

Between-plant interactions in Scots pine are not impaired by air pollutants

Corresponding Author: Dr Tihomir Simin

This file contains all editorial decision letters in order by version, followed by all author rebuttals in order by version.

Version 0:

Decision Letter:

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Dear Dr Simin,

Your manuscript titled "Between-plant interactions in the field are unimpaired by air pollutants" has now been seen by 2 reviewers, whose comments are appended below. You will see that they find your work of some potential interest. However, they have raised quite substantial concerns that must be addressed. In particular, a clearer representation of the results, an improved discussion on VOC-mediated signaling, and a deeper investigation or discussion of potential root-root interactions in the experiments is requested. An explanation of the choice of the studied species as well as a more detailed description of the methods used is also recommended.

In light of these comments, we cannot accept the manuscript for publication, but would be interested in considering a revised version that fully addresses these serious concerns.

In revision, please address the editorial thresholds as follows:

**** Provide a compelling case that volatile-mediated interactions between Scots pine seedlings are not impaired by air pollutants, including full discussions on mechanisms driving the plant responses, especially plant-to-plant interactions, to air pollutants.**

**** Make a clear description of experimental methods and acknowledge potential limitations of data/methods.**

We hope you will find the reviewers' comments useful as you decide how to proceed. Should additional work allow you to address (that is, either incorporate or refute) these criticisms, we would be happy to look at a substantially revised manuscript. If you choose to take up this option, please either highlight all changes in the manuscript text file, or provide a list of the changes to the manuscript with your responses to the reviewers.

When resubmitting, please provide a point-by-point response to the reviewers' comments. Please submit your responses as a separate file, distinct from your cover letter where you can add responses to the Editors' comments that you do not want to be made available to the reviewers. Word files are preferred. We recommend that any figures, tables or graphs that are included in the response to reviewers are also included in the main article or Supplementary Information.

Please bear in mind that we will be reluctant to approach the reviewers again in the absence of substantial revisions.

If the revision process takes significantly longer than three months, we will be happy to reconsider your paper at a later date, as long as nothing similar has been accepted for publication at Communications Earth & Environment or published elsewhere in the meantime.

We are committed to providing a fair and constructive peer-review process. Please do not hesitate to contact us if you wish to discuss the revision in more detail.

Please use the following link to submit your revised manuscript, point-by-point response to the reviewers' comments with a list of your changes to the manuscript text (which should be in a separate document to any cover letter), a tracked-changes version of the manuscript (as a PDF file) and any completed checklist:

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Please do not hesitate to contact us if you have any questions or would like to discuss the required revisions further. Thank you for the opportunity to review your work.

Best regards,

Nora Zannoni, PhD
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Communications Earth & Environment
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REVIEWER COMMENTS:

Reviewer #1 (Remarks to the Author):

Summary

This study examined how air pollutants—tropospheric ozone (O₃) and nitrogen oxides (NO_x) from diesel exhaust—affect volatile-mediated plant–plant communication in Scots pine seedlings, using a Free-Air Diesel and Ozone Enrichment system. The findings demonstrate that receiver seedlings exposed to herbivore-induced plant volatiles (HIPVs) from weevil-damaged neighbors experienced a 49% reduction in bark damage and a 15% increase in net photosynthesis, regardless of pollution exposure. VOC emissions increased by 158% in these seedlings, with altered chemical blends, notably a higher abundance of β-elemene, which was negatively correlated with herbivory. While O₃ and diesel exhaust independently influenced plant physiological traits such as photosynthesis and stomatal conductance, they did not disrupt the ability of seedlings to respond defensively to neighbor cues. Overall, the study highlights that VOC-mediated defenses in Scots pine are resilient to ambient air pollution, suggesting that plant–plant signaling can remain functional even under environmentally stressful conditions.

Main comments

This study presents an important contribution to our understanding of plant-plant communication in Scots pine seedlings under air pollution stress. The topic is timely and the experimental design appears well-executed. However, several critical issues must be addressed to strengthen the clarity, rigor, and interpretation of the findings.

First, the introduction contains excessive anthropogenic framing and lacks focus on key ecological mechanisms, particularly what is currently known about volatile-mediated interactions between Scots pine seedlings. A deeper contextualization of existing knowledge, including the role of specific volatiles and known plant-plant signaling mechanisms in conifers, is necessary to establish a stronger foundation for the study's aims.

Second, the figures require improvement to better communicate essential findings. For example, although the manuscript states that green leaf volatiles (GLVs) are induced after HIPV exposure (line 267), this pattern is difficult to discern in the current stacked bar chart due to the minimal representation of GLVs. If GLVs or other compound groups are central to the discussion or linked to palatability effects, their presentation should be visually clearer—perhaps through separate panels or grouped bar plots highlighting specific VOC categories. The current visualization underrepresents key data that are otherwise emphasized in the text.

Third, the discussion of photosynthetic parameters (e.g., stomatal conductance G_s and net assimilation rate A) is too superficial. These physiological responses deserve a more thorough interpretation, particularly given that the results differ from earlier studies (e.g., Yu et al. 2022, 2024). A critical comparison with these previous findings and potential explanations for the discrepancies would enhance the manuscript's depth.

Additionally, the role of root-root interactions is underexplored. While the authors argue that such effects are likely negligible due to slower response times, this assertion is not well substantiated. Evidence from studies (cited in this manuscript) such as Rasheed (2022) indicates that root-mediated communication can lead to rapid (within 24 hours) physiological changes in trees. The possibility that belowground signaling contributed to the observed effects, especially under conditions where VOCs might be less reliable (e.g., wind disruption or pollution), warrants a more balanced and comprehensive discussion. In fact, the lack of air pollution effect observed in this study might itself suggest that non-VOC pathways—such as root-root interactions—could be mediating plant responses across treatments.

Finally, the potential for herbivore manipulation of host plant signaling should be acknowledged. Given the specialized ecological relationship between pine weevils and Scots pine, and the known ability of herbivores to influence plant volatile profiles, the possibility that some induced volatiles may serve insect, rather than plant, interests should be considered.

