Essential ingredients in Joint Species Distribution Models: influence on interpretability, explanatory and predictive power

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Abstract

1. *Joint Species Distribution Models* (*jSDM*) are increasingly used to explain and predict biodiversity patterns. *jSDMs* account for species co-occurrence patterns and can include phylogeny or functional traits to better capture the processes shaping communities. Yet, several factors may alter the interpretability and predictive ability of *jSDMs* : missing abiotic predictors, omitting ecologically-important species, or increasing the number of model parameters by adding phylogeny and/or trait information.

2. We developed a novel framework to comprehensively assess the interpretability, explanatory and predictive power of *jSDMs* at both species and community levels. We compared performances of four alternative model formulations : (1) a *Benchmark jSDM* with only abiotic

predictors and residual co-occurrence patterns, (2) a *jSDM* adding phylogeny to the *Benchmark*, (3) a *jSDM* adding traits to model 2, and (4) the *Benchmark jSDM* with additional non-target species that are not of direct interest but potentially interact with the target assemblage. Models were fitted on both presence/absence and abundance data for 99 target polychaete species sampled in two coastal habitats over 500km and 8 years, along with information on 179 non-target species and traits data for the target species.

3. For both presence/absence and abundance data, explanatory power was good for all models but their interpretability and predictive power varied. Relative to the *Benchmark* model, predictive errors on species abundances decreased by 95% or 53%, when including non-target species, or phylogeny, respectively. These differences across models relate to changes in both species-environment relationships and residual co-occurrence patterns. While considering trait data did not improve explanatory or predictive power, it facilitated interpretation of trait-mediated species response to environmental gradients.

4. This study demonstrates that any *jSDM* formulation comes with tradeoffs between either explaining or predicting the occurrence or abundance of species. Hence, it highlights the need to compare alternative model formulations using the original and comprehensive assessment framework proposed in this study. Overall, this work contributes to a better understanding of *jSDM*s' performances across multiple facets and provides insights and tools for model selection based on specific objectives and available data.

Introduction

Community ecology aims at describing, explaining, and predicting changes in communities (Tredennick et al. 2021). Understanding the processes that determine species distribution is a prerequisite to characterize and predict community structure and associated ecological dynamics, which is critical to inform effective management or restoration measures in a rapidly changing world (Dietze et al. 2018; Brudvig and Catano 2022). *Joint Species Distribution Models* (*jSDM*) are particularly well-suited tools to address these challenges, whether to characterize the processes that shape observed communities (Warton et al. 2015; Ovaskainen, Tikhonov, Dunson, et al. 2017), or to predict future changes in species assemblages (Norberg et al. 2019; Pollock, O'Connor, et al. 2020).

jSDMs are multivariate (i.e. multi-species) extensions of *Species Distribution Models* (*SDMs*), which have been broadly applied over the past decades - across all terrestrial and marine realms - to understand and predict both species occurrences (Elith et al. 2006; Norberg et al. 2019) and species abundances (Howard et al. 2014; Waldock et al. 2022) using a set of covariates (e.g. climatic variables). Relative to *SDMs*, *jSDMs* explanatory power can benefit from accounting for species assembly rules (Ovaskainen, Tikhonov, Norberg, et al. 2017). In particular, relative to single-species *SDMs* that only consider the abiotic niche of species (i.e. the Grinellian niche), *jSDM* can theoretically also account for interspecific interactions (i.e. the Eltonian niche).

In *jSDMs*, the variability in community composition not explained by covariates is captured by a residual covariance matrix representing species co-occurrence patterns potentially representing biotic interactions (Ovaskainen, Tikhonov, Norberg, et al. 2017). This feature is highly attractive to ecologists because it provides a way to disentangle the relative influence of abiotic and biotic processes on biodiversity patterns (Godsoe, Franklin, and Blanchet 2017) while also improving model's predictive power (Giannini et al. 2013; Staniczenko et al. 2017). However, in practice, inferring and interpreting residual co-occurrence patterns using *jSDMs* remains challenging for several reasons (Blanchet, Cazelles, and Gravel 2020; Holt 2020).

