

Reviewer #1 Comments		
Line # (in original script)	Comment	Response
19	I suggest two other relevant and key references for the snow melt rate statement: <i>Ganey et al. 2017 Nature Geosciences</i>, and <i>Roussel et al. 2024 PNAS</i>. Kahn et al. is very relevant as well.	- Added the Ganey and Roussel references to this statement - Kahn et al. was already included, assuming this is a comment indicating approval
20	Mechanism likely to intensify under climate change -> I would be really careful with this statement. Liang et al. has not used prediction model to evaluate the effect of climate change under different scenarios. This question however is clearly investigated in <i>Roussel et al. 2024 PNAS</i> which does suggest the opposite FOR the Alps (not necessary the case for Antarctica), shorter snow melt duration -> less snow algal bloom	- Thank you for this observation, we understand and agree. Line 20 has been changed to: “Snow algal proliferation is linked to meltwater presence and the subsequent release of nutrients (Hoham & Ling, 2000; Hoham & Mullet, 1997). How these relationships may respond under future climate change scenarios remains an important question and requires further investigation.”

24	About the thermal range and definition, I would suggest to double check what range defines a cryophilic species. It sometimes commonly accepted that cryophilic species optimally grow below 10°C, and temperature above would be lethal (i.e. 15°C) as clearly described in <i>Détain et al. 2025</i> using TPC (already cited in this review). “<i>Hoham 1975, Arctic and Alpine Research</i>” is the first original and key reference for these definitions in snow algae. As an additional reference with a screening of snow algae for thermal preference is <i>Suzuki et al 2023 FEMS</i>, despite not perfect since only 2 temperatures are tested, it shows many species with more cryotolerant-mesophilic traits, a true cryophilic and an absolute mesophilic.	- Added the Hoham reference - Added the Suzuki reference - Moved the Hulatt reference to the portion of the sentence referring to biotech (more relevant) - Added the Leya reference Regarding the thermal range and definition, after referring to Hoham’s work on optimum temperature ranges for a wide array of snow algal species in Table 5 (https://doi.org/10.1080/00040851.1975.12003805), we do feel it would be more appropriate to say below 10°C. This has been altered in the text and the Hoham reference has been added to the sentence.
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	<i>Hulatt et al. 2017 & Leya et al 2009 FEMS</i> are the two great reference for biotech application, alongside <i>Schoeter</i> .	
31	This is really COOOL. I feel this is an interesting application honestly. However, I feel this microswimmer application is not essentially related to snow algae. Is it the right place to mention this? What do you think about the Ice-Binding-Proteins from snow algae that could have biotech application, to add in this section? (if you really want to mention biotech application)	- We appreciate this comment and do agree that targeted drug delivery (using phototaxis and magnetotaxis) in mammalian bodies is not a direct application of snow algae themselves, but rather mesophilic (<i>Cd. reinhardtii</i>) algae used in the study. However, we felt this example was relevant because it illustrates how understanding the navigation of microswimmers through porous, complex environments can have broader applications, including in healthcare. Snow algae inhabit and migrate through heterogenous, porous media formed by snow crystals, which much of this review focuses on this (e.g. section 3.1.2). Studies of active matter and microswimmer interaction with obstacles are, in our opinion, therefore relevant. Highlighting these adjacent applications and areas of study help highlight the

		transferability of knowledge in the snow algae studies we review and further justify the understanding of topics such as tactic behaviour. - Regarding the ice-binding-protein (IBP) comment, although there is evidence for ice-binding-protein's use in cryobiology and food storage etc., to our knowledge, there don't appear to be studies outlining demonstrable use of IBPs extracted from microalgae to any scale, whereas the biotech related studies we cite represent more developed and experimentally established application areas
36	Could you make a smoother transition, indicating that snow algae have a motile stage. Probably, just something like <i>“motile microalgae (like some snow algae) are considered...”</i>	- Changed to: “Motile microalgae, including many species of snow algae, are considered self-propelled Brownian particles, or active matter (a class of non-equilibrium soft matter), whose motion, unlike most other

		particles', cannot be explained solely by equilibrium physics.”
42	About the term “Flagella”. There is no microtubule in a flagellum, flagella are made of flagellin and only found in bacteria. Cilia are membrane delimited and articulated by microtubule sliding (Kahn & Scholey et al 2018 Current Biology). I acknowledge that most people understand and still many misuse this term, but I would raise your attention on the fact that a flagella is protein-based structure found in bacteria ONLY (prokaryotes) that propel the particle, while microalgae use cilia (a cellular protrusion membrane delimited) that pull the cell particle in its environment (Kahn & Scholey et al 2018 Current Biology). From a biological perspective as well as biophysical perspective the two structures are clearly different.	Thank you for your comment, respectfully, the correct widespread use of the term eukaryotic “flagella” is present in a vast amount of literature, particularly related to the biophysics of microswimmers and the characterisation of snow algae species. Flagella referred to in said subject areas is distinct from bacterial flagella or prokaryotic flagella. Since the appendages of snow algae are widely referred to as flagella we feel changing flagella to cilia throughout the review could potentially cause unnecessary confusion or limit visibility to the intended audiences during literature searches.

	I would suggest consistency and either use only flagella or cilia, knowing that “cilia” is the correct biological term, and cells are biciliated as defined in (Raymond et al. 2019 Current Biology for Sanguina aurantia, and Lynn Quarmby’s work.).	
41	I could suggest something like “propel themselves through ciliary-beating, a biological process where...”. So, it indicates what kind of movement drives the propulsion mentioned in the next sentence.	- Incorporated this into line 41, it now reads as: “Motile microalgae propel themselves through flagellar-beating, a biological process where...”
43-46	This is very interesting, but considering the target audience, would you have a way to make this statement a bit more digestible for a wider audience? while keeping the message.	- We understand your concern. These lines have been changed to: “The aforementioned propulsion process can be contrasted with synthetic active particles such as catalytic Janus particles, which self-propel by catalysing chemical reactions on one of their two differently coated hemispheres. This reaction generates local concentration gradients in the surrounding fluid producing an uneven distribution of molecules around

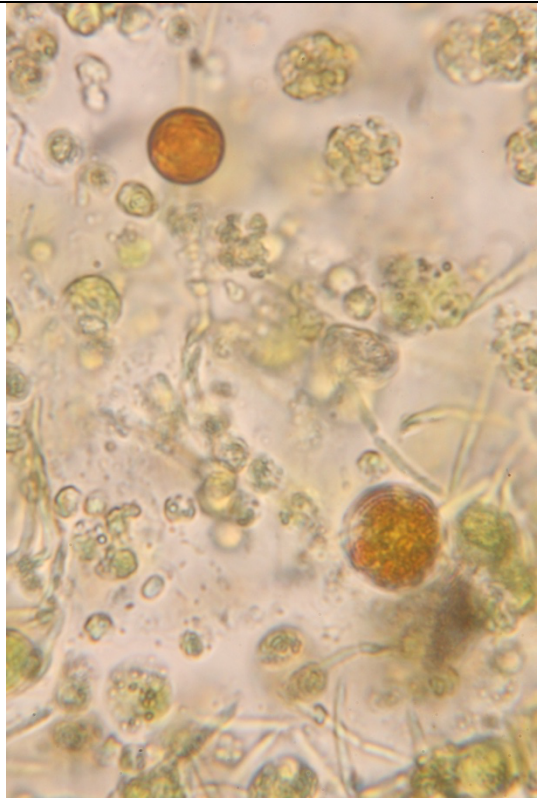
		the particle, leading to interfacial pressure differences that drive its motion (Ebbens and Gregory, 2018). Mechanisms such as this one which enable microscopic particles to be propelled within a fluid without externally applied fields are called self-diffusiophoresis (Ganguly et al., 2023).”
58	<i>Cd. reinhardtii</i>	- This was not the incorrect/inconsistent use of <i>C. reinhardtii</i> in passing, it was the explanation of the reasoning behind writing Chlamydomonas as Cd. instead of C. (which is much more common in literature) for the sake of this study: “ <i>Cd. reinhardtii</i> although more commonly written as <i>C. reinhardtii</i>, will be written as such for the purpose of distinguishing between multiple genera beginning with the same letter.”
66-70	I think the dynamic in which species names arose from one another is complicated. I would recommend a more straightforward sentence where genetic	- The Rea and Dial citation removed - Engstrom et al., 2024 reference has been moved so it immediately follows acknowledgement of the <i>Rosetta</i> genus

	characterisation and differentiation led to the definition of new genus including <i>Sanguina</i> (Prochazkova et al 2019), <i>Rosetta</i> (Engstrom et al 2024), <i>Chlainomonas</i> (Novis et al. 2008 <i>J. Phycology</i>), <i>Chloromonas</i> (Matsuzaki et al 2019 <i>Plos One</i>, FYI major polyphyletic group of snow algae) and <i>Limnomonas</i> (Tesson & Proschold 2022, <i>Diversity</i>). Remove Rea & Dial from this section (still relevant for the vertical migration within the snowpack). Important note: The genus <i>Chlainomonas</i> is a very outstanding group of microswimmer which was omitted in this review. It has a biciliated stage as well and a Quadri-ciliated stage with bulky swimming. This is very outstanding. Please refer to both <i>Novis et al. 2008 and 2023 Journal of Phycology</i>) in this review.	- Quadri-flagellated stage (found in the <i>Chlainomonas</i> genera) acknowledged on line 74 and 75 “this review will focus on motile snow algae with biflagellated and quadriflagellated stages e.g.: <i>Chloromonas typhlos</i>, <i>Chlainomonas rubra</i>, <i>Limnomonas spitsbergensis</i> and <i>Sanguina nivaloides</i>.” - Removed lines 63-66: “The <i>Chlamydomonas</i> genus is now recognised as polyphyletic (Matsuzaki et al., 2015, Engstrom et al., 2024, Prochazkova et al., 2019, Raymond et al., 2024). Polyphyly is where a group of organisms are deemed to have multiple distinct ancestral groups as opposed to a single common ancestor, making it no longer appropriate to classify them in the same taxonomic group; a genus in the case of <i>Cd. nivalis</i>.”
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77	Well, as suggested before I would go for “use of cilia”. Can cilia really rotate?	The “cilia” comment was addressed above. The description of flagellar motion was changed for accuracy: “Motile microorganisms, sometimes referred to as microswimmers, have evolved a range of methods of self-propulsion, including flagellar action typically involving the waving or breast-stroke like motion of flagella...”
79-81	To my knowledge, cilia of cells like Chlamydomonas-like are symmetric, beating can be asymmetric to give directional change, like in response to light stimuli. Not sure this specific asymmetry refers to the positioning of cilia on a Chlamydomonas-like cell like snow algae? Or clarify what asymmetry you are specifically talking about in here (maybe an illustration?) Important note: The genus <i>Hydrurus</i> (golden snow algae <i>Chrysophyceae</i>) have asymmetric cilia, please find a way to describe this heterogeneity in cilia configuration and potential implication in microswimming (this corresponds to	Lines 78-81 and onwards were changed to: Motile microorganisms, sometimes referred to as microswimmers, have evolved a range of methods of self-propulsion, including flagellar action typically involving the waving, undulation or rotation of flagella (Pedley et al., 1992), which are elongated structural extensions to the cell (the appendages attached to the cell bodies in Figure 2. The motile snow algae focused on in this review are biflagellated, meaning they have two flagella (Raymond et al., 2022). Motile algal cells of the same species can be identified by the distinct gait that they exhibit due to factors such as the symmetry of their flagella and

	the Chrysophyte in Détain et al 2025, and please refer to (<i>Prochazkova et al 2026 Journal of Phycology</i>) Maybe the numbering of section, 2 and 2.1 is not optimal, you should have a 2. with 2.1 diversity and taxonomy and 2.2 Use of cilia	the fibres which attach the flagella to the basal body (Wan et al., 2016). For example, the model species <i>Cd. reinhardtii</i> has two physically symmetric flagella. The flagella's basal apparatus is structured so that it results in a non-planar, three-dimensional, flagellar beat (Wilson & Bees, 2025). Flagellar beating has been proven to be critical to phototactic response in <i>Cd. reinhardtii</i> (Wang et al., 2026) and is hypothesized to be relevant to other tactic responses, although this has not yet been proven. This, combined with the flagella having different phases, controls <i>Cd. reinhardtii</i>'s helical swimming pattern (Cortese et al., 2021). Microalgae can also have morphologically asymmetric flagella. Golden snow algae from the genus <i>Hydrurus</i> such as <i>H. nivalis</i> and <i>H. svalbardensis</i> have physically asymmetric flagella, one long and one very short, only a fraction of the size of the other Prochazkova et al., 2026, though little is known about <i>Hydrurus</i>'s swimming pattern as many of the species have only recently been characterised.
144-147	Yes, but this is hypothetic, it not shown. Figure 4 shows two snow color, but the green cells are maybe not the same as the	Lines 144-147: have been changed to reflect this: Current knowledge suggests that with the onset of spring snow melt, the cysts germinate into green, motile flagellated cells which respond to spring

	red cells. So I would suggest phrasing it as: “it is suggested that...”	meltwater, light and the subsequent release of nutrients by migrating upward toward the newly accumulated snow surface formed during autumn and winter, as shown in Figure 4. At the snow surface, or from another environmental cue, the microalgae transform into non-motile cells once again, appearing in colours including green, yellow, gold, orange and red. There is evidence for this lifecycle in the <i>Chloromonas</i> genus (e.g. Rea et al., 2024, Schuler et al., 2023) but it has been only theorised for other algae genera and species. Regarding the colours of the snow in Figure 4, Dr Matthew Davey, the photographer of this photo, confirmed that there were singular species which transitioned from green to red present, though there would have been mixed species in the snowpack as well. In the supplementary attachments portion of the reply to your comments we have provided a microscopic image where some cells from this image can be seen transitioning, with a blend of red and green pigment within their cellular body.
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150	UV-protection from astaxanthin is not really sure, astaxanthin is a strong antioxidant that shield the cell from excessive and damaging energy transfer from light to the photosynthetic machinery (Ezzedine et al. 2023 Nature communication).	These sentences and citations have been added to the end of the “Snow algae physiology and taxonomy” section to reflect these points and create a better flow throughout the review: “The colour of a snow algal bloom depends on cyst maturity and the astaxanthin to chlorophyll-a ratio present within the cells (Prochazkova et al., 2020; impacts on

		snow albedo and melt rate have been shown to differ amongst snow algal bloom colours (Khan et al., 2021). Astaxanthin is an antioxidant which provides algal cells with protection from damage brought on by intense solar radiation and oxidative stress at the snowpack surface (Gorton et al., 2007), not necessarily specific protection from ultra-violet radiation as once thought (Ezzedine et al., 2023).
161	Roussel et al 2024 PNAS suggests that liquid water for at least 46 days is required for bloom formation, shouldn't be assumed that it is upward migration.	Line 161 changed to: "Roussel et al., 2024 reported that the formation of red algal blooms (when snow algal cells reach their non-motile, red cyst phase on a snowpack surface) in the European alps requires the presence of liquid water throughout the whole snow column for at least 46 days. One would hypothesise that this value would differ for differing species."
170	No, cysts have not been seen germinating, in this study they only observed the effect of blocking the way between the ground and the surface. Important note: Please check <i>Matsumoto et al 2024 Journal of Phycology</i>. About Chlainomonas, this study has more convincing evidences of	Line 170 and the following paragraph have been changed to: To investigate life cycle linked migration, during summer, Rea and Dial (2024) applied a bleach-containing mat to the surface of a subsection of an Alaskan ice field snowpack colonised by snow algae. Cell abundance beneath the mat, in the untreated areas surrounding the mat, and at a distant control site was measured the

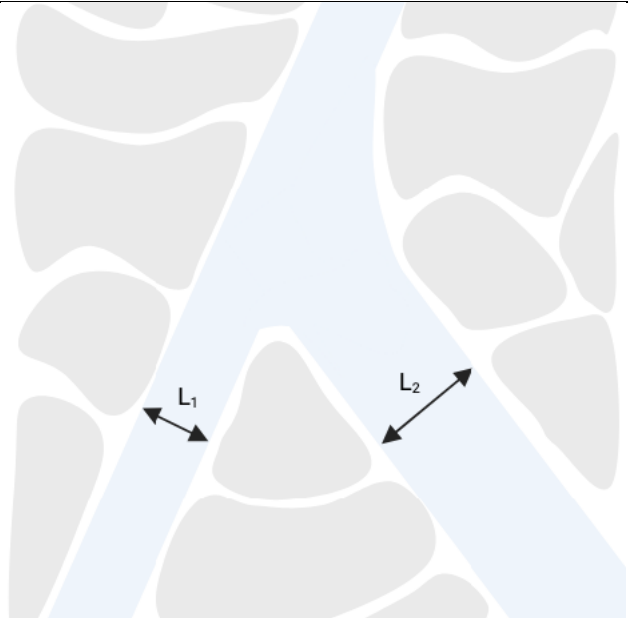
	germination, but it is not absolutely proven that it works that way. Mind that this is for a snow-lake environment.	following summer after the treatment. The researchers defined two pathways for algae to recolonise the snow each year: active resurfacing and passive dispersal. Active resurfacing was hypothesised to occur when algal cysts germinate at the bottom of the snowpack entering the green motile phase in response to light and nutrient gradients, then transforming into non-motile, red cysts once again on top of the snowpack, dividing clonally (exhibiting mitosis and reproducing a genetically identical child cell). Passive dispersal was described as algal cells being introduced through passive transportation methods such as wind, water and birds. The authors concluded that at the peak of the growing season actively resurfacing cells were responsible for 65% of microalgal surface abundance and that passive dispersion accounted for the remaining 35%. Regarding the comment about <i>Chlainomonas</i>' lifecycle, as hypothesized in: https://doi.org/10.1111/jpy.13454, it is our opinion that the description of this lifecycle is too habitat specific to be of value to the review by being described in specific detail. Saying this, we
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		acknowledge the relevance and expand on our description of the generalised snow algae life cycle hypothesis by mentioning this at the beginning of section 3.1.1: “... There is evidence for this lifecycle in the <i>Chloromonas</i> genus (e.g. Rea and Dial (2024); Schuler and Mikucki (2023)), as well as a similar lifecycle in the <i>Chlainomonas</i> genus (though habitat specific in a snowy lake environment) (Matsumoto et al., 2024), but it has been only theorised for other algae genera and species.”
182	I would suggest the introduce the notion of quasi-liquid layers QLLs before referring to it	Line 182: We have included a brief overview of quasi-liquid layers before going into further detail later in the section: “On a microscopic scale, snow algae have been thought to inhabit the quasi-liquid layer (Grinde et al., 1983) a thin film of liquid water that surrounds snow crystals and persists at sub-zero temperatures, forming on the crystal surface within approximately 20 Kelvin of the melting point (Yasuda et al., 2024).
194	40µm for a motile vegetative cell is quite big (except Chlainomonas), I would suggest checking the typical size of	Line 194 changed to: “In contrast, motile snow algae cells in their flagellated phase are several orders of magnitude larger, typically measuring 6–20 µm (Gálvez et al., 2021; Procházková et al.,

	vegetative motile cells (more between 6 and 20µm).	2019; Remias et al., 2005), and up to 40 µm in species of larger genera such as <i>Chlainomonas</i> (Matsumoto et al., 2024).” - Clarified the documented sizes and added a specific citation for <i>Chlainomonas</i>
200	I am not sure about the interpretation of <i>Ono and Takeuchi 2025</i>. It says non-motile SA (cysts) do not migrate/change layer in the snowpack, and do not seem to be affected by meltwater flow, no significant percolation effect. And this would explain why the cells accumulate on the surface as the snowpack melts. However, cysts can be found within the liquid layer as shown in <i>Ezzedine et al.</i>, maybe percolating at a microscale, but not a macroscale. <i>In fine</i>, both study don't contrast, they are more complementary, one describing the microscale (with a cm²), the other one the macroscale (with dozens of cm²).	Thank you for your feedback on this, we appreciate the confusion on our perspectives when comparing these studies. Both studies referred to non-motile snow algal cysts and their positions within the snow structure. Ezzedine et al. (2023) commented on the cells being within liquid channels (possibly due to melt during sample transport) and Ono and Takeuchi (2025) reported that non-motile cells did not seem to drain into the snowpack through the liquid channels. We have added the comment about cells travelling during transport in the Ezzedine study to a later point in the paragraph and have also covered the macro/microscale issue in detail that you pointed out. This paragraph, including line 200, has been rewritten: Ezzedine et al. (2023), using X-ray tomography at a µm resolution and focused-ion-beam scanning-electron-microscopy,

		observed field samples of <i>S. nivaloides</i> and found that dormant red cysts from this species were only present in the liquid water fraction of the snowpack, none appearing within the ice grain cores. These findings contrast with those of Ono and Takeuchi (2025), who reported that non-motile snow algal cysts were not transported through meltwater channels between snow crystals during daylight hours when snowmelt and channels of liquid water would have likely occurred. It is possible that Ono and Takeuchi (2025) were focused on migration at a macroscopic scale, with their most shallow samples being taken three centimetres from the snowpack surface, whereas Ezzedine et al. (2023) were doing up to a subcellular resolution of sample investigation. This could mean that there was potentially cell transport from percolation and cells present in liquid channels occurring in both studies, just not reported at a fine enough resolution for comparison purposes in the (Ono and Takeuchi, 2025) study. Additionally, the difference in findings could be related to potential melt and refreezing during sample transport during the Ezzedine et al. (2023)
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		study. Or, lastly, the difference could also relate to the timescales of the studies or the environment that the microalgae were observed in, which could modify the microstructure of the snow, as we continue to discuss below.
214-238	This is a really great section, maybe the most valuable and novel information/perspective you bring in this review. Do you think it would be possible to illustrate i) comparison between narrow and wider channel in terms of physical forces, ii) how the interfacial pre-melting could enhance migration, or whatever you think is worth illustrating.	An image captioned: A diagram of water channels within a snowpack, where $L1 < L2$. Water flowing in the narrower channel (L1) has a shorter viscous diffusion timescale than water flowing in the wider channel (L2) made in biorender: https://BioRender.com/1oc2605 was added to this section to give context to the equations found on these lines.

		
240	Agree with the taxis definition but I could suggest improving with something more like: “... a stimulus from biological, chemical or physical origin” so it includes all components of taxis, including chemo-, photo-, thermos- and gravi-. For the equation of the different taxes, it is a bit confusing how the different equations build. What is preceding the	We agree with this suggested improvement. Line 240 has been changed from: “Tactic behaviour is a bias in swimming direction towards or away from a stimulus such as light or chemicals.” To “Tactic behaviour is a bias in swimming direction towards or away from a stimulus of biological, chemical or physical origin.” The + signs in equation 6 follow the line above them, this is standard in mathematics and physics. See this study for example by Pedley et al. (1988): 10.1017/S0022112088002393

	“+” ? (this maybe due to my ignorance in equation syntaxes)	
285-286	I would rephrase with something explaining like: “light sensing by photoreceptor triggers modulation of intracellular calcium current (Ca ²⁺ signature), which in turn induces an asymmetric ciliary beating followed by a movement toward or away from the light source.”	Line 285-286 changed from: “Through the modulation of intracellular calcium currents, cellular and molecular structures allow for control of flagellar steering of cells towards light sources (Pivato and Ballottari, 2021).” to “Photoreceptor activation modulates intracellular calcium currents, inducing asymmetric flagellar beating and thereby steering cell movement toward or away from light sources (Pivato and Ballottari, 2021).
289	Phototaxis was examined at only 1 temperature (except for <i>Cd. reinhardtii</i>) in Détain et al. 2025. Following this, I invite you to discuss the discussion (section “Occurrence of stigmas in snow Chloromonads”) in Novis et al. 2024 Phycologia (on <i>Chloromonas fuhrii</i>) regarding the role and evolution of the eyespot in <i>Chloromonas</i> species. Their perspectives are interesting and worth mentioning at the end of this section. Especially that not having an eyespot in snow algae is to avoid confusing signals	This is a great paper that was missed – thank you for pointing this out. This short paragraph was added onto line 294: “In this context, Novis et al. (2024) described a new species of snow algae in the <i>Chloromonas</i> genus, <i>C. fuhrii</i>, which among other unique defining characteristics does not have an eyespot (or a stigma as referred to in this study). The two nearest relatives of <i>C. fuhrii</i> reported, <i>C. cf. platystigma</i> and <i>C. muramotoi</i> both have eyespots, suggesting that its loss was recent. The authors speculated that the higher frequency of eyespot absence in species such as those from the <i>Chloromonas</i> genus which

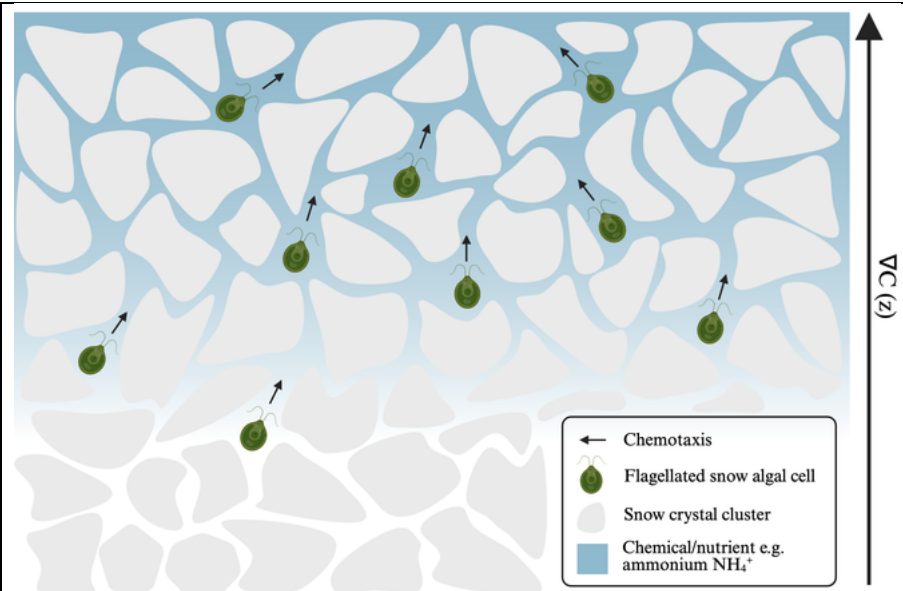
	from light reflecting from numerous directions off snow crystals.	live in snow versus other habitats is potentially due to the dynamic of response to light in snow, suggesting that cells may need to avoid confusing signals from light reflecting from numerous directions off snow crystals. Eyespots are helpful for phototactic precision but have been proven to be unnecessary for phototactic behaviour itself as shown using <i>Chlamydomonas</i> mutants with no eyespot (Morel-Laurens and Feinleib, 1983).”
306	What species are you referring to with Prochazkova 2019. <i>Cd. nivalis</i> is not <i>Sanguina</i>. According to the literature, <i>Sanguina</i> species are only available in culture in two laboratories so far, <i>S. aurantia</i> from 2022 in Canada and now in France. And <i>S. nivaloides</i> from 2025 in Norway. Important note: Light quality is also affecting mating/sexual reproduction in snow algae (Hoham et al. 1998, Hydrol Process). It is not directly related to phototaxis, but somewhere in this review, it would be necessary to highlight that the motile stage of snow	- The Prochazkova et al. 2019 reference was removed from line 306, we understand, thank you - We note the comment about light quality impacting sexual reproduction and although very interesting and important for future work, it is our opinion that this is beyond the scope of the review which aims to introduce the biophysics of snow algal migration specifically

	algae is suggested to play a key role in the life cycle and strategy of snow algae, through sexual reproduction by cilia pairing. Refer to other Hoham et al. paperS and Matsumoto et al 2024 Journal of Phycology for the life cycle of Chloromonas snow algae. Maybe introduce the notion in introduction, since mating is also discussed in the chemotaxis section	
326	Other molecules than ions are sensed for chemotaxis	Line 326 changed from: “To sense chemicals, microalgae use receptors in their cellular membrane to detect ions in their surrounding environment (Amaral et al., 2023).” to “Microalgae use receptors in their cell membrane to detect chemical cues, including ions and organic compounds, present in their surrounding environment (Amaral et al., 2023).”
328-333	Not convinced the results from Almela et al. 2024 needs to be developed that much. Results from different regions or bloom types suggest different scenario, where there is not much of a consensus. Davey 2019 New Phytol highlights the	We have changed the chemotaxis Figure 7 to include ammonium instead of potassium, this has been updated through the biorender reference as well: https://BioRender.com/inc0hfl

metabolic difference between nutrient deprived red blooms and green metabolically active blooms. *Ezzedine et al. 2023 Nat comm* and *Suzuki et al. 2025 The Plant Journal* highlight the adaptability of snow algae to low Phosphorus condition with an adapted lipidome. *Suzuki et al. 2023 FEMS* shows that biciliated motile *Chloromonas reticulata* accumulate lipid droplets and specific lipids under N-starvation in the same way as *Sanguina nivaloides* does (Ezzedine et al. 2023).

Therefore, green bloom supported by higher nutrient content in Davey 2019, as well Ono and Takeuchi 2025 in the wood, are metabolically active and can fuel motility, enhanced by chemotaxis for better success??

I suggest to better introduce the context or relationship between nutrients and snow algae



We agree that the Almela et al. 2024 paper was emphasized disproportionately. We have cut lines 328-333 to: “Phosphorus is a limiting nutrient for the snow alga *C. typhlos*, whereas nitrogen deposition is hypothesized to have a limited effect on bloom occurrence and size (Almela et al., 2024). This conclusion is based on a 38-day incubation experiment at 4.5 °C using 24 nitrogen-to-phosphorus (N:P) treatments representative of nutrient availability in snow. Maximum biomass occurred at N:P molar ratios of 4–7, indicating that phosphorus availability is more important for

	Figure 7: Great figures, I would only suggest using NH_4^+ instead of K^+ as your example, to better match the key nutrients discussed layer. I would suggest looking into Quorum sensing behaviour in <i>Chlamydomonas reinhardtii</i> from Folcik et al 2020, <i>iScience</i>	optimising <i>C. typhlos</i> growth, although blooms developed across a wide range of nutrient conditions.” We also acknowledge that “snow algal nutrient preference will vary across species, environment and lifecycle phase.” With regards to the rest of the studies mentioned, we thank you for bringing them to our attention but feel that the chemistry-related specifics are beyond the scope of the review. We felt it was more appropriate to mention for example Choi et al., 2016 and Nelson et al., 2023 as these provide specific examples of flagellated microalgae exhibiting chemotactic behaviour. Regarding the comment about better introducing the relationship between nutrients and snow algae, these lines have been added starting on line 328: “Snow algae inhabit snowpacks which are classified as oligotrophic environments where essential nutrients are often scarce and unevenly distributed (Maccario et al., 2015). Since nutrients such as nitrogen and phosphorus are required for algal growth and metabolism (Stibal et al., 2009),
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		their spatial distribution may influence the movement of motile cells. Chemotaxis therefore represents a potential mechanism by which snow algae could respond to localised nutrient gradients.”
446	I think it should be: “orient (Pedley and Kessler 1992)” In this paragraph, would you have anything to suggest about the effect of gyrotaxis and bioconvection pattern for snow algae, in the snowpack? What about snow-covered alpine lakes with Chlainomonas species (Matsumoto et al) ?? Important note: <i>Hulatt et al 2024 G3</i> (genome paper on Limnomonas) has a nice illustration of the culture with accumulation of biomass at the surface (very gravitactic) and the cells (biciliated with very long cilia (Tesson & Pröschold 2022)) are even climbing the walls of the	Yes, it should be. This has been changed to “orient (Pedley and Kessler, 1992)” with brackets. The formation of bioconvection patterns relies on negative buoyancy-driven large scale fluid flows. These would suppressed in ‘dry’ snow with small channels: the space between snow grains is not sufficiently large to allow fluid flow, as argued in section 3.1.2. In ‘wet’ snow with large channels, the flow induced by the snow draining would also prevent the formation of bioconvection patterns. However, if the flows are not too strong, it could be that gyrotaxis will cause algae to focus in the flow. We have added a paragraph about this after line 488, response to this comment by the reviewer.

	flasks. You may have a comment on this behaviour and the ecological relevance in snow in term displacement?	“A final observation is that gyrotaxis may play a role in melting snow at the onset of the formation of draining flows through the snow. Cells advected by these downward flows may be gyrotactically focused toward the centre of the flow, where they drift down faster than the mean flow velocity (Croze et al. 2017). By this mechanism gyrotaxis may increase the transport of swimming algae to the bottom of the snowpack.” Regarding the note on the <i>Limnomonas</i> genome paper specifically, we have included a scanning electron microscopic image of a <i>Limnomonas</i> sp. Cell in Figure 2 a). Although the Tesson & Pröschold 2022 paper does show the presence of plumes within a <i>Limnomonas</i> sp. culture, we feel that the bioconvection image we include in Figure 10 more clearly demonstrates the phenomenon, as well as providing a comparison between a model mesophilic alga and snow alga bioconvection pattern.
490	Cryotolerant species are somehow mesophilic but tolerate the cold, do they necessarily have lower speed compared	We thank you for pointing out this oversight. The sentence starting on line 492 has been changed from: “Both psychrophilic and psychrotolerant

	to the pure mesophilic? maybe not? The list of species in Détain et al. is too small to compare cryophilic vs. cryotolerant vs. mesophilic. But it does contrast pure cryophilic from mesophilic with or without cryotolerance.	species of snow algae display maximum swimming speeds at colder temperatures than mesophilic species (Détain et al., 2025)” to “Psychrophilic species of snow algae display maximum swimming speeds at colder temperatures than mesophilic species (Détain et al., 2025).”
496	As previously suggested, the range for cryophilic is probably 0 to 10°C; most cryophilic are happy between 5 and 10°C, but do not survive above 15°C. In the table, the Chrysophyte has a T_{opt} of 9.9°C, but it doesn’t survive much above 12°C. Comment: would you have any thoughts about the effect of temperature on ciliary beating and consequently trajectory? Have a look at <i>Geyer et al. 2022 Nature physics</i> Fig 2. And 3.	In line 496 the temperature range has been changed from 0-10°C, as it has earlier in the text as well. Thank you for bringing the Geyer et al. 2022 paper to our attention. Geyer et al. found that beat frequency in <i>Chlamydomonas reinhardtii</i> increases with temperature studied at temperatures ranging from 24 – 38 °C. It would be interesting to see how cryophilic species’ beat frequencies and trajectories are impacted by changes in temperature. As flagellar beat frequency is a contributing factor and not a proxy for swimming speed and hasn’t been studied in cryophilic microalgae we don’t feel the reference or its contents would be particularly relevant to add to this line.
General Comment	This review discusses the potential for active microbial motility in snow algae, a functionally important group of	We are very appreciative of the reviewer’s detailed assessment of our work; their comments have helped us add clarity and rigour to our review.

	unicellular algae in the cryosphere ecosystems. It provides an updated overview of their ecological context and environmental impact, followed by a concise review of the snow algal diversity and motility in green algae. The remainder and core of the manuscript explores current knowledge and perspectives on active microalgal migration within snowpacks and examines how environmental stimuli influence these movements. Overall, this work provides valuable insights for the research community. It highlights promising directions for future investigations into the dynamics and assembly of snow algae communities and contributes to improving our understanding of their potential global impacts. The sections addressing micro-motility and its biophysical basis are very well	Although we have taken the vast majority of their insightful suggestions on board, we disagree with the last portion of your general comment: “I also suggest ensuring that each subsection concludes with a brief synthesis highlighting the ecological relevance of the feature discussed, particularly in relation to motility of snow algae within snowpacks. This would help improving the coherence of the review.”. Since this is a review focusing on biophysics, we think that continuously emphasizing the ecological relevance of algae-snowpack interaction and tactic behaviour after each subsection would distract from our messaging and potentially confuse the reader. We agree that ecological aspects are very important, but these should be best considered in another paper.
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	explained and accessible to snow algae biologists and ecologists. The quality and clarity of illustration is appreciated. My comments mainly suggest a better integration of the snow-algal literature to better link the ecological context and integrate the diversity of algal species and behaviours. It seems that several special cases of motile species and behaviour have been omitted, remember that snow algae is a diverse group with diverse life strategies. I also suggest ensuring that each subsection concludes with a brief synthesis highlighting the ecological relevance of the feature discussed, particularly in relation to motility of snow algae within snowpacks. This would help improving the coherence of the review.	
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Reviewer #2 Comments		
Line # (in original script)	Comment	Response
68	Include reference to Engstrom <i>et al</i> for the description of the new <i>Rosetta</i> genus.	- A reference to Engstrom et al., 2024 for the description of the <i>Rosetta</i> genus specifically has been added on line 69
69	Please include <i>Chlamydomonas</i> on this list. As I understand there are still snow algal species assigned as such, the definition of <i>Sanguina</i> did not backdate to other species previously assigned as <i>Chlamydomonas</i> . I also feel that the omission of <i>Chlainomonas</i> from further discussion in this review is an oversight, especially as this is one of the only snow algal species that has it's life cycle documented in detail.	Respectfully, we don't believe that it is appropriate to include <i>Chlamydomonas</i> as a genus in this paragraph as we are referring to the most globally ubiquitous and unambiguous genera responsible for creating red algal blooms. The <i>Chlamydomonas</i> genus is now recognised as polyphyletic (Matsuzaki et al., 2015, Engstrom et al., 2024, Prochazkova et al., 2019, Raymond et al., 2024), despite some snow algae possibly still being referred to as a part of this genus in literature.

		We do remove the portion of the text that alludes to <i>Sanguina</i> backdating to <i>Chlamydomonas</i>, thank you for your input. We agree that information on the <i>Chlainomonas</i> genus was lacking in the initial submission of this review. We have acknowledged a species of this genus on line 74 as well as acknowledging that snow algae can have a quadriflagellated stage as shown with <i>Chlainomonas</i> species. We also note on line 151 that the hypothetical <i>Chlainmonas</i> lifecycle has been documented in detail, being one of the few snow algal species to have been examined in this way.
70	Include further references for these other groups, including Ochrophytes responsible for golden-brown snow.	We have included specific species examples and three further references, the sentence on line 70 has been changed from: “Other genera are responsible for golden-brown, orange and green70 blooms, equally as striking visually, but proven to have a different impact on snow albedo and melt rate (Khan et al., 2021).”

		To “Snow algae species can also be responsible for creating yellow/golden-brown, orange and green blooms in snow, for example <i>Kremastochrysopsis austriaca</i> and <i>americana</i> (Remias et al., 2020) can create yellow blooms, <i>Chloromonas krienitzii</i> (Prochazkova et al., 2020) can create orange blooms and <i>Chloromonas kaweckae</i> (Prochazkova et al., 2023) green blooms. The colour of a snow algal bloom depends on cyst maturity and the astaxanthin to chlorophyll-a ratio present within the cells (Prochazkova et al., 2020); impacts on snow albedo and melt rate have been shown to differ amongst snow algal bloom colours (Khan et al., 2021).”
74	The life cycle of <i>S. nivaloides</i> is unknown as, to my knowledge, no cultivable strain exists, and so is theorised. Therefore <i>S. nivaloides</i> should not be named here as a motile flagellated snow algae. It should be made clearer throughout the review that the life cycles of many common snow algal species are only theorised to date, with more care to name the species for which this transition	<i>Sanguina</i> species have been shown to be cultivable, for example: <i>Sanguina aurantia</i> (Canada), Raymond et al., 2024 https://doi.org/10.1093/g3journal/jkae181 <i>Sanguina nivaloides</i> (Norway), Détain et al., 2025 https://doi.org/10.1128/mbio.02954-24 With this said, we do understand your concern.

	from vegetative motile to encysted cells has been observed.	We have updated lines 141-151 to emphasize the fact that lifecycles for some species are theorized, with the lifecycle of the majority of snow algae species not having been studied: “An original overview by Hoham and Duval (2001) described snow algae participating in a cyclical process where they overwinter as dormant cysts on a summer snowpack surface and/or the soil-snowpack interface. Current knowledge suggests that with the onset of spring snow melt, the cysts germinate into green, motile flagellated cells which respond to spring meltwater, light and the subsequent release of nutrients by migrating upward toward the newly accumulated snow surface formed during autumn and winter, as shown in Figure 4. At the snow surface, or from another environmental cue, the microalgae transform into non-motile cells once again, appearing in colours including green, yellow, gold, orange and red. There is evidence for this lifecycle in the <i>Chloromonas</i> genus (e.g. Rea & Dial, 2024; Sculer et al., 2023), as well as a similar lifecycle in the <i>Chlainomonas</i> genus (Matsumoto et al., 2024) (though habitat specific in a snowy lake environment), but it has been only theorised for other algae genera and species.”
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141	Similar to above, please make clear in this section that not all snow algal species are known to experience this life cycle, and for many it is only theorised.	Lines 144-147: have been changed to reflect this: Current knowledge suggests that with the onset of spring snow melt, the cysts germinate into green, motile flagellated cells which respond to spring meltwater, light and the subsequent release of nutrients by migrating upward toward the newly accumulated snow surface formed during autumn and winter, as shown in Figure 4. At the snow surface, or from another environmental cue, the microalgae transform into non-motile cells once again, appearing in colours including green, yellow, gold, orange and red. There is evidence for this lifecycle in the <i>Chloromonas</i> genus (e.g. Rea et al., 2024, Schuler et al., 2023) but it has been only theorised for other algae genera and species.
152	Include Ganey et al 2017 for further information on the contribution of wide scale snow algal blooms to albedo reduction.	This reference has been added on line 152.
159	Please include the species this study is focused on.	Line 159: This line and the following sentence have been changed to include the genera in this study: “The temporal aspect of snow algal migration and lifecycle in <i>Chlamydomonas</i> and <i>Chloromonas</i> species has been described by Kviderova et al., 2010, having found snow algae at a study site in the

		Giant Mountains, Czech Republic to complete their entire lifecycle within a snowpack in a span of several weeks.
163	The Roussel et al study is focused on the analysis of remote sensing data and so is not centred specifically on <i>S. nivaloides</i> . Perhaps rephrase to more general language.	Line 163: The specific mention of <i>S. nivaloides</i> was removed, this was a misinterpretation of the paper. Line 163 was re-written as: “Roussel et al., 2024 reported that the formation of red algal blooms (when snow algal cells reach their non-motile, red cyst phase on a snowpack surface) in the European alps requires the presence of liquid water throughout the whole snow column for at least 46 days. One would hypothesise that this value would differ for differing species.”
170	Again please include the exact species/genera this study was focused on, or whether there were multiple snow algal species present. This allows for better context throughout the review with much diversity present within the motility and life stages of different snow algal species.	The study states “No effort was made to classify cells beyond identifying red pigmented spherical cells as members of the <i>Chlamydomonadaceae</i> family” on page 5 under the “Sampling and cell counts” heading: https://doi.org/10.1080/15230430.2024.2370905 . Saying that, we understand your comment and will include this statement. At the end of the paragraph beginning on line 168 we have now added: “The authors stated that no effort was made to classify the cells beyond being members of the <i>Chlamydomonadaceae</i> family.”

177	It is not clear through this study that these red algal blooms are dominated by <i>S. nivaloides</i> so please rephrase this section accordingly.	We acknowledge this, thank you. Line 177 and onwards has been rephrased: “These findings are consistent with (Roussel et al., 2024) where Sentinel-2 satellite data from the European Alps displayed red algal blooms that persisted in environments where the ground was not permanently frozen. This pattern is notable in light of evidence that <i>S. nivaloides</i> cysts irreversibly lose photosynthetic capacity when exposed to -5 °C (Ezzedine et al., 2023; Roussel et al., 2024). Although the relationship remains speculative, inhibited photosynthetic ability would presumably impact upwards swimming behaviour motivated by phototaxis. If the active resurfacing pathway is curtailed, bloom dynamics should be similarly impacted.
206:	This short paragraph is lacking an overall point I find. What does it mean for the discussion of the paper that the mean swimming speed is negligible?	We thank the reviewer for their comment. The purpose of this comparison was not to say that swimming speed is universally negligible and unimportant, but many studies refer to the presence of meltwater and the implication that this allows snow algae to swim and migrate. We wanted to contextualise this by saying that in regions of sustained flow due to melting, advective velocity from the meltwater exceeds reported swimming

		speed by several orders of magnitude. This prefaces the subsequent discussion of snowpack conditions under which flow may be reduced or effectively stagnant, allowing active motility to play a more important role.
235	Please include specific references as to these mechanisms being observed in snow or other microalgae.	Lines 233-235 changed from: “Active particles such as biota have also developed unique survival strategies when trapped in ice, such as producing exopolymeric substances and antifreeze glycoproteins which increase interfacial melting, enhancing their motility and survival ability in harsh, icy conditions.” to “Active particles such as biota have also developed unique survival strategies when trapped in ice, such as producing exopolymeric substances and antifreeze glycoproteins which increase interfacial melting, enhancing their motility and survival ability in harsh, icy conditions e.g. (Meiners et al., 2003; Riedel et al., 2006). It has also been shown that motile microalgae in the genus <i>Chlamydomonas</i> can produce ice-binding proteins (Raymond and Morgan-Kiss, 2017), which bind to the surfaces of ice crystals and hinder their growth (Bar Dolev et al., 2016).”

		- 4 references added - 2 examples of microorganisms (sea algae/diatoms) producing exopolymeric substances - 1 reference specifically about <i>Chlamydomonas</i> - 1 contextual reference about ice-binding proteins
335	It may also be worth mentioning here the capacity for snow algal to demonstrate plasticity to the available nutrient conditions as opposed to moving to where they are optimal (see Broadwell et al 2023). Although not focused on movement, it demonstrates the range of mechanisms present across motile snow algae.	This is an important point. We have added to line 339: “It is also worth noting that snow algae have demonstrated plasticity in response to the nutrient conditions available to them (Broadwell et al 2023). For example, Broadwell et al. (2023) demonstrated considerable stoichiometric plasticity across multiple snow algal strains, with cellular C:N ratios varying substantially under nitrate concentrations representative of natural snowpacks. Despite reduced growth under nutrient-limited conditions, the algae maintained growth across a broad range of nitrate availabilities, suggesting an ability to acclimate to nutrient-poor environments rather than relying solely on movement towards more favourable conditions. This has particular

		implications for the portion of cells belonging to motile snow algal species which are immobile either temporarily due to lifecycle stage, environmental stressors or other reasons.”
General Comment	This review investigates the mechanisms underlying the motility in snow algae, a phenomena that is still not fully understood. There is an updated overview of the importance of snow algae in the global context, including some updates to the known diversity of this group of microalgae. The majority of the review then gives an in-depth overview of the different environmental parameters that can trigger this motility, and the mechanisms behind this. This is a detailed and well-reasoned review that synthesises a wide range of relevant literature to provide new insights into the responses of mobile snow algae to different environmental parameters. There are many interesting arguments raised as to what may govern the movement of snow algae within	We thank you kindly for your thorough review of this manuscript and hope that the revisions made in response to each of your comments have addressed the identified generalisations and potential oversights.

	snowpacks, alongside how these understandings could be scaled up to larger scales and possibly into the future. The explanations given for the biophysical mechanisms described are very accessible, alongside clear illustration. That said, there are a number of generalisations and potential oversights that this review feels needs to be addressed before publication.	
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