method has the advantage that annual GPP for each pixel is derived with a LUE model and hence, should be more accurate than assuming that GPP for all MODIS

pixels is identical to GPP at the EC tower. For the years 2004 and 2012, when there was little refoliation in the area (Table 3), Methods 1 and 2the two methods -resulted in similar estimates of the GPP loss with slightly larger decrease in GPP for Method 2. In 2013, the difference between the methods was larger with the highest decrease in annual GPP for method 1. One possible explanation for the smaller decrease in annual GPP according to Method 2 for the year 2013 is that the growing

- 5 season seems to have been shorter and that refoliation started earlier and was stronger in 2013 compared to 2004; this is indicated by the seasonal developments of NDVI. Both methods resulted in similar GPP reductions, with marginally larger decrease for Method 2, also for the year 2004 when refoliation was widespread in the study area (Table 3). The larger difference between the methods in 2013 could be due to substantial refoliation, which was captured by method 2, and which resulted in a lower GPP reduction. However, since there was refoliation also in the year 2004, when there were only minor
- 10 differences between Method 1 and 2, the large differences could also be due to uncertainties in $\varepsilon_{max, def}$ which was estimated from one year with defoliation only. It should also be noted that higher NDVI might be due to increasing growth of understory grasses favoured by the changed light conditions due to defoliation (Karlsen et al. 2013) rather than recovering birch. More data from the EC tower would be required to confirm this. It is, however, likely that Method 2 will result in more accurate estimates of the decrease in GPP if data are available to make more robust estimates of $\varepsilon_{max, def}$.
- 15 The impact of insect outbreaks on the carbon balance has been quantified in earlier studies: Heliasz et al. (2011) studied the impact on NEE of the autumnal moth and winter moth outbreak in Abisko in 2004, but these measurements started on July 2, which was around 10 days after the larvae reached peak densities, which most likely resulted in an underestimated reduction in NEE. To facilitate a comparison between the outbreak years 2004 and 2012, we computed GPP for the period July 2 to September 30 for all years with EC data. This indicated that the two outbreak years had similar impact on the carbon balance
- during the period studied with a GPP loss of $\frac{205-210 \text{ g}}{205-210 \text{ g}}$ C m⁻² yr⁻¹ in 2004 and $\frac{199-200 \text{ g}}{200 \text{ g}}$ C m⁻² yr⁻¹ in 2012 compared to years without disturbance. Furthermore, the loss of $\frac{199-200 \text{ g}}{200 \text{ g}}$ C m⁻² yr⁻¹ in the year 2012 and for the same time period as studied in the year 2004, compared to the GPP loss of $\frac{260 \text{ g}}{260 \text{ g}}$ C m⁻² yr⁻¹ for the entire growing season in 2012, suggests that the impact on NEE was underestimated by Heliasz et al. (2011). Clark et al. (2010) found the highest difference in NEE between undisturbed years and years with severe defoliation by the gypsy moth in New Jersey, USA, to be 266–480 g C m⁻²
- 25 yr⁻¹ and Clark et al (2014) found that mid-day NEE during complete defoliation was 14% of pre-defoliation rates. Allard et al. (2008) noted that cumulative NEE was lower during a year with insect defoliation compared to years without disturbances; however, the low NEE value might to a large extent have been caused by a dry spring. Brown et al. (2010) found that a mountain pine beetle outbreak turned a forest into a carbon sinksource; no pre-outbreak EC data were available to quantify the impact on NEP, but recovery after the outbreak was faster than anticipated (Brown et al. 2012). It should be
- 30 noted that the mountain pine beetle feed within the phloem and directly kills trees, while the moth species discussed above are defoliators that usually only kill trees in cases of severe and repeated outbreaks (Hicke et al. 2012). Modeling studies have also found that forests have changed from sinks into sources of carbon, in some cases for extended periods (Kurz et al. 2008a; Dymond et al. 2010; Schäfer et al. 2010; Medvigy et al. 2012). However, to our knowledge, this is the first study that

has utilized remote sensing data and applied-developed a LUE model, calibrated with EC data, to both quantify and map the spatial extent of the impact of <u>defoliating insects</u> outbreaks on GPP.

