Letter of responses to the recommender and the reviewers

Authors' replies to the recommender and the reviewers' comments are highlighted in blue

#Recommender's comments

Dear authors

Thanks for sending this nice text to PCI, and sorry for the time taken to get a first decision on it; summer holidays and the difficulties we all are struggling with this year of confinations delayed the process of getting two sound reviews and reviewing the text myself.

Both the two reviewers and myself believe that it is a solid piece of work, and is in general well written. The reviewers highlight some minor problems with yhe understandability of certain parts of the text, including the need for specific clarifications and presenting further information on data and traits. Among these, I would like to highlight the need to be a bit more critical with the limitations of SDM approaches to model invasions. They certainly are one of the best tools we have to forecast the potential areas of impact of invaders, but as one of the reviewers states, their accuracy depends on the quality of the original data (on both species occurrence and climate). Besides that, for many (if not most) species the environmental conditions they occupy now do not comprehend the whole range of conditions where their populations could present positive growth rates (i.e. their potential distributions). This difficults forecasting all the conditions where these species could thrive and become succesfully naturalized during the process of invasion. This limitation does not diminish the value of your study, specially in the extreme conditions of the seldom studied archipelagos you work with. But calls for being cautious about the limitations of the results you obtain. Please try to make clear for the reader these limitations, in the paragraph of the introduction indicated by the reviewer, and also in the discussion, (around current lines 380-400), where you can also indicate the gains of having been able to develop a more mechanistic model using high-quality data on species abundances, as indicated by the other reviewer. You can take a look to Jiménez-Valverde et al (2011) Biological Invasions 13, 2785–2797 or Srivasta et al (2019) CAB Reviews Perspectives in Agriculture Veterinary Science Nutrition and Natural Resources 14:1-13 for a more critical view on the use of SDM to model invasions.

Authors:
Dear Prof. Hortal,

First of all, we would like to thank you for the time and effort you spent in handling and reviewing our manuscript. We are glad that you appreciated our work and we hope that you will appreciate even more our revised version. Please find below our detailed responses to your comments as well as to the reviewers' comments.

We completely agree on the need to interpret our results with care when using correlative SDMs for modelling the distribution of alien species. We are aware that modelling the occurrence of alien species showing limited range filling can provide at best a snapshot of the current species-environment relationship net of dispersal and biotic constraints (i.e. realized), while necessarily underestimating the species potential distribution (*sensu* Jackson and Overpeck, 2000). To address your comment, we now acknowledge in both the introduction and the discussion sections, the inherent weaknesses of using SDMs to model biological invasions (see lines 99-104 and lines 460-462).

Jackson, S. T., & Overpeck, J. T. (2000). Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology*, *26*(sp4), 194-220.

#Reviewers' comments

Prof. Convey

The threat and impacts of biological invasions have justifiably received much increased attention in recent years across the entire Antarctic region, but in particular in the sub-Antarctic islands, across which over 90% of known non-natives in Antarctica are recorded from. Of these, around half of the known species are of 'higher' (flowering/vascular) plants, with the largest numbers recorded from the extensively impacted Kerguelen archipelago in the Indian Ocean. This study focuses on the Crozet archipelago, a separate (also French-administered) island group also in the Indian Ocean which closely shares human historical and biological features with Kerguelen. This is the first detailed analysis of this type that I am aware of for drivers of plant invasions in these (or other sub-Antarctic) island groups, although a number of more general studies and reviews are available. The results described provide important information that will be helpful to those responsible for risk management and conservation in this region.

The paper is generally clearly written and appropriately and thoroughly referenced; very minor language editing would be helpful throughout. My comments are generally minor and offered more to stimulate discussion than being critical.

Authors:
Dear Prof. Convey,

We would like to thank you for the time you spent reviewing our manuscript and for your nice words regarding our study. We are really pleased that you appreciated our work and we really appreciate your positive feedback and helpful comments. We integrated all your suggestions in the main text and thoroughly answered to all of your comments (following a list of point-by-point replies).

L44-46 – this is an inevitably brief reference to the impacts of climate change in this region, but is in danger of being a bit simplistic….warming trends have been identified in some sub-Antarctic islands, although perhaps more important are some quite drastic changes in precipitation and drying regimes, while studies have also noted that some of these changes can have serious negative impacts on various native plant species (especially I think on Marion and Macquarie Islands). The very widespread impacts of non-native vertebrates on most of the sub-Antarctic islands also deserve mention. Taken together, these points highlight the potentially very complex interactions between several major factors, which may have both positive and negative impacts on both native and non-native biota.

Authors: you are right, and we thus rephrased lines 44-46 (lines 45-48 in the revised version) to fully account for the complex interaction between abiotic (e.g. changes in temperature and precipitation regimes) and biotic (e.g. impacts of introduced large herbivores) factors that have affected both native and non-native biodiversity of sub-Antarctic islands in the last decades.

L48 – I believe the Molina-Montenegro et al study refers to the South Shetland Islands and Antarctic Peninsula, in the maritime Antarctic. Perhaps there should be a line early in the paper defining what is included in the term 'sub-Antarctic' for the purposes of this paper.

Authors: yes, Molina-Montenegro et al. (2012) indeed referred to the South Shetland Islands and to Antarctic Peninsula. We therefore deleted this reference, and followed your recommendation by adding a geographical definition of sub-Ant. islands (see line 34 of the revised manuscript).

L85 – I do strongly accept the usefulness and increasing application of SDM approaches for modelling non-native species distributions. Perhaps one caution I would raise is that a regular feature of some biological invasions in the wider invasion literature is that at least some such non-native species appear capable of making 'jumps' that take them beyond what would be expected to be a suitable/viable habitat based on the available ecophysiological and physical climatic characteristics of their native ecosystems. One example of this is the global pest moth species Plutella xylostella which has been introduced to and spread quite widely on sub-Antarctic Marion Island. In the early 2000s, when this was first reported, the annual climatic characteristics of Marion Island appeared to place it beyond the capabilities (in the published literature) of this moth to survive year-round and establish there. This highlights that modelling approaches such as SDM may only be as 'good' as the data available to input to them (this is further to the caveats recognised at l95-97).

Authors: indeed, this is a very valid and important point on which we completely agree. We are aware that modelling the occurrence of an alien species using correlative SDMs provides, at best, a snapshot of the realized species-environment relationship, while not being informative of the species (current and more so future) potential distribution. To address your comment (and an analogue one raised by Prof. Hortal, the recommender), we now highlight this inherent weakness to the application of SDMs for alien species in the introduction and discussion sections (see lines 99-104 and lines 460-462).

For completeness in the use of citations to the use of this approach in the Antarctic Peninsula region, two further recent studies on, respectively, invading and native invertebrates are pertinent: Pertierra et al 2019 J Biogoeg on the invading midge Eretmoptera murphyi and Contador et al 2020 Sci Rep on the maritime Antarctic native Parochlus steinenii.

Authors: we thank you for the suggested references. However, lines 85-91 (original version of the manuscript) exclusively (and intentionally) referred to studies that used SDMs to analyse plant invasion in the sub-Antarctic, while Pertierra et al. (2019) and Contador et al. (2020) focused on an alien and a native insect, respectively. We therefore prefer keeping the

references as they are and focus more specifically on plants. We will be anyway glad to rephrase the paragraph if you deem it necessary to mention SDMs studies which are not strictly focused on alien plants and were carried out in the sub-Antarctic and Antarctic regions.

L120 – it would seem appropriate to have explicit reference to a good map figure in this subsection.

Authors: thank you for this suggestion. We added a map of the study area (now 'Figure 1').

L123 – what is 'EPSG'?

Authors: 'EPSG' is the acronym of the European Survey Petroleum Group. The EPSG provided a list of numeric codes to unambiguously identify coordinates reference systems. In the original version of the manuscript, we provided a coordinates pair and the associated EPSG code to allow the reader inspecting the study area on any Geographic Information System. However, following your suggestion, we added a map of the study area and removed the coordinates pair (and associated EPSG code) from the text.

L137 – perhaps be explicit and name the herbivores that impacted Possession.

Authors: as reported in Convey & Lebouvier (2009), sheep were the largest introduced herbivores on Possession Island. We accordingly indicated this information in line 147.

L141 – although a weblink is given, and not knowing this journals' policy with supplementary material, I suspect many readers would appreciate having direct access to a list of these recorded species directly linked to this paper, including the subsets that are persistent and invasive.

Authors: the weblink provides access to the latest management plan of the "*Reserve naturelle des terres australes françaises*", which, among other issues, reports the most updated list of the alien plant species recorded on Possession Island (personal communication, Marc Lebouvier). The document can be accessed without restriction as it is fully public. However, as the document is quite vast, we agree that the reader may benefit from a more direct access to this list. We therefore added in the manuscript a reference to page 99 of the management plan (see line 150), where the list of the alien plant species colonizing Possession Island is reported along with other relevant information.

L182 – if 'flowering' includes mechanisms of non-insect fertilisation (wind pollination, self fertility) then is it appropriate to exclude all these traits? With reference to seed characteristics, are any of the selected species known to have seeds that can facilitate dispersal either within vertebrate guts or attached to their fur/feathers?

Authors: information on the role of animals in facilitating the dispersal of seeds is not univocal in the literature for the species considered in our study. Vidal et al. (2003) reported that penguins might accidentally spread alien plant seeds (regardless of specific seeds characteristics) on Possession Island, though they also stressed that the effects of penguins on seed dispersal are likely to be marginal and limited to littoral areas (where penguins establish rookeries). On the contrary, Mathakutha et al. (2019) listed *Poa annua*, *Cerastium fontanum* and *Sagina procumbens* (high-spread species in our study) among the alien species recorded on Marion Island associated with unassisted dispersal. Furthermore, the authors did not include dispersal mode among the traits relevant for discriminating invasive and non-invasive alien plants.

Although there is some evidence (and it is reasonable to think) that animals, in particular birds, may facilitate seeds dispersal within and among islands (see Gremmen & Smith 1999 & Ryan et al. 2003), it is certainly true that humans remain the most important vectors of propagules introduction and spread on sub-Antarctic islands (as widely reported in Frenot et al. 2001 and Whinam et al. 2005 to cite a few). We are aware that explicitly accounting for the role of birds, especially petrels and skuas, in spreading alien plants propagules might have enhanced models performance (in terms of both goodness-of-fit and predictive power). However, data on the nesting sites of these species on Possession Island are scarce, and, more importantly, reliable information on their movement and, therefore, potential influence on seed dispersal is absent.

References:

Frenot, Y., Gloaguen, J. C., Massé, L., & Lebouvier, M. (2001). Human activities, ecosystem disturbance and plant invasions in subantarctic Crozet, Kerguelen and Amsterdam Islands. *Biological conservation*, *101*(1), 33-50.

Gremmen, N. J. M., & Smith, V. R. (1999). New records of alien vascular plants from Marion and Prince Edward Islands, sub-Antarctic. *Polar Biology*, *21*(6), 401-409.

Mathakutha, R., Steyn, C., le Roux, P. C., Blom, I. J., Chown, S. L., Daru, B. H., ... & Greve, M. (2019). Invasive species differ in key functional traits from native and non-invasive alien plant species. *Journal of Vegetation Science*, *30*(5), 994-1006.

Ryan, P. G., Smith, V. R., & Gremmen, N. J. M. (2003). The distribution and spread of alien vascular plants on Prince Edward Island. *African Journal of Marine Science*, *25*(1), 555-562.

Vidal, E., Jouventin, P., & Frenot, Y. (2003). Contribution of alien and indigenous species to plant-community assemblages near penguin rookeries at Crozet archipelago. *Polar Biology*, *26*(7), 432-437.

Whinam, J., Chilcott, N., & Bergstrom, D. M. (2005). Subantarctic hitchhikers: expeditioners as vectors for the introduction of alien organisms. *Biological Conservation*, *121*(2), 207-219.

194 – could some explicit examples be given of such areas?

Authors: we rephrased the sentence as we agree that it was unclear in the former version. In particular, we clarified that we compiled functional traits data from the scientific literature and specifically focusing on measured/collected data in areas environmentally analogous to Possession Island, explicitly mentioning in the text the areas we referred to (see lines 203-205 of the revised manuscript).

L307 – I certainly don't question the finding, but is there any surprise that J. bufonius shows this negative relationship with precipitation? I would have assumed members of this genus would be positively associated with wet habitats? Is high precipitation associated with lower temperature?

Authors: yes, we agree that the results for *Juncus bufonius* might appear surprising at first glance. We speculate that the low occurrence probability predicted for this species on the western side of the island might be the result of multiple (possibly combined) issues:

- Species distribution models rely on the assumption of the species being in equilibrium with the environment. In some circumstances, such as biological invasions, this assumption is hardly, if never truly, met. As pointed out above, modelling the occurrence of an alien species using observational data necessarily leads to the underestimation of the area environmentally suitable for the species to establish and maintain a viable population. The introduction of *J. bufonius* on the island is rather recent, and the species is likely to be at an intermediate invasion stage. Therefore, the low occurrence probability predicted on the western side of Possession Island for this species could be the result of the simultaneous effect of abiotic, biotic and historical (dispersal-related) factors, while not necessarily pointing to the lack of suitable habitats on that side of the island.
- *Juncus bufonius*, likewise the other low-spread species we identified here (*Poa pratensis* and *Stellaria alsine*), may effectively lack key functional traits that would allow this alien plant species to spread far from places where anthropogenic propagule pressure is high (notably, areas close to the research station and *Baie Américaine*). Moreover, as stated in lines 389-391, we speculate that the precipitation pattern observed on Possession Island substantially overlaps with human presence and activity across the island, and that the resulting lower anthropogenic propagule pressure may prevent the establishment of less invasive species, such as *J. bufonius*.
- Precipitation abundance does not seem to correlate with temperature as it rains more on the western side of the island, whereas temperature decreases moving towards the inner higher sectors. At extreme latitudes, higher precipitation might induce a higher frost stress, which, in turn, might have detrimental effects on the establishment of alien species lacking specific adaptations to cope with the harsh sub-Antarctic climate. As underlined in lines 402-405, the lack of high spatial resolution data on variables such as number of frosting days or snow cover (and other processes acting at a much finer scale, e.g. plant-soil microbiota, soil properties) might have reduced our capacity to control for these important factors, which are likely to affect the distribution of *J. bufonius*.

L380 (para) – a couple of thoughts that might be added to discussion in this para: first, would it pertinent to draw analogy with the way P. annua on King George Island (maritime Antarctic) appears to have escaped from local human influence

in its rapid recent expansion from its original introduction site at the Polish research station there? And partly drawing on that example, it would be appropriate to mention the potential role of some species being able to establish seed banks which ensure some level of extended viability even if it were possible to eradicate a proportion of the visible plants.

Authors: the analogy with the invasion of *Poa annua* on King George Island is absolutely pertinent. We integrated some thoughts about it in lines 399-401 to further support our findings on the invasion pattern observed for high-spread species. Moreover, we mentioned the important role of seed banks in supporting alien plants establishment and spread in lines 450-453.

L394 – a similar point is emphasised generally for terrestrial studies in both Arctic and Antarctic regions by Convey et al. 2018 (Polar Biol).

Authors: thank you for the suggested reference, which we included in line 413. In particular, we cited:

Convey, P., Coulson, S. J., Worland, M. R., & Sjöblom, A. (2018). The importance of understanding annual and shorter-term temperature patterns and variation in the surface levels of polar soils for terrestrial biota. *Polar Biology*, *41*(8), 1587-1605.

L441-443 – while this closing sentence is certainly true, it is also something of a motherhood statement – readers might be interested in the inclusion of a para in the paper (Introduction and/or Discussion) on whether control measures have been carried out or are planned directed towards such non-native plants – the statement of 'they might be', on its own, is rather irrelevant if they are not!

Authors: we agree that the closing sentence sounded a bit rhetorical and inconclusive. Up to our knowledge, there are no management actions currently undertaken to control the spread of the alien plant species we considered on Possession Island, while, for instance, eradication plans focusing on mammals have been carried out on both Crozet and Kerguelen archipelagos (e.g. rats on Possession Island; rats, cats and reindeers on Kerguelen).

We would anyway prefer not to integrate new paragraphs about alien species management in the introduction and discussion sections. We feel that a focus on management actions and practices would deserve a proper discussion and, more importantly, could be out of scope in the manuscript, as our main aims were specifically to explore the drivers of plant invasion on sub-Antarctic islands and highlight key functional traits conferring plant invasiveness therein. To address your comment, we rephrased the sentence to read less sensationalist and more in line with the study aims (see lines 464-467).

Dr. Matos

Dear authors and recommender

First of all, I would like to apologize for my delay in the review process. Having said that, I would like to say that it was a pleasure to read this work. The topic is very interesting, the paper is very well written, it follows a very clear outline, the methodologies applied are, in my opinion, appropriate for the aim of the paper (from the downscaling of the climate variables, a key point to me in this work and a major constraint in ecological studies in polar or sub-polar regions, to the SDMs), and the results are clear and very interesting. I have just some minor comments that I feel could improve even more the manuscript.

Authors:
Dear Dr. Matos,

We thank you for the time and effort you dedicated in reviewing our manuscript. Also, we thank you for your positive and constructive comments, which helped us improving the content of our manuscript. We did our best to integrate all your suggestions, and we carefully replied to your comments (see below our point-by-point responses).

Title

I really like the title, but I miss something there related to the traits, which are in my opinion a key aspect of this work. As it is, it seems that you only address the drivers of invasion, and not the plant traits conferring invasiveness. Rephrasing the second part of the title would make it easier to pass both messages to the reader.

Authors: very good point. Thanks a lot for highlighting that. We agree that the original title was missing a clear reference to the role of functional traits in determining plant invasiveness. We therefore changed the title to: "*Once upon a time in the far south: Influence of local drivers and functional traits on plant invasion in the harsh sub-Antarctic islands*".

Abstract

Line 21 shouldn't it be "being more invasive" or "being the most invasive" instead of "being most invasive"?

Authors: yes, we corrected this sentence.

Material & methods

1. In the M&M, when describing species traits, it would be important to add a table with the six species traits. That, in my opinion, would facilitate understanding the results, as the readers would already have in mind if a species is, e.g., tall or short, or an old or new resident. Not all readers will be familiar with the species, and this would make the flow of the paper easier to follow and would be helpful to understand the invasion patterns related to the traits. It would prevent readers to go back and forth in results to try to figure this out in the text (as happened to me).

Authors: we agree that a table reporting the species-specific values of the traits might facilitate the reading and the understanding of the manuscript. We therefore integrated information on all traits used in the analyses in table S1.1, which was already reported in supplementary material S1, but only provided data on old *vs* new residents species groups.

Discussion

2. In the Discussion, line 363 when you first introduce the two main invasion patterns, I missed here, along with what you said, a clear description on the traits associated with each of these strategies. Similar to what you have in the abstract. In my opinion, it is always good to first clearly state these key findings in the first sentences of the discussion. This will serve as an interest teaser to the reader and engage him to read the rest. And would make this clear, because I felt that, apart from the abstract, this was not clearly mentioned in the main text.

Authors: as suggested, we added a clear statement about the functional traits affecting alien species invasiveness in lines 377-379.

3. Also, in the discussion, sentences in lines 359, 377 and 403, are somewhat confusing to read, because it seems you are concluding something based on your results, but then you attribute other works references to those sentences content. Is it a mix of both? You saw that, and those patterns had already been highlighted in previous works? It wasn't clear to me what the intention was. Please clarify these sentences.

Authors: thank you for pointing out these unclear sentences. We modified lines 372 and 422 (revised manuscript version) to better link our findings with those reported in the cited studies, while we deleted the reference from line 379 (original version of the manuscript), as it was unnecessary.

4. Line 391 maybe you mean "temperate latitudes" instead of temperature?

Authors: yes, we meant "temperate" indeed. Thank you for highlighting this typo, we corrected it.

5. Line 392 maybe remove "only" from the "a single weather station only"

Authors: we deleted "only".

6. When you highlight the limitations of your work, I feel you missed an important one. This work was based on presence/absence data. How do you feel the results would be with abundance data? Would the patterns observed sustain? Do you feel it could have, e.g., helped emerged relationships in the traits whose relationships were weak or inexistent (e.g. reproduction, or leaf traits)? Could this be the reason why models weren't as good for those two species? Maybe these environmental variables are related to their abundance patterns and not their presence. I suggest you add something related to this issue in the limitations.

Authors: we agree that abundance data would have been more informative than presence/absence data to inform alien species responses to environmental and human-related variables, and would have probably enhanced both fit and SDMs predictive performance. At the same time, we think that some of the limitations inherent to the use of SDMs for modelling biological invasion would have anyway remained, e.g. underestimation of the species invasion potential due to "false" absences (absences due to dispersal constraints more than to environmental unsuitability). Also, we think that the low predictive performance obtained for the high-spread species SDMs was strongly due to the lack of information on

processes influencing species distribution at a fine spatial resolution (e.g. soil properties, plant-soil microbiota interactions). Including these variables into model specification would have allowed further explaining the distribution patterns observed for the high-spread species.

As regard to the functional traits, we agree that using abundance data to fit both the single-SDMs and the multi-SDM could have favoured the emergence of other important interactions between species features and human-related variables.

Unfortunately, we did not have high-quality abundance data of the selected alien species.

To address your comment, we added some thoughts about the potential benefit of using abundance data (and possible drawbacks of not using them) in the discussion (see lines 405-408, 458 and 460-461).

Finally, just as an extra suggestion, I believe that a graphical scheme summarizing the results would help readers grasp better the message, and it could also serve as a graphical abstract. A scheme (maybe with icons) showing the main drivers of invasiveness, the two strategies of invasion and the traits mediating them.

Authors: we agree that a graphical abstract may help conveying the take-home messages of the manuscript. Therefore, we drew one that will be submitted along with the revision material.