Jensen et al. present a novel and interesting study of soils and streamwater from northeast Greenland and probe the biological composition of their samples using filtration and a number of DNA analysis techniques, finding correlations between bacterial and primarily fungal species with INP concentrations. The manuscript is well written and the work is generally very thorough, while the results add to our knowledge of INPs in the environment and open up new avenues of exploration. This manuscript is suitable for publication pending a handful of major questions and comments below.
Major comments:

1) Line 253 (and throughout the paper when referring to onset temperatures): "Our results showed higher onset temperatures (between -1.5 °C and -4.7 °C) compared to previous studies of Arctic soils (Fig. 3)" and the sentences thereafter – This could be a result of using larger droplet volumes (30 ul) in the droplet freezing assays compared to the literature, allowing the rarer particles to be detected (i.e. better sensitivity) rather than the soils being more active here than elsewhere. This needs to be discussed, at least as a caveat. Generally speaking, the use of onset temperatures or T50 values can only be compared in "like-for-like" experiments, and are not necessarily suitable for literature comparisons.

We agree with this concern regarding the comparability of onset freezing temperatures across studies using different droplet volumes or different input amount of soils in freezing assays. We have revised the manuscript to explicitly discuss the potential implications of methodological differences. Specifically, we added a section that acknowledges that larger droplet volumes are more sensitive to detecting rarer INPs. Many of the studies we compare our results to, used larger volumes and therefore their sensitivity is higher than in our assays, supporting the statement that INPs observed in our study indded show a higher onset temperature than other studies. In these revisions, we now emphasize both the methodological context and the unique INP activity observed in the Arctic soils we studied. By addressing these points, we believe the discussion now provides a balanced interpretation of the results while maintaining scientific rigor.

"Our results showed higher onset temperatures (between -1.5 °C and -4.7 °C) compared to previous studies of Arctic soils (Fig. 3). Methodological differences, such as droplet volume used in freezing assays, must be considered when interpreting this trend. Studies using smaller volumes (e.g. 5 µL in Tobo et al., 2019), have a lower sensitivy and cannot be directly compared to our study. However, several studies used larger droplet volumes (e.g., 50 µL in Conen et al., 2018; Barry et al., 2023b, and 100 µL in Conen et al., 2012), which have a higher sensitivity than the micro-Pinguin asssay and a comparable potential to detect rare highly active INPs. Therefore, the higher freezeing onset that we observe does not seem to only be linked to methodological differences but reflects differences in the INP popoluations in these environments. INPs active at such high temperatures are generally proteinaceous (Santl-Temkiv et al., 2022) and are often associated with microbial sources, including bacteria and fungi (Barry et al., 2023b; Tobo et al., 2019; Conen et al., 2011). The presence of higher onset temperatures in this study may indicate differences in either the identity or in the activity of their microbial producers across Arctic terrestrial environments."

2) Figure 2 and 6: Some of the data goes below -25oC, but it is not written or shown anywhere in the paper or Supporting Information what the freezing temperatures of the pure water controls were. In what range do the pure water droplets freeze and does it overlap with the sample data? It would be helpful to include the pure water data in the fraction frozen plots in the Supporting Information. If there is overlap between the control and sample data then

background-corrections may need to be applied, as per Vali 2019 (https://amt.copernicus.org/articles/12/1219/2019/).

Thank you for pointing this out. We have added the control data to the fraction frozen plots, as shown in Supplementary Figures 1 and 7. These controls demonstrate onset freezing temperatures consistently below -15°C. Therefore, background subtraction is not required in the temperature range of primary interest, specifically between 0°C and -15°C, as there is no overlap between the control data and the sample data.

3) The streams are all defined as freshwater, but was there any formal analysis of their salinity, even if low? Did salinity levels vary at all across the streams (some samples appear to be from near the coastline) and could this be reflected in the INP spectra, e.g. do the INP concentrations decrease with salinity?

Thank you for your observation. We analyzed the salinity across the streams, measuring concentrations of Na^+ and Cl^- ions to calculate NaCl levels and salinity. Salinity values ranged from 0.0012 ppt to 0.0184 ppt, confirming that all streams fall well within the freshwater range (below 0.5 ppt). Even for the stream with the highest salinity (Kærelv C, 0.0184 ppt), the salinity is extremely low, and any freezing point depression would be negligible.

4) Supplementary figure 8 should ideally be in the main paper, particularly being that it is the equivalent of Figure 5 for the stream samples. Most of the factors shown in the figure are not discussed in the main paper but should also be mentioned.

