

Discussion of “Divergent response of evergreen needle-leaf forests in Europe to the 2020 warm winter”

Gharun et al.

Reviewers' comments are in italic. The Author's responses are marked in blue.

Author Response to Referee 2

1. General comments

This is an interesting and ambitious attempt to disentangle the impact of an extremely warm winter on forest productivity (the netto balance between respiration and CO₂ uptake). Using high-resolution (temporal) data from multiple forest sites across Europe, linked to locally measured environmental conditions, the authors try to disentangle a) how local microclimatic conditions were different from baseline conditions the years before, and b) how these differences impact winter productivity.

While I applaud this effort, the paper might be falling short of answering the actual questions convincingly, perhaps largely due to the extreme complexity of the whole system. Effects are highly site-specific, and the analysis fall short – if I understand all correctly – of showing the direction of trends resulting from the differences in temperature between the warm year and baseline conditions. I'm not sure the answer to the above is more analysis – the paper already has plenty of figures trying to make sense of the complex story – but perhaps a refocus towards figures that synthesize the actual relationship between NEP changes and temperature differences, both within and between sites is needed to bring the story. Also, the figures that are there might need some clarifications to make them more intuitive (see comments at the end).

We thank you for your feedback. In the revised version we will revise our questions (to make the logic of the paper more clear) and restrict the analysis to answering those questions. In addition we will add figures that synthesize the actual relationship between NEP (and GPP and Reco) changes and temperature differences (see details below).

The questions that we ask are:

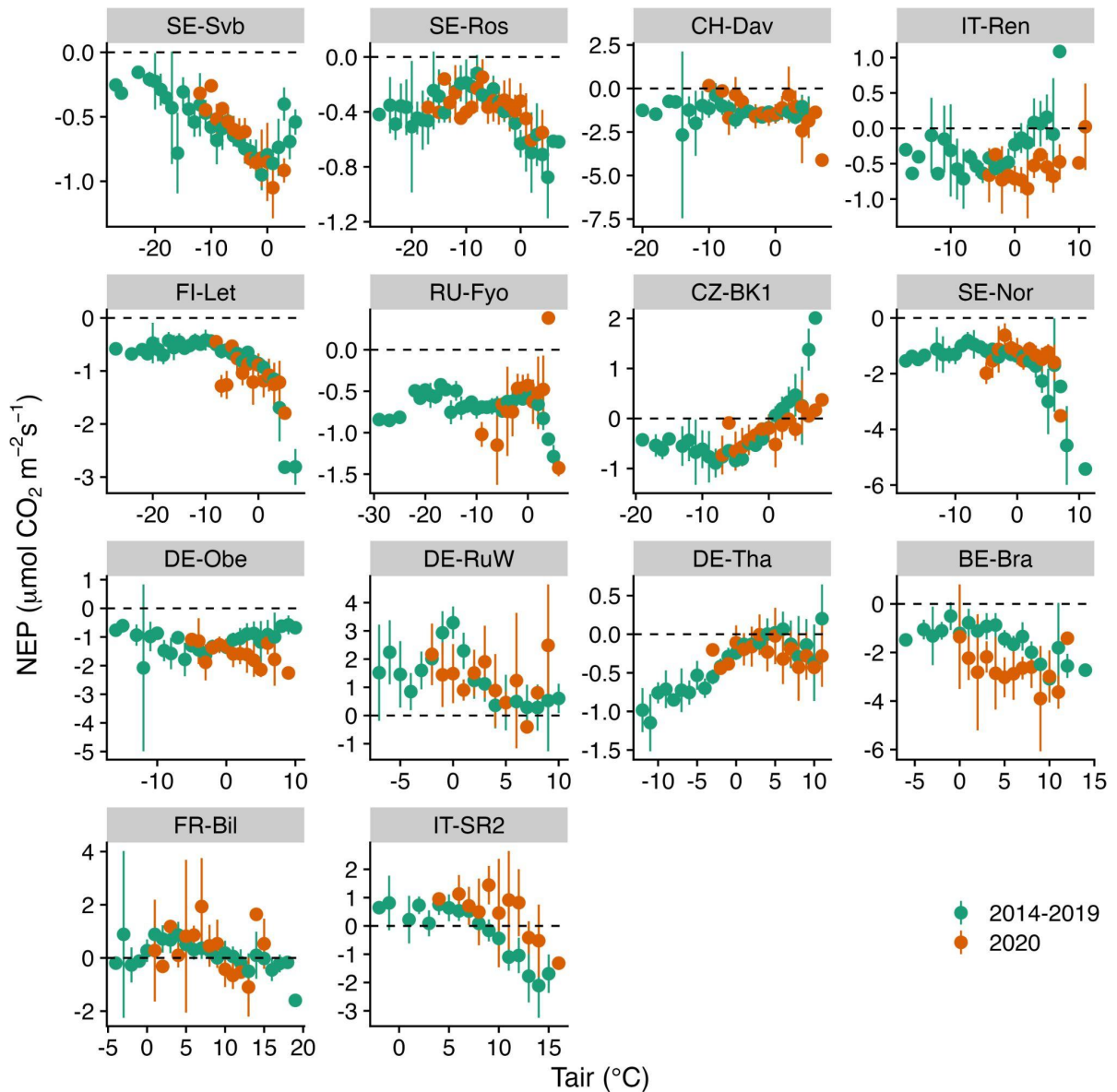
- 1) How much warmer was winter 2020 at each site in terms of air temperature?
- 2) How did the warming of the air in winter 2020 affect snow depth and soil temperature?
- 3) How did net carbon uptake change at each site in winter 2020 compared to the reference period?
- 4) How different was the temperature sensitivity of GPP, Reco, and NEP across different sites and how did this temperature sensitivity of CO₂ fluxes change in winter 2020 compared to the reference winter conditions?

Question 1 and Question 2 are answered by Figures 2, 3, 4, 5 that describe the environmental conditions in 2020 compared to the reference period.