The results of this study could help to reduce uncertainties in the impact of insect outbreaks on primary productivity as well as to improve carbon budgets by including insect induced defoliation. For the mountain birch forests in this study the

- 5 estimated reduction in annual GPP, compared to years without disturbances, was 50% when there was limited refoliation in the study area. For years with widespread refoliation, the annual GPP losses were about 1/3 of GPP for years without disturbances. In addition, the spatial and temporal mapping of insect defoliation provided by remote sensing is important for accurate simulation of the carbon dynamics, since it has been suggested that the spatial distribution of defoliation has a strong influence on carbon dynamics (Medigvy et al. 2012). Furthermore, the outbreak area included in this study is only a
- 10 fraction of the 10,000 km² estimated to having been severely defoliated in northern Fennoscandia during the period 2000– 2008 (Jepsen et al. 2009). Assuming that the conditions were similar over northern Fennoscandia, the insect defoliation over these vast areas would result in a potential total regional GPP loss for the time period of the magnitude 2–3 <u>Tg C.Extrapolating the reduction in annual GPP over these vast defoliated areas would result in a GPP loss of the magnitude</u> 2–3 Tg C in northern Fennoscandia for that time period. Models not accounting for such disturbance events would seriously
- 15 overestimate the ability of these forests to absorb atmospheric CO₂.

5 Conclusions

This study <u>demonstratedshowed</u>, with the aid of MODIS NDVI and eddy covariance data, a substantial loss in <u>regional</u> GPP due to insect induced defoliation in subarctic deciduous forests in northern Fennoscandia. The estimated <u>mean annual total</u> decrease in <u>regional</u> GPP in the study area of 100 km² due to insect outbreaks since the year 2000 for a year with insect

20 <u>outbreak</u> was <u>15±5 Gg C yr⁻¹44.6 ±±13 Gg C for three disturbance events, in the study area of 100 km², <u>comparable This</u> should be compared with the average annual GPP of 41.1 ± 12 Gg C yr⁻¹ for years without disturbances. In the most severe outbreak year (2012) 76% of the birch forests were defoliated and annual GPP was merely 50% of GPP for years without disturbances.</u>

The study also demonstrated the use of remote sensing data to both monitor the spatial extent of the defoliation and to

25 estimate the impact on the primary productivity of these defoliation events. The insect disturbance is shown to have major impacts on the primary production of the sub-arctic forest; consequently, the derived methods, based on combining remote sensing and eddy covariance measurements, are of major importance to support carbon balance estimates over large areas.

The authors declare that they have no conflict of interest.

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References

Abisko Scientific Research Station: Temperature data, 1913-2014, 2015. Available from Abisko Scientific Research Station. http://www.polar.se/abisko.

- 10 Adelabu, S., Mutanga, O., and Cho, M. A.: A review of remote sensing of insect defoliation and its implications for the detection and mapping of Imbrasia belina defoliation of Mopane Woodland, Afr. J. Plant Sci. Biotechnol, 6, 1-13, 2012. Allard, V., Ourcival, J. M., Rambal, S., Joffre, R., and Rocheteau, A.: Seasonal and annual variation of carbon exchange in an evergreen Mediterranean forest in southern France, Global Change Biology, 14, 714-725, 10.1111/j.1365-2486.2008.01539.x, 2008.
- 15 Ammunét, T., Bylund, H., and Jepsen, J.U.: Northern Geometrids and Climate Change: From Abiotic Factors to Trophic Interactions. In Björkman., C., and Niemelä, P. (Eds.), Climate Change and Insect Pests (pp. 235–247). Boston: CABI, 2015. Asrar, G., Fuchs, M., Kanemasu, E. T., and Hatfield, J. L.: Estimating Absorbed Photosynthetic Radiation and Leaf Area Index from Spectral Reflectance in Wheat1, Agronomy Journal, 76, 10.2134/agronj1984.00021962007600020029x, 1984.
- Babst, F., Esper, J., and Parlow, E.: Landsat TM/ETM+ and tree-ring based assessment of spatiotemporal patterns of the
 autumnal moth (Epirrita autumnata) in northernmost Fennoscandia, Remote Sensing of Environment, 114, 637-646, http://dx.doi.org/10.1016/j.rse.2009.11.005, 2010.