In conclusion, while this manuscript offers valuable insights into plant signaling under pollution stress, its current conclusions are too strongly framed around volatile signaling alone. The claim that “plants can emit and receive informative chemical signals even in air-polluted environments” should be tempered, as root-mediated signaling or other mechanisms may also be involved. A more cautious and integrative conclusion would better reflect the complexity of the system studied.

Minor comments

- Line 52: Consider using more neutral language than “developed vs. developing countries,” which may be perceived as outdated or politically insensitive. Terms such as “high-income vs. low- and middle-income countries” are often preferred in academic writing.
- Line 53–54: The statement regarding ozone levels in rural areas is unclear. Does this refer to absolute increases in ozone over time in rural areas, or to relatively higher levels in rural versus urban areas? Clarifying this comparison would help readers understand the context.
- Line 58: The term “long-distance” VOC signaling is vague. Providing an approximate spatial range (in meters or kilometers) would help the reader grasp the scale and significance of this phenomenon.
- Line 69: The phrase “they increase their VOC emissions” anthropomorphizes plants. Consider rephrasing to emphasize physiological processes (e.g., “VOC emissions are elevated in response to...”).
- Line 71: The phrase “help plants manage abiotic stress” is both anthropogenic and vague. Specify the physiological responses or mechanisms (e.g., modulation of stomatal conductance, antioxidant production) rather than using general terms.
- Line 99: The claim that VOCs are the main medium of seedling interaction may be too strong. Root-root signaling is well documented in conifers and may play a role here. A more balanced phrasing would acknowledge this uncertainty.
- Line 155: The discussion could benefit from mentioning host plant selection behaviors, which are central to understanding herbivore responses to induced volatiles.
- Line 161: Since photosynthesis is sensitive to environmental conditions and diurnal variation, and the methods are only introduced later, it would be helpful to mention here whether timing of measurement (e.g., time of day post-HIPV exposure) may have influenced the results.
- Line 166: Since the observed difference is non-significant, this should be explicitly addressed in the text to avoid overinterpretation.
- Line 197: Emission factors are not a common metric in plant VOC research. The authors should explain what this measure represents and why it was chosen. Additionally, reporting the raw emission data would provide valuable context for interpretation.
- Line 210 & 215: Figure 2 (and related panels) are not clearly labeled or designed. It is unclear if panel (b) reflects the HIPV treatment results. The figure should be revised to improve clarity and ensure it aligns with the text description.
- Line 218: The term “emission increase” is ambiguous. Is this a fold-change, absolute difference, or a standardized factor? Clarify terminology and ensure consistency with the terminology used in the figures.
- Line 234–235 & 242: The ecological significance of certain VOCs (e.g., those correlated with bark damage) deserves more detailed treatment. Consider adding a figure that shows their actual concentrations across treatments.
- Line 274: The discussion begins to diverge toward global modeling and scaling-up topics, which are peripheral to the main findings. Refocusing on more relevant issues—such as belowground communication—would be more appropriate and insightful.
- Line 280: The claim that carbon assimilation increases after HIPV exposure should be presented more cautiously, since all cited studies come from the same research group. This should be acknowledged explicitly, and the need for broader replication emphasized.
- Line 286: “Potentially open” is unclear. Consider rephrasing this sentence for clarity.
- Line 315: The suggestion that volatile changes reflect herbivore manipulation should be considered. For example, linalool is attractive to many herbivores and pollinators. Given that pine beetles are specialists and can influence host physiology, this possibility should be discussed.
- Line 326: The conclusion implies effects on tree survival, yet survival data are not presented. Please revise this statement accordingly.
- Line 327: It would strengthen the paper to include data on whether HIPV exposure alters emissions of volatiles that are attractive to pine beetles. This could reveal important aspects of the defense strategy.
- Line 332: The suggestion of follow-up directions appears somewhat disconnected from the main focus. It may be better to limit the discussion to implications that are directly supported by the current findings.
- Line 339: The conclusion currently assumes that VOCs are solely responsible for the observed interactions. However, root-root communication may also contribute. A more nuanced conclusion acknowledging this possibility is warranted.

Reviewer #2 (Remarks to the Author):

What are the major claims of the paper?

- The paper highlights the disruption of plant to plant signaling via HIPVs (herbivore-induced plant volatiles) when under herbivory attack (specifically weevil and Scots pine) under air pollution (O₃ and NO_x). The authors found physiological effects (A, gs, VOCs emission) after a weevil attack. O₃ suppress the VOC reaction after being primed with HIPVs. However, the combination of O₃ and NO_x had no effect on the plant-to-plant interaction.

Are they novel and will they be of interest to others in the community and the wider field?

- Yes, it's novel and interesting to the community, however the choice of species is rather uncommon. Since Scots pine grows more often in forests, rather than urban or industrial areas with high NO_x levels.

On a more subjective note, do you feel that the paper will influence thinking in the field? Please feel free to raise any further questions and concerns about the paper.

- It will contribute well to the field of VOCs, herbivory attacks, air pollution.

- Further detailed comments:

Introduction

Line 66 – would not talk about the smell here. Its not relevant later on????

Line 67 – "... and can be stored in special structures...". Now it sounds as if they are either synthesized OR stored.

Line 70 – "...such as GLVs which are synthesized de novo and other isoprenoids which were stored..." induced emissions would be the wording for an emission answer on a certain stress.

Line 71 – "these VOCs" better would be "constitutive and induced VOCs"

Line 77 – remove "even"

Line 92 – why are they discouraged? Bc not environmentally friendly? I think you want to say, that seedlings can developed their own strategies if not spayed. Try connect these two sentences with "because", "the reason is", etc. In general, at several points your text reads as if the sentences and statements/story are/is not connected.

Materials and Methods

How did you damage the emitter plants with herbivores? Did you place the beetles beforehand to do some damage? Were they damaged the year before? How much were they damaged?

Double check if all devices mentioned are given the name, company, country. E.g., line 415

Line 382-385 – missing the verb, also this sentence is rather into

Line 389 – of what? How much % soil moisture content is saturated? Specific info about this soil?