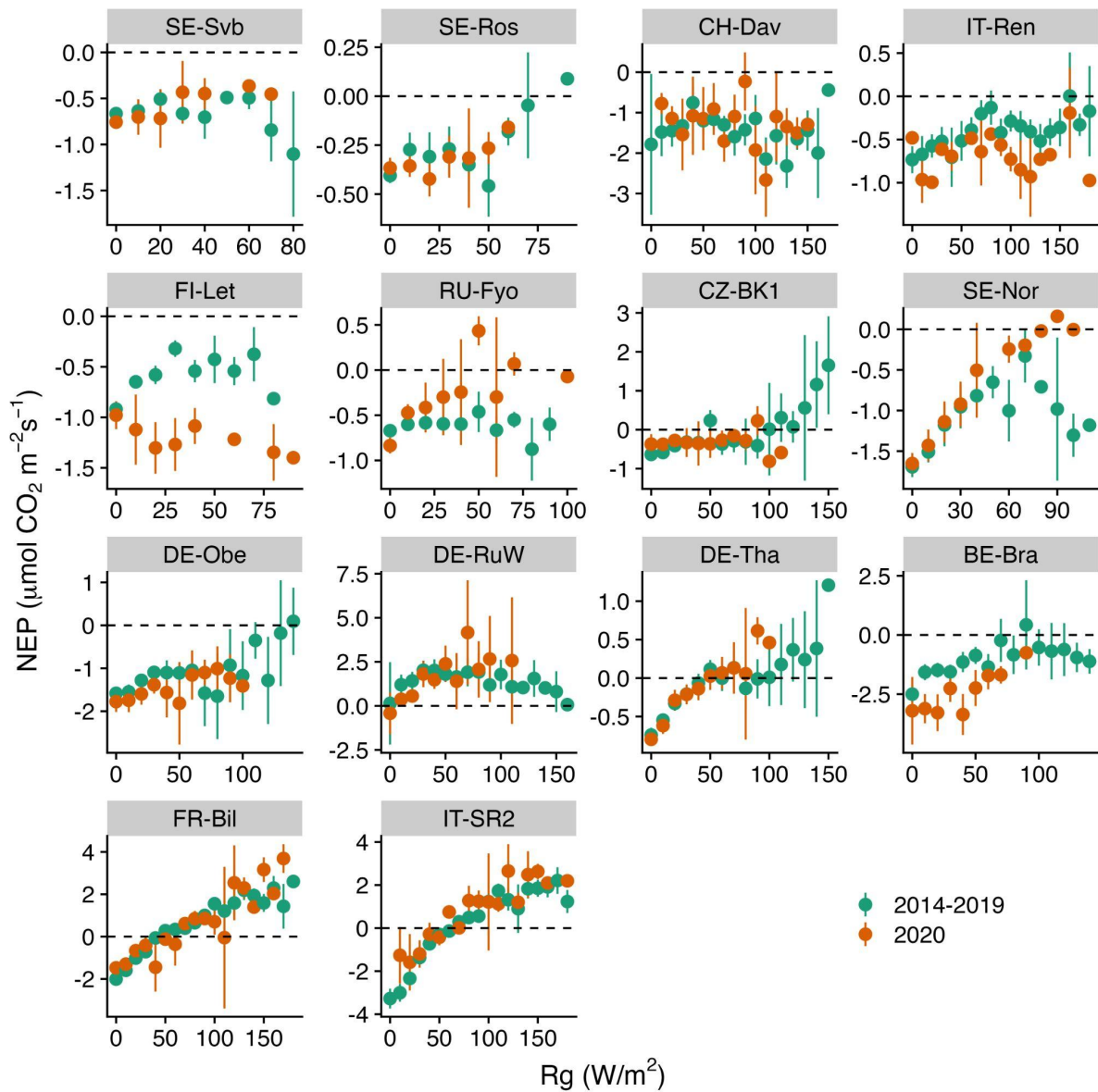
Question 3 is answered by Table 2 and Figure 6 that show changes in mean net carbon uptake (NEP) in winter 2020 compared to the reference winter (2014-2019), in each of the forest sites.

Question 4 is answered by the following figures which we will add to the main body of the manuscript:

NEP (positive values denote a sink) response to air temperature in winter:

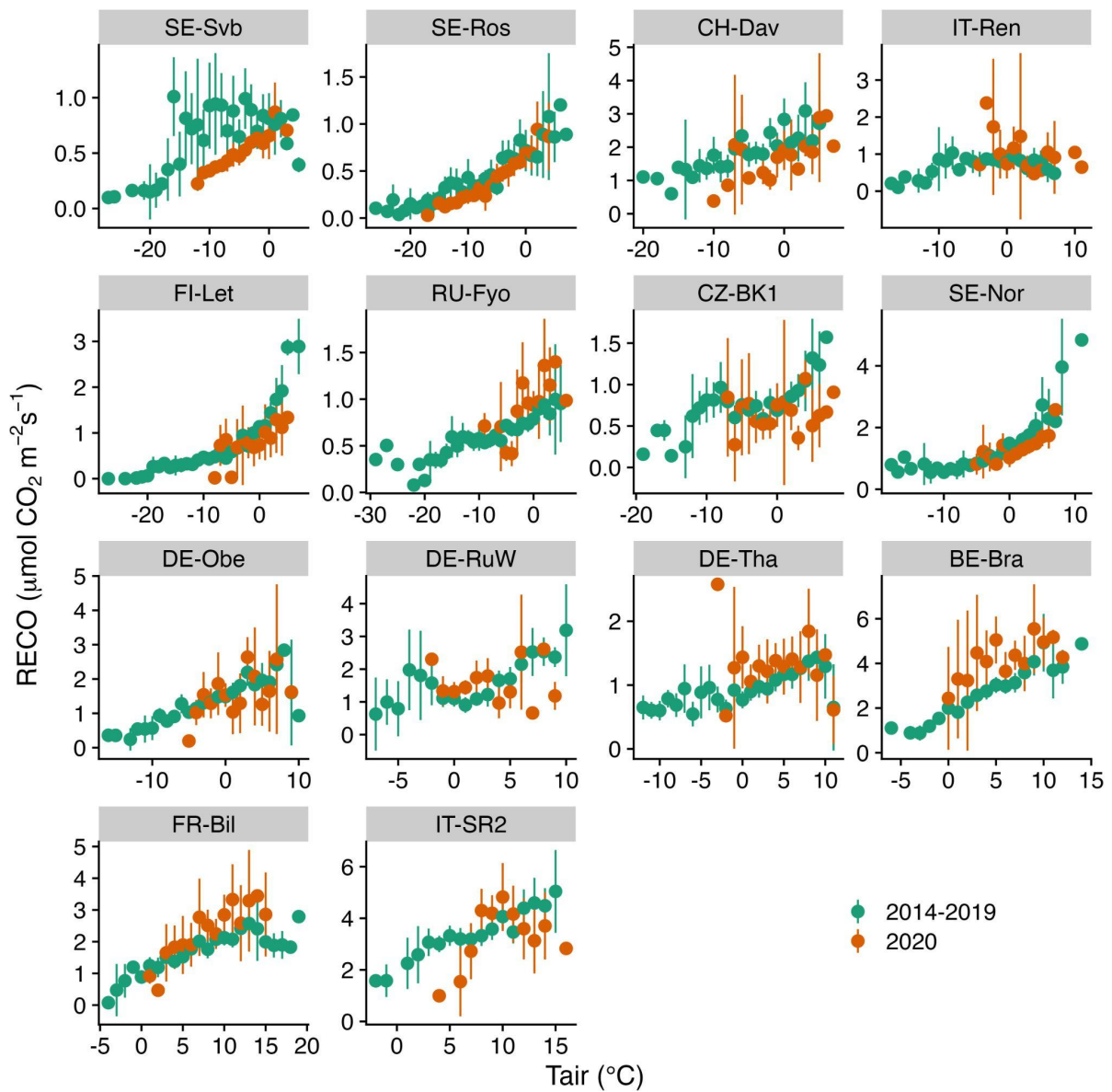


NEP response to light in winter:

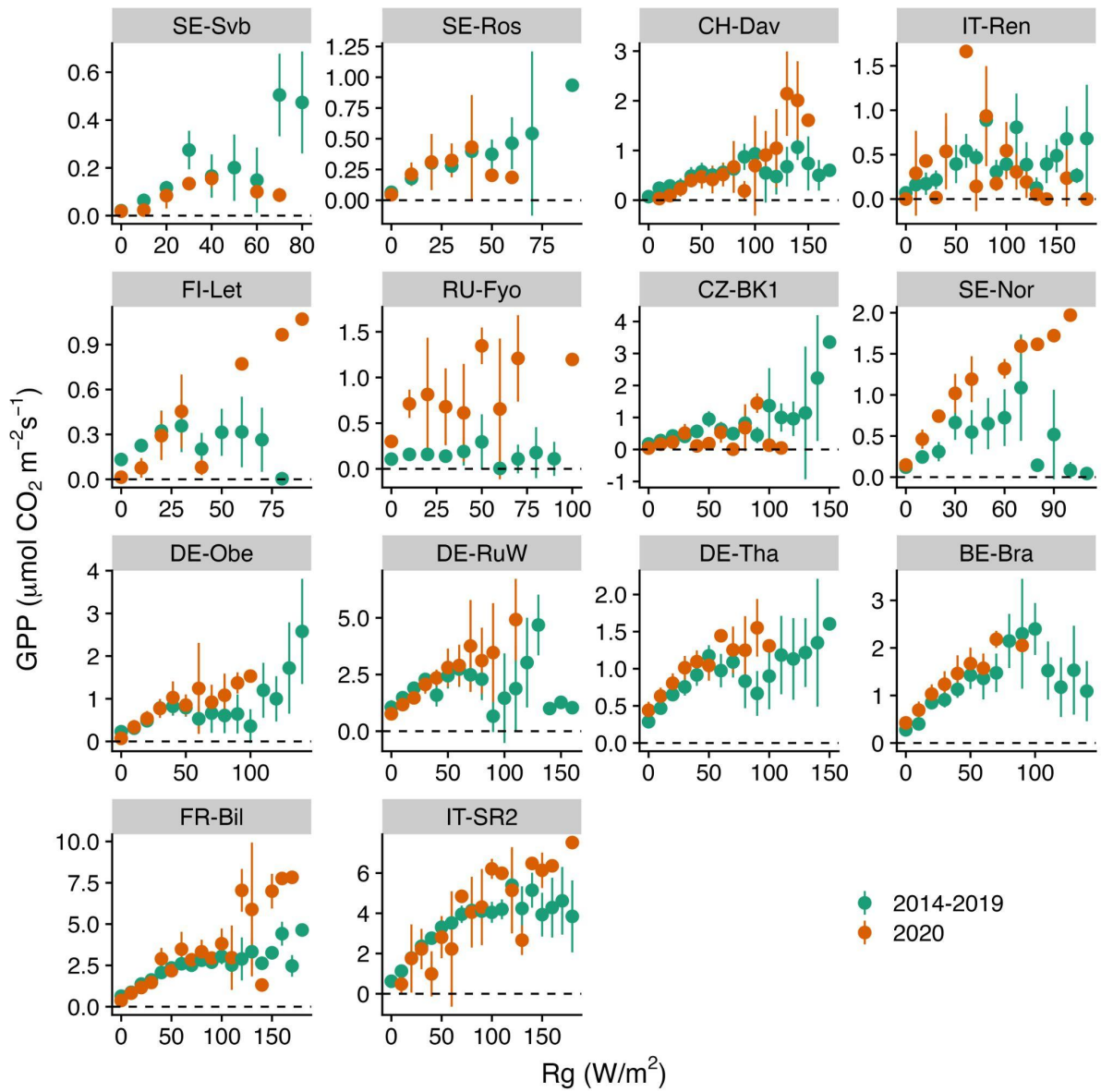


And the following figure that will be added to the Supplementary Material:

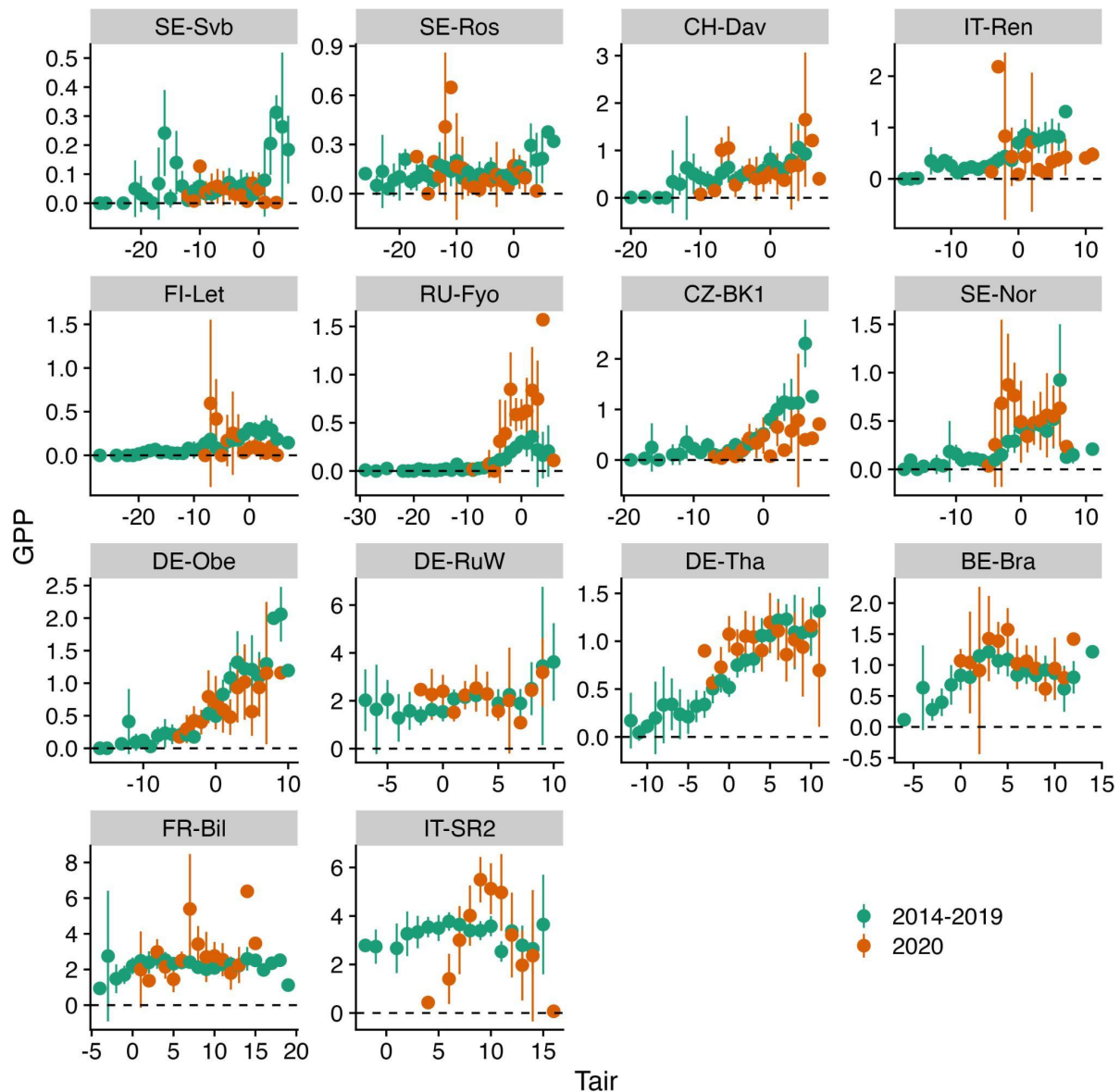
Reco response to air temperature in winter:



GPP response to light in winter:



GPP response to air temperature in winter:



In addition we will provide clarification of all figures and make them more intuitive as the reviewer suggested. Please see more specific responses below.