Bergh, J., McMurtrie, R. E., and Linder, S.: Climatic factors controlling the productivity of Norway spruce: a model-based 25 analysis, Forest ecology and management, 110, 127-139, 1998.

Boisvenue, C., and Running, S. W.: Impacts of climate change on natural forest productivity – evidence since the middle of the 20th century, Global Change Biology, 12, 862-882, 10.1111/j.1365-2486.2006.01134.x, 2006.

Bonan, G. B.: Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests, Science, 320, 1444-1449, 10.1126/science.1155121, 2008.

30 Bright, B. C., Hicke, J. A., and Meddens, A. J. H.: Effects of bark beetle-caused tree mortality on biogeochemical and biogeophysical MODIS products, Journal of Geophysical Research: Biogeosciences, 118, 974-982, 10.1002/jgrg.20078, 2013.

Battisti, A.: Forests and climate change - lessons from insects, iForest-Biogeosciences and Forestry, 1, 1-5, 10.3832/ifor0210-0010001, 2008.

Brown, M., Black, T. A., Nesic, Z., Foord, V. N., Spittlehouse, D. L., Fredeen, A. L., Grant, N. J., Burton, P. J., and Trofymow, J. A.: Impact of mountain pine beetle on the net ecosystem production of lodgepole pine stands in British Columbia, Agricultural and Forest Meteorology, 150, 254-264, http://dx.doi.org/10.1016/j.agrformet.2009.11.008, 2010. Brown, M. G., Black, T. A., Nesic, Z., Fredeen, A. L., Foord, V. N., Spittlehouse, D. L., Bowler, R., Burton, P. J.,

5 Trofymow, J. A., Grant, N. J., and Lessard, D.: The carbon balance of two lodgepole pine stands recovering from mountain pine beetle attack in British Columbia, Agricultural and Forest Meteorology, 153, 82-93, http://dx.doi.org/10.1016/j.agrformet.2011.07.010, 2012.

Bylund, H.: Long-term interactions between the autumnal moth and mountain birch: the role of resources, competitors, natural enemies, and weather. , PhD, Swedish University of Agricultural Sciences, 1995.

10 Callaghan, T. V., Bergholm, F., Christensen, T. R., Jonasson, C., Kokfelt, U., and Johansson, M.: A new climate era in the sub-Arctic: Accelerating climate changes and multiple impacts, Geophysical Research Letters, 37, L14705, 10.1029/2009GL042064, 2010.

Clark, K. L., Skowronski, N., and Hom, J.: Invasive insects impact forest carbon dynamics, Global Change Biology, 16, 88-101, 10.1111/j.1365-2486.2009.01983.x, 2010.

