

Reduced BVOC emissions from birch forest understory during coupled insect outbreak and microclimatic forcing

Corresponding Author: Mr Simon Nyboe Laursen

This file contains all reviewer reports in order by version, followed by all author rebuttals in order by version.

Version 0:

Reviewer comments:

Reviewer #1

(Remarks to the Author)

Dear authors,

I have finished my assessment of the manuscript titled 'Severe insect outbreak suppresses understory BVOC emissions through canopy-mediated microclimate feedbacks.' The manuscript presents an interesting blocked study design in which three different arctic understory vegetation types (graminoid, *Empetrum*, *Vaccinium*) are compared in their responses to canopy defoliator geometrid outbreaks (comparing 2022 to 2023, the latter being a heavy outbreak year). Responses recorded include microclimatic conditions, greenness, and the emission of biogenic volatiles.

The authors find that the outbreak year resulted in substantially more open and exposed conditions that resulted in shifts in climatic conditions and a lower greenness of the plots. Contrary to expectations, there was a lower release of biogenic VOCs in the outbreak year than before.

Although I think the work is largely done to very high standards, there are some general remarks that the authors could consider, to hopefully improve their work further:

1) In the intro, the authors immediately jump into BVOCs. I was thinking whether it would make sense to break down BVOCs into the most commonly found components (including HIPVs, which are only mentioned in the discussion). I think breaking them down, and then highlighting which contributors to BVOC pools are investigated here would feel more intuitive to the reader?

2) From the figure presenting the branch beating caterpillar yields, it seems to me that 2022 was also quite the heavy year. This is also clearly discussed by the authors. If it is possible, it would be quite insightful to compare the two years to a 'low' year, to see how this compares. I realize that this may be difficult if no such samples exist.

3) The authors present clear evidence of 2023 being much lower in BVOCs than 2022. This is interesting. However, in the results and discussion, the authors repeatedly refer to increases in specific concentrations between years. I believe these refer to increased relative concentrations, and the difference in wording could be important. What may seem like a massive increase (or decrease), may actually not represent a change in the environment (i.e. the absolute concentration) at all. Would it not be useful to present the absolute concentrations, as stacked bars, perhaps in a supplement?

4) The correlation plots show a very clear link between environmental conditions and BVOC emissions. To me, these are totally sensible. However, it was not completely sure to me whether these values were for 2022, 2023, or both years combined. Especially as the environmental exposure to irradiation increases – which you would expect to increase emissions – but the actual BVOC concentrations decreases in 2023, I am not sure how this could still lead to such significant effects. Would it make sense to break these down by year?

5) I struggled slightly with the link with the outbreak herbivores. The geometrids feed mainly on birch, which they seem to defoliate almost entirely. However, it is not completely clear to me whether the authors have actual evidence of the geometrids entering the plots and feeding (i.e. consumption inducing HIPVs), or that the loss in green actually represents a shift in color, i.e., due to exposure to sunlight or drier conditions? Was there any recorded evidence of the herbivore abundance, or even better, defoliation in the plots? Even a categorical estimate from none at all ranging to completely defoliated would have been extremely insightful. If we do not know conclusively what caused the shift in greenness, we can only rely on indirect evidence (as the authors also indicate with specific VOCs, etc.).

6) I am a bit confused by the loading PCAs. I only know loading plots as plots with vectors, where each vector represents a species variable (compound), and the relative contribution represented as some shade or color. (Often as biplots). Are the dots here the end of those vectors? This is probably just me, as I am by no means an expert at multivariate statistics, but I struggled to see how I could get a relative contribution from this plot?

I hope some of these suggestions may help the authors to improve their work further.

Best wishes,
Robin Heinen, Technical University of Munich

Reviewer #2

(Remarks to the Author)

This is very fine manuscript that explores an important topic: the impact of herbivory on BVOCs in a subarctic ecosystem. The manuscript explains that subarctic ecosystems are changing rapidly in terms of climate, which in turn is increasing herbivory. BVOC emissions are important from an ecosystem physiological perspective and from their influence on chemistry and particular matter.

The experiment is sound and the methodology is well explained. My comments are relatively minor. I support publication of the manuscript once these minor comments are addressed.

Minor comments:

Abstract: The last sentence in the abstract (lines 33-36) needs to be modified. While you do say “can”, your Future Directions (section 3.3, lines 353-376) does a nice job stating that the interaction between herbivory, vegetation and BVOCs is complex and “context-dependent and “species-specific.” Please bring some of this complexity to the final sentence of your abstract.

You do not expect every herbivory outbreak to follow this same pattern.

Line 72: remove “contrasting” or explain what the contrast is between the two growing seasons.

Line 74: italicize species names. Check other instances in manuscript.

Lines 92-95: do you have evidence that 2022 followed typical phenology? Even a personnel communication from a site manager/technician?

Lines 268-272: is it possible that climate played a role too? Isn't 2023 warmer and drier overall? Please comment on this in the manuscript.

Lines 273-282: are graminoids also more physiologically resilient to increased light and temperature compared to the other plot-dominant species? Is there evidence for this in the literature? If so, please include in the manuscript.

Lines 297-316 and 346-352: this non-linear response is not unique to herbivory. For example, the basic BVOC (particularly isoprene) temperature response is non-linear: the sharp increase eventually collapses at very high temperatures. Drought can also lead to a nonlinear response: mild drought can increase emissions via leaf energy balance, while emissions decline with severe drought (leaf senescence).

Lines 450-454: You reference section 2.4.1, but I believe it should be 4.4.1.

Figure 2: I find the closed symbols (sampling dates) a little difficult to interpret. You are putting the symbols at non-zero positions on the graph. This makes sense for the open symbols, since they are directly related to phenology. Your BVOC measurement dates are not derived from phenology. I suggest that you put these closed symbols along the 0 line.

Figure 3: I understand this may not fit, but check if you could include species (*nigrum*, graminoids, *myrtillus*) in the figure itself, instead of putting it in the caption. You do include the names in Figure 5 (vertically).

Reviewer #3

(Remarks to the Author)

The study linking insect outbreaks with understory BVOC emissions is interesting and relevant. The authors' effort to measure a wide range of variables related to microclimate, vegetation condition, and BVOC emissions is commendable. However, I have concerns that should be addressed before the conclusions can be fully supported.

A major concern is that the manuscript presents the insect outbreak as the cause of reduced BVOC emissions, but this causal link does not appear to be directly statistically tested. The authors connect lower BVOC emissions to changes in light, temperature, soil moisture, drought stress, and loss of green vegetation. However, without a formal analysis linking outbreak severity to BVOC emissions, the claim that the insect outbreak “suppresses” BVOC emissions is an interpretation than a directly tested result. The authors could test direct and indirect mediation pathways from outbreak severity to BVOC emissions, for example using causal analysis or structural equation modelling. If this cannot be done with the available data, the wording should be toned down.

It is also unclear how the authors separate outbreak effects from year effects. I assume that 2021 and or 2022 may function as a lower-outbreak or reference year, but this is not clearly explained. Because the study compares two growing seasons, differences between years could reflect annual variation of parameters that not measured rather than insect damage alone.

The sampling design and statistical analysis are not sufficiently clear. It would be helpful to have a table summarizing what was measured, where (which block), and when. For example, it is not clear whether green ratio, microclimate, and BVOC measurements were taken from the same blocks or plots, or how the selected blocks were used as random variable, if the parameters are not measured in same blocks.

The discussion also needs links referred back to the results. Most statements in the discussion are not supported by citations to specific figures or tables, and some sections lack citations to results altogether. This makes it difficult to read the manuscript and verify which results support each statement.

Version 1:

Reviewer comments:

Reviewer #2

(Remarks to the Author)

Thank you for addressing my comments from my initial review. I am satisfied with the responses to my comments.