Line 422 – leaves = needles

Line 429 – remove "on average"

Line 430 – refer to section 5.5 or say e.g. "described below"

Line 448 – leaf = needle, throughout the whole text

Line 452 – it is not clear how you come to this formula. Can you make a more abstract formula, by not using the constants 4.2235 and 15.6835? Details can be mentioned in the supplements.

Line 473 – GLVs are not used as a chemical term as SQTs (C15) or MTs (C10). Maybe add that GLVs are C6 compounds, as the reader who is unfamiliar to this topic might not know what you mean. Or give a list in the supplements what you define as GLVs.

Line 482 – did you measure the Cin [VOCs] also in the field? I can only find you measured it in the lab "in situ". Your hydrocarbon trap is a charcoal filter I suppose? They are often quite good, but can exhaust until a certain point. Did you use the carbon filter as well in the lab for your blanks?

Line 522 – "was not given" instead of "violated"

Line 521 – not necessary to report all significance levels. Only $p < 0.05$. Is it necessary to mention $p < 0.1$?

Line 525 – not necessary to mention which axis is Y and which is X. better use dependent and independent variables.

Statistics well executed.

Results

Line 118 – date 1st

Line 118 – 122 usually O₃ thresholds are given per a certain timeframe. Per 8h mean for example. I would add this to each O₃ level you mention

Figure 1 b – legend: better order it as (top) O₃, NO_x, NO₂, NO (bottom), not quite sure what happened with the grey writing there. something is underneath.

Line 160 – I figure, from here you say, exposure to HIPVs is what happens to the receiver tree, during phase 1 (emitter tree with beetle). It's a break in the reading process. Please lead the reader towards this understanding. I would find it better to state those two phases clearer in the text and the figures. Or at least: it becomes not clear from the M&M that you fumigated trees with HIPVs(?). In the M&M the first time you mention HIPV treatment is in the statistics. Pretty sure, it's only a problem of wording.

Line 172 – O₃ + D treatment – until here you were always writing the O₃ and diesel. Keep consistency.

Figure 2 a – DA (y axis) probably not necessary

Figure 2 – confusing what you want to say with H*, A*, P*, AxP*. Change, maybe put in a table. Does not fit in the figures.

Figure 3 – please change the unfilled phase 1 bars. Increase the contrast, it is hard to see. Check your whole text on American and English writing (normalised, normalized)

Figure 3 c – use emission rates not factors. Not necessary to write “needle area” on the y axis.
Figure 4 – remove DA abbreviation. Check legend of 4c.

Discussion

Line 263 – remove “leaf”

Line 264 – processes

Line 290 – interestingly in the discussion, you do not mention D or diesel, here you use NO_x. Better, to have it everywhere the same. I suggest to use NO_x.

Line 296 – damage to leaf tissue/cell membranes. I would rather think, the damage comes from internal structures, rather than surface structures. NO_x and O₃ enter through the stomata into stomatal cavity, reaching the mesophyll. There it has severe effects on the hydration shell of the cells + membranes etc. I guess you focus too much on outer structures, since you work with the visible damages of the bark by beetles.

Conclusion

You could add, that there is a high need to figure out how plants detect HIPVs.

Reads a too much like an abstract.

References

Check for O₃, NO_x etc to put 3 and x in subscript and species names in italic, DOIs?

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Version 1:

Decision Letter:

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Dear Dr Simin,

Your manuscript titled "Between-plant interactions in the field are unimpaired by air pollutants" has now been seen by our reviewers, whose comments appear below. In light of their advice we are delighted to say that we are happy, in principle, to publish a suitably revised version in Communications Earth & Environment.

We therefore invite you to revise your paper one last time to address the remaining concerns of our reviewers. At the same time we ask that you edit your manuscript to comply with our format requirements and to maximise the accessibility and therefore the impact of your work.

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Please review our specific editorial comments and requests regarding your manuscript in the attached "Editorial Requests Table".

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We hope to hear from you within two weeks; please let us know if you need more time.

Best regards,

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Mengjie Wang
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Consulting Editor, Communications Sustainability
Bluesky: @commsearth.nature.com; @ commssustain.nature.com

REVIEWERS' COMMENTS:

Reviewer #1 (Remarks to the Author):

Dear Authors,

Thank you for your careful and thorough revisions. You have addressed the main comments in a satisfactory way, and the manuscript is now clearer and better structured. In particular, the revised introduction, improved figures, and expanded discussion of physiological responses and possible belowground signaling pathways have strengthened the overall interpretation. The more cautious framing of conclusions is also appropriate.

Overall, I am satisfied with the changes and believe the manuscript is now suitable for publication, pending the editor's final decision.

Reviewer #2 (Remarks to the Author):

Minor revisions

I like this introduction much better. Small changes and some things still do not come to me easily.

Line 108 – 113 in the introduction is actually part of the results already and might better fit in the abstract

Line 102 thank you for explaining the Diesel exhaust in your in-line answers from my previous review. Maybe here is the best moment to explain that Diesel exhaust mainly contains NO_x but will be handled throughout the text as Diesel exhaust/Diesel.

Line 477,501, etc: you should decide now on NO_x or Diesel Exhaust 😊 pick one and stay consistent. I think you should take Diesel.

Line 52 – 53 would be nice to say here as well that VOCs are changing from species to species and can be cited from

<https://doi.org/10.3389/fgc.2019.00050>

Line 486 better practice would be to not speak of a specific date but say in the year 2023 the experiment was conducted and when using specific days you say this is the day of the year (DOY) so 4 May 2023 is 124 DOY.

Line 509 – 511 I think here you explain that the second bars of all plots showing BVOCs is the one which is of the second phase, right? In the description of figure 4 you do not say what the difference is between the lighter and darker colorful bars.

Line 523 – 524 the information about the wind direction is not mentioned in the rest of the text. I would not mention it at all.

Line 545,547 check the unit here ml min⁻¹ is better (check the whole text), also throughout your text double check for wrong spellings, missed full stop and missed spaces.

Line 326 Place "(LMM)" after Linear mixed models. Later you use just the abbreviation.