- 15 Clark, K. L., Skowronski, N. S., Gallagher, M. R., Renninger, H., and Schäfer, K. V. R.: Contrasting effects of invasive insects and fire on ecosystem water use efficiency, Biogeosciences, 11, 6509-6523, 10.5194/bg-11-6509-2014, 2014. Dymond, C. C., Neilson, E. T., Stinson, G., Porter, K., MacLean, D. A., Gray, D. R., Campagna, M., and Kurz, W. A.: Future Spruce Budworm Outbreak May Create a Carbon Source in Eastern Canadian Forests, Ecosystems, 13, 917-931, 10.1007/s10021-010-9364-z, 2010.
- 20 Eklundh, L., Jin, H., Schubert, P., Guzinski, R., and Heliasz, M.: An Optical Sensor Network for Vegetation Phenology Monitoring and Satellite Data Calibration, Sensors, 11, 7678, 2011.
 Field, C. B., Randerson, J. T., and Malmström, C. M.: Global net primary production: Combining ecology and remote sensing, Remote Sensing of Environment, 51, 74-88, http://dx.doi.org/10.1016/0034-4257(94)00066-V, 1995.
 Gamon, J. A.: Reviews and Syntheses: optical sampling of the flux tower footprint, Biogeosciences, 12, 4509-4523,
- 10.5194/bg-12-4509-2015, 2015.
 Goodale, C. L., Apps, M. J., Birdsey, R. A., Field, C. B., Heath, L. S., Houghton, R. A., Jenkins, J. C., Kohlmaier, G. H., Kurz, W., Liu, S., Nabuurs, G.-J., Nilsson, S., and Shvidenko, A. Z.: Forest Carbon Sinks in the Northern Hemisphere, Ecological Applications, 12, 891-899, 10.1890/1051-0761(2002)012[0891:FCSITN]2.0.CO;2, 2002.
 Goward, S. N., and Huemmrich, K. F.: Vegetation canopy PAR absorptance and the normalized difference vegetation index:
- An assessment using the SAIL model, Remote Sensing of Environment, 39, 119-140, http://dx.doi.org/10.1016/0034-4257(92)90131-3, 1992.
 Heliasz, M.: Spatial and Temporal Dynamics of subarctic Birch Forest Carbon Exchange, PhD thesis, Dep. of Geography and Ecosystem Science, Lund Univ., Lund, Sweden, 2012.

Heliasz, M., Johansson, T., Lindroth, A., Mölder, M., Mastepanov, M., Friborg, T., Callaghan, T. V., and Christensen, T. R.: Quantification of C uptake in subarctic birch forest after setback by an extreme insect outbreak, Geophysical Research Letters, 38, L01704, 10.1029/2010gl044733, 2011.

Hicke, J. A., Allen, C. D., Desai, A. R., Dietze, M. C., Hall, R. J., Hogg, E. H., Kashian, D. M., Moore, D., Raffa, K. F.,

Sturrock, R. N., and Vogelmann, J.: Effects of biotic disturbances on forest carbon cycling in the United States and Canada,
 Global Change Biology, 18, 7-34, 10.1111/j.1365-2486.2011.02543.x, 2012.
 Hoogesteger, J., and Karlsson, P. S.: Effects of Defoliation on Radial Stem Growth and Photosynthesis in the Mountain
 Birch (Betula pubescens ssp. tortuosa), Functional Ecology, 6, 317-323, 10.2307/2389523, 1992.

Holmgren, B., and Tjus, M.: Summer Air Temperatures and Tree Line Dynamics at Abisko, Ecological Bulletins, 159-169, 1996.

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Interact: Abisko Scientific Research Station, 2016. http://www.eu-interact.org/field-sites/sweden-2/abisko/ (accessed 09-02-16).

Jepsen, J. U., Hagen, S. B., Ims, R. A., and Yoccoz, N. G.: Climate change and outbreaks of the geometrids Operophtera brumata and Epirrita autumnata in subarctic birch forest: evidence of a recent outbreak range expansion, The Journal of animal ecology, 77, 257-264, 10.1111/j.1365-2656.2007.01339.x, 2008.

Jepsen, J. U., Hagen, S. B., Høgda, K. A., Ims, R. A., Karlsen, S. R., Tømmervik, H., and Yoccoz, N. G.: Monitoring the spatio-temporal dynamics of geometrid moth outbreaks in birch forest using MODIS-NDVI data, Remote Sensing of Environment, 113, 1939-1947, 2009.

Jepsen, J. U., Biuw, M., Ims, R. A., Kapari, L., Schott, T., Vindstad, O. P. L., and Hagen, S. B.: Ecosystem impacts of a 20 range expanding forest defoliator at the forest-tundra ecotone, Ecosystems, 16, 561-575, 2013.