Thank you for your comment. We appreciate the suggestion to move Supplementary Figure 8 to the main paper. The figure is primarily intended to support specific arguments made in the discussion, rather than to present critical results. Considering the fact that the correlations displayed in the figure do not reveal any significant novel findings, we decided to keep the figure in the SI to keep the manuscript focussed on the key findings.

5) I was expecting more of a clear discussion about the links or their absence between the soil and water studies, for example what portion of microbial species were found in the soils that then also appeared in the water samples, and how did their relative amounts change, particularly for those that were ice nucleating. A weak positive correlation of INP concentration is mentioned in part 3.5, but there is not much discussion about the nature of the INPs between the two samples (unless I have missed it). This is a little lacking considering the abstract and introduction point to this link, e.g. "In addition, the transfer of bioINPs from soils into freshwater and marine systems has not been quantified. This study aimed at addressing these open questions…". Perhaps there is a reason why it may not be suitable to discuss, but it is not clear, and so if possible I would like to see at least some discussion of the potential links between the soils and streams, or otherwise make clear that this is not one of the points of the manuscript.

Thank you for your insightful comment. We agree that understanding the microbial links between soils and streams would be very important. Unfortunately, in this study, we could not conduct amplicon sequencing on the stream microbial community due to technical difficulties during the field campaign. This limits our ability to directly track specific microbial taxa or quantify their transfer from soils to streams. We have revised the manuscript to acknowledge this limitation and added a sentence in the discussion section emphasizing the need for future

studies that include parallel analyses of both soil and stream microbial communities. This would allow for a more detailed assessment of microbial transfer dynamics, particularly for ice-nucleating taxa.

"To better understand the microbial transfer dynamics between soils and streams, future studies should include parallel analyses of both soil and stream microbial communities. This would enable a more detailed assessment of microbial transfer, particularly for ice-nucleating taxa, which is crucial for understanding the links between these two environments."

6) The plots should have error bars where possible, for example the INP plots.

Thank you for your suggestion. The analysis of INP data in this study does not involve binning the data into temperature intervals, as we rely on cumulative freezing spectra derived from individual droplets or wells. This approach provides precise freezing temperatures for each droplet, without aggregating the data into bins. Consequently, there is no statistical variation across temperature intervals to calculate error bars.
Furthermore, each sample is analyzed using 80 droplets, instead of analyzing smaller numbers of droplets in replicates, as has been recommended by Polen et al (2018) (Polen et al., 2018). This also means a high coverage of the freezing temperature distribution within the sample. This high number of droplets allows us to capture the variability of freezing events across the sample population with high confidence, minimizing the need for additional statistical representation such as error bars.

Minor comments:
1) Line 304: "The gradual loss of INA during filtration at the different locations suggests a mixture of different-sized INPs, predominantly originating from fungi." – What would suggest that they cannot originate from bacteria?

Thank you for your comment. The statement that the INPs predominantly originate from fungi might at this point in the manuscript be a to strong statement. However, there are some evidence that they might be the predominant type compared to bacterial INpro:

Retention of Activity After 0.2 µm Filtration: In most samples, INPs retained activity after filtration through a 0.2 µm filter, which suggests that they are not membrane-bound. Bacterial INpro are typically associated with the bacterial outer membrane, as demonstrated in the literature (Santl-Temkiv et al., 2022). Retention of activity post-filtration is therefore inconsistent with a predominantly bacterial origin.

1. **Size Distribution of Soluble INPs:** Soluble INPs in the majority of samples were found to be smaller than 0.2 µm while >1000 kDa, consistent with fungal INpro aggregates or oligomers. For example, Fusarium acuminatum produces INpro aggregates up to ~700 kDa (Schwidetzky et al., 2023a). Others samples were more similar to INpro produced by Mortierella sp. and Fusarium sp. in the range of 300–100 kDa (Kunert et al., 2019; Schwidetzky et al., 2023). These size ranges align with the predominant INPs observed in our samples after filtration.
2. **Binding to Clay Particles:** The observed decrease in activity in some samples (e.g., West 4 and Aucella) following filtration could be explained by fungal INPs binding to clay particles, which are abundant across all soil samples (Supplementary Fig. 2). Such

interactions are well-documented for fungal INPs (O'Sullivan et al., 2016), while bacterial INPs are not typically associated with clay particles in this manner.

Given this body of evidence, we have concluded that the gradual loss of INA during filtration is most likely due to a mixture of different-sized INPs predominantly originating from fungi and bacteria.

This has now been updated in the manuscript:

"The gradual loss of INA during filtration at the different locations suggests a mixture of different-sized INPs, predominantly originating from fungi and bacteria (Fig. 4)."