First, while *jSDMs* have been applied to a large number of species presence/absence datasets (Norberg et al. 2019; Wilkinson et al. 2019; Wilkinson et al. 2021), simulation studies showed that inferred co-occurrence networks do not necessarily provide evidence for species interactions (Dormann et al. 2018; Blanchet, Cazelles, and Gravel 2020) but only capture spatial and temporal associations between species (Keil et al. 2021). Some authors speculated that *jSDMs* applied to abundance data - instead of presence/absence data - could provide a better proxy for biotic interactions (Blanchet, Cazelles, and Gravel 2020; Momal, Robin, and Ambroise 2020). Accordingly, *jSDM* have increasingly been applied to abundance data (Hui 2016; Ovaskainen, Tikhonov, Norberg, et al. 2017; Chiquet, Mariadassou, and Robin 2021). While challenges related to modelling abundance data was recently explored in the context of species distribution modelling (Waldock et al. 2022), the predictive and the explanatory power of *jSDM* fitted to abundance data remains relatively untested compared to presence/absence data (Norberg et al. 2019; Wilkinson et al. 2021).

Second, regardless of the type of data considered (i.e. presence/absence or abundance), several factors may limit or affect the interpretability and predictive ability of *jSDM*. For instance, co-occurrence patterns estimated in *jSDM* are affected by unaccounted environmental variables im-

83 plying that *jSDMs* cannot fully separate the environmental and the biotic niche of species (Blanchet,

84 Cazelles, and Gravel 2020; Poggiato et al. 2021). Beyond missing environmental predictors, ac-

85 counting for extra species that can influence the target community (e.g. competitors) is key to

86 improve *jSDMs*' inference and predictions. However, because many ecological studies only focus

87 on particular taxonomic groups (Pollock, Tingley, et al. 2014; Häkkilä et al. 2018) and disregard

88 non-target taxa, co-occurrence patterns estimated from *jSDMs* are almost always skewed by missing

89 ecological actors (Momal, Robin, and Ambroise 2021). How this bias affects the predictive ability of

90 jSDM remains untested.

91 Finally, similar to *SDMs*, *jSDMs* can theoretically be extended to include additional sources of

92 information about modelled species (Niku et al. 2019; Ovaskainen, Tikhonov, Norberg, et al. 2017).

93 For instance, accounting for phylogenetic relationships between species (Ives and Helmus 2011) or

94 for the link between functional traits and environmental responses (Pollock, Morris, and Vesk 2012)

95 can improve both the explanatory and the predictive powers of *SDMs* (Morales-Castilla et al. 2017;

96 Vesk et al. 2021). These findings support the hypothesis that similar species, in terms of traits and/or

97 recent evolutionary history, usually share similar environmental preferences. While inclusion of

98 species-specific information in *jSDMs* should yield similar benefits (Ovaskainen, Tikhonov, Norberg,

99 et al. 2017), the relative influence of additional sources of information on their interpretability and

100 predictive power remains untested (Norberg et al. 2019; Wilkinson et al. 2019; Abrego, Bässler, et al.

101 2022).

102 Overall, many practical questions remain concerning the application of *jSDMs* to ecological com-

103 munity monitoring data, in particular related to inclusion of additional sources of information within

104 the models. While some comparative assessments of *jSDM* performance exists (e.g. Norberg et al.

105 (2019) ; Wilkinson et al. (2021)), including some comparison of the benefit of trait and phylogenetic

106 data in some phyla (e.g. Abrego, Bässler, et al. (2022)), there has been no formal assessment of

107 the relative importance of species-specific information (trait and/or phylogeny) compared to the

108 role of missing species. Furthermore, comparative assessments have rarely been performed on

109 both presence/absence and abundance data. To a few exceptions (Waldock et al. 2022), most

110 assessments were made considering presence/absence data (Norberg et al. 2019; Wilkinson et al.

111 2019) and mostly focused on predictive power (Norberg et al. 2019; Wilkinson et al. 2019), hence

112 disregarding the interpretability/explanatory aspects of the models (Tredennick et al. 2021). Yet,

113 *jSDMs* are increasingly fitted on abundance data (Brimacombe, Bodner, and Fortin 2021) and used

for explanatory purposes (Abrego, Dunson, et al. 2017). Hence, there is a mismatch between current understanding of *jSDMs* performance and their application by ecologists. In practice, most *jSDM* applications consider a single model structure and do not explore the effects of including additional sources of information. Perhaps this shortcoming relates to the high-dimensionality of *jSDMs* which makes their comparison challenging.