Reviewer #3

(Remarks to the Author)

I thank the authors for addressing my comments. I have no further comments.

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Dear Editor and Reviewers,

Thank you for the opportunity to revise our manuscript and for your constructive comments and recommendations, which have helped to improve the quality of our manuscript. We have now followed the guidance of all three reviewers and carefully addressed the comments raised.

During the revision of our manuscript, we identified a conversion error in the calculation of BVOC emission rates. This error has now been corrected throughout the manuscript, including the main text, figures, tables, and supporting information where relevant. The correction did not change the statistical interpretation, or conclusions of the manuscript.

Please find below our detailed responses to the reviewer comments in **blue text** with changes highlighted in **bold**. All line numbers (Line XXX-XXX) refer to the tracked changes version of the reviewed manuscript.

Best regards on behalf of all co-authors,

Simon Nyboe Laursen

Reviewer #1 (Remarks to the Author):

Dear Authors,

I have finished my assessment of the manuscript titled 'Severe insect outbreak suppresses understory BVOC emissions through canopy-mediated microclimate feedbacks.' The manuscript presents an interesting blocked study design in which three different arctic understory vegetation types (graminoid, *Empetrum*, *Vaccinium*) are compared in their responses to canopy defoliator geometrid outbreaks (comparing 2022 to 2023, the latter being a heavy outbreak year). Responses recorded include microclimatic conditions, greenness, and the emission of biogenic volatiles. The authors find that the outbreak year resulted in substantially more open and exposed conditions that resulted in shifts in climatic conditions and a lower greenness of the plots. Contrary to expectations, there was a lower release of biogenic VOCs in the outbreak year than before.

Although I think the work is largely done to very high standards, there are some general remarks that the authors could consider, to hopefully improve their work further:

We thank Robin for his careful and thoughtful comments and for the positive evaluation of the overall quality of our work. We believe that by addressing his comments, the quality of the manuscript has improved substantially. Please see our detailed reply point by point below.

1) In the intro, the authors immediately jump into BVOCs. I was thinking whether it would make sense to break down BVOCs into the most commonly found components (including HIPVs, which are only mentioned in the discussion). I think breaking them down, and then highlighting which contributors to BVOC pools are investigated here would feel more intuitive to the reader?

We thank the reviewer for this constructive suggestion and agree that the *introduction* would benefit from a clearer overview of BVOC composition and especially herbivory-induced plant volatiles (HIPVs). This may also widen the audience for our study. We have therefore revised the introduction to distinguish constitutive from stress-induced emissions and to introduce some of the most well-known HIPVs.

Line (55-73): "Geometrid feeding is also known to strongly enhance plant emissions of biogenic volatile organic compounds (BVOCs) **and their composition**, which function in plant defence by repelling herbivores, attracting natural enemies, and signalling to neighbouring plants ^{19,20}. **Herbivore-induced plant volatiles (HIPVs) include compounds such as green leaf volatiles (GLVs), which are emitted immediately upon physical herbivore damage²¹, (E)-4,8-Dimethylnona-1,3,7-triene ((E)-DMNT), which plants use to attract natural enemies of herbivores ²² and indole, which is known as a key stress-signalling compound ²³**. Experimental studies have shown that geometrid feeding on mountain and dwarf birch foliage can

increase BVOC emissions by up to two orders of magnitude ^{24,25}, with herbivory-induced emissions potentially representing a dominant BVOC source in high-latitude ecosystems ²⁶. **BVOCs therefore serve as early biochemical indicators of ecosystem stress, as their release is closely linked to plant physiological responses to biotic disturbance ^{27–29}. In addition to stress-induced emissions, plants also emit BVOCs constitutively as part of their normal metabolic activity, while the magnitude of these emissions is regulated by abiotic drivers such as temperature and solar radiation ^{27,30}.** Once emitted, BVOCs participate in the formation of tropospheric ozone and secondary organic aerosols (SOA), thereby influencing air quality, cloud condensation nuclei, and regional radiative forcing ^{31,27,32,33}. In relatively pristine Arctic environments with low anthropogenic pollution, plant BVOCs may have higher relative importance in atmospheric chemistry than in more polluted regions ³⁴.”

We also now clarify that our study quantifies total BVOC emissions and emission composition across major compound groups, including compounds commonly associated with herbivore stress.

Line (86-97): “To address this, we conducted extensive enclosure BVOC sampling (n = 132) across two growing seasons spanning increasing herbivory (2022) to the peak of a geometrid outbreak (2023) ^{43,44} in a subarctic mountain birch forest in northern Sweden (Fig. 1). **We quantified total BVOC emissions and their composition across major BVOC groups, including isoprene, monoterpenes, sesquiterpenes, GLVs, homoterpenes, oxygenated BVOCs, and other BVOCs. Several of these BVOC groups include compounds commonly associated with herbivory, allowing us to assess whether outbreak conditions altered not only total emission rates but also the relative composition of the emitted blend.** Focusing on plots dominated by three understory plant groups (*Empetrum nigrum*, *Vaccinium myrtillus*, and graminoids), we combined BVOC measurements with near-surface proxies of vegetation greenness and microclimatic observations to quantify how canopy defoliation alters understory conditions and, in turn, BVOC emission rates and composition.”

2) From the figure presenting the branch beating caterpillar yields, it seems to me that 2022 was also quite the heavy year. This is also clearly discussed by the authors. If it is possible, it would be quite insightful to compare the two years to a ‘low’ year, to see how this compares. I realize that this may be difficult if no such samples exist. We agree with the reviewer that comparison with a true low-herbivory/background year would be valuable for our study. Unfortunately, such *in situ* BVOC measurements are not available for this ecosystem prior to the outbreak. We have clarified this limitation in both the Introduction and Discussion:

Line (456-461): “**Because BVOC samples were not available for the non-herbivory baseline year of 2021, we used 2021 only as a reference for site-level above-canopy meteorological conditions and phenology.**”

Line (456-461): “Additionally, given that 2022 represents an intermediate level of herbivory^{43,49} rather than a true non-herbivory baseline year, our two-year comparison may underestimate **the full extent of outbreak-associated reduction in GreenRatio and BVOC emissions. Future comparisons with a true low-herbivory baseline would provide valuable insight into the full magnitude of these effects.**”

3) The authors present clear evidence of 2023 being much lower in BVOCs than 2022. This is interesting. However, in the results and discussion, the authors repeatedly refer to increases in specific concentrations between years. I believe these refer to increased relative concentrations, and the difference in wording could be important. What may seem like a massive increase (or decrease), may actually not represent a change in the environment (i.e. the absolute concentration) at all. Would it not be useful to present the absolute concentrations, as stacked bars, perhaps in a supplement?

We thank the reviewer for this important comment and agree that the distinction between absolute emission rates and the relative proportion to total emissions is vital. We have therefore revised the wording throughout the *Results* and *Discussion* sections to distinguish clearly between absolute BVOC emissions and relative contributions to the total BVOC blend. Absolute emission rates (estimated marginal means) for the discussed HIPVs are already presented in Table S8. We have therefore not added an additional stacked bar plot, as this would duplicate the information already provided in the supplementary table.

4) The correlation plots show a very clear link between environmental conditions and BVOC emissions. To me, these are totally sensible. However, it was not completely sure to me whether these values were for 2022, 2023, or both years combined. Especially as the environmental exposure to irradiation increases – which you would expect to increase emissions – but the actual BVOC concentrations decreases in 2023, I am not sure how this could still lead to such significant effects. Would it make sense to break these down by year?