Line 153, 175, 171, 209 etc: Here in the results, you often use "(p=x.xxx, F=xx.x, LMM/Pearson, Figure XX)". This information is quite much. "LMM" is not necessary to tell, as you mention it in the methods. Also, the F-value is not necessary. (So, no F-value and statistical test)

Line 157, Table 1: I rather would like to read mean +- SE or SD values and give asterisk for significance levels. F- values are rather information for supplements. Also, if it is not significant better say n.s.

I understand, BVOC emissions are often not significantly changing. Every change is a result. But I would say therefore you raised the reporting P-value already to 0.1, which should be enough.

Line 169 here you speak of A and Gs. You say in the first sentences A is affected by diurnal patterns, but in the next sentences you say it was not. Also the window of 6h is quite large and contains high likely the midday depression (you could simplify)? So you Gs is following a diurnal pattern, am I right? You should write the same about Gs as you do about A (sentences line 171-176). (Not for this manuscript, but just to say: the more important parameter is Gs, as this actually influences VOC emission, together with T, PAR, daily pattern. A is more the result and a "trait-off"/"price the tree is paying" of taking in C and releasing C via VOCs.)

Line 239 find a reference. Maybe <https://doi.org/10.1111/nph.12887>.

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Dear Reviewers,

Thank you for reviewing our manuscript.

Your comments have been very useful for making meaningful improvements.

We are sending the new version of our manuscript with tracked changes along with this letter.

We apologize for the time needed to implement all the changes You asked for. We appreciate your patience and understanding.

Please find the detailed replies (in red) to the review comments (in blue) below.

Kind regards,

Tihomir Simin and the coauthors

Kuopio, Finland

November 2025

Reviewer #1:

Summary

This study examined how air pollutants—tropospheric ozone (O₃) and nitrogen oxides (NO_x) from diesel exhaust—affect volatile-mediated plant–plant communication in Scots pine seedlings, using a Free-Air Diesel and Ozone Enrichment system. The findings demonstrate that receiver seedlings exposed to herbivore-induced plant volatiles (HIPVs) from weevil-damaged neighbors experienced a 49% reduction in bark damage and a 15% increase in net photosynthesis, regardless of pollution exposure. VOC emissions increased by 158% in these seedlings, with altered chemical blends, notably a higher abundance of β -elemene, which was negatively correlated with herbivory. While O₃ and diesel exhaust independently influenced plant physiological traits such as photosynthesis and stomatal conductance, they did not disrupt the ability of seedlings to respond defensively to neighbor cues. Overall, the study highlights that VOC-mediated defenses in Scots pine are resilient to ambient air pollution, suggesting that plant–plant signaling can remain functional even under environmentally stressful conditions.

Reply (R): Thanks for a comprehensive summary.

Main comments

This study presents an important contribution to our understanding of plant–plant communication in Scots pine seedlings under air pollution stress. The topic is timely and the experimental design appears well-executed. However, several critical issues must be addressed to strengthen the clarity, rigor, and interpretation of the findings.

First, the introduction contains excessive anthropogenic framing and lacks focus on key ecological mechanisms, particularly what is currently known about volatile-mediated interactions between Scots pine seedlings. A deeper contextualization of existing knowledge, including the role of specific volatiles and known plant–plant signaling mechanisms in conifers, is necessary to establish a stronger foundation for the study's aims.

R: Thank you for your suggestions. We have revised the introduction entirely, so now it leads the reader more clearly to the aims of the manuscript.

Second, the figures require improvement to better communicate essential findings. For example, although the manuscript states that green leaf volatiles (GLVs) are induced after HIPV exposure (line 267), this pattern is difficult to discern in the current stacked bar chart due to the minimal representation of GLVs. If GLVs or other compound groups are central to the discussion or linked to palatability effects, their presentation should be visually clearer—perhaps through separate panels or grouped bar plots highlighting specific VOC categories. The current visualization underrepresents key data that are otherwise emphasized in the text.

R: We have modified all figures. Figure 3 was changed the most and now we show the emission rates of all VOC groups along with total emissions in panel a). In panel b) we decided to show the emission of smaller groups, i.e. all groups other than monoterpenes. Now they are more easily visible. Similarly, we show the damage-based emission increase for all groups in panel c) and smaller groups in panel d). The PCA and the emission factors panels have been moved to the Supplementary material. In addition, we have removed the results of the linear mixed model from the graphs and made a table that contains this information in detail (F and p values for all variables).

Third, the discussion of photosynthetic parameters (e.g., stomatal conductance G_s and net assimilation rate A) is too superficial. These physiological responses deserve a more thorough interpretation, particularly given that the results differ from earlier studies (e.g., Yu et al. 2022, 2024). A critical comparison with these previous findings and potential explanations for the discrepancies would enhance the manuscript's depth.

R: Very good point. We expanded the discussion about these parameters and proposed explanations for the differences and possibilities for further studies.

Additionally, the role of root-root interactions is underexplored. While the authors argue that such effects are likely negligible due to slower response times, this assertion is not well substantiated. Evidence from studies (cited in this manuscript) such as Rasheed (2022) indicates that root-mediated communication can lead to rapid (within 24 hours) physiological changes in trees. The possibility that belowground signaling contributed to the observed effects, especially under conditions where VOCs might be less reliable (e.g., wind disruption or pollution), warrants a more balanced and comprehensive discussion. In fact, the lack of air pollution effect observed in this study might itself suggest that non-VOC pathways—such as root-root interactions—could be mediating plant responses across treatments.

R: Another very good point. We made sure to include much more open discussion on the possibility of underground pathway of mediating between-plant interactions in the manuscript.

Finally, the potential for herbivore manipulation of host plant signaling should be acknowledged. Given the specialized ecological relationship between pine weevils and Scots pine, and the known ability of herbivores to influence plant volatile profiles, the possibility that some induced volatiles may serve insect, rather than plant, interests should be considered.

R: Interesting point. We have added a paragraph in the discussion about weevils and benzenoid compounds.

In conclusion, while this manuscript offers valuable insights into plant signaling under

pollution stress, its current conclusions are too strongly framed around volatile signaling alone. The claim that “plants can emit and receive informative chemical signals even in air-polluted environments” should be tempered, as root-mediated signaling or other mechanisms may also be involved. A more cautious and integrative conclusion would better reflect the complexity of the system studied.