I have a bunch of more detailed comments below, which I hope identify where for me as a reader the uncertainties arise.

L95: why does the risk for photo-oxidative frost damage increase? Is that due to the lost winter hardiness mentioned earlier? Might be good to make the reason explicit.

The risks of photo-oxidative frost damage increases with winter warming, because warmer winter temperatures can lead to an accumulation of photosynthetically active compounds in plants, and when sudden frost events occur, during periods of high radiation, the combination

of low temperatures and intense sunlight can induce photo-oxidative stress in plant tissues. This occurs because the photosynthetic machinery is still active, but the low temperatures impair the plant's ability to dissipate excess energy, leading to the production (and imbalance) of reactive oxygen species (ROS) that can damage cells and tissues.

Having said this, photochemical damage can also happen in the case of high radiation, low water content in the leaf tissue and low temperature, when photosynthesis and protein turnover become inhibited by low temperatures and when non photochemical, heat dissipation mechanisms are insufficient to deal with excess excitation (hence the negative effect of freezing temperatures after de-hardening) (Anderson & Osmond 1987; Öquist & Huner 2003).

We will add this clarification to the text.

L99: 'the interaction of light quality and photoperiod': unclear to me what this implies

Light quality means the type of light in terms of intensity of the red, far red, blue wavelengths, and photoperiod means day length. We meant here that the triggering of cold acclimation in evergreen conifers is not only controlled by temperature but also controlled by daylength, and light properties that change with seasons. The phytochrome system of plants that triggers many different processes is sensitive to the type of light (e.g., to the ratio of red to far-red wavelength).

We will add a clarification to the text.

L103: 'thus': this word implies that the previous sentences explain why cold periods play an important role in forming the photosynthetic capacity, but to me there is a step missing: why are these pathways resulting in improved photosynthetic capacity. The previous paragraph hints to this, perhaps, by mentioning that a lack of these would result in damage (and thus reduced photosynthesis as a result). But all of this feels a bit implicit and disconnected. Just adding a sentence might already help.

We will revise this section to make it more clear. The new text will read:

“Environmental cues such as temperature, photoperiod, and light quality control a network of signalling pathways that coordinate cold acclimation and cold hardiness in trees that ensure survival during long periods of low temperature and freezing (Öquist and Hüner 2003; Ensminger et al. 2006). These signalling pathways include the gating of cold responses by the circadian clock, the interaction of light quality and photoperiod, and the involvement of phytohormones in low temperature acclimation (Chang et al. 2021). Soluble carbohydrates, including sucrose (most abundant) accumulate in response to low temperatures, starting from late autumn throughout winter (Strimbeck & Schaberg 2009; Chang et al. 2015). Persistent uninterrupted cold periods thus play an important role in forming the photosynthetic capacity of the trees as warmer winter temperatures increases the chance of photo-oxidative frost damage during earlier stages of the growing season (Gu et al. 2008; Chamberlain et al. 2019) which would compromise the capacity of the forest for CO₂ uptake throughout the year (Desai et al. 2016).”

L104-106: now here you continue with examples. Again, I feel the need for a better structuring of this introduction, disconnecting the theoretical cause-and-effect relationship from the examples.

Our response to the previous comment will address this comment too.

L112: might there be a need to define respiration, or can we assume this concept to be sufficiently well-known?

For the readership of this paper we expect the definition of respiration to be clear. However we will add “emission” to make this clear. The new text will read:

“Forest net ecosystem productivity (NEP) depends on the balance between gross ecosystem CO₂ uptake (gross primary productivity, GPP) and CO₂ emission (ecosystem respiration, Reco).”

L131-132: this sentence is a bit too dense in information for me to fully understand

We will revise this sentence to make it easier to understand. The new text will read:

The temperature sensitivity of ecosystem respiration incorporates both the direct response of ecosystem respiration to temperature, and indirect influences from other climatic and physiological variables such as moisture, leaf area index, photosynthate input, litter quality, microbial community (Reichstein et al. 2002; Fierer et al. 2005; Lindroth et al. 2008; Migliavacca et al. 2011; Karhu et al. 2014; Collalti et al. 2020). Previous studies have shown that the temperature sensitivity of ecosystem respiration increases with a decrease in site mean temperature (e.g., Chen et al. 2020).

L133-135: I feel like we're missing some information to make the distinction between direct and indirect effects on respiration clear: what happens in the direct pathway, and can you give some examples on how the other factors are affecting respiration indirectly?

The direct pathway is that with increase in temperature the metabolic activity of plants and microorganisms increases, leading to higher respiration rates. The indirect pathway is that soil moisture affects the microbial activity and decomposition rates, which in turn influence respiration rates. In moist conditions, microbial activity is larger, leading to increased decomposition and respiration rates. Conversely, in dry conditions, microbial activity slows down, reducing the respiration rates. LAI affects the amount of plant material available for decomposition. Higher LAI means more plant litter, which increases substrate availability for decomposers and leads to higher respiration rates. The amount of organic matter produced through photosynthesis affects the availability of substrates for microbial decomposition. Higher photosynthate input results in increased carbon availability, stimulating microbial activity and respiration rates. The chemical composition of plant litter influences decomposition rates and microbial activity. Litter with high nutrient content decomposes more readily, leading to higher respiration rates. The composition and diversity of the microbial community in the soil influence decomposition rates and respiration. Different microbial species have varying metabolic capabilities, affecting the efficiency of decomposition and subsequent respiration.

L140: to me the ‘on record’ doesn’t match too well with the cut-off of 1981, as intuitively I think we have older records than that (although not in that source). Perhaps rephrase to ‘in the last four decades’?

We will replace this term with “in the last four decades”.

L150: soil temperature comes a bit out of the blue here – there has been very little discussion on how it can affect respiration in addition to air temperature. Similar for radiation, for which it’s even the first time the word is mentioned.

We will add a paragraph to the introduction on how the different environmental variables (air temperature, soil temperature and radiation) will affect respiration and GPP fluxes.

L192: ‘the forest’?

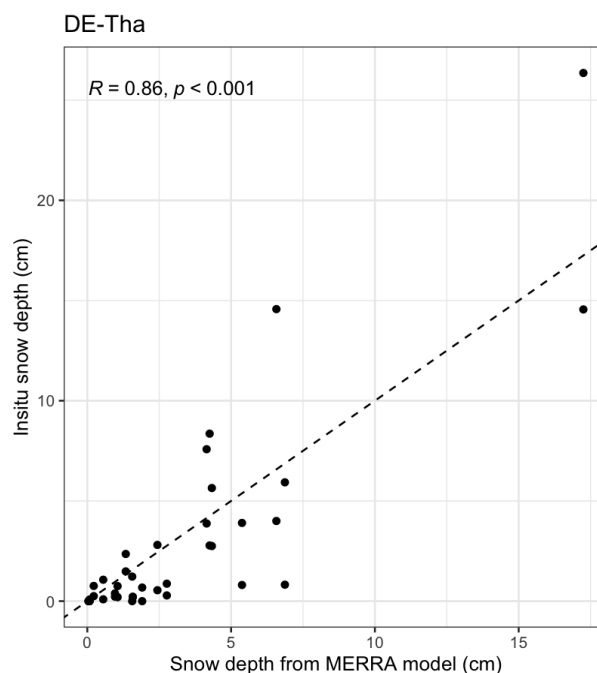
We will rewrite the sentence as suggested.