We thank the reviewer for this helpful suggestion and agree that showing pooled relationships across years may mask important year-specific patterns, especially because 2023 was characterized by warmer and drier conditions but lower overall BVOC emissions. To address this, we have revised the analysis and figure accordingly. Specifically, we now present year-specific marginal trends from the linear mixed models when the ANOVA (Table S11) indicated a significant Year × Group × environmental-driver interaction. Where no significant interaction was detected, trends are shown pooled across years. We have also included the backward model selection

results in the Supplementary Information (Table S12, S13 and S14) to make the model structure and retained interaction terms more transparent.

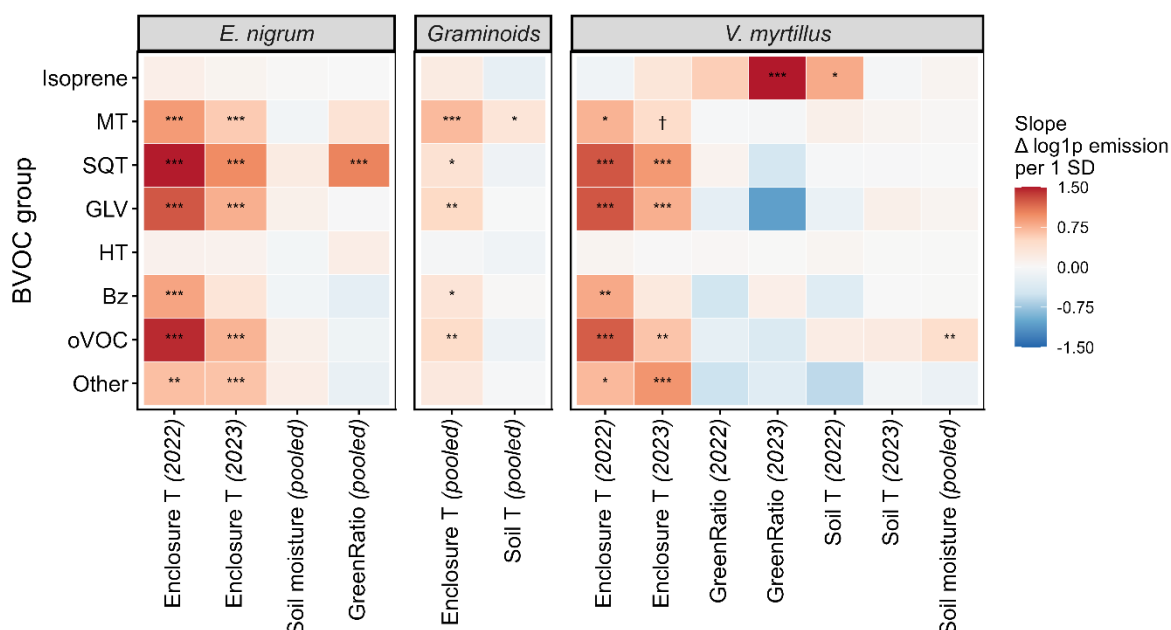
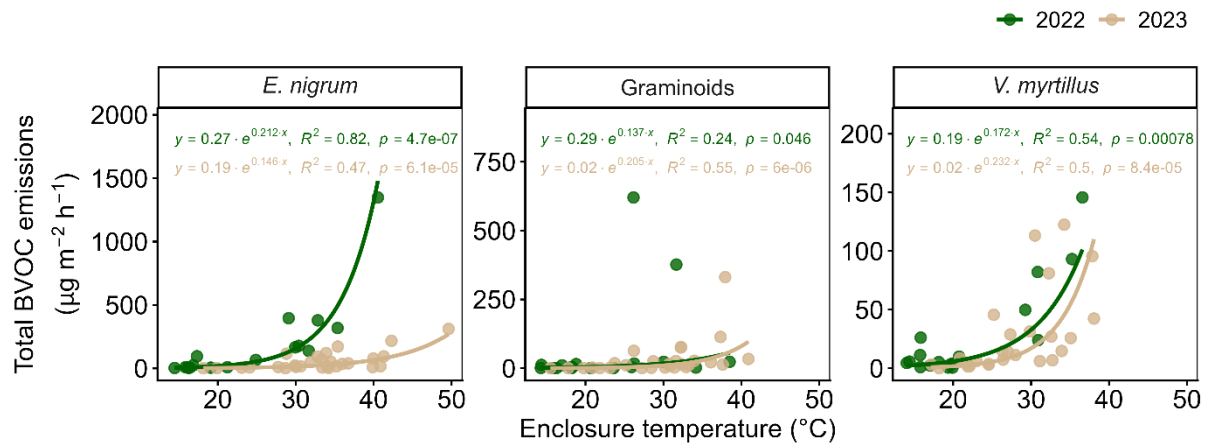


Figure 7: BVOC emission rates sensitivities to environmental drivers. Heatmaps of marginal trends estimated from LMM, showing BVOC group-specific sensitivities of BVOC emissions rates and environmental drivers. Tile colours indicate the estimated marginal trend ($\Delta \log_{10}$ emission per 1 SD), and symbols denote Benjamini–Hochberg-adjusted significance ($\dagger p < 0.1$, $* = p < 0.05$, $** = p < 0.01$, $*** = p < 0.001$). **Only environmental drivers retained in the final models are shown. Environmental drivers are displayed separately by year when the ANOVA (Table S11) indicated a significant Year $\times$ Group $\times$ driver interaction; otherwise, marginal trends are shown pooled across years. See Supplementary Table S13 for backward model selection results.** BVOC groups include isoprene, monoterpenes (MT), sesquiterpenes (SQT), green leaf volatiles (GLV), homoterpenes (HT), other oxygenated BVOCs (oBVOC), and Other BVOCs. Marginal-trend statistics for total emissions are given in Supplementary Table S9, and BVOC group-specific trends are given in Supplementary Table S10.

In the revised figure, year-specific enclosure-temperature sensitivity differed significantly in *E. nigrum* and *V. myrtillus*-dominated plots. Here, all BVOC groups, except for other BVOCs, showed weaker coupling with enclosure temperature in 2023 than in 2022 (Table S10), although enclosure temperature remained a strong and significant positive driver in 2023. In graminoid dominated plots, temperature sensitivity did not differ significantly between years across BVOC groups (Table S11). Thus, enclosure temperature remained an important positive driver of BVOC emissions, but its effect was not significantly year-dependent in these plots. This suggests that temperature continued to stimulate emissions from residual green tissues, while total emissions in 2023 were constrained by reduced BVOC-emitting green vegetation.

For clarity, we also examined yearly raw total BVOC emissions against enclosure temperature for each plot-dominant species, although this plot was not included in the revised manuscript. These data showed that emissions generally increased with enclosure temperature within both years, but that 2023 emissions were generally lower

at high enclosure temperatures, particularly in *E. nigrum* plots. This supports our interpretation that temperature continued to promote BVOC emissions from remaining green tissues, while outbreak-year emission capacity was constrained by reduced BVOC-emitting vegetation.