Jin, H., and Eklundh, L.: In Situ Calibration of Light Sensors for Long-Term Monitoring of Vegetation, IEEE Transactions on Geoscience and Remote Sensing, 53, 3405-3416, 10.1109/TGRS.2014.2375381, 2015.
Josefsson, M.: The Geoecology of Subalpine Heaths in the Abisko Valley, Northern Sweden – A study of periglacial conditions. Uppsala University Report 78, 1990.

25 Jönsson, P., Eklundh, L.: Seasonality extraction by function fitting to time-series of satellite sensor data, PISCATAWAY, 2002, 1824-1832,

Jönsson, P., Eklundh, L.: TIMESAT—a program for analyzing time-series of satellite sensor data, Computers and Geosciences, 30, 833-845, 10.1016/j.cageo.2004.05.006, 2004.

Kalman, R. E.: A New Approach to Linear Filtering and Prediction Problems, Journal of Fluids Engineering, 82, 35-45, 10.1115/1.3662552, 1960.

Karlsen, S., Jepsen, J., Odland, A., Ims, R., and Elvebakk, A.: Outbreaks by canopy-feeding geometrid moth cause statedependent shifts in understorey plant communities, Oecologia, 173, 859-870, 10.1007/s00442-013-2648-1, 2013.
<u>Karlsson, P. S., Bylund, H., Neuvonen, S., Heino, S., and Tjus, M.: Climatic Response of Budburst in the Mountain Birch at</u> Two Areas in Northern Fennoscandia and Possible Responses to Global Change, Ecography, 26, 617-625, 2003. Kaukonen, M., Ruotsalainen, A. L., Wäli, P. R., Männistö, M. K., Setälä, H., Saravesi, K., Huusko, K., and Markkola, A.: Moth herbivory enhances resource turnover in subarctic mountain birch forests?, Ecology, 94, 267-272, 2013.

Kurz, W. A., Dymond, C. C., Stinson, G., Rampley, G. J., Neilson, E. T., Carroll, A. L., Ebata, T., and Safranyik, L.: Mountain pine beetle and forest carbon feedback to climate change, Nature, 452, 987-990, http://www.nature.com/nature/journal/v452/n7190/suppinfo/nature06777 S1.html, 2008a.

Kurz, W. A., Stinson, G., and Rampley, G.: Could increased boreal forest ecosystem productivity offset carbon losses from increased disturbances?, Philosophical Transactions of the Royal Society of London B: Biological Sciences, 363, 2259-2268, 10.1098/rstb.2007.2198, 2008b.

5

30

Lagergren, F., Eklundh, L., Grelle, A., Lundblad, M., Mölder, M., Lankreijer, H., and Lindroth, A.: Net primary production

10 and light use efficiency in a mixed coniferous forest in Sweden, Plant, Cell & Environment, 28, 412-423, 10.1111/j.1365-3040.2004.01280.x, 2005.

Landry, J. S., Price, D. T., Ramankutty, N., Parrott, L., and Matthews, H. D.: Implementation of a Marauding Insect Module (MIM, version 1.0) in the Integrated BIosphere Simulator (IBIS, version 2.6b4) dynamic vegetation–land surface model, Geosci. Model Dev., 9, 1243-1261, 10.5194/gmd-9-1243-2016, 2016.

Lantmäteriet: Produktbeskrivning: GSD-Marktäckedata, GSD, Geografiska Sverigedata. Dokumentversion 1.2, 2010-03-26, 2010.

Liljedahl, A. K., Hinzman, L. D., Harazono, Y., Zona, D., Tweedie, C. E., Hollister, R. D., Engstrom, R., and Oechel, W. C.: Nonlinear controls on evapotranspiration in arctic coastal wetlands, Biogeosciences, 8, 3375–3389, 10.5194/bg 8–3375–2011, 2011.

20 Lloyd, J., and Taylor, J. A.: On the Temperature Dependence of Soil Respiration, Functional Ecology, 8, 315-323, 10.2307/2389824, 1994.