R: Thank you for your comments. We have tried to temper the conclusions based on your recommendations.

Minor comments

- Line 52: Consider using more neutral language than “developed vs. developing countries,” which may be perceived as outdated or politically insensitive. Terms such as “high-income vs. low- and middle-income countries” are often preferred in academic writing.

R: Thank you for your comment. However, the current version of the Introduction does not contain this sentence anymore.

- Line 53–54: The statement regarding ozone levels in rural areas is unclear. Does this refer to absolute increases in ozone over time in rural areas, or to relatively higher levels in rural versus urban areas? Clarifying this comparison would help readers understand the context.

R: It refers to absolute concentrations of ozone. Thank you for this comment. This comment might relate to Line 64 in the current version of the Introduction.

- Line 58: The term “long-distance” VOC signaling is vague. Providing an approximate spatial range (in meters or kilometers) would help the reader grasp the scale and significance of this phenomenon.

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- Line 71: The phrase “help plants manage abiotic stress” is both anthropogenic and vague. Specify the physiological responses or mechanisms (e.g., modulation of stomatal conductance, antioxidant production) rather than using general terms.

R: Thank you for your comment. However, the current version of the Introduction does not contain this sentence anymore.

- Line 99: The claim that VOCs are the main medium of seedling interaction may be too strong. Root-root signaling is well documented in conifers and may play a role here. A more balanced phrasing would acknowledge this uncertainty.

R: Good point. We addressed the uncertainty in our current version of the Introduction.

- Line 155: The discussion could benefit from mentioning host plant selection behaviors, which are central to understanding herbivore responses to induced volatiles.

R: We go into more nuance about bark palatability later in the discussion. While we understand your concerns about host plant selection behaviours and we agree that this an interesting topic, we cannot discuss this topic in our paper because weevils were placed on the seedlings “against their will” and were not free to choose the host plant themselves. We can assure you that a work on this topic has been conducted in our group last year and will be submitted at some point in the future.

- Line 161: Since photosynthesis is sensitive to environmental conditions and diurnal variation, and the methods are only introduced later, it would be helpful to mention here whether timing of measurement (e.g., time of day post-HIPV exposure) may have influenced the results.

R: Thank you for this comment. We’ve added a short discussion on this topic in the beginning of the section. Currently at Line 176.

- Line 166: Since the observed difference is non-significant, this should be explicitly addressed in the text to avoid overinterpretation.

R: Good point. We addressed this more directly now. Currently at Line 186.

- Line 197: Emission factors are not a common metric in plant VOC research. The authors should explain what this measure represents and why it was chosen. Additionally, reporting the raw emission data would provide valuable context for interpretation.

R: The reason why we showed the emission factors initially is because, unlike the measurements in the lab, the influence of temperature and light on VOC emissions was deemed as significant. Therefore, we thought that comparing the emission factors would be a better way of showing the effect of the treatments in our experiment on VOC emissions. However, we do agree with you that emission rates are the most commonly used metric to compare in VOC. In fact, LMM actually showed a very similar response between emission rates and emission factors. Therefore, we removed the results and

discussion on emission factors. However, the bark-damage-based VOC emission increase is based on the emission factors, so the normalisation to temperature and light is still present in our paper. We think this is a good solution to your concerns.

- Line 210 & 215: Figure 2 (and related panels) are not clearly labeled or designed. It is unclear if panel (b) reflects the HIPV treatment results. The figure should be revised to improve clarity and ensure it aligns with the text description.

R: Thank you for the feedback. As explained earlier, we moved the PCA result to Supplementary material and have introduced emission rates in panel a (for all groups and total) and b (for oMTs, STQs, BZs, GLVs and ONIs). In c and d panels the bark-damage-based VOC increase is presented similarly and the figure description follows appropriately.

- Line 218: The term “emission increase” is ambiguous. Is this a fold-change, absolute difference, or a standardized factor? Clarify terminology and ensure consistency with the terminology used in the figures.

R: The increase is based on difference between phase 2 and phase 1 of emissions standardized for temperature and light and divided by bark damage. This is a measure to see which VOC emissions are primed by the exposure to damaged emitters. The details are provided in the Materials and Methods. We made sure to explain it better in the figure description (Bark damage area (DA)-based increase in emissions for individual VOC groups and total VOCs ($\text{mg m}^{-2} \text{h}^{-1} \text{cm}^{-2} \text{DA}$), based on emission factors = emission rates standardized to a temperature of 30°C and a photosynthetic photon flux density (PPFD) of $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) and we keep the terminology even across the manuscript.

- Line 234–235 & 242: The ecological significance of certain VOCs (e.g., those correlated with bark damage) deserves more detailed treatment. Consider adding a figure that shows their actual concentrations across treatments.

R: We added a panel in Figure 4 showing the emission rates of the VOCs that correlated significantly to bark damage in the PLS. We also described the emission of these compounds across treatments.

- Line 274: The discussion begins to diverge toward global modeling and scaling-up topics, which are peripheral to the main findings. Refocusing on more relevant issues—such as belowground communication—would be more appropriate and insightful.

R: We removed the scaling-up topics and focused more on the underground interactions aspects.

- Line 280: The claim that carbon assimilation increases after HIPV exposure should be

presented more cautiously, since all cited studies come from the same research group. This should be acknowledged explicitly, and the need for broader replication emphasized.

R: Thank you for your comment. We have expressed this uncertainty more clearly and openly now in line 363.

- Line 286: “Potentially open” is unclear. Consider rephrasing this sentence for clarity.

R: We rephrased the sentence and adopted your suggestion of addressing the possibility of underground mode of interaction more openly throughout the manuscript.

- Line 315: The suggestion that volatile changes reflect herbivore manipulation should be considered. For example, linalool is attractive to many herbivores and pollinators. Given that pine beetles are specialists and can influence host physiology, this possibility should be discussed.

R: We considered this possibility with benzenoid compounds between lines 421 and 428.

- Line 326: The conclusion implies effects on tree survival, yet survival data are not presented. Please revise this statement accordingly.