2) Was there any consideration of using heat treatments or peroxide treatments of the samples followed by reanalysis of the droplet freezing temperatures? These treatments have high uncertainties in that they do not necessarily "prove" the presence of biological (or entities produced by biological species), but can be a useful indication. On the other hand, DNA analysis allows direct detection of biological species including identification and even quantification, but appears to suffer from other issues, for example PCR would be used for the identification of specific known INP species (but could miss others), while sequencing informs on the identification of populations but not whether they are INPs or produce INpro. While not ideal, heat or peroxide treatments would at least allow an indication of the potential impact of INpro versus the mineral or clay particles that would presumably form the "background" signal.

We appreciate the reviewer's suggestion regarding heat treatments or peroxide treatments followed by reanalysis of droplet freezing temperatures. It is well-established in the literature that highly active INPs are predominantly of biological origin. Specifically, temperature treatments have been shown to significantly reduce the activity of INPs and close to 100% of INP-10 activity was lost after heat treatments (Daily et al., 2022; Barry et al., 2023b; Barry et al., 2023a). While heat treatments would confirm proteinaceous origin of the INPs that we observed, they would have not given specific insights into the microbial producers of the INPs. We therefore chose to perform filtration analysis as well as microbial community analysis attempting to more specificaly identifying the INP-producers.

3) Lines 420-429: While the soil results were compared to the literature in Figure 3, there is no such figure for the stream water results despite a description of several relevant datasets. While not essential, this would be easier to follow in a visual format rather than trying to compare numbers.

Thank you for the suggestion, which we agree with. However, most cited datasets are unfortunately not publically available and we have therefore decided not to include such a figure.

4) Could the fraction frozen and Nm/Nv data for the filtered samples be included in the Supplementary figures? Only the T50 values are discussed but this does not show whether there were any other influences on the INP populations, for example changes in the shape of the Nm curves upon filtering.

Thank you for your suggestion. We have now included the fraction frozen data for the filtered samples in Supplementary Figures 1 and 7.

5) What is the temperature uncertainty of the micro-PINGUIN technique?

The measurement accuracy of the micro-PINGUIN instrument is primarily influenced by the vertical temperature gradient within the well. A detailed breakdown of the uncertainty contributions can be found in (Wieber et al., 2024), Section 2.5 and Appendix A1–A7.
In summary, the largest contribution to the uncertainty arises from the vertical gradient in the well. This gradient was measured to be 0.20 °C at 0 °C, increasing by 0.015 °C for each degree below 0 °C. To account for this, temperature readings are corrected by half of the vertical gradient at each temperature point, ensuring that the surface temperature measured by the infrared camera is accurate.
We have included Table A1 from Wieber et al. (2024), which demonstrates that while the temperature correction increases with decreasing temperature, it never exceeds 1 °C. Hence, in the temperature range that we are interested in ie., 0 to -15 °C the uncertainty will be quite small and within the range of other ice nucleation setups uncertainty which is usually ranging between 0.5 to 1 °C (Lacher et al., 2024).

Temperature	Correction	Uncertainty ($k = 2$)
0 °C	−0.27 °C	±0.59 °C
−5 °C	−0.38 °C	±0.70 °C
−10 °C	−0.48 °C	±0.81 °C
−15 °C	−0.59 °C	±0.93 °C
−20 °C	−0.69 °C	±1.04 °C
−25 °C	−0.80 °C	±1.16 °C

Table A1 Measurement uncertainty and temperature corrections for various temperatures at 5 °C steps. The measurement uncertainties are expanded to a coverage of 95 %.

6) Lines 368-370: How does this compare to ice nucleating phyla found in other soil INP studies? Likewise Line 375 for fungi.

Thank you for your comment.
The ASVs that correlate with the INP concentrations are from microbial taxa that were previously unknown to produce ice-nucleation-active proteins. While some of them belong to the same phyla as known INA microorganisms, they do not affiliate to the same genera.

7) Line 126: How many pure water droplets were analysed per experiment? And were the control experiments performed in the same plate as the samples?

Thank you for raising this point. In each plate we included a negative control, which consisted of 64 Milli-Q water droplets. While this is slightly lower compared to 80 droplets analyzed for the samples, the impact on the calculation of INP concentrations is minimal. As described in our methods, the term:

$\alpha \cdot \ln\left(\frac{\alpha}{\alpha-1}\right)$

becomes negligible when α >> 1 making the calculations robust to slight variations in the number of droplets analyzed. Consequently, the use of 64 droplets (α =1.007895) vs 80 droplets (α =1.006303) does not significantly influence the accuracy or interpretation of the INP data.