LPDAAC: Surface Reflectance 8-Day L3 Global 250m, Land Processes Distributed Active Archive Center, 2016a. https://lpdaac.usgs.gov/dataset_discovery/modis/modis_products_table/mod09q1 (accessed 09-02-16).

LPDAAC: Surface Reflectance 8-Day L3 Global 500m, Land Processes Distributed Active Archive Center, 2016b. 25 https://lpdaac.usgs.gov/dataset_discovery/modis/modis_products_table/mod09a1 (accessed 09-02-16).

McCallum, I., Franklin, O., Moltchanova, E., Merbold, L., Schmullius, C., Shvidenko, A., Schepaschenko, D., and Fritz, S.: Improved light and temperature responses for light-use-efficiency-based GPP models, Biogeosciences, 10, 6577-6590, 10.5194/bg-10-6577-2013, 2013.

Medlyn, B. E.: Physiological basis of the light use efficiency model, Tree Physiology, 18, 167-176, 10.1093/treephys/18.3.167, 1998.

Medvigy, D., Clark, K. L., Skowronski, N. S., and Schäfer, K. V. R.: Simulated impacts of insect defoliation on forest carbon dynamics, Environmental Research Letters, 7, 045703, 2012.

Monteith, J. L.: Solar Radiation and Productivity in Tropical Ecosystems, Journal of Applied Ecology, 9, 747-766, 10.2307/2401901, 1972.

Monteith, J. L., and Moss, C. J.: Climate and the Efficiency of Crop Production in Britain [and Discussion], Philosophical Transactions of the Royal Society of London B: Biological Sciences, 281, 277-294, 10.1098/rstb.1977.0140, 1977. Myneni, R. B., and Williams, D. L.: On the relationship between FAPAR and NDVI, Remote Sensing of Environment, 49, 200-211, 1994.

Myneni, R. B., Hoffman, S., Knyazikhin, Y., Privette, J. L., Glassy, J., Tian, Y., Wang, Y., Song, X., Zhang, Y., Smith, G.
 R., Lotsch, A., Friedl, M., Morisette, J. T., Votava, P., Nemani, R. R., and Running, S. W.: Global products of vegetation leaf area and fraction absorbed PAR from year one of MODIS data, Remote Sensing of Environment, 83, 214-231, http://dx.doi.org/10.1016/S0034-4257(02)00074-3, 2002.

Nabuurs, G.-J., Lindner, M., Verkerk, P. J., Gunia, K., Deda, P., Michalak, R., and Grassi, G.: First signs of carbon sink saturation in European forest biomass, Nature Clim. Change, 3, 792-796, 10.1038/nclimate1853, 2013.

Nemani, R. R., Keeling, C. D., Hashimoto, H., Jolly, W. M., Piper, S. C., Tucker, C. J., Myneni, R. B., and Running, S. W.:
 <u>Climate-Driven Increases in Global Terrestrial Net Primary Production from 1982 to 1999, Science, 300, 1560-1563, 10.1126/science.1082750, 2003.</u>

Netherer, S., and Schopf, A.: Potential effects of climate change on insect herbivores in European forests-General aspects

- and the pine processionary moth as specific example, Forest Ecology and Management, 259, 831-838, 10.1016/j.foreco.2009.07.034, 2010.
 Olofsson, P., and Eklundh, L.: Estimation of absorbed PAR across Scandinavia from satellite measurements. Part II: Modeling and evaluating the fractional absorption, Remote Sensing of Environment, 110, 240-251, 2007.
- Olofsson, P., Eklundh, L., Lagergren, F., Jönsson, P., and Lindroth, A.: Estimating net primary production for Scandinavian
 forests using data from Terra/MODIS, Advances in Space Research, 39, 125-130, http://dx.doi.org/10.1016/j.asr.2006.02.031, 2007.

Olsson, P.-O., Kantola, T., Lyytikäinen-Saarenmaa, P., Jönsson, A., and Eklundh, L.: Development of a method for monitoring of insect induced forest defoliation – limitation of MODIS data in Fennoscandian forest landscapes, 2, 2016a.