Based on the new correlation plots (Fig. 7) we have revised the Results and Discussion sections:

Line (251-263): "Across plot-dominant species, enclosure air temperature was the most consistent positive driver of BVOC emissions (Fig. 7; Table S9-10), in line with previous studies from Arctic and alpine tundra ecosystems^{40,47,48}. For total BVOC emissions, enclosure temperature showed strong positive trends in *E. nigrum* ($1.09 \pm 0.2 \Delta \log_{10} p$ per 1 SD; $p < 0.001$), graminoids (0.95 ± 0.17 ; $p < 0.001$), and *V. myrtillus* plots (1.25 ± 0.2 ; $p < 0.001$; Fig. 7). Enclosure temperature was also positively associated with emissions of the major BVOC groups (benzenoids, GLVs, monoterpenes, sesquiterpenes, oBVOCs, and Other BVOCs) across all plot-dominant species (Fig. 7). Homoterpenes and isoprene showed no detectable enclosure temperature sensitivity in any plot-dominant species ($p \geq 0.205$, Fig. 7). **For *E. nigrum* and *V. myrtillus* plots, year-specific enclosure temperature sensitivities were in general stronger in 2022 than in 2023 across BVOC groups (Fig. 7; Table S10).**"

Line (264-282): "In contrast, GreenRatio, soil moisture and soil temperature showed weaker and more selective trends with BVOC emissions. **For total emissions in *E. nigrum* plots, soil moisture was marginally positive in 2023 (0.30 ± 0.17 ; $p = 0.098$), but not in 2022 (-0.35 ± 0.32 ; $p = 0.276$).** GreenRatio also showed a marginal positive relationship with total emissions in *E. nigrum* plots (0.61 ± 0.29 ; $p = 0.090$), whereas neither soil moisture nor GreenRatio was related to total emissions in graminoid or *V. myrtillus* plots (Table S9). At the BVOC group level in *E. nigrum* plots, GreenRatio showed a strong positive trend with sesquiterpene emissions (1.03 ± 0.21 ; $p < 0.001$; Fig. 7). Soil moisture showed no significant trends for any BVOC groups for the *E. nigrum* plots. In graminoid plots, soil temperature showed only a significant positive trend for monoterpenes (0.32 ± 0.13 ; $p = 0.049$, Fig. 7). In *V. myrtillus* plots, a significant positive trend for GreenRatio was observed for isoprene in 2023 ($3.03 \pm$

0.54; $p < 0.001$), but not in 2022 (0.58 ± 0.29 ; $p = 0.164$). Soil temperature showed a significant positive trend for isoprene in 2022 (0.80 ± 0.30 ; $p = 0.034$), but not in 2023 (-0.05 ± 0.12 ; $p = 0.990$), whereas soil moisture showed a positive trend only for oVOCs (0.44 ± 0.14 ; $p = 0.009$; Fig. 7; Table S10)."

Line (440-449): "At the same time, enclosure air temperature emerged as the most consistent positive driver of emissions across plot-dominant species, for both total BVOCs (Table S9) and majority of the BVOC groups (Fig. 7; Table S10). Warmer and brighter understory conditions would typically be expected to stimulate BVOC emissions because higher temperatures enhance enzymatic activity in BVOC biosynthetic pathways and volatilization from leaf tissues^{30,69,80}. **However, this positive temperature effect may weaken when heat or drought stress becomes severe, as prolonged stress can reduce photosynthesis, carbon substrate availability, and green leaf metabolic activity, thereby constraining BVOC production despite warmer conditions**⁸¹. The net emission response therefore likely reflects a balance between *i*) reduced BVOC-emitting leaf areas and *ii*) temperature- and light-driven stimulation of BVOC synthesis and volatilization in residual leaf tissues."

5) I struggled slightly with the link with the outbreak herbivores. The geometrids feed mainly on birch, which they seem to defoliate almost entirely. However, it is not completely clear to me whether the authors have actual evidence of the geometrids entering the plots and feeding (i.e. consumption inducing HIPVs), or that the loss in green actually represents a shift in color, i.e., due to exposure to sunlight or drier conditions? Was there any recorded evidence of the herbivore abundance, or even better, defoliation in the plots? Even a categorical estimate from none at all ranging to completely defoliated would have been extremely insightful. If we do not know conclusively what caused the shift in greenness, we can only rely on indirect evidence (as the authors also indicate with specific VOCs, etc.).

We thank the reviewer for this important comment, and appreciate the opportunity to clarify this point. A similar comment was given by reviewer #3.

We did not directly quantify insect abundance or feeding damage within the BVOC sampling plots, because a direct assessment of feeding damage would have required destructive harvesting or cutting of the sampled vegetation. Such disturbance could have altered plant stress responses and potentially induced artificial BVOC emissions during subsequent measurements. Instead, we used the non-destructive GreenRatio metric derived from repeated close-up camera images of the plot vegetation, as a proxy for changes in green vegetation cover. However, we acknowledge that this metric cannot fully distinguish between direct herbivory-induced defoliation and browning caused by e.g. accelerated senescence and/or desiccation as a result of altered microclimate. This is also stated in method section: Line (600-603): "Because GreenRatio is a greenness-based metric, it is used as a proxy for green canopy fraction rather than a direct measure of defoliation i.e. lower values may also reflect browning/senescence or other pigment-related changes."

Yet, we agree that this should also be stated more clearly in the discussion, so we added the following paragraph, acknowledging the limitation of not measuring herbivore abundance and feeding damage directly in the sampling plots:

Line (295-303): **“Geometrid abundance and feeding damage were not directly quantified in the BVOC understory sampling plots, as assessment of precise leaf area damage requires destructive sampling i.e. cutting the vegetation after the BVOC sampling which could induce additional stress emissions of the plants ⁵⁰. We therefore used GreenRatio as a non-destructive proxy for changes in green vegetation cover, while recognizing that declines in this metric may result from both direct herbivore-induced defoliation and indirect canopy-mediated microclimatic stress. Consequently, we cannot fully separate the effects of these mechanisms on the observed declines in green vegetation cover and BVOC emissions.”**

Line (333-341): **“Thus, the reduction in understory GreenRatio likely reflects a coupled effect of geometrid herbivory and canopy-mediated heat-, light-, and drought stress, rather than direct herbivore feeding alone. In addition, carry-over effects from winter or early-season stress, including freezing damage and winter drought ⁶⁰⁻⁶³, may also have contributed to reduced GreenRatio in 2023, although these effects were not directly quantified in the present study.”**

Line (456-461): **“Additionally, given that 2022 represents an intermediate level of herbivory ^{43,49} rather than a true non-herbivory baseline year, our two-year comparison may underestimate the full extent of outbreak-associated reduction in GreenRatio and BVOC emissions. Future comparisons with a true low-herbivory baseline would provide valuable insight into the full magnitude of these effects.”**

Moreover, we have revised the manuscript throughout to clarify that both mechanisms likely contributed to the observed changes in GreenRatio and BVOC emissions e.g.

Line (33-37): **“We suggest that this decline is due to a combined effect of direct herbivory on susceptible understory species** and canopy-mediated feedbacks following mountain birch defoliation. These feedbacks **likely** intensified radiative, thermal, and drought stress in the understory, leading to widespread loss of BVOC-emitting green vegetation.”

Lastly, we have also changed the title from:

“Severe insect outbreak suppresses understory BVOC emissions through canopy-mediated microclimate feedbacks” to **“Reduced BVOC emissions from birch forest understory during coupled insect-outbreak and microclimatic forcing”**, to better reflect the coupled effects of herbivory and microclimatic change.

6) I am a bit confused by the loading PCAs. I only know loading plots as plots with vectors, where each vector represents a species variable (compound), and the relative contribution represented as some shade or color. (Often as biplots). Are the dots here the end of those vectors? This is probably just me, as I am by no means an expert at

multivariate statistics, but I struggled to see how I could get a relative contribution from this plot?

The reviewer is correct that the points in our loading plots represent the endpoints of the loading vectors for each VOC compound. We chose to show only the vector endpoints because including all vectors made the figure visually cluttered and difficult to read. However, we agree that this was not sufficiently clear. We have therefore revised the figure caption to explicitly state that each point represents the endpoint of a loading vector, and that the distance from the origin reflects the strength of the loading on PC1 and/or PC2.

Line (1059-1067): **“Figure 6: Principal component analyses (PCA) of BVOC emission profiles.** PCAs analyses are based on the proportional contribution of individual compounds to total emissions, across plot-dominant species in 2022 and 2023. Left panels show compound loadings for a) *E. nigrum* and c) *V. myrtillus* plots. **Each point represents the endpoint of a loading vector for one compound. Compounds farther from the origin have stronger loadings on PC1 and/or PC2 and therefore contribute more to variation along these axes.** Loadings are coloured by BVOC group: isoprene (Iso), monoterpenes (MT), sesquiterpenes (SQT), green leaf volatiles (GLV), homoterpenes (HT), other oxygenated BVOCs (oBVOC), and Other BVOCs. Right panels display sample scores (each point represents one BVOC sample) for b) *E. nigrum* and d) *V. myrtillus*, with point size indicating plot GreenRatio and colour denoting sampling year.”