R: We revised the conclusions to reflect more on the need to separate the aboveground and belowground pathways for interactions.

- Line 327: It would strengthen the paper to include data on whether HIPV exposure alters emissions of volatiles that are attractive to pine beetles. This could reveal important aspects of the defense strategy.

R: We included this data in Figure 4d. Exposure to damaged emitters did not directly induce or prime higher emissions of VOCs that correlated with bark damage. But there was still plenty to discuss about them. :)

- Line 332: The suggestion of follow-up directions appears somewhat disconnected from the main focus. It may be better to limit the discussion to implications that are directly supported by the current findings.

R: Good point. We restructured the follow-up directions.

- Line 339: The conclusion currently assumes that VOCs are solely responsible for the observed interactions. However, root-root communication may also contribute. A more nuanced conclusion acknowledging this possibility is warranted

R: We tempered the conclusions.

Reviewer #2:

What are the major claims of the paper?

- The paper highlights the disruption of plant to plant signaling via HIPVs (herbivore-induced plant volatiles) when under herbivory attack (specifically weevil and Scots pine) under air pollution (O₃ and NO_x). The authors found physiological effects (A, gs, VOCs emission) after a weevil attack. O₃ suppress the VOC reaction after being primed with HIPVs. However, the combination of O₃ and NO_x had no effect on the plant-to-plant interaction.

R: Thank you for the positive summary.

Are they novel and will they be of interest to others in the community and the wider field?

- Yes, it's novel and interesting to the community, however the choice of species is rather uncommon. Since Scots pine grows more often in forests, rather than urban or industrial areas with high NO_x levels.

R: Thank you for your comment. We chose the Scots pine because it is actually common to have it in the cities in Finland and other Nordic countries. It is also a very common tree in the northern forests and the pollution can travel long distances from the place of origin, so even though it might not be obvious, it is important to study how air pollution affects the open-air between-plant interactions using Scots pine as a model organism.

On a more subjective note, do you feel that the paper will influence thinking in the field?

Please feel free to raise any further questions and concerns about the paper.

- It will contribute well to the field of VOCs, herbivory attacks, air pollution.

R: Thank you for your assessment.

- Further detailed comments:

Introduction

Line 66 – would not talk about the smell here. Its not relevant later on????

R: Thank you for your comment. However, we have revised the Introduction, so it does not contain this sentence anymore.

Line 67 – "... and can be stored in special structures...". Now it sounds as if they are either synthesized OR stored.

R: Thank you for your comment. However, we have revised the Introduction, so it does not contain this sentence anymore.

Line 70 – "...such as GLVs which are synthesized de novo and other isoprenoids which were stored..." induced emissions would be the wording for an emission answer on a certain stress.

R: Thank you for your comment. However, we have revised the Introduction, so it does not contain this sentence anymore.

Line 71 – “these VOCs” better would be “constitutive and induced VOCs”

R: Thank you for your comment. However, we have revised the Introduction, so it does not contain this sentence anymore.

Line 77 – remove “even”

R: Thank you for your comment. However, we have revised the Introduction, so it does not contain this sentence anymore.

Line 92 – why are they discouraged? Bc not environmentally friendly? I think you want to say, that seedlings can developed their own strategies if not spayed. Try connect these two sentences with “because”, “the reason is”, etc. In general, at several points your text reads as if the sentences and statements/story are/is not connected.

R: Thank you for your comment. We revised this paragraph of the text and made sure to connect the sentences better throughout the manuscript. Currently it is situated in line 84 and reads: “While insecticides have been used to mitigate this damage, their use is increasingly regulated due to environmental concerns. Therefore, understanding and enhancing the interactions between Scots pine seedlings could provide a sustainable alternative for protecting these economically vital forests.”

Materials and Methods

How did you damage the emitter plants with herbivores? Did you place the beetles beforehand to do some damage? Were they damaged the year before? How much were they damaged?

R: We described how the damage was done in section 5.1

Here’s the updated section about this process:

“The herbivory treatment (to emitter or receiver seedlings) consisted of placing three adults of the large pine weevil, *H. abietis* (Figure 1f), onto the bark of selected trees and enclosing the insects and the bark in a white mesh bag (Eurokangas, Orimattila, Finland). The weevils were starved for 24 hours before placement. They were collected from tree trunks in Scotland the previous year, kept in captivity at low temperature (16 °C at night and 9 °C during the day) and fed pine and spruce branches regularly. The experiment had two phases: the first involved placing the weevils onto the emitter tree for 5 days and then measuring the receiver trees’ responses. The second phase involved placing weevils onto the receiver trees for 38 hours and measuring bark damage, in addition to repeating the measurements from the first phase.”

Double check if all devices mentioned are given the name, company, country. E.g., line 415

R: Good idea. Checked!

Line 382-385 – missing the verb, also this sentence is rather into

R: We modified the sentence slightly.

Line 389 – of what? How much % soil moisture content is saturated? Specific info about this soil?

R: Volume. The probe returns a volumetric water content. We provided some references for readers that would be interested in reading more about this type of soil mixture. It is in line 496 now.

Line 422 – leaves = needles

R: Corrected.

Line 429 – remove “on average”

R: Removed.

Line 430 – refer to section 5.5 or say e.g. “described below “

R: Good idea. We added “as described in section 5.5” in line 540.

Line 448 – leaf = needle, throughout the whole text

R: Well spotted. Now we refer to needles throughout the text.

Line 452 – it is not clear how you come to this formula. Can you make a more abstract formula, by not using the constants 4.2235 and 15.6835? Details can be mentioned in the supplements.

R: Explaining this formula would take a considerable amount of space. The article by Flower-Ellis and Olsson 1993 goes into the detail of this conversion. Essentially, it was the best fit regression between different morphological aspects of the needles (breadth, thickness, perimeter and area of serial transverse sections) measured by projection microscopy and total needle area. This was performed on pines from Sweden, so the formula should fit well with the trees from Scotland that we used in our experiment. We

adjusted the formula slightly (defined the constants) and encouraged the readers to see the original article.