L194: what do you mean with climate variables that overlapped? Data availability within your dataset? Or overlapping values?

We mean data availability within our dataset. We will revise this sentence to make it clear.

L197: for those sites that measured snow depth, could you make a test of the accuracy of the remotely-sensed snow depth measurements, as this is notoriously hard to get right?

For most sites we do not have long-term snow depth measurements. We compared the measured snow depth against the remotely-sensed snow depth for one site (DE-Tha) where these measurements were available during the study period. This comparison is shown below. Since we do not have this comparison across all sites we do not include this new figure in the paper and instead address this points within the text (in the Methods section).



L216: 'were'

We will rewrite the sentence as suggested.

L235: *there is a 'the' that doesn't seem to fit there*

We will rewrite the sentence as suggested.

L235: *what exactly are these anomalies here?*

As already explained in the Methods, these anomalies are changes in a variable during 2020 (v_{2020}) compared to the reference period ($v_{\text{reference}}$) based on its relative anomaly (Δv_r) and absolute anomaly (Δv_a) as per equations 3 and 4.

L247: *'lowest positive anomaly of 0.87°C': what about the even smaller anomalies in Fig. 3, in FR-Bil and DE-RuW?*

Those changes were not significant. We only compare the values when the change was significant at $p < 0.05$. We will make this clear in the text by adding “significantly largest anomaly” and “significantly smallest anomaly”.

L254: *first time soil temperature depth is mentioned – feels like more something for the methods*

We will make sure this is mentioned in the Methods section.

L263: *315 days? Table says 365*

Thank you for pointing out this typo. The correct number is 315. We will correct this in Table 2.

L272: *'IT-SR2... shifted towards being a smaller source in winter' Is that true? I thought that we saw in Supplementary Table 2 that the value actually showed it turned into a CO2 sink?*

We will rewrite this sentence to avoid future confusion.

L274-275: *why are the values described here different from those in Fig. 6? Are they describing something different? If so, why refer to Fig. 6?*

Thank you for this comment. The correct values are 331% (and not 346%) and -98% (and not -97%) as shown in Figure 6. We will correct the typo in the text.

L276: *'increased significantly' -> remind the reader that increasing here means a decrease in value? As the previous comments also reflect, this part was pretty hard to follow.*

We will clarify in the text by adding “indicated by a negative anomaly in nighttime NEP” to make sure it is not confusing to the readers.

L285: *'winter respiration fluxes': remind the reader which panel in the figure that is*

This is shown in Figure 7 panel c that displays Reco as the panel title shows. We will add this info in the text.

L324: where do we see this result?

In Figure 6 as the next sentence says. We will add this info here too.

L325: 'high latitude-high elevation': this is either/or, right, not both together? Unclear from the way it's written

We mean either/or not both together. We will add this info.

L329: 'dominated': is the difference that strong? Can you quantify that?

When sites are ranked by mean temperature, in the 5 colder sites (SE-Nor, RU-Fyo, FI-Let, IT-Ren, SE-Svb) out of 8 affected sites (IT-SR2, BE-Bra, DE-RuW, SE-Nor, RU-Fyo, FI-Let, IT-Ren, SE-Svb) temperature dominated.

L333: what are the implications of those relationships in Table 3? They feel a bit disconnected from the story now (although, as I ask down below regarding Fig. 7 and 8, they might be critical)

We will remove this Table as we have revised our research questions and this information no longer helps with our story.

L336-339: the role of LAI feels a bit like an afterthought now, and the way it's currently analyzed (basically qualitatively rather than quantitatively) makes it hard to build strong conclusions on it. You could at least model the relationship between Tair-Tsoil and LAI?

This was based on Table 3 which we will remove in the revised version (see previous comment please).

L435: weaker snow buffering effect often results in lower winter temperatures, as snow tends to buffer against freezing temperatures. This makes sense, as snow is usually present when air temperature is below zero, and then soil temperature stays at zero. You see this in Lembrechts et al – Global maps of soil temperature – that soil temperatures in cold regions are usually higher than air temperatures. Here, you have a reduced snow cover, so the only way in which soil temperature can be higher, is if air temperature is also unusually high (i.e., positive).

We will remove this statement as the previous sentence already sufficiently points to the link between snow cover and changes in the soil temperature.

L436-438: can you specify which sites this are? I'm getting a bit lost in trying to link the different figures on snow and temperature.

At these sites both soil temperature increased and snow depth declined significantly: SE-Svb, IT-Ren, FI-Let, RU-Fyo, SE-Nor, DE-Obe, DE-RuW, DE-Tha. We will mark these sites on Figure 4.

L449: Supplementary Figure 5 shows very little trend to me (the blue and red dots are basically randomly distributed?)

We will remove this Figure as we have revised our research questions and this information no longer helps with our story.

L445 and following: in these paragraphs lies one of my main questions. Here indeed you are connecting everything together (soil temperature, air temperature, NEP, ...). You have an analysis (the machine learning model) that does this as well, but I am missing figures and/or analyses of the relationships between these things. Now, it requires juggling of all figures and tables to connect everything together, but the machine learning model is only used to show the SIZE of the effect, not the actual relationships themselves.

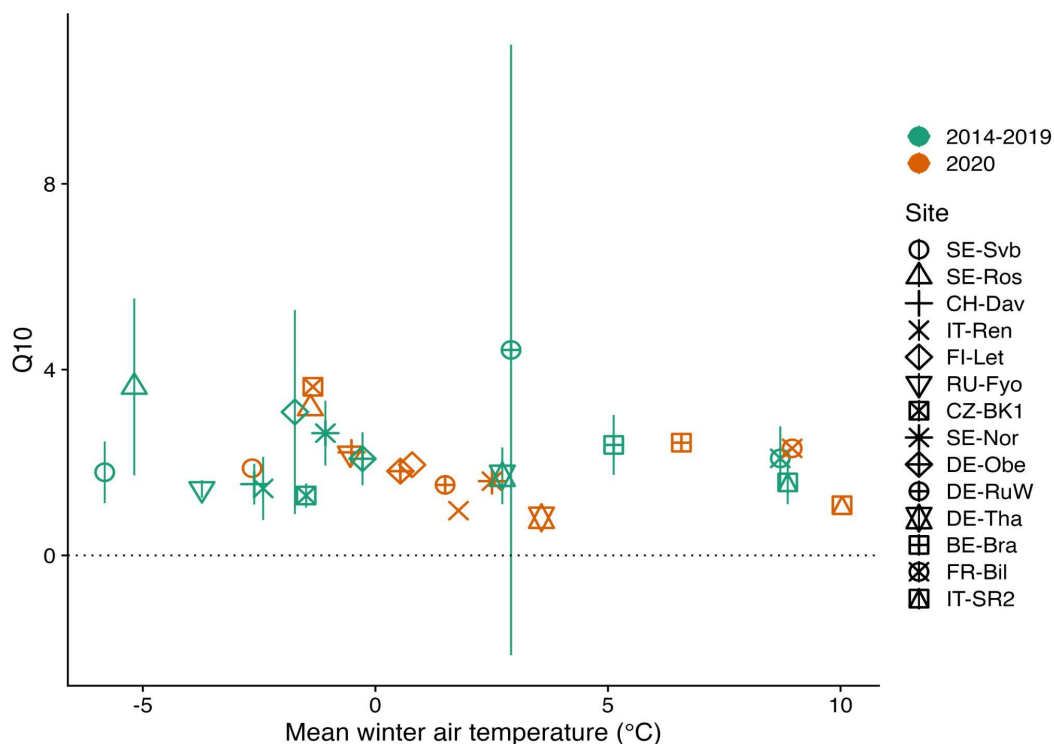
For example, if you say: 'warmer sites however (low altitude or low latitude sites) winter warming also increased the productivity and CO₂ uptake' then this should be supported with a figure showing delta productivity/CO₂ uptake as a function of delta T in winter and background T, and their interactions (for example, a separate line for the relationship for warmer versus colder sites).