I hope some of these suggestions may help the authors to improve their work further. We thank the reviewer for his constructive and thoughtful comments. The suggestions were very helpful and have improved the clarity and interpretation of the manuscript substantially.

Best wishes,
Robin Heinen, Technical University of Munich

Reviewer #2 (Remarks to the Author):

This is very fine manuscript that explores an important topic: the impact of herbivory on BVOCs in a subarctic ecosystem. The manuscript explains that subarctic ecosystems are changing rapidly in terms of climate, which in turn is increasing herbivory. BVOC emissions are important from an ecosystem physiological perspective and from their influence on chemistry and particular matter. The experiment is sound and the methodology is well explained. My comments are relatively minor. I support publication of the manuscript once these minor comments are addressed.

We thank the reviewer for this positive assessment of our manuscript and for recognizing the importance of understanding how herbivory (directly/indirectly) affects BVOC emissions from understory vegetation in rapidly changing subarctic ecosystems. We are thankful for the constructive comments and the support for publication. We have carefully addressed each of the comments in the revised manuscript, and we believe that these revisions have improved the manuscript substantially. Please see our detailed reply point by point below.

Minor comments:

Abstract: The last sentence in the abstract (lines 33-36) needs to be modified. While you do say “can”, your Future Directions (section 3.3, lines 353-376) does a nice job stating that the interaction between herbivory, vegetation and BVOCs is complex and “context-dependent and “species-specific.” Please bring some of this complexity to the final sentence of your abstract. You do not expect every herbivory outbreak to follow this same pattern.

We thank the reviewer for this helpful suggestion. We agree that the final sentence of the abstract should better reflect the context-dependent and species-specific nature of BVOC responses to herbivory. We have therefore revised the final sentence that now reads:

Line (37-40): “Our findings demonstrate that severe geometrid outbreaks can suppress, rather than enhance, BVOC emissions by shifting emission control from abiotic stimulation to green biomass limitation, **while highlighting that BVOC responses to herbivory are context-dependent and species-specific.**”

Line 72: remove “contrasting” or explain what the contrast is between the two growing seasons.

We have removed “contrasting” from the sentence.

Line 74: italicize species names. Check other instances in manuscript. Thanks for pointing this out. We have revised here and throughout the manuscript.

Lines 92-95: do you have evidence that 2022 followed typical phenology? Even a personnel communication from a site manager/technician?

We thank the reviewer for pointing this out. We do not have independent evidence that 2022 represented a typical phenological year, and have therefore removed this wording. The revised sentence now reads:

Line (114-118): “Phenology of both the mountain birch canopy and the understory vegetation varied markedly among the three growing seasons (Fig. 2b–c). In 2022, the **mountain birch canopy (Fig. 2b) developed progressively during spring** with leaf flush **beginning** in late May (**start of season (SOS) = DOY 148**), **reaching** peak of season (POS = DOY 172), and then declined gradually towards the end of season (EOS = DOY 254).”

Lines 268-272: is it possible that climate played a role too? Isn't 2023 warmer and drier overall? Please comment on this in the manuscript.

We thank the reviewer for this helpful comment and agree that the increased light exposure and temperature in 2023 likely amplified heat and drought stress in the *E. nigrum* dominated plots. Especially since that *E. nigrum* is known to be drought sensitive. We have now revised the section accordingly to make that clearer:

Line (365-377): “**In addition, the altered understory microclimate following canopy defoliation may also have contributed to the reduced GreenRatio observed in 2023. *E. nigrum* is considered drought sensitive^{63,66}, and recent experimental evidence shows that photosynthesis in *E. nigrum* mesocosms was strongly reduced under drought, but not under heat-wave conditions alone⁶⁷. This indicate that water limitation may be a key constraint on *E. nigrum* functioning under warmer Arctic conditions. This aligns with our BVOC measurements, where reductions in total BVOC emissions from *E. nigrum* plots were most pronounced under dry conditions (Table S6). Together, these direct and indirect effects suggest that the low GreenRatio in 2023 reflected a combination of direct feeding on *E. nigrum*, limited recovery from previous herbivory, and increased exposure to stressful microclimatic conditions, resulting in reduced BVOC-emitting green vegetation cover and, consequently, a reduced ability to mount a strong BVOC emission response during the outbreak year.**”

We have also elaborated on the role of climate on the response observed for *V. myrtillus* (see below) and Graminoids (see reply to next comment):

Line (409-417): “**In addition, *V. myrtillus* is also known to be vulnerable to severe drought stress under more exposed understory conditions^{61,62,76}. Experimental work shows that drought-related stress can accelerate leaf senescence in mature *V. myrtillus* leaves, while also producing carry-over effects in stems across years ^{61,62}. Increased radiation and temperature following canopy defoliation may therefore have amplified drought stress ⁷⁶, contributing to reduced green tissue cover and lower BVOC-emitting green vegetation in 2023.**”

Thus, the response observed in the *V. myrtillus* plots likely reflects **the coupled effects of direct** herbivory and elevated drought stress.”

Lines 273-282: are graminoids also more physiologically resilient to increased light and temperature compared to the other plot-dominant species? Is there evidence for this in the literature? If so, please include in the manuscript.

We thank the reviewer for this helpful comment and agree that elaborating on the light and temperature resilience of graminoids is highly relevant in this context. We have now revised the Discussion to address this:

Line (385-395): “**The limited response to the geometrid outbreak** is in line with graminoids generally being avoided by geometrids ^{15,63,64}, **but may also reflect greater tolerance of the warmer and brighter microclimate following canopy defoliation** ^{60,70}. **Experimental evidence from subarctic plant communities show that graminoids can be less vulnerable than evergreen dwarf shrubs to abiotic stress, including extreme warming** ⁶⁰. **Long-term Arctic vegetation observations also show increasing graminoid cover under recent climatic change, suggesting that graminoids may persist or increase under warmer conditions**⁷⁰. Together, this suggests that the graminoid plots were structurally more resilient and chemically conservative under the geometrid outbreak. Accordingly, the moderate reduction in GreenRatio likely reflects indirect, microclimate-mediated stress, rather than direct geometrid feeding.”

Lines 297-316 and 346-352: this non-linear response is not unique to herbivory. For example, the basic BVOC (particularly isoprene) temperature response is non-linear: the sharp increase eventually collapses at very high temperatures. Drought can also lead to a nonlinear response: mild drought can increase emissions via leaf energy balance , while emissions decline with severe drought (leaf senescence).

We thank the reviewer for this helpful comment. We agree that non-linear BVOC responses are not unique to herbivory and can also arise from abiotic controls such as temperature and drought. We have therefore revised this section to clarify that temperature- and light-driven stimulation of BVOC emissions may weaken or reverse under severe heat or drought stress, when photosynthesis, carbon substrate availability, green leaf metabolic activity, or leaf area become constrained. The revised section now reads:

Line (440-449): “At the same time, enclosure air temperature emerged as the most consistent positive driver of emissions across plot-dominant species, for both total BVOCs (**Table S9**) and majority of the BVOC groups (**Fig. 7; Table S10**). Warmer and brighter understory conditions would typically be expected to stimulate BVOC emissions because higher temperatures enhance enzymatic activity in BVOC biosynthetic pathways and volatilization from leaf tissues ^{30,69,80}. **However, this positive temperature effect may weaken when heat or drought stress becomes severe, as prolonged stress can reduce photosynthesis, carbon substrate availability, and green leaf metabolic activity, thereby constraining BVOC**

production despite warmer conditions⁸¹. The net emission response therefore likely reflects a balance between *i*) reduced BVOC-emitting leaf areas and *ii*) temperature- and light-driven stimulation of BVOC synthesis and volatilization in residual leaf tissues.”