Line 473 – GLVs are not used as a chemical term as SQTs (C15) or MTs (C10). Maybe add that GLVs are C6 compounds, as the reader who is unfamiliar to this topic might not know what you mean. Or give a list in the supplements what you define as GLVs.

R: We added a short description of GLVs: oxygenated hydrocarbons containing 6 C atoms in line 589.

Line 482 – did you measure the Cin [VOCs] also in the field? I can only find you measured it in the lab “in situ”. Your hydrocarbon trap is a charcoal filter I suppose? They are often quite good, but can exhaust until a certain point. Did you use the carbon filter as well in the lab for your blanks?

R: OK, we understand how the “in situ” statement could be confusing. The blanks were collected at the FADOE site every day- we modified the text to reflect this. Yes, the filter was charcoal from the Supelco company (added the info). No, we didn’t measure the Cin, because the filters were fresh, so we could safely assume that there were working well and that the Cin was minimal or zero.

Line 522 – “was not given” instead of “violated”

R: We replaced “violated” with “not met” in line 640.

Line 521 – not necessary to report all significance levels. Only $p < 0.05$. Is it necessary to mention $p < 0.1$?

R: Alright, so the reason why we decided to include the $p < 0.1$ in this study is because this study is based on fieldwork. The conditions outside can differ quite a lot, compared to a controlled study in the laboratory. Therefore, to capture the possible correlations and especially to compare to the lab-based studies, we decided to keep the 0.1 level, but we always follow up with appropriate language (for example, “potentially significant”, “marginally significant”, “possible correlation”, etc.). We show the results of the LMM in Table 1 and while we do point out the $p < 0.1$ significance, we don’t put those results in bold letters.

Line 525 – not necessary to mention which axis is Y and which is X. better use dependent and independent variables.

R: Done.

Statistics well executed.

R: Thank you!

Results

Line 118 – date 1st

R: Done.

Line 118 – 122 usually O₃ thresholds are given per a certain timeframe. Per 8h mean for example. I would add this to each O₃ level you mention

R: In the manuscript, the reported pollutant concentrations from the FADOE rings represent overall averages calculated from sequential measurements taken every second during 60-second sampling periods per ring, which were conducted throughout the system's daily operational hours (approximately 10 hours per day, aligned with daytime periods to simulate realistic exposure regimes). These measurements were averaged across the entire study duration for each treatment. We have revised the text to make it clear that these are 'overall means over the 10-hour daily operational periods, averaged across the study duration.' Where we report O₃ concentrations measured from local monitoring stations we have specified that this is an 8h mean. Please note the 8h standard is used to account for prolonged exposure effects for humans. Our operational periods already approximate typical daytime exposure windows where O₃ peaks are most relevant ecologically.

Figure 1 b – legend: better order it as (top) O₃, NO_x, NO₂, NO (bottom), not quite sure what happened with the grey writing there. something is underneath.

R: Ordered the legend according to your suggestion. We increased the font size to make the writing above the grey lines more easily visible. They represent the 2024/2881 directive on air pollution for O₃ and NO_x.

Line 160 – I figure, from here you say, exposure to HIPVs is what happens to the receiver tree, during phase 1 (emitter tree with beetle). It's a break in the reading process. Please lead the reader towards this understanding. I would find it better to state those two phases clearer in the text and the figures. Or at least: it becomes not clear from the M&M that you fumigated trees with HIPVs(?). In the M&M the first time you mention HIPV treatment is in the statistics. Pretty sure, it's only a problem of wording.

R: We have decided to rename the HIPV treatment to exposure to damaged (vs control) emitters. That's what it is and this way it should also be clearer for the reader what the treatment is. Thank you for this comment.

Line 172 – O₃ + D treatment – until here you were always writing the O₃ and diesel. Keep consistency.

R: Good point. Corrected.

Figure 2 a – DA (y axis) probably not necessary

R: Removed. Also, we changed the terminology, referring to damaged and control emitters, instead of HIPV and control treatments, so this is reflected in the labels

Figure 2 – confusing what you want to say with H*, A*, P*, AxP*. Change, maybe put in a table. Does not fit in the figures.

R: Thanks for the comment. We have moved these statistical analysis results to a separate table (Table 1).

Figure 3 – please change the unfilled phase 1 bars. Increase the contrast, it is hard to see.

R: We filled the bars with grey colour. Also, we increased the width of the coloured lines, so that they are more easily visible.

Check your whole text on American and English writing (normalised, normalized)

R: Good point. We chose the British spelling.

Figure 3 c – use emission rates not factors. Not necessary to write “needle area” on the y axis.

R: We changed this figure to show the emission rates in panels a and b and damage-based emission increase in panels c and d. Our reasoning was that the monoterpenes make the most of the emissions, so the second panel is showing all groups of VOCs, other than MTs. We took out the “needle area” from the description.

Figure 4 – remove DA abbreviation. Check legend of 4c.

R: Removed. Checked.

Discussion

Line 263 – remove “leaf”

R: Removed.

Line 264 – processes

R: Corrected!

Line 290 – interestingly in the discussion, you do not mention D or diesel, here you use NO_x. Better, to have it everywhere the same. I suggest to use NO_x.

R: We understand your preference to use NO_x. However, even though the diesel exhaust treatment was introduced because of the NO_x, it contains many other inorganic and organic compounds such as PAHs, sulphates, metals and trace compounds (<https://doi.org/10.1080/08958370701498075>), so for the sake of accuracy we refer to the diesel exhaust treatment in general and NO_x where appropriate.

Line 296 – damage to leaf tissue/cell membranes. I would rather think, the damage comes from internal structures, rather than surface structures. NO_x and O₃ enter through the stomata into stomatal cavity, reaching the mesophyll. There it has severe effects on the hydration shell of the cells + membranes etc. I guess you focus too much on outer structures, since you work with the visible damages of the bark by beetles.

R: Good point. We added a discussion about how the O₃ and NO affect the internal leaf structures at the beginning of the section in line 367. In addition, we added a longer discussion about the photosynthetic traits starting at line 319, as suggested by the other reviewer.

Conclusion

You could add, that there is a high need to figure out how plants detect HIPVs.
Reads a too much like an abstract.