Similarly, if you say (L453-454) that when soil temperature reaches above freezing level, CO₂ uptake increases, this should be shown by a figure showing daytime NEP as a function of soil temperature.

These are just two examples, but this comment is valid throughout the chapter. The main conclusions (the relationships between local climatic conditions and NEP are not really shown in the results, if I'm not mistaken.

Thank you for the suggestion. Yes, it is true that we show the size of the effects and not the actual relationships. This is because our analysis is based on non-linear decision-tree based machine learning models where depicting the actual direction of the relationship is not possible (as it is in linear models with coefficients).

In order to clarify this part we added two new analysis: 1) analysis of the temperature sensitivity for respiration based on Q₁₀ since RECO is the dominant flux component in winter (new Figure below, error bars show the 95% confidence interval) 2) functional relationships between NEP, GPP and RECO with light, air temperature and soil temperature as written in response to the first comment (see Figures above please).



L461: how does Fig. 7 show that baseline climate conditions are a good proxy for this? Do you mean that if you order sites from warm to cold that there is a rough trend emerging in the amount of variance explained? If so, then I'm not super convinced that 1) this is a 'good proxy', and 2) that it says anything on 'how'.

In response to the previous comment we will add a new analysis which will address this point too. We will show the relationship between each of the local climatic conditions and NEP.

L472: perhaps add half a sentence on what a higher Q10 means in practice for these soils.

We will add how this means that in these soils a higher Q10 means that soil respiration increases faster in response to warming.

L474: where do these labile C inputs have to come from?

Labile C are organic compounds that are simple in structure and highly reactive which makes them easily decomposable during respiration. They come from plant material such as leaf and root litter, root exudates. Seasonal changes in labile C input is thus positively related to NPP (Pausch and Kuzyakov, 2018, Wu et al., 2011, Yin et al., 2013). During winter the warming can increase respiration but the lower NPP (and thus lower labile C input) could limit the increase of respiration (Sullivan et al., 2020).

We will add this information to the text to make it more clear for the readers.

L475: Supplementary Figure 3 is not mentioned in the results, so it's very hard to link this to the story. In this figure, the differences between 2020 and reference are also very hard to spot. If the story in L445 and following is indeed true, then it should show up somehow in figures correlating NEP to temperature (or better perhaps, delta NEP to delta temperature)

In the revised version of the manuscript we will quantify the temperature response of NEP in 2020 and compare that with the temperature response during the reference period, via a SHAP value analysis. We will remove Supplementary Figure 3 and add a new figure that shows NEP to air temperature response in 2020 compared to the reference period.

In addition we have added to the Abstract that: “Except the southernmost site, warming declined mean winter NEP across all sites where we observed a significant change to previous years”.

Fig. 2 and Supplementary Fig. 1: x- and y-axis labels are not entirely intuitive, yet not explained

We will add in the figure caption that “pr_anom” and “ta_anom” are precipitation and temperature anomalies.

Fig. 3: anomalies are in °C?

Yes. Temperature anomalies should be expressed in °C.

Fig. 3: unclear from this figure which sites are high latitude or high-altitude sites (L 246)

In this figure sites are listed in the decreasing order of mean annual temperature (as mentioned in the figure caption). We will revise the text and instead write:

“Positive air temperature anomalies in winter 2020 were larger in the colder sites (Figure 3)”.

Fig. 6: could you change the color scheme so it is white at zero?

We will change the color scheme so that zero is marked with white, positive anomaly in red and negative anomaly in blue. The updated Figure 3 and Figure 6 will look as following:

Figure 3:

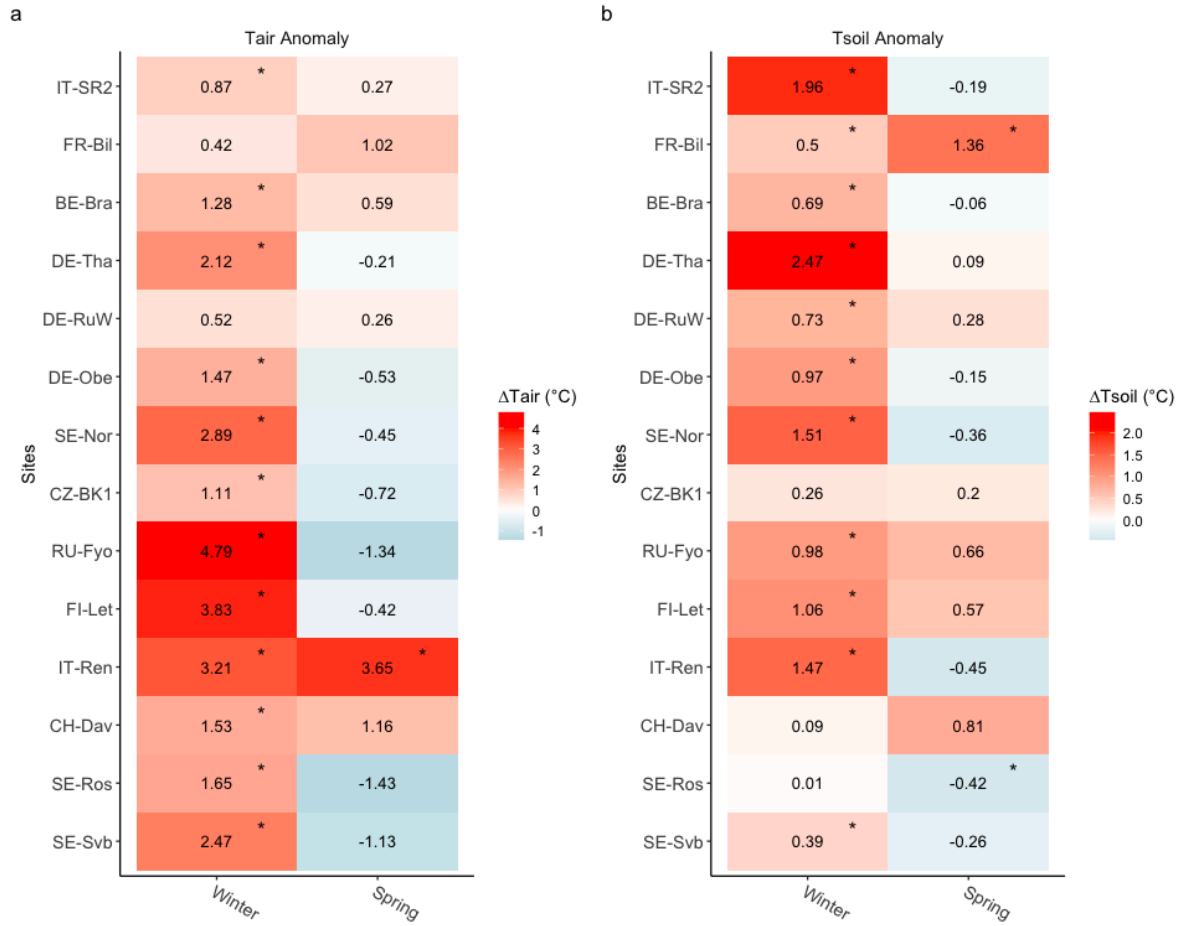


Figure 6:

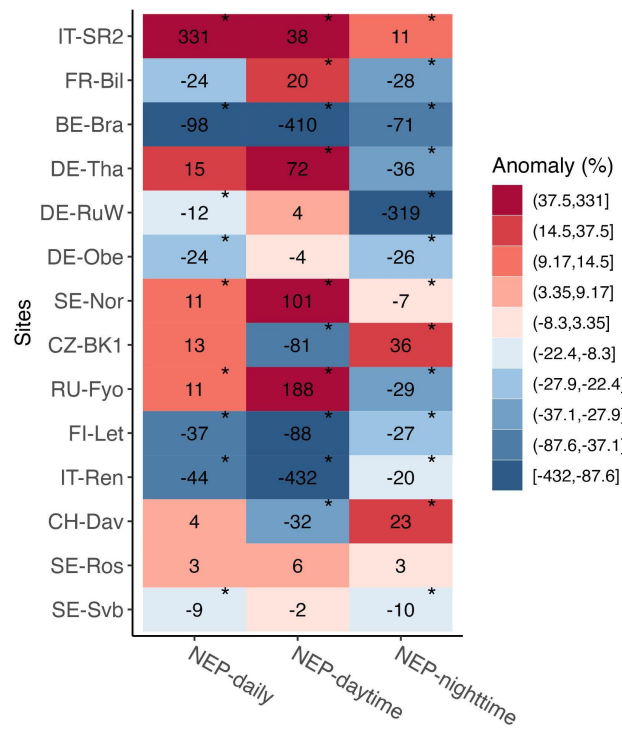


Fig. 7: ‘overall variable explained’, shouldn’t that be variance?

We will change this everywhere to “variance explained (R^2)

Fig. 7: ‘three climatic variables’: why is there a fourth one – not mentioned in the legend – for the bottom panel? Even more confusing: it doesn’t seem to be mentioned in the main text on Fig. 7 either?

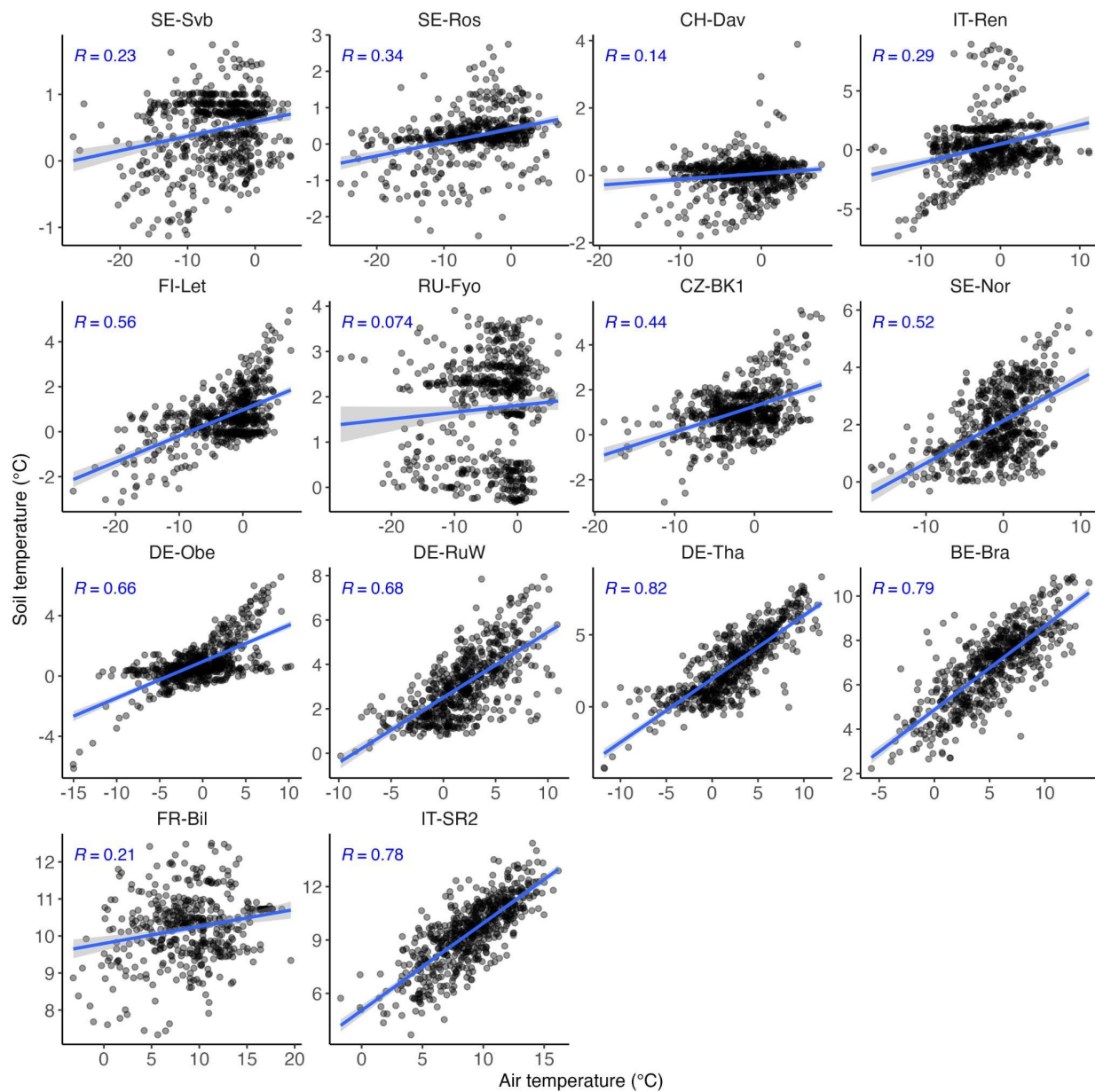
We will adjust the caption and mention it in the main text as well.

