





Peer Community In Ecology

Combining Joint Species Distribution Models and multivariate techniques allows understanding biogeographical and micro-habitat community responses

Joaquín Hortal  based on peer reviews by **André Mira** , **Sergio Chozas**  and 1 anonymous reviewer

Ruben Van De Walle, Maxime Dahirel, Ward Langerhaert, Dries Benoit, Pieter Vantiegheem, Martijn L. Vandegheuchte, François Massol and Dries Bonte (2025) Drivers of plant-associated invertebrate community structure in West-European coastal dunes. BioRxiv, ver. 4, peer-reviewed and recommended by Peer Community in Ecology.

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Community structure is determined by the regional species pool – which for simplicity can be assumed to be filtered through dispersal limitations, abiotic conditions, and species coexistence mechanisms (Cornell & Harrison 2014). This filtering involves macroecological constraints, such as energy and space availability, and assembly rules that determine species composition (Diamond 1975; Weiher & Keddy 1995; Guisan & Rahbek 2011; Hortal et al. 2012). But also by a series of processes that determine species distributions across scales, including biogeographical and stochastic processes (e.g., large-scale dispersal and occupancy dynamics within the landscape) and deterministic niche-based responses to abiotic and biotic conditions, which interact across scales (Soberón 2010; Hortal et al. 2010; Brousseau et al. 2018). These processes collectively determine the persistence of species assemblages within communities. It follows that, to understand the processes determining the structure of these communities it is necessary to combine methods analyse the effects of drivers acting on both species distributions and community responses.

Van de Walle et al. (2025) take this integrative approach. The final revised version of their work combines multivariate techniques (in this case a RDA) and Joint SDMs to model the small-scale distribution and structure of the invertebrate communities inhabiting a series of coastal dunes in Southern England, France, Belgium and the Netherlands. The paper builds upon well-designed stratified field surveys, which allow them to identify

variations at different scales, from geographical to local. These high-quality field data, together with the combination of different modelling techniques, allows them to identify both a clear biogeographical zonation in the structure of these communities, and the existence of a series of neat responses of species to the spatial structure and vigour of the tussocks created by the marram grass fixing the sand dunes. Their models also include the body size, feeding guild and phylogenetic relationships between co-occurring species, although their effects are smaller compared to those of biogeographical differences –which, arguably, are determined by differences in the species pool of each dune system, and species responses to the microhabitat conditions created by the tussocks. They can however identify a trade-off between generalist and specialist species within each community.

Note that here I'm using model in the sense of tools for understanding and explaining complex ecological systems, as advocated by Levins (1966). Which is precisely what Van de Walle et al. (2025) do here. By combining techniques tailored to model species distributions and community-level responses, they (we) gain a much improved understanding of how both species pools and the spatial structure of habitats determine the composition of ecological communities. Importantly, Van de Walle et al. (2025) use this knowledge to obtain key insights about how to manage and restore these endangered habitats, thereby proving the value of this kind of integrative approaches.

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Reviews

Evaluation round #2

DOI or URL of the preprint: <https://doi.org/10.1101/2024.06.24.600350>

Version of the preprint: 3

Authors' reply, 12 February 2025

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Decision by [Joaquín Hortal](#) , posted 13 January 2025, validated 15 January 2025

Minor revisions

Dear authors

Both reviewers and myself have revised this new version of your manuscript, and we all agree in that in only requires minor revisions before being ready to be recommended.

Besides the comments made the reviewers, I have some recommendations. Perhaps the most important one is about using the term "biogeographical area", which is commonly used in historical biogeography (aka cladistic biogeography) to refer to (relatively large) areas inhabited by two or more endemic taxa (which, arguably, implies that a number of species/clades in the area share a common evolutionary history). This term is not used in ecology, nor it is used by non-cladist biogeographers such as myself, but it can indeed create some confusion. I'm sorry not to have noticed this before in the first revision, but I would advice to change it for another term that is not equivocal, such as "biogeographic sector" or just "region". "Biogeographic region" is often attributed to larger areas that have distinct species pool, but it could be adequate to use it here, if you justify it in the first paragraph of the methods by changing the sentence "The study area can be divided into six distinct biogeographical areas, which differ in soil characteristics because of their geological history and climate (Bonte et al. 2003a)." as follows:

"The studied dune systems can be divided into six distinct biogeographical [regions/sectors], which differ in soil characteristics because of their geological history and climate (Bonte et al. 2003a), and may host different species pools." This, or any paraphrasis you may see fit, would be enough to use biogeographical region or sector, or just "areas". Whatever term you choose, please make sure that it is consistently used throughout the text and in the figure captions, as mentioned by one of the reviewers.

about minor issues:

page 3, 2nd paragraph, biogeographical clustering can be also expected due to the relative isolation/limited connectivity between the different dune systems, as you correctly say below; mention it also in this sentence

page 6, last paragraph, "take fully advantage" should be "take full advantage"

pag7, 3rd para, note that "biogeographical areas" may also host different species pools (coming from the limited connectivity between the different metacommunities), as commented above, so some differences between them may not be due to environmental differences... I would indicate this here, saying something like "Although some differences may be due to the different species composition of the metacommunities from each region, this factor would account for large-scale differences in climate and soil characteristics."

pag7, last para, it is odd to say "explained spatially", in particular because space is not explanatory in this context; rather, say "spatially structured"

pag 9, 1st para, "within the latter regions" seems to refer to the last regions of a list that is not in the text here, indicate which regions

pag 16, 1st para, substitute "transect, rather than individual tussock scale are in play" for "transect, rather than at individual tussock, scale are in play"; this would clarify the alternative between transect and tussock scales

pag 16, last para (and 1st of pag 17), a minor remark here; are land use/management histories similar in all these dune systems?

Reviewed by Sergio Chozas , 19 November 2024

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Reviewed by André Mira , 11 January 2025

The revised version of the manuscript entitled "Drivers of Plant-Associated Invertebrate Community Structure in West-European Coastal Dunes" demonstrates a commendable effort by the authors to address the reviewers' suggestions. Most recommendations have been incorporated, and where they were not, the authors provided valid reasoning for their decisions. Consequently, the manuscript has been elevated to an even higher standard, already being a compelling and well-written piece. In my opinion, no further substantial improvements are necessary for publication, aside from the minor corrections noted below.

I suggest the following small amendments:

Line 314: Remove the extra space after "variation."

Line 447: Eliminate the double space before "While."

Line 509: Remove the duplicated word "preferentially."

Evaluation round #1

DOI or URL of the preprint: <https://doi.org/10.1101/2024.06.24.600350>

Version of the preprint: 2

Authors' reply, 25 October 2024

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Decision by Joaquín Hortal , posted 18 September 2024, validated 18 September 2024

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 naive, 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 it 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 analysis 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.

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).

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 laid by the reviewers.

Reviewed by anonymous reviewer 1, 11 September 2024

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Reviewed by [André Mira](#) , 17 September 2024

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.

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

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 phyla and how they interact.

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.

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

- 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.

- 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 $127 \pm \text{SD}$ 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

- 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."

- 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: "(Bonté"

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