R: Thank you for the suggestion. We have added the part that you suggested in line 434 and modified the conclusions, so please feel free to read the full version now.

References

Check for O₃, NO_x etc to put 3 and x in subscript and species names in italic, DOIs?

R: We fixed the formatting and added the DOIs!

Dear Reviewers,

Thank you for reading the new version of our manuscript.

Please find the detailed replies (in red) to your comments below (in blue).

Kind regards,

Tihomir Simin and the coauthors

Kuopio, Finland

December 2025

Reviewer #1:

Dear Authors,

Thank you for your careful and thorough revisions. You have addressed the main comments in a satisfactory way, and the manuscript is now clearer and better structured. In particular, the revised introduction, improved figures, and expanded discussion of physiological responses and possible belowground signaling pathways have strengthened the overall interpretation. The more cautious framing of conclusions is also appropriate. Overall, I am satisfied with the changes and believe the manuscript is now suitable for publication, pending the editor's final decision.

Reply (R): Thank you for positive assessment of the revised manuscript. We are grateful for all the useful comments provided that contributed to the new and improved version.

Reviewer #2:

Minor revisions

I like this introduction much better. Small changes and some things still do not come to me easily.

Line 108 – 113 in the introduction is actually part of the results already and might better fit in the abstract

R: The reason for this section in the introduction is because it is specifically requested for the Introduction section in Style and Formatting guidelines for the Communications journals (<https://www.nature.com/documents/commsj-phys-style-formatting-guide-accept.pdf>):

“The final paragraph should be a brief summary of the major results and conclusions.” To comply with journal guidelines, we have decided to keep this paragraph.

Line 102 thank you for explaining the Diesel exhaust in your in-line answers from my previous review. Maybe here is the best moment to explain that Diesel exhaust mainly contains NO_x but will be handled throughout the text as Diesel exhaust/Diesel.

R: We say that diesel exhaust is rich in NO_x with this phrase in the brackets:

“diesel exhaust (primarily rich in NO_x but due to presence of other compounds, referred to as diesel exhaust in this article)”

We will stick with diesel exhaust throughout the text.

Line 477,501, etc: you should decide now on NO_x or Diesel Exhaust ☺ pick one and stay consistent. I think you should take Diesel.

R: Thank you for pointing this out. We are now focused on expressing diesel exhaust wherever relevant.

Line 52 – 53 would be nice to say here as well that VOCs are changing from species to species and can be cited from <https://doi.org/10.3389/ffgc.2019.00050>

R: We added a sentence about the variability of VOC emissions at the end of this paragraph.

“ The blend of emitted VOCs is often highly dependent on plant species and intraspecific variation between individual plants^{24,25}. “

Line 486 better practice would be to not speak of a specific date but say in the year 2023 the experiment was conducted and when using specific days you say this is the day of the year (DOY) so 4 May 2023 is 124 DOY.

R: We have added the DOY indicator of the date in the brackets, but we also left the date in the original format, for clarity.

Line 509 – 511 I think here you explain that the second bars of all plots showing BVOCs is the one which is of the second phase, right? In the description of figure 4 you do not say what the difference is between the lighter and darker colorful bars.

R: Thank you for pointing it out. We have now added this information to the description of Figure 4.

Line 523 – 524 the information about the wind direction is not mentioned in the rest of the text. I would not mention it at all.

R: Fair enough. For the detailed description of the site, readers are directed to the paper by Mofikoya et al. 2024, so they can find all the information about the sensors used at the FADOE platform. The information about wind speed measurement is now removed.

Line 545,547 check the unit here ml min⁻¹ is better (check the whole text), also throughout your text double check for wrong spellings, missed full stop and missed spaces.

R: Well spotted. Corrected and double checked.

Line 326 Place “(LMM)” after Linear mixed models. Later you use just the abbreviation.

R: Done.

Line 153, 175, 171, 209 etc: Here in the results, you often use “(p=x.xxx, F=xx.x, LMM/Pearson, Figure XX)”. This information is quite much. “LMM” is not necessary to tell, as you mention it in the methods. Also, the F-value is not necessary. (So, no F-value and statistical test)

R: OK, so we have modified the text in the following manner. When the information in the brackets refers to the Table 1 with LMM results, we deleted the F value and LMM abbreviation and referred to Table 1 instead. We have modified the table according to your suggestion. We have left the other markings of the tests, because there are different ones that we present here, like Pearson correlation, Dunnett's test and MANOVA, so we believe it's important to be transparent about that.

Line 157, Table 1: I rather would like to read mean $\pm$ SE or SD values and give asterisk for significance levels. F- values are rather information for supplements. Also, if it is not significant better say n.s.

I understand, BVOC emissions are often not significantly changing. Every change is a result. But I would say therefore you raised the reporting P-value already to 0.1, which should be enough.

R: We understand your concerns and preference for averages with standard errors. However, this information is presented in Figures 2 and 3 and we would like to avoid presenting the same information twice, in form of graphs and figures. So we decided to keep the Table 1, but we did edit it following your recommendation.

Line 169 here you speak of A and Gs. You say in the first sentences A is affected by diurnal patterns, but in the next sentences you say it was not. Also the window of 6h is quite large and contains high likely the midday depression (you could simplify)? So you Gs is following a diurnal pattern, am I right? You should write the same about Gs as you do about A (sentences line 171-176). (Not for this manuscript, but just to say: the more important parameter is Gs, as this actually influences VOC emission, together with T, PAR, daily pattern. A is more the result and a "trait-off"/"price the tree is paying" of taking in C and releasing C via VOCs.)

R: We have expanded the result section on Gs and now it reads as follows:

"The Gs of receivers, unlike AN did not correlate with leaf temperature (Pearson, $r=0.06$, $p=0.47$ $n=160$). The Gs of receivers was also not significantly affected by exposure to damaged emitters or direct herbivory (phase 2 of the experiment; Figure 2c, Table 1). The acclimation of GS to time of day-related growth light variations can be an important strategy for maintaining AN in field conditions."

Line 239 find a reference. Maybe <https://doi.org/10.1111/nph.12887>.

R: Added the reference.