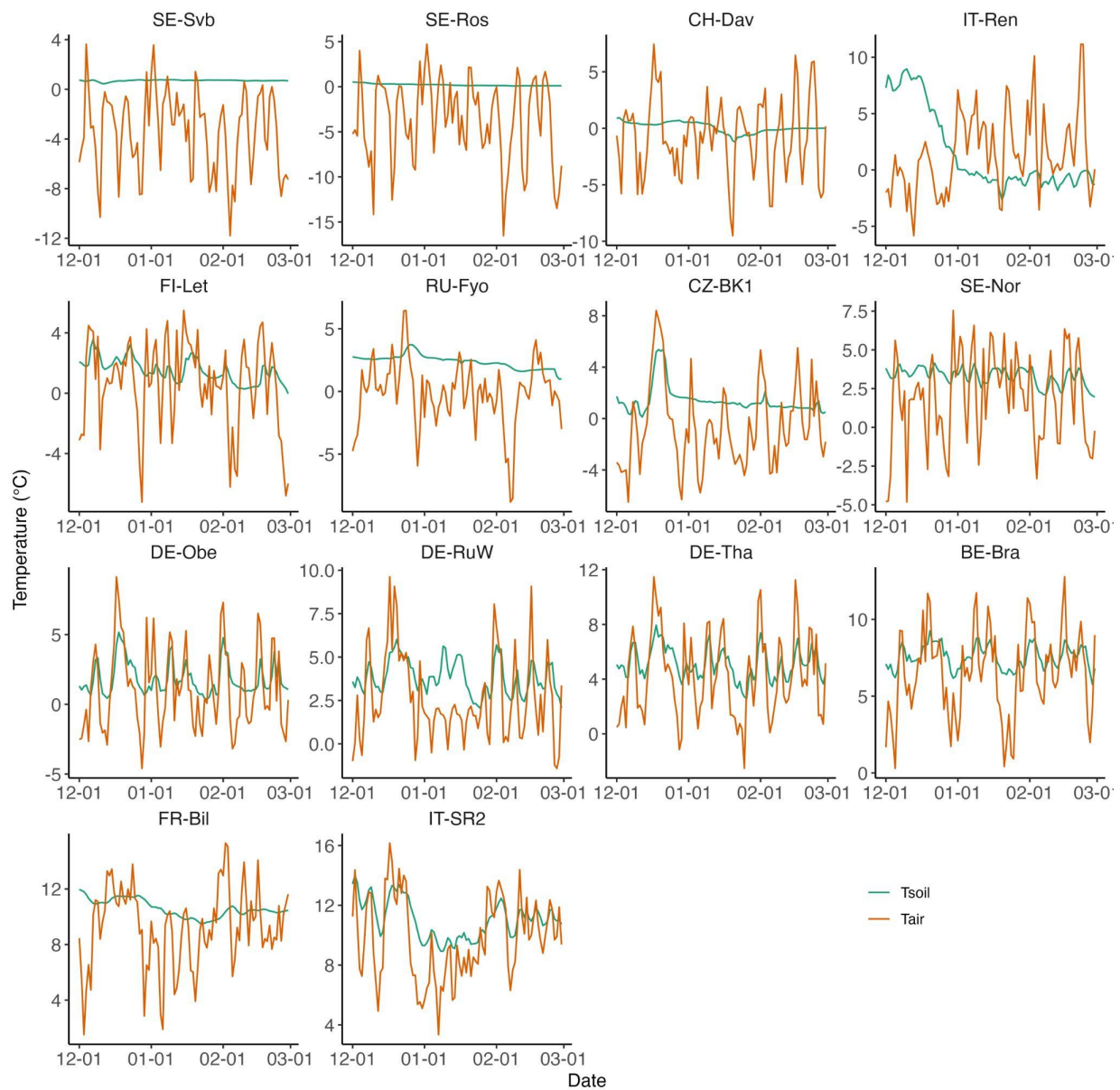
Fig. 7 and 8: isn’t there a correlation between Tsoil and Tair? If so, how can the model decide which of the two explains the variance (and have this sum up to 100%)? This is different from the way I’m used to variance partitioning,

Yes, there is a correlation (not significant for all sites) between Tsoil and Tair during winter as shown in the Figure below. The correlation is not perfect (varies from 0.07 to 0.82) with both Tsoil and Tair showing a different day-to-day variation, i.e., Tsoil showing a damped variation compared to Tair (also shown in Figure below). We used random forest regression for modelling NEP/GPP/Reco, which uses decision trees to form relationships between dependent (NEP/GPP/Reco) and the independent variables (here Tair, Tsoi and Rg).

Decision trees are constructed based on impurity measures known as Gini impurity. When selecting the best split at each node for constructing the decision tree, the algorithm chooses the feature that maximizes the information gain (or minimizes the error), which is a measure of how much the split reduces mse (mean square error) in the target variable. Therefore, even if two correlated variables are available for splitting, the algorithm chooses the one that results in the lowest mse, which then gives an indication of the importance of the variable (or variable importance). In this study, we used conditional variable importance (which is shown in Figures 7 & 8) as demonstrated by Strobl et al. (2008) which indicates the variable importance taking into account its correlation of the variable with another variable (thus ‘conditional’). This variable importance approach of random forest does not provide information about the proportion of variance explained (i.e., variance partitioning) in the target variable but rather quantifies the relative contribution of features to predictive accuracy.

We will include the above mentioned clarification in the ‘Statistical analysis’ section.





Supplementary Fig. 1: SE-Ros or FI-Ros?

Thank you for pointing out this typo. We will write SE-Ros.

Supplementary Fig. 4: legend doesn't seem to explain the figure

Supplementary Fig. 4 shows the performance of the random forest model using a 2-D kernel density scatter plot. We have now modified the legend and the figure caption to indicate the density of the data as shown below.

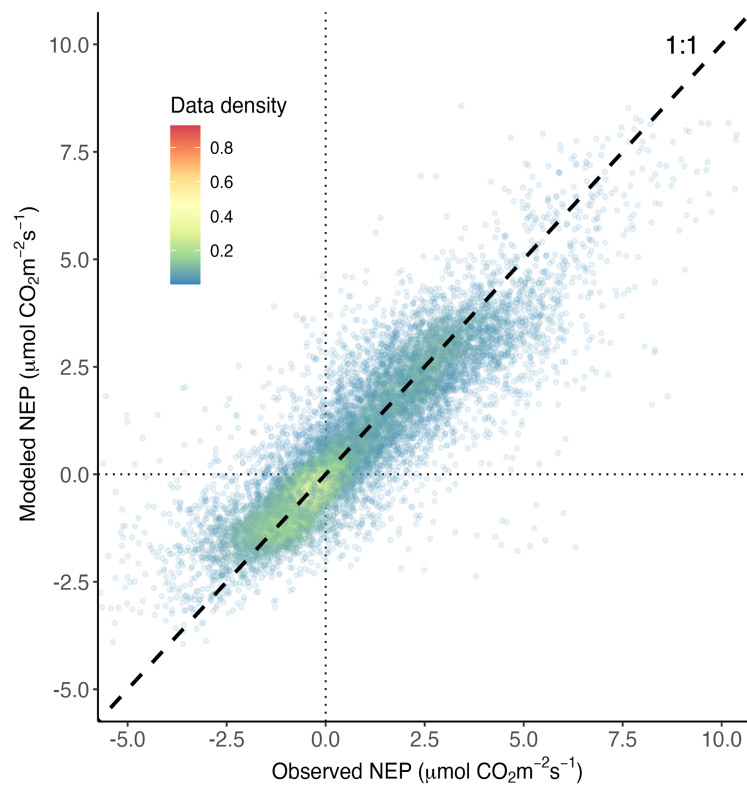


Figure S4. Density scatter plot showing the performance of the random forest regression model used to explain the variation of wintertime NEP. The average variance explained (across all sites) by the random forest model was 78% ($r^2 = 0.78$).

Figure numbers are not always in the right order throughout the manuscript, which muddies the water unnecessarily.

We found the incident that happened and we will fix these and check thoroughly in the revised version.

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