Olsson, P.-O., Lindström, J., and Eklundh, L.: Near real-time monitoring of insect induced defoliation in subalpine birch 25 forests with MODIS derived NDVI, Remote Sensing of Environment, 181, 42-53,

http://dx.doi.org/10.1016/j.rse.2016.03.040, 2016b.
Page, E. S.: Continuous Inspection Schemes, Biometrika, 41, 100-115, 10.2307/2333009, 1954.
Potter, S. C., Klooster, S., and Brooks, V.: Interannual Variability in Terrestrial Net Primary Production: Exploration of

Trends and Controls on Regional to Global Scales, Ecosystems, 2, 36-48, 10.1007/s100219900056, 1999.

Prince, S. D.: A model of regional primary production for use with coarse resolution satellite data, International Journal of Remote Sensing, 12, 1313-1330, 10.1080/01431169108929728, 1991.
 Prince, S.D., and Goward, S.N.: Global Primary Production: A Remote Sensing Approach. Journal of Biogeography, 22,

Prince, S.D., and Goward, S.N.: Global Primary Production: A Remote Sensing Approach. Journal of Biogeography, 22, 815–835, 1995.

Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N., Gilmanov, T., Granier, A., Grünwald, T., Havránková, K., Ilvesniemi, H., Janous, D., Knohl, A., Laurila, T., Lohila, A., Loustau, D., Matteucci, G., Meyers, T., Miglietta, F., Ourcival, J.-M., Pumpanen, J., Rambal, S., Rotenberg, E., Sanz, M., Tenhunen, J., Seufert, G., Vaccari, F., Vesala, T., Yakir, D., and Valentini, R.: On the separation of net ecosystem exchange into

5 assimilation and ecosystem respiration: review and improved algorithm, Global Change Biology, 11, 1424-1439, 10.1111/j.1365-2486.2005.001002.x, 2005.

Rouse, J. W., Haas, R. H., Shell, J. A., and Deering, D. W.: Monitoring vegetation systems in the Great Plains with ERTS-1, Third Earth Resources Technology Satellite Symposium, 309–317, 1973.

Ruimy, A., Saugier, B., and Dedieu, G.: Methodology for the estimation of terrestrial net primary production from remotely sensed data, Journal of Geophysical Research: Atmospheres, 99, 5263-5283, 1994.

Rullan-Silva, C. D., Olthoff, A. E., Delgado de la Mata, J. A., and Pajares-Alonso, J. A.: Remote Monitoring of Forest Insect Defoliation -A Review, 2013, 22, 15, 10.5424/fs/2013223-04417, 2013.

Running, S. W., Nemani, R. R., Heinsch, F. A., Zhao, M., Reeves, M., and Hashimoto, H.: A Continuous Satellite-Derived Measure of Global Terrestrial Primary Production, BioScience, 54, 547-560, 10.1641/0006-15 3568(2004)054[0547:ACSMOG]2.0.CO;2, 2004.

Saravesi, K., Aikio, S., Wäli, P. R., Ruotsalainen, A. L., Kaukonen, M., Huusko, K., Suokas, M., Brown, S. P., Jumpponen,A., and Tuomi, J.: Moth Outbreaks Alter Root-Associated Fungal Communities in Subarctic Mountain Birch Forests,Microbial ecology, 69, 788-797, 2015.

Schäfer, K. V. R., Clark, K. L., Skowronski, N., and Hamerlynck, E. P.: Impact of insect defoliation on forest carbon balance as assessed with a canopy assimilation model, Global Change Biology, 16, 546-560, 10.1111/j.1365-2486.2009.02037.x,

2010. Schubert, P., Eklundh, L., Lund, M., and Nilsson, M.: Estimating northern peatland CO 2 exchange from MODIS time series data, Remote Sensing of Environment, 114, 1178-1189, 2010.