8) Line 152: Why is 5% of the droplets freezing used as the onset freezing value?

Thank you for your question. The 5% freezing threshold is used as the onset freezing value to account for the probabilistic nature of ice nucleation experiments. Ice nucleation can be viewed as a probability distribution, where droplets have varying likelihoods of containing an ice-nucleating particle capable of nucleating at a specific temperature. Removing the first and last 5% of the data effectively excludes the tails of this distribution, which represent the extremes. This approach corresponds to a 5% confidence interval on either end, ensuring that the reported onset temperature reflects the more statistically robust and reproducible freezing behavior of the majority of droplets, rather than potential outliers.

9) Line 174: Add the word "respectively" after discussing bacteria and fungi to make clear that the 16S and ITS sequencing refers to specifically to one or the other.

Thank you for your comment. This has been implemented in the new version.

10) Line 181: Please define BSA.

Thank you for your comment. This has been implemented in the new version.

11) Line 184: Missing degree symbols in temperatures.

Thank you for your comment. This has been implemented in the new version.

12) Line 187: What are V3 and V4?

Thank you for your comment. The V3 and V4 regions refer to two variable regions within the 16S rRNA gene, which are widely used in microbial community studies. These regions contain sufficient sequence variability to allow differentiation between bacterial taxa while remaining flanked by conserved regions for primer design. By amplifying these regions, we can achieve high-resolution taxonomic identification of the bacterial communities in our samples. This has been clarified in the revised manuscript.

13) Lines 189-190: The description of the PCR mix is a little confusing. What were the volumes of the components, and what is meant by "2 template DNA" (e.g. should this be 2 ul?) and "2 x KAPA….."?

Thank you for pointing this out. We have clarified the description of the PCR mix in the revised manuscript.

14) Lines 203-204: Why are the products re-quantified after pooling? Due to losses when transferring between vials? Is the total concentration required for the sequencing?

Thank you for your question. The pooled library is re-quantified after pooling to ensure accurate equimolar representation of each sample in the final library. This step is critical because the pool will be multiplexed with other libraries on the Illumina MiSeq platform. Accurate quantification ensures optimal cluster generation during sequencing, preventing over- or under-representation of specific samples and maximizing the quality and consistency of the sequencing output.

15) Line 214: Define ASVs.

Thank you for your comment. This has been implemented in the new version.

16) Figures 1 and 2: It would help the reader to color code the locations in Figure 1 with the same colors as used in Figure 2, especially when trying to determine whether there are regional grouping of INP concentrations etc. Ideally the same color coding would be used throughout (e.g. in Supplementary Figures 2, 5 and 6, although it is less important for the Supporting Information compared to the main paper).

We appreciate the suggestion to streamline the color coding for clarity and consistency. We have revised the color scheme to ensure that the locations in Figures 1 and 2, as well as Supplementary Figures 2, 5, and 6, now use the same color coding.

17) During the Introduction or Results sections, the authors may want to consider the recent work of Herbert et al. using fertile soil representations of INPs rather than simply desert dust: https://egusphere.copernicus.org/preprints/2024/egusphere-2024-1538/

Thank you for this comment and pointing us to this recent research. Since the manuscript mentioned is still in review as a preprint we have decided to leave it out of our manuscript, since we already in our opinion cover relavant litterature.

18) Line 244: Data for total carbon (TC) is discussed, but this TC data is not shown for the samples (likewise for nitrogen).

Thank you for pointing this out. The data for total carbon (TC) and nitrogen has now been included in Supplementary Table 1, alongside the 16S rRNA gene copy numbers per gram of soil.

19) Line 251: The sampling of Barry is discussed since they used bulk soil rather than sieved soil, but how was the soil in Tobo and Conen sampled/treated.

Thank you for pointing this out. We have now clarified the sampling and treatment methods used in Conen et al. (2011, 2018) in the manuscript. Both studies prepared their soils by air-drying before sieving to isolate finer fractions. Conen et al. (2011, 2018) used a 63 µm mesh. After sieving, they further separated particles smaller than 5 µm using differential settling techniques. We have added this information to the manuscript to provide a clearer comparison of the methodologies.