Lines 450-454: You reference section 2.4.1, but I believe it should be 4.4.1.
Thanks for pointing this out. Now revised.

Figure 2: I find the closed symbols (sampling dates) a little difficult to interpret. You are putting the symbols at non-zero positions on the graph. This makes sense for the open symbols, since they are directly related to phenology. Your BVOC measurement dates are not derived from phenology. I suggest that you put these closed symbols along the 0 line.

Good suggestion. We have revised the figure accordingly and now show the BVOC sampling dates as colored rectangles placed along the zero line.

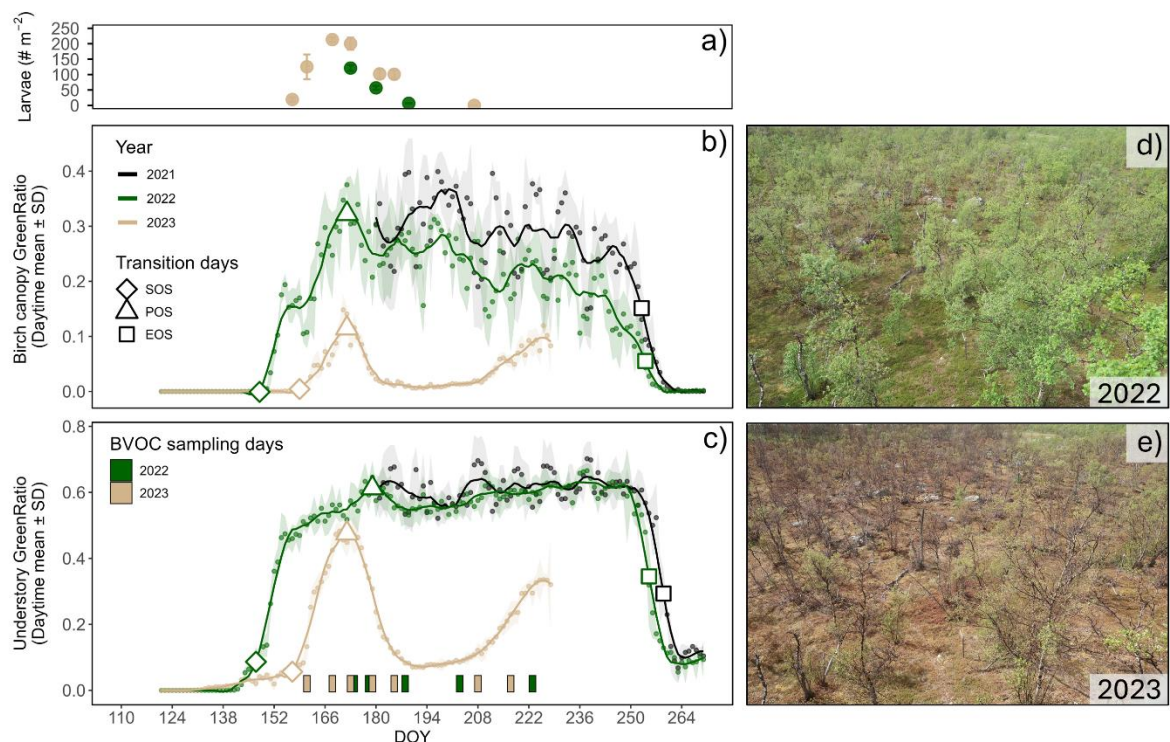


Figure 2: Seasonal dynamics of geometrid abundance and vegetation phenology. a) Geometrid larvae abundance on birch branches from insect beating surveys conducted in 2022-2023. For more information on the insect beating surveys, see Rieksta et al. (2026). Seasonal trajectories of b) birch canopy and c) understory GreenRatio derived from tower RGB time-lapse imagery. Lines show Savitzky–Golay–smoothed daytime means with shaded ribbons indicating ± 1 SD. Open symbols mark phenological transition dates derived from the smoothed curves: start of season (SOS), peak of season (POS) and end of season (EOS). Filled circles in c) denote BVOC sampling days in 2022–2023. A full summary of phenological transition dates is provided in Table S1. (d–e) Raw RGB time-lapse images of the birch forest on d) DOY 188 (7 July) in 2022 and e) on the same day in 2023, illustrating the contrast between a fully foliated and a heavily defoliated canopy.

Figure 3: I understand this may not fit, but check if you could include species (nigrum, graminoids, myrtillus) in the figure itself, instead of putting it in the caption. You do include the names in Figure 5 (vertically).

Good suggestion. We have revised Figure 3, 4 and 7, accordingly (see revised plots below).

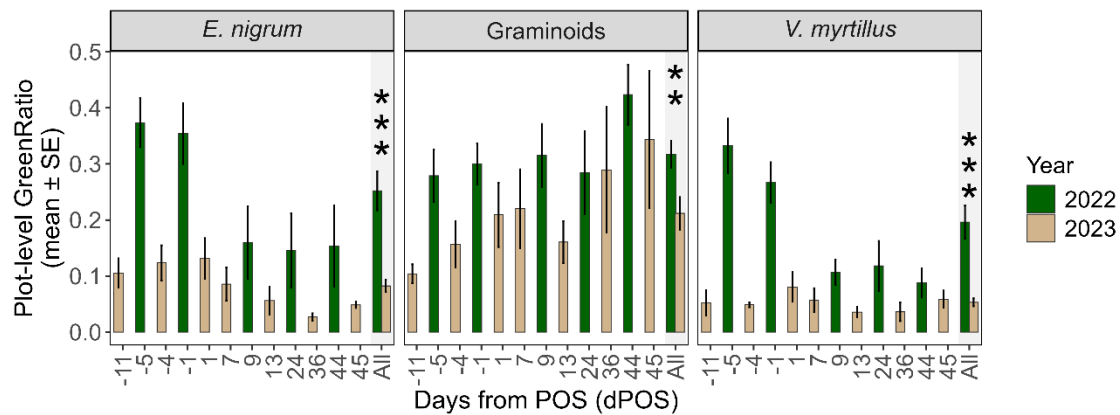


Figure 3: Interannual differences in understory GreenRatio across plot-dominant species. Mean GreenRatio ($\pm$ SE) of plot-dominant species across days from peak of season (dPOS) in 2022 and 2023. The vertical dashed line marks peak of season (POS), derived from the time-lapse images. The shaded "All" bar summarizes means across all dPOS of each year. Asterisks indicate year contrasts from LMM, $p < 0.01$ (**), and $p < 0.001$ (***).

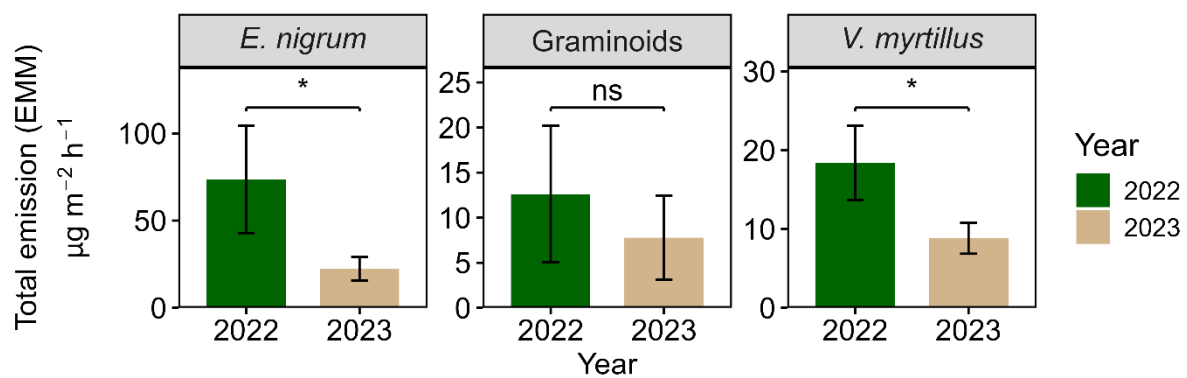


Figure 4: Interannual variation in total BVOC emission rates across plot-dominant species. Back-transformed estimated marginal means (EMMs $\pm$ SE) of total BVOC emission rates ($\mu\text{g m}^{-2} \text{h}^{-1}$) from LMM of each plot-dominant species in 2022 and 2023. Significance symbols above brackets denote the pairwise Year contrast (* = $p < 0.05$, ns = not significant). Note different scaling on y-axis.