Seidl, R., Schelhaas, M. J., Rammer, W., and Verkerk, P. J.: Increasing forest disturbances in Europe and their impact on

- 25 carbon storage (vol 4, pg 806, 2014), Nat. Clim. Chang., 4, 930-930, 10.1038/nclimate2393, 2014. Sellers, P.: Canopy reflectance, photosynthesis, and transpiration, II. The role of biophysics in the linearity of their interdependence, Remote sensing of Environment, 21, 143-183, 1987. Senn, J., Hanhimäki, S., and Haukioja, E.: Among-Tree Variation in Leaf Phenology and Morphology and Its Correlation with Insect Performance in the Mountain Birch, Oikos, 63, 215-222, 10.2307/3545381, 1992.
- 30 Sonesson, M., and Lundberg, B.: Late Quaternary Forest Development of the Torneträsk Area, North Sweden. 1. Structure of Modern Forest Ecosystems, Oikos, 25, 121-133, 10.2307/3543633, 1974. Tenow, O.: The outbreaks of Oporinia autumnata Bkh. & Operophthera spp. (Lep., Geometridae) in the Scandinavian mountain chain and northern Finland 1862–1968. Zoologiska Bidrag Från Uppsala, Supplement 2, 1972. Tenow, O.: Hazards to a Mountain Birch Forest: Abisko in Perspective, Ecological Bulletins, 104-114, 1996.

Tenow, O., and Bylund, H.: Recovery of a Betula pubescens Forest in Northern Sweden after Severe Defoliation by Epirrita autumnata, Journal of Vegetation Science, 11, 855-862, 2000.

Tenow, O., Nilssen, A. C., Bylund, H., and Hogstad, O.: Waves and synchrony in Epirrita autumnata /Operophtera brumata outbreaks. I. Lagged synchrony: regionally, locally and among species, Journal of Animal Ecology, 76, 258-268, 10.1111/j.1365-2656.2006.01204.x, 2007.

Tømmervik, H., Høgda, K. A., and Karlsen, S. R.: in: Nordic mountain birch ecosystems, edited by: Wielgolaski, F. E., The Parthenon Publishing Group., London, 241-249, 2001.

5

10.1016/j.foreco.2005.09.021, 2006.

Tucker, C. J.: Red and photographic infrared linear combinations for monitoring vegetation, Remote Sensing of Environment, 8, 127-150, 1979.

- 10 Turner, D. P., Urbanski, S., Bremer, D., Wofsy, S. C., Meyers, T., Gower, S. T., and Gregory, M.: A cross-biome comparison of daily light use efficiency for gross primary production, Global Change Biology, 9, 383-395, 2003. Vanhanen, H., Veteli, T., Päivinen, S., Kellomäki, S., and Niemelä, P.: Climate change and range shifts in two insect defoliators: gypsy moth and nun moth a model study, 4, 2007. Wielgolaski, F.E.: Vegetation sections in northern Fennoscandian mountain birch forests. In F.E. Wielgolaski (Ed.), Nordic
- 15 Mountain Birch Ecosystem. (pp. 23–46). London: The Parthenon Publishing Group, 2001. Wu, C., Munger, J. W., Niu, Z., and Kuang, D.: Comparison of multiple models for estimating gross primary production using MODIS and eddy covariance data in Harvard Forest, Remote Sensing of Environment, 114, 2925-2939, http://dx.doi.org/10.1016/j.rse.2010.07.012, 2010.
- Wulder, M. A., Dymond, C. C., White, J. C., Leckie, D. G., and Carroll, A. L.: Surveying mountain pine beetle damage of 20 forests: A review of remote sensing opportunities, Forest Ecology and Management, 221, 27-41, DOI:

Xiao, X., Zhang, Q., Braswell, B., Urbanski, S., Boles, S., Wofsy, S., Moore Iii, B., and Ojima, D.: Modeling gross primary production of temperate deciduous broadleaf forest using satellite images and climate data, Remote Sensing of Environment, 91, 256-270, http://dx.doi.org/10.1016/j.rse.2004.03.010, 2004.