"We prepared soil samples for ice nucleation analysis as previously described, with slight modifications (Conen and Yakutin, 2018). The soil samples were placed in a small petri dish and freeze dried overnight (Edwards Micro Modulyo Freeze Dryer). Freeze-drying was chosen

instead of air-drying to minimize the potential for microbial activity during the drying process and preserving the original composition of INPs, as prolonged air-drying could induce microbial activity, potentially altering INP concentrations due to production or degradation. The freeze-dried samples were kept in a desiccator to prevent rehydration and subsequently comminuted in a mortar by hand. Mortaring was performed to break down aggregates formed during freeze-drying and ensured effective sieving. Samples were dry sieved with a 125 µm and 63 µm sieve for two minutes using a vibratory sieve shaker (Analysette 3 PRO, Fritsch). The <63 µm fraction was collected for analysis, as this size range represents particles most likely to aerosolize (Fröhlich-Nowoisky et al., 2016).”

20) Lines 376-377: “While this phylum is known to be encompass many different lifestyles, only saprotrophic, pathogenic and lichenized fungi are known to produce INPs.” – Are there appropriate references that could be used to support this statement?

Thank you, we have now added the following references:
(Pouleur et al., 1992; Fröhlich-Nowoisky et al., 2015; Huffman et al., 2013; Morris et al., 2013).

21) Line 390: Consider citing Meinander 2022 (https://acp.copernicus.org/articles/22/11889/2022/) and Bullard 2016 (https://pubs.usgs.gov/publication/70190769) when discussing emission of dusts and soils from these high Arctic locations.

Thank you for your comment. This has been implemented in the new version.

22) Figure 5 and caption: Is the concentration in terms of Nm (g-1 of particles) as in Figure 2? If so, please make this clear and have the formatting of parameters/units across the plots be more consistent.

Thank you for noting this. It is indeed in terms of Nm (g-1 of particles), as indicated in Figure 2. We have clarified this in the caption for Figure 5 and ensured that the formatting of parameters and units is consistent across all plots in the manuscript.

23) Line 440: Could biofouling be another possible mechanism for the loss of proteinaceous material via non-specific adsorption to the membrane material?

Thank you for the idea.
Given that we observe an increase in ice nucleation activity after filtration, it seems less likely that biofouling is the main mechanism responsible for this phenomenon. As mentioned biofouling typically involves the non-specific adsorption of proteins, particles, or other macromolecules to the filter material, which might lead to a decrease in the concentration of active species in the filtrate.
However, if cell lysis were occurring during filtration, this could release cellular contents, including INPs, into the filtrate, potentially leading to an increase in ice nucleation activity.

24) Line 520: “…while at other locations they are present in solution” – what is meant by this?

Thank you for your comment. The phrase "present in solution" refers to the fact that the remaining INPs in these cases were found in the soluble fraction, indicating that they were likely excreted or detached from microbial membranes.. We have clarified this in the revised manuscript.

"Additionally, using filtration through a series of filters with decreasing cut-offs, we found that soil INPs at some locations were associated with soil particles or microbial membranes, while at other locations they were present in the soluble fraction, likely excreted or detached from microbial membranes."

25) Supplementary Figure 1: Is this data for the 63 um sieved samples? Please provide further details about the samples in the caption. Also, provided it does not make the plot too busy, please add the fraction frozen plots for the filtered samples too.

Thank you for your comment regarding Supplementary Figure 1 and for pointing out the need for clarification and additional details. We have addressed your concerns as follows:

1. We have clarified in the caption that the data correspond to soil samples that were pre-sieved to <63 µm before the freezing activity analysis.
2. We have added a detailed explanation of the filtration treatments for each category (<63, Soluble > 1000 kDa, 1000-300 kDa, 300-100 kDa, and <100 kDa).
3. We have added the negative controls (Milliq water samples)

26) Supplementary Figure 2: It would be helpful to the reader to show more sizes on the x-axis, e.g. steps of 20 um or 50 um. The samples all seem to peak at around the 50-60 um region, please note the number in the caption.

Thank you for the suggestion. We have updated Supplementary Figure 2 to show more particle size intervals on the x-axis, now displayed in steps of 20 µm together with gridlines, for improved readability. Additionally, as noted, the samples predominantly peak in the 40–60 µm region, which is now mentioned explicitly in the updated figure caption.

27) Page 6 of the Supporting Information is blank.

Thank you for your comment. This has been corrected in the new version.

28) Supplementary Figure 8: Please include in the caption the definitions of the various parameters shown in the plot.

Thank you for your suggestion. We have updated the caption for Supplementary Figure 8 to include the definitions of the various parameters shown in the plot.

29) There are occasional minor spelling and grammatical errors throughout that can be picked up on a thorough proofread.

Thank you for your comment. We have proofread the manuscript to remove spelling and grammatical errors.

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