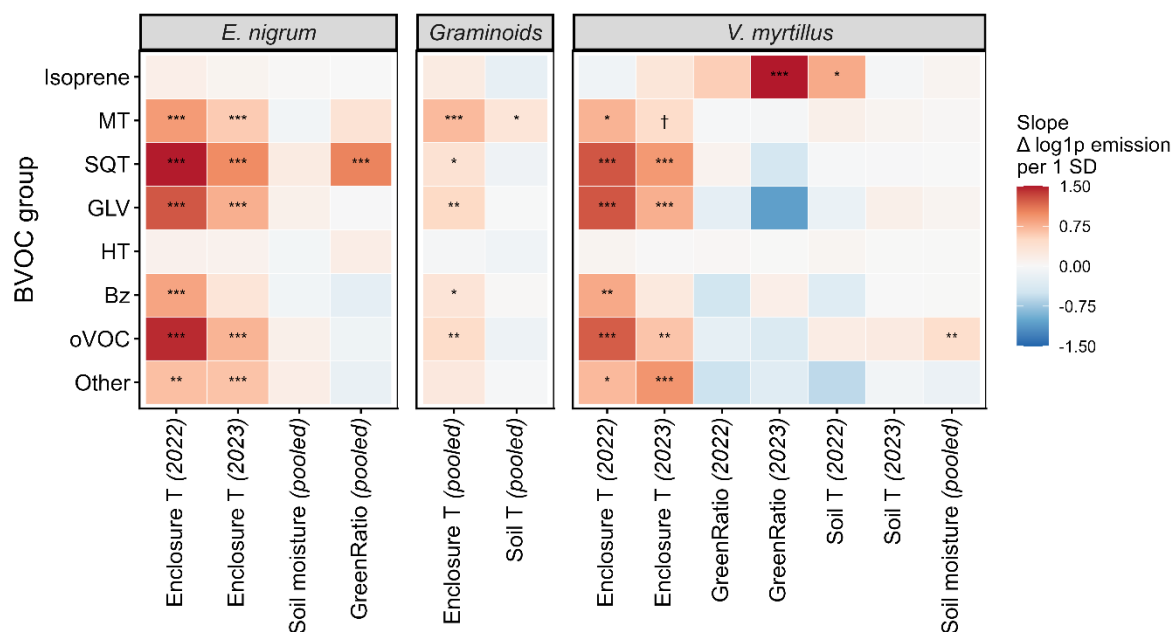


Figure 7: BVOC emission rates sensitivities to environmental drivers. Heatmaps of marginal trends estimated from LMM, showing BVOC group-specific sensitivities of BVOC emissions rates and environmental drivers. Tile colours indicate the estimated marginal trend ($\Delta \log_{10} p$ emission per 1 SD), and symbols denote Benjamini–Hochberg–adjusted significance ($\dagger p < 0.1$, $* = p < 0.05$, $** = p < 0.01$, $*** = p < 0.001$). Only environmental drivers retained in the final models are shown. Environmental drivers are displayed separately by year when the ANOVA (Table S11) indicated a significant Year $\times$ Group $\times$ driver interaction; otherwise, marginal trends are shown pooled across years. See Supplementary Table S13 for backward model selection results. BVOC groups include isoprene, monoterpenes (MT), sesquiterpenes (SQT), green leaf volatiles (GLV), homoterpenes (HT), other oxygenated BVOCs (oBVOC), and Other BVOCs. Marginal-trend statistics for total emissions are given in Supplementary Table S9, and BVOC group-specific trends are given in Supplementary Table S10.

Reviewer #3 (Remarks to the Author):

The study linking insect outbreaks with understory BVOC emissions is interesting and relevant. The authors' effort to measure a wide range of variables related to microclimate, vegetation condition, and BVOC emissions is commendable. However, I have concerns that should be addressed before the conclusions can be fully supported.

We thank the reviewer for the positive assessment of our work and for recognizing the value of the multi-variable field dataset. We believe that by addressing the reviewers comments the quality of the manuscript has improved substantially. Please see our detailed reply point by point below.

1) A major concern is that the manuscript presents the insect outbreak as the cause of reduced BVOC emissions, but this causal link does not appear to be directly statistically tested. The authors connect lower BVOC emissions to changes in light, temperature, soil moisture, drought stress, and loss of green vegetation. However, without a formal analysis linking outbreak severity to BVOC emissions, the claim that the insect outbreak “suppresses” BVOC emissions is an interpretation than a directly tested result. The authors could test direct and indirect mediation pathways from outbreak severity to BVOC emissions, for example using causal analysis or structural equation modelling. If this cannot be done with the available data, the wording should be toned down.

We thank the reviewer for this important comment. A related comment was also given by reviewer #1.

We agree that a formal causal analysis would indeed strengthen our claim, that it was the insect outbreak that directly and/or indirectly caused the reduction in BVOC emissions. Unfortunately, our dataset does not support such an analysis. Herbivore abundance and herbivory feeding damage was not quantified directly in the sampling plots, as such sampling would be destructive to the vegetation within the plots (i.e. cutting and harvesting the vegetation for accurate assessment of leaf area damage) that could lead to induced artificial BVOC emissions. Instead, we used the non-destructive GreenRatio metric derived from repeated close-up camera images of the plot vegetation, as a proxy for changes in green vegetation cover. However, we acknowledge that this metric cannot fully distinguish between direct defoliation and browning caused by e.g. accelerated senescence and/or desiccation. This is also stated in the method section; Line (600-603): “Because GreenRatio is a greenness-based metric, it is used as a proxy for green canopy fraction rather than a direct measure of defoliation i.e. lower values may also reflect browning/senescence or other pigment-related changes.”

We therefore rely on indirect evidence from the GreenRatio signal and the BVOC emission blend, showing an increase in the relative contribution of herbivory-induced plant volatiles. Based on this, we have toned down the wording throughout the

manuscript. For example, we changed the wording to acknowledge that both direct herbivory and canopy-mediated microclimate feedbacks likely caused the reduction in GreenRatio and BVOC emissions.

Line (33-36): “We suggest that this decline **reflect a combined effect of direct herbivory on susceptible understory species** and canopy-mediated feedbacks following mountain birch defoliation. **These feedbacks likely intensified** radiative, thermal, and drought stress in the understory, leading to widespread loss of BVOC-emitting green vegetation.”

We also changed the title from “Severe insect outbreak suppresses understory BVOC emissions through canopy-mediated microclimate feedbacks” to “**Reduced BVOC emissions from birch forest understory during coupled insect-outbreak and microclimatic forcing**”, to better reflect the coupled effects of herbivory and microclimatic change.

We have also added a paragraph to the Discussion explicitly acknowledging the limitation of not measuring herbivore abundance and feeding damage directly in the sampling plots.