In this study, we developed a multi-faceted assessment framework to evaluate the extent to which alternative parameterization of *jSDM* can lead to a better interpretability or predictability at the species and community levels. To illustrate its usefulness, we applied this general framework to a case study presenting typical features of community ecology datasets. Specifically, by comparing predictions obtained from a *Bench*mark model excluding additional sources of information (i.e. a classical *jSDM*), we tested the effect of (1) including phylogeny alone and in combination with trait data, (2) incorporating monitoring information related to non-target species and (3) considering abundance instead of presence/absence data. We hypothesized that all these sources of information should improve *jSDM* predictive and explanatory powers, but did not assume a priori that a given modeling strategy would lead to greater improvements in model performances.

Materials & Methods

We used the *HMSC* (*Hierarchical Modeling of Species Communities*) framework applied to a long-term monitoring dataset. The following subsections sequentially describe our workflow (as illustrated in fig. 1): (1) the *HMSC* framework, (2) the data used in this study, (3) data splitting between train and test datasets to assess the explanatory and predictive powers of models, respectively, (4) the rationales for the suite of alternative models considered and, (5) a multi-faceted framework developed to assess tradeoffs in jSDMs' performances in relation to different study purposes.

Hierarchical Modelling of Species Community (*HMSC*)

HMSC is a multivariate hierarchical generalized linear mixed model using Bayesian inference (Ovaskainen and Abrego 2020). It has two parts: one for fixed effects and another for random effects. The fixed part models the species' realized niche, where each dimension of the niche is a covariate (e.g. temperature; fig. 1). Including trait data can improve species niche estimates by accounting for trait-environment relationships, where species with similar traits are expected to respond similarly along environmental gradients (Ovaskainen, Tikhonov, Norberg, et al. 2017).

143 Including phylogenetic data can help capture residual ecological information not included in the

144 available trait data, as phylogenetically-close species tend to share similar traits and niches (Wiens

145 et al. 2010). Alongside traits, phylogeny can improve niche estimates for rare species by borrowing

146 information from similar species (Ovaskainen, Tikhonov, Norberg, et al. 2017; Ovaskainen, Tikhonov,

147 Dunson, et al. 2017; Ovaskainen and Abrego 2020). The random part of *HMSC* relies on latent

148 variables, i.e. covariates that capture residual variance, including missing environmental features or

149 biotic interactions (Ovaskainen, Tikhonov, Norberg, et al. 2017; Ovaskainen, Tikhonov, Dunson, et al.

150 2017; Ovaskainen and Abrego 2020). The H matrix (site loadings) estimates missing covariate values,

151 while the Λ matrix (species loadings) represents species' response to these missing covariates

152 (fig. 1).

Datasets

Faunistic data

155 The *REBENT* program (rebent.ifremer.fr) is an ongoing monitoring of benthic macrofauna across

156 multiple stations along Brittany's coastline (Western France). Here, we used data from Boyé,

157 Thiébaut, et al. (2019), covering 23 sites and two intertidal soft-bottom habitats: bare sands and

158 seagrass meadows (Fig. S1) where infaunal communities were monitored yearly using the same

159 protocol between 2006 and 2014. A detailed description of the sampling methodology is provided

160 in (Boyé, Legendre, et al. 2017; Boyé, Thiébaut, et al. 2019). At each site, three faunal samples

161 (0.03 m^2 cores) were taken at each of three fixed sampling points distributed 200 m apart. These

162 samples were then pooled together to estimate abundances at the site level. For each sampling

163 event, individuals were identified to the lowest taxonomic level possible (mostly species level; for

164 simplicity we hereafter refer to "species").

165 Overall, across a total of 375 sampling units (i.e. unique combination of years, sites and habitats),

166 152,583 individuals belonging to 519 species were collected and identified. To avoid convergence

167 issues and poor model inference, we filtered out species occurring less than four times (across the

168 180 samples used as train set, see below), resulting in the removal of 241 species. The remaining

169 278 species included 99 polychaete species (the targeted assemblage) and 179 non-target species

170 of bivalves, molluscs, and amphipoda, which may predate or compete with polychaetes (Grall et al.

171 2006; Jankowska et al. 2019). We chose to focus on polychaetes as this taxonomic group exhibits

172 diverse lifestyles (Jumars, Dorgan, and Lindsay 2015), can be used to monitor the health of benthic
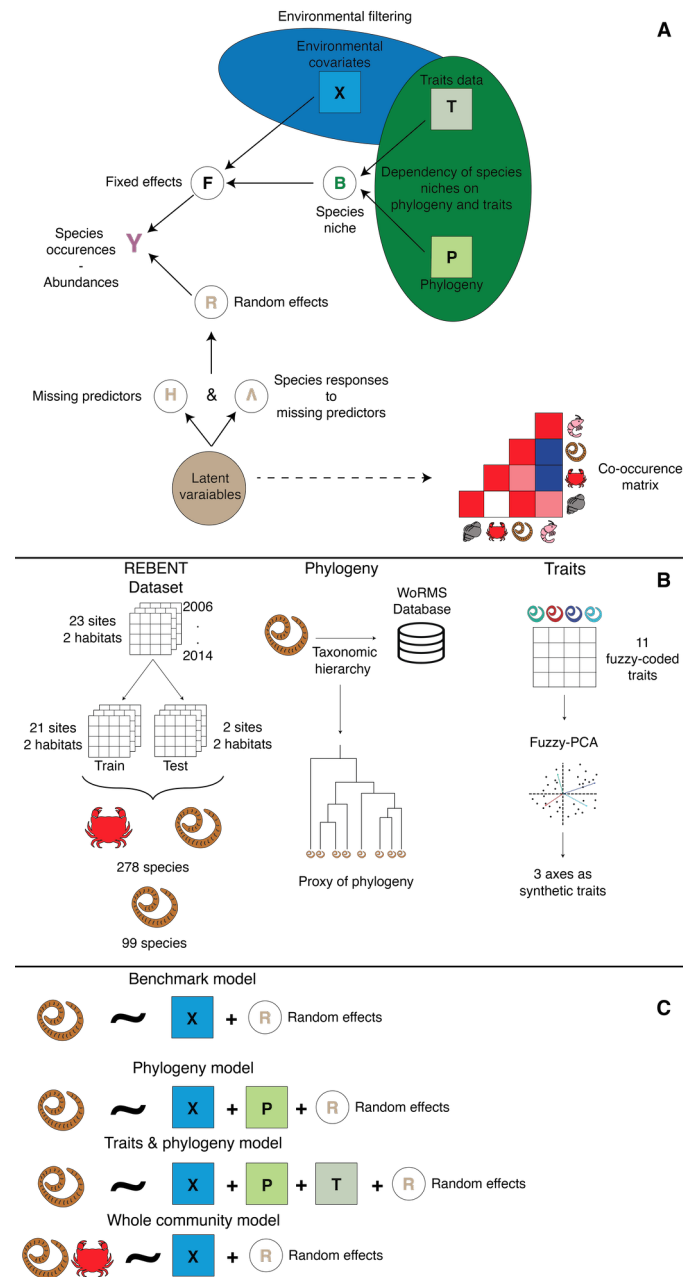
Figure 1. Study workflow. A. *Hierarchical Model of Species Community* (*HMSC*) structure, incorporating environmental variables, phylogeny, and species-specific traits. B. Data pre-processing: partitioning community data into train and test datasets, estimating phylogenetic distance (using taxonomic classification), and dimension reduction of species-trait matrix using fuzzy-PCA. C. Summary of the four alternative model structures fitted to presence/absence and abundance data: the *Bench*mark, Phylogeny, Traits & Phylogeny models only consider the targeted polychaetes, while the Whole Community model includes additional species potentially interacting with the target assemblage. Random effects for sampling year, site, and habitat were included in all models.

173 habitats (Giangrande, Licciano, and Musco 2005), and because trait data and ecological information

174 were available from previous studies (Boyé, Thiébaut, et al. 2019).

Traits and phylogeny data

176 Traits data were retrieved from (Boyé, Thiébaut, et al. 2019) for the 99 polychaete species present

177 in the train set (see below). The 11 fuzzy-coded traits available (see Boyé, Thiébaut, et al. (2019)

178 for details) were synthetized using a fuzzy-PCA, with the *fpca* function from the *ade4* R package

179 (Thioulouse et al. 2018). The first three axes, which account for 59% of the total variance of the trait

180 matrix, were included in the model as synthetic traits data (fig. 1). The first axis distinguishes mobile

181 predatory species from sessile microphages; the second axis differentiates semelparous species

182 from iteroparous species; and, the third axis separates burrowers from tube-dwellers (Fig. S2).

183   Phylogeny was not available, hence we followed common practices (Ovaskainen and Abrego

184 2020) and retrieved the taxonomic classification of these 99 polychaetes through the WoRMS

185 database (www.marinespecies.org; january 2020) and used this information as a proxy for phylo-

186 genetic relationships (fig. 1 ; Ovaskainen and Abrego (2020)). Phylogenetic distances were then

187 estimated using the ape R package (Paradis and Schliep 2019).

Environmental data

189 Following Boyé, Thiébaut, et al. (2019) (see Appendix A for details about data sources), we selected

190 seven environmental variables to characterise the ecological niche of each species. These seven

191 variables quantify different components of coastal environmental variability including hydrology

192 (sea water temperature, salinity and current velocity), sedimentology (mud and organic matter

193 content), substrate heterogeneity (Trask index) and local wave exposure (fetch). For each of these

194 seven variables, the first- and second-degree polynomials were computed to account for non-linear

195 responses.

Comparison of alternative model structures

197 The first model (denoted *Bench*) only considers data for the 99 target polychaete species and the 7

198 environmental covariates (fig. 1). The second model (denoted *Ph*) adds phylogenetic data to the

199 *Bench* model (fig. 1). The third model (denoted *TrPh*) adds traits data to the *Ph* model. The fourth

200 model (denoted *WhC*) has the same structure as the *Bench* model but includes data on the whole

201 community (278 species, including 179 additional non-target species; fig. 1). *WhC* excludes traits

₂₀₂ (unavailable for the non-target taxa) and phylogenetic data for faster computation. Each model was

₂₀₃ fitted twice, either with presence/absence or abundance data, using probit and lognormal Poisson

₂₀₄ distributions respectively. All models include the same random effects (fig. 1): temporal, spatial

₂₀₅ (sites), and habitats (bare vs seagrass).

Model fitting

₂₀₇ We estimated model parameters by running 5 chains using a MCMC sampling algorithm over

₂₀₈ 375,000 iterations. The first 125,000 iterations were discarded as burn-in while the remaining

₂₀₉ were thinned every 250 iterations yielding 1,000 posterior samples per chain for an overall total of

₂₁₀ 5,000 posterior samples for each parameter. We assessed convergence for each model parameter

₂₁₁ using both potential scale reduction factor (Gelman and Rubin 1992) and effective sample size as

₂₁₂ reported in supplementary materials (Appendix B). All models were fitted using the DATARMOR

₂₁₃ supercomputing facility.

Assessing model performance and interpretability

₂₁₅ For independent assessment of models' predictive performance, the dataset was split into a train

₂₁₆ and a test set, instead of using strict cross-validation procedure that would have considerably

₂₁₇ increase the computational burden (see also Norberg et al. (2019)). The train dataset consisted of

₂₁₈ 180 sampling units (21 sites; one or two habitats, and six to nine years per site; Fig. S1). The test

₂₁₉ set comprised 35 sampling units covering a 9-year period at two specific sites with both seagrass

₂₂₀ and bare sand habitats. These sites were chosen as representative of both regional macrofaunal

₂₂₁ species diversity (all the species observed in the test set are also observed in the train set) and

₂₂₂ mean environmental conditions (which limits model extrapolation outside of the trained parameter

₂₂₃ space; Fig. S3-S4; Boyé, Legendre, et al. (2017) ; Boyé, Gauthier, et al. (2022) ; Toumi et al. (2023)).

₂₂₄ To assess *jSDM's* performance, we used a set of complementary metrics to evaluate both their

₂₂₅ explanatory and predictive abilities on the train and test dataset, respectively (Table 1). AUC and

₂₂₆ RMSE, calculated only for the 99 target species (i.e. polychaetes) even for the *WhC* model that

₂₂₇ includes a total of 278 species, were used to assess overall and species-level performance for

₂₂₈ presence/absence and abundance models, respectively. Relationships between observed and

₂₂₉ predicted mean species abundances across all sites were also visualized for abundance models.

₂₃₀ Along with the raw AUC and RMSE values, we also visualized and quantified changes relative

to the *Bench* model for the *Ph*, *TrPh* and *WhC* models. For abundance models, we computed the overall relative change in mean RMSE across species as:

$$\text{Relative change} = \frac{\text{mean}\left(\text{RMSE}_{\text{focal model}}\right) - \text{mean}\left(\text{RMSE}_{\text{Bench}}\right)}{\text{mean}\left(\text{RMSE}_{\text{Bench}}\right)} \times 100 \tag{1}$$

AUC and RMSE only partially capture model accuracy at the community scale (Table 1). To explore this aspect, we focused on differences between predicted and observed assemblage richness and total abundances (for abundance models). We also compared observed and predicted Sørensen (for presence/absence) and Bray-Curtis (abundance) pairwise-dissimilarity matrices to explore how well β-diversity patterns were reproduced by the models. For these three metrics, we computed relative change for both the train and test datasets between mean predicted and mean observed values as follows:

$$\text{Relative change} = \frac{\text{mean}\left(\text{Metric}_{\text{predict}}\right) - \text{mean}\left(\text{Metric}_{\text{obs}}\right)}{\text{mean}\left(\text{Metric}_{\text{obs}}\right)} \times 100 \tag{2}$$

where "Metric" is a community-based measure (e.g. species richness, total abundance, dissimilarity matrices) estimated from model predictions or observations at the sample level (i.e. unique combination of site, habitat and year; or, pairs of samples for dissimilarity). To evaluate model interpretability, we calculated the amount of explained variance per species and the proportion that can be attributed to environmental covariates (fixed effects) and random effects. We compared the overall relative change in the proportion of variance explained by the covariates and by the random effects for the *Ph*, *TrPh* and *WhC* relative to the *Bench* model (by comparing mean values across species similarly to eq. 1). We also propose a novel way of exploring species-environment relationships (Table 1) by classifying the response curves estimated from the different models based on their shapes, considering both their direction (decline, null, or increase) and their acceleration (decelerated, constant, or accelerated) (Rigal, Devictor, and Dakos 2020). Finally, we compared the residual co-occurrence patterns associated with each random effect of the *Bench* model with those of the best performing model (*WhC*). We quantified differences in magnitude and sign of residual species-species correlations using the following index:

$$\delta = |corr_{\text{best model}} - corr_{\text{Benchmark}}| \times sign(corr_{\text{best model}} \times corr_{\text{Benchmark}}) \tag{3}$$

Table 1. Multi-assessment framework providing a list of useful metrics to assess, interpret or compare jSDMs across different ecological facets (rows) at the species, community or overall level. Italicized metrics are used in this study.

	Model outputs	Example of derived-metrics for model interpretation	Example of derived-metrics for model evaluation		Example of performance measures to assess the explanatory/predictive power of models[1]	
			Presence/Absence	Abundance	Presence/Absence	Abundance
Species level	Abundance, occurrence probability, environmental coefficients	Variable importance (e.g. LIME, SHAP[2]), Heatmap of environmental coefficients, *Response curves*[3], *Variance partitioning*	Number of Presence/Absence, Proportion of occupied sites	Total abundance, site-specific abundance	*AUC*, Kappa, F1-Score	*RMSE*, MAE, R2, Correlation between predicted and observed values
α-diversity	Site-specific community composition	Diversity index (e.g. Shannon entropy, Simpson-Gini index), *Total abundance*, *Total richness*, Proportion of rare/abundant species			*Differences between predicted and observed values*, RMSE, MAE, R2, Correlations (e.g. Kendall, Pearson) between observed and predicted alpha or beta diversity indices	
β-diversity		*Pairwise dissimilarity* (e.g. Jaccard/Bray-Curtis),[4,5] Total Beta diversity, Turnover,Nestedness, Local Contribution to Beta Diversity (LCBD), