Comments by the recommender

Your manuscript has been reviewed by two researchers with good knowledge on dune communities, and proficient in different statistical methods. Unfortunately I did not manage to secure a reviewer with deep knowledge on JSDMs, but the reviewers are not statistically naïve, and I'm aware that took some time to review the literature on these methods. From their review and my own knowledge the application of this methods seems well performed. So based on the strong points of the quality and coverage of the data, and the appropriate use of JSDMs to assess community-level responses, I'm certain that a new version of this preprint will merit my recommendation.

However, for your work to reach such status it needs to undergo major revisions. The final purpose of the peer review system is that in enables scientific conversation and, as a result, improves the work that will be finally published, or recommended in this case. The comments of the reviewers go in that direction. I find particularly interesting the proposal that you include explicit analyses on abundance; I believe that they will finish "drawing the whole picture" that JSDMs start providing. I'm not sure which analysis would be better; perhaps a multivariate analyisis that accounts for species abundances may be a good complement, as stressed by the other reviewer. I believe that if you accept the challenge of including these analyses may help making your work a milestone in community ecology; but I concur it will make it longer. In any case, please consider adding this approach or another analysis based on species abundances seriously.

Our answer: thanks for this suggestion. We added two distance-based approaches to contrast with JSDM.

Also, given the importance of phylogenetic signal, it is quite possible that providing separate analyses into arthropods and molluscs, in addition to the analysis of the whole community, may give some deeper insights about the dynamics of these two groups. It can be argued that JSDMs account for the whole community, but it is also fair to argue that the interactions within each one of these groups are likely to be stronger than between groups (if we leave apart predation of molluscs by arthropods, of course).

Our answer: we discussed this as well. Separating both showed to be challenging as molluscs show some collective underrepresentation in those regions with less calcareous soils.

The reviewers also provide many other comments aimed to raise the overall quality of your work to a highest level. Besides reviewing your preprint, please provide a point-by-point response to all their comments. I'm looking forward to see a new version of this manuscript along the path lied by the reviewers.

Our answer: thanks. We implemented all changes, and address how we dealt with their comments in the separate referee reports.

Comments by referee 1

“Drivers of plant-associated invertebrate community structure in West-European coastal dunes”.
This work studies the factors that influence the community structure of invertebrates growing on marram grass. They performed a stratified sampling design into six biogeographic areas across the North Sea. They evaluated the degree to which plant spatial organisation affects local species composition by sampling marram grass tussocks that are spatially arranged differently. To understand how species traits and their phylogeny influence the makeup of species communities, they used a quite novel approach, the joint species distribution models. The most significant factor they found affecting invertebrate community structure was biogeography, followed by species-specific responses to the cover and vitality of marram grass. They also found that functional traits and phylogeny had a minor impact on the species distribution patterns while the residual species covariation suggested negative interactions between groups of specialist and generalist species.
Overall, the manuscript is well-written and easy to follow. The objectives are certainly interesting, and the results and discussion are clear. The use of JSDM is particularly noteworthy, as this relatively new approach enables a deeper study of community structures by analysing community-level responses to different drivers, capturing biotic interactions, and assessing the influence of missing covariates on residual species associations.
The title clearly represents the contents of the article, and the abstract is concise and addresses the study's main results. The objectives of the study are explained in detail in the introduction, which also presents the hypotheses or the study and relies on relevant, previous and current, research in the subject.

Our answer: thanks for this positive evaluation

Enough information is given about the methods and analysis that allows other researchers to replicate the research. The author should, however, provide a more thorough explanation of the rationale behind the selection of the sampled locations, particularly the reason why there are only two widely separated sites in the UK and four regularly distributed sites within the European coast. The topic is especially important since biogeographic areas are the main structuring factor determining the invertebrate community structure of the marram dunes.
The statistical analyses seem feasible and suitable for the research's goals, but since I'm not a specialist on JSDM, I'll leave this part of the review for reviewers who are. I also would like to stress that the authors were honest and accurately detailed the limitations and challenges they faced while analysing the data, particularly the need to limit their analysis to species that were sufficiently represented across the sampling.

Our answer: thanks for this positive evaluation. As you will notice, we now argue why we have only two sites in the UK (two most important areas in the ‘two seas region’ with sandy coasts and developed marram dunes) and also provide in the supplement a more detailed analysis of the differences in climatology among the regions.

Regarding the results, again, and after reading several works on JSDMs, statistical analysis

results seem sound and make sense to me, also from an ecological point of view; however, since this isn't really my area of expertise, I'll leave this part of the review to others who know more about it.
Additionally, the research from the field, current as well as past, is included in the discussion. The findings support the conclusions and prove that the analysis's interpretation is reasonable rather than overstated. However, as already stated, more thorough explanation of the sampling site characteristics should be provided, as biogeographic areas are the main structuring factor determining the invertebrate community structure.

Our answer: thanks for this positive evaluation. We now elaborated on these differences

I probably would not stress so much that traditional multivariate analyses can lead to oversimplified results, but that with this approach is possible to address different questions and, specially, to deepen into singular species responses and community's inter-species relationships. I would also discuss the complementarity of both approaches. Indeed, I am quite sure that multivariate studies will also be able to identify major biogeographic areas as the most important structuring component of marram dune invertebrate community structure. In fact, it would be wonderful to test that (just a suggestion/challenge).

Our answer: This is a good suggestion. As you will see, we now added RDA/Permanova analyses as well. These distance-based approached yield indeed the same general insights, but underperform with respect to species-specific drivers of the complex community organisation. Differences between both approaches are now discussed.

Minor comments:
Line 22: remove space before the comma. Additionally, plant common names should be written in lower case (marram), as you have done throughout the rest of the manuscript.
If the colours used in Figure 2 (or small icons) were used on every figure for all the categories (orders and classes), the figures would all become easier to interpretate.
Figure 6 requires an explanation of the abbreviations.

Our answer: thanks for this comment – we followed these suggestions.

Comments by referee 2 (André Mira)

The manuscript entitled “Drivers of Plant-Associated Invertebrate Community Structure in West-European Coastal Dunes” presents a compelling study that effectively deconstructs the drivers of community assembly and examines their significance in shaping the species composition within these coastal environments. The manuscript is based on a high-quality dataset collected for this study, and it was thoroughly analyzed. While the paper successfully achieves its objectives, I believe a few changes could further enhance its overall quality:

1) I really miss a proper analysis based on abundance. Although they partially account for it by reducing the number of species in the study to the 50 more abundant species, there were still some issues with the occurrence data as it was mentioned in the discussion. Although I can understand that such problems may be amplified if analyzing abundance explicitly, this does not necessarily have to be the case. And importantly, it would give us a new layer of complexity that, I believe, will improve the final quality of this work, providing novel insights on the dynamics of dune communities.

Our answer: this is the same suggestion as reviewer one and we followed this. We added an abundance (distance) based analysis and critically compare both with respect to the yielded insights (generally similar) and precision/conclusiveness (JSDM outperforms RDA/Permanova).

2) I believe some analysis of how local environmental factors vary across districts would greatly strengthen the discussion.

Our answer: this is now reported in appendix with respect to climatic variation. Other major differences of the regions are clarified in the methods section

3) Furthermore, given the significance of phylogenetic signals, it would be valuable to explore how the Arthropoda and Mollusca classes are influenced by the studied factors separately. Such addition would improve our knowledge on the influence of the used environmental drivers inside these phylums and how they interact.

Our answer: this is considered. As explained in the response to the recommender, such a split was not a real success as models failed to converge because of the underrepresentation of the molluscs in specific areas. We nevertheless add this information to the discussion.

4) Finally, I think the conclusions of this work should be expanded to emphasize the crucial conservation measures needed, as marram grass plays a vital role in the stability and biodiversity of these West-European dune systems.

Our answer: this is a good suggestion. This was already touched, but we now expanded. We specifically focus on conflicts between functioning and biodiversity

Besides that, I would like to propose a few minor changes:

Our response: Thank you. As you will see, we implemented all suggestions. We here and there used an alternative wording though. We add some specific comments below when relevant.

- Introduction -

Row 35: “Biodiversity is organized” sounds too strong; I would change organized for shaped/arranged/influenced

r. 35-36: “biogeographic, regional, and local factors, each operating at a different spatial scale” double confirmation - biogeographic, regional, and local factors already give away a spatial scale specificity

r. 36-40: Detailing factors that occur in biogeographical and regional scale, but not in local

r. 46-47: I’m suggesting you rephrase like this: Herbivory is a key factor that shapes community dynamics depending on the identity, abundance, and traits of the involved species.

r. 64: Would change the definitive tone of the sentence: heterogeneous habitats have the ability to sustain more species

r. 74: Consider improving this passage “All of these traits are ultimately shaped by evolution.”. It could be even replaced/modified by the sentence in r. 77-78

r. 83-84: If I correctly understood, sand dynamics affect horizontal structural complexity but it’s unclear how only dead plant material affects vertical complexity.

Our response: all edits considered and followed

- Material & Methods -

r. 112: districts sounds a bit too much like an administrative sectorization, at least to me; what about using “sections” instead of “districts”? If you agree, you’ll have to change this in the whole document

Figure 1: Consider adding colors to represent acidic and calcareous dunes. Furthermore, improve the quality of the satellite picture present in the inset, or change it by another depiction format of the area.

r. 126-135: Sampling methodology requires clarifications (see below).

r. 127-128: “The mean transect length 127 ± SD was 1212 ± 786 m” what defined/limited the length of transect?

r. 18-129: Samples were only in the first 100 m inland from the seaward side of the foredunes? Not clear why the remaining transect was not qualified for sampling.

r.130: “with individual samples separated by at least 20 m” Which results in a maximum of 5 sampling points for each transect?

r. 131-132: “surrounded by pure marram grass vegetation 131 and bare sand (e.g., no shrubs, trees, or large quantities of other species).” Consider replacing “pure” by “only” and state the radius of species limitation.

Figure 2: Consider placing this figure after the “Invertebrate sampling” section

r.169: Define “spatial configuration”

r.195: Why Bernoulli and not Binomial? Note that rather than a single event (which is what Bernoulli is meant to represent), you measure occurrence in districts, transects and sampling areas, thus making several events that could lead to occurrence

Our response:

(1) there was some confusion on the transect design. These were not orthogonal to the coastline, but parallel within a zone of 100m. This is now reworded and hopefully clarified (see also Fig 1).

(2) quality of inset is improved, but we decided not to add any labelling with respect to the lime content of the soil. We did not measure this, and some areas (e.g. UK) consist of mosaics of calcareous dunes and dune heaths. We prefer to keep this textual

(3) bernouilli versus binomial. This is correct, but we would like to stress that local factors play at the single sample. So presence/absence with respect to marram properties follow a bernouilli distribution. At a district or biogeographical scale, these bernouilli distributions scale up to binomial ones. We preferred not to elaborate on this, as the wording is correct.

- Results -

r. 267 - 270: Consistent brackets placement is required.

Figure 3: I would move this figure to S.I.

r. 288: “For the majority of species…”

Figure 6: I suggest specifying the local environmental parameters in the description.

Figure 9: Why is there a color scale when only four possible outcomes? Furthermore, consider passing Figure 9 below the “Residual species co-occurrence patterns” section

r. 349 - “Only strong “residual” correlations (absolute value of the mean posterior > 0.75) were highlighted in the figure as being significantly different from 0.”

Our response. All followed. The color scale is indeed a scaling, but most of the correlations were either strong or absent, hence falsely suggesting a categorical separation.

- Discussion -

r.366: Consider changing “We here used” by “Here, we applied”

r.402-405: I recommend you to rephrase like this: “Since this species of spider is an effective disperser by air (through ballooning (Bonte et al. 2003b, 2004)), the prevailing land-inward winds on the continent typically prevent the species from drifting into coastal systems. However, in the UK, the pattern of mass immigration via wind-driven drift may be more pronounced.”

r.405-406: Consider changing “(and thus by extension biogeographical districts)” by “(and by extension, biogeographical districts)

r.411: Consider restructuring as: ”vegetation as measured by its cover (P%), spatial contagion (Moran’s I) and/or the marram grass vitality.”

r.415: Eliminate one parentheses in: “((Bonte”

r.421-422: “Only one species was preferentially associated with overdispersed marram plants” Would be interesting explaining the reason for this result.

Our response: all followed. Last issue was an error as we referred to cover not to contagion or clustering. This is corrected