Line (448-453): “**In addition, geometrid abundance and feeding damage were not directly quantified in the BVOC sampling plots, because destructive sampling or repeated disturbance of the vegetation could have artificially induced BVOC emissions. Therefore, we cannot fully separate the effects of direct herbivory from canopy-mediated microclimatic stressors on the observed decline in green vegetation cover and BVOC emissions. Resolving their relative contributions warrants further investigation.**”

2) It is also unclear how the authors separate outbreak effects from year effects. I assume that 2021 and or 2022 may function as a lower-outbreak or reference year, but this is not clearly explained. Because the study compares two growing seasons, differences between years could reflect annual variation of parameters that not measured rather than insect damage alone.

We thank the reviewer for this important comment and agree that the distinction between outbreak effects and general year effects needed to be clarified. The reviewer is correct, that we use 2021 as a baseline year for above-canopy meteorological conditions (Ambient air temperature and PAR measured above the forest canopy) and the phenology signal from the timelapse RGB-images. However, BVOC sampling was first initiated in 2022 and therefore represents a moderate herbivory year rather than a true baseline year. We have not stated this more explicitly in the Introduction:

Line (86-89): “To address this, we conducted extensive enclosure BVOC sampling (n = 132) across two growing seasons spanning **increasing herbivory (2022) to the peak of a geometrid outbreak (2023)** ^{43,44} in a subarctic mountain birch forest in northern Sweden (Fig. 1).

Line (97-99): **“Because BVOC samples were not available for the non-herbivory baseline year of 2021, we used 2021 only as a reference for site-level above-canopy meteorological conditions and phenology.”**

We have also clarified in the Discussion that 2022 should be interpreted as a intermediate herbivory year rather than a true non-herbivory baseline year:

Line (456-461): **“Additionally, given that 2022 represents an intermediate level of herbivory^{43,49} rather than a true non-herbivory baseline year, our two-year comparison may underestimate the full extent of outbreak-associated **reduction in GreenRatio and BVOC emissions. Future comparisons with a true low-herbivory** baseline would provide valuable insight into the full magnitude of these effects.”**

That said, we do believe that several lines of evidence support our interpretation that the 2023 response was strongly associated with the geometrid outbreak and canopy defoliation rather than reflecting background annual variation alone.

- First, larvae abundance in the mountain birch canopy was substantially higher in 2023, documenting stronger outbreak pressure in the year when understory greenness and BVOC emissions declined.
- Second, above-canopy meteorological measurements from the MET tower showed no significant difference in ambient PAR or air temperature between 2022 and 2023 growing seasons, suggesting that the strong differences observed within the understory were not simply caused by warmer or brighter regional weather conditions.
- Third, the observed changes were consistent with canopy-mediated effects of birch defoliation, including increased understory light and temperature, reduced soil moisture, reduced GreenRatio, and lower BVOC emissions from green understory vegetation.

At the same time, we acknowledge that unmeasured annual factors, such as winter freezing events or other carry-over effects, may also have contributed to the observed reduction in GreenRatio and associated BVOC responses. We have added this limitation to the Discussion:

Line (333-341): **“Thus, the reduction in understory GreenRatio likely reflects a coupled effect of geometrid herbivory and canopy-mediated heat-, light-, and drought stress, rather than direct herbivore feeding alone. In addition, carry-over effects from winter or early-season stress, including freezing damage and winter drought^{60–63}, may also have contributed to reduced GreenRatio in 2023, although these effects were not directly quantified in the present study.”**

3) The sampling design and statistical analysis are not sufficiently clear. It would be helpful to have a table summarizing what was measured, where (which block), and when. For example, it is not clear whether green ratio, microclimate, and BVOC measurements were taken from the same blocks or plots, or how the selected blocks were used as random variable, if the parameters are not measured in same blocks.

We thank the reviewer for the opportunity to clarify the sampling design and statistical structure and agree that this was not described sufficiently clearly in the original manuscript. We have therefore added a new supplementary table summarizing which variables were measured, at which spatial scale, in which blocks/plots, and during which sampling campaigns (Table S15; also attached below).

Line (656-658): “See Supplementary Table S15 for an overview of all environmental variables measured during the study, including their spatial scale, timing relative to BVOC sampling, and whether they were included as plot-level covariates in the linear mixed-effects models.”

Table S15: Overview of variables measured during the study, their spatial scale, timing relative to BVOC sampling, and inclusion in the linear mixed-effects models (LMMs). Plot-level variables were measured in the corresponding BVOC sampling plots and during the same sampling campaigns as the BVOC measurements. Site- and landscape-level variables were used contextually to characterize the broader ecosystem response to the geometrid outbreak, but were not included as plot-level predictors in the LMMs.				
Variable	Spatial scale	Measured in BVOC plots?	Timing relative to BVOC sampling	Used in LMM?
BVOC emissions	Plot	Yes	Sampling event	Response
Enclosure air temperature	Plot	Yes	During BVOC sampling	Yes
Ambient air temperature	Plot	Yes	During BVOC sampling	Yes*
Ambient PAR	Plot	Yes	During BVOC sampling	Yes*
Soil temperature	Plot	Yes	During BVOC sampling	Yes
Soil moisture	Plot	Yes	During BVOC sampling	Yes
Close-up GreenRatio	Plot	Yes	Prior to BVOC sampling	Yes
Ambient above forest canopy air temperature (from MET-tower)	Site	No	Continuous/site-level	No / contextual
Ambient above forest canopy PAR (from MET-tower)	Site/landscape	No	Continuous/site-level	No / contextual
Time-lapse GreenRatio (from MET-tower)	Site/landscape	No	Continuous phenology	No / contextual
Time-lapse Canopy surface temperature (from MET-tower)	Site/landscape	No	Continuous canopy surface temperature	No / contextual
Larvae abundance on mountain birch canopies	Site/landscape	No	Campaign-level	No / contextual

Note: * Ambient air temperature and PAR were excluded in the LMM due to collinearity with enclosure air temperature.

To clarify, all variables included in the linear mixed models (LMMs) were measured at the BVOC sampling-plot level and at the time of BVOC sampling for all samples. We now state this explicitly in the manuscript: Line (622-624): **“Only covariates measured directly in the corresponding BVOC sampling plots and during the same sampling campaigns were included in the models.”** The experimental design consisted of repeated measurements of plots nested within blocks over the growing season. We therefore used block as a random effect to account for the non-independence of repeated measurements from the same block. This is also stated in the method section: Line (625-629): “All models included a random intercept for Block (Fig. 1b) to account for repeated measurements within blocks. For the BVOC group and selected-BVOC models, an additional random intercept for Sample ID was included to account for multiple BVOC group responses derived from the same sample.”

We also clarified that some variables were measured at the site/landscape scale and were not used as plot-level covariates in the LMMs. For example, above-canopy meteorological measurements from the MET tower, including air temperature and PAR, represent site-level environmental conditions, with the tower location shown in Fig. 1. Similarly, GreenRatio derived from time-lapse images mounted on the MET tower was used to describe continuous seasonal phenology and landscape-level GreenRatio of the study area, rather than as a plot-level predictor in the LMMs.

Line (97-99): **“Because BVOC samples were not available for the non-herbivory baseline year of 2021, we used 2021 only as a reference for site-level above-canopy meteorological conditions and phenology.”**

Thus, site- and landscape-level measurements were used only as contextual evidence to assess the broader ecosystem response to the geometrid outbreak, and not as plot-level predictors in the LMMs.

4) The discussion also needs links referred back to the results. Most statements in the discussion are not supported by citations to specific figures or tables, and some sections lack citations to results altogether. This makes it difficult to read the manuscript and verify which results support each statement.

Thanks for pointing this out. We agree that several statements in the Discussion needed clearer links back to the Results. We have now revised the Discussion and added references to the relevant figures and tables where appropriate. We believe that this improves the readability of the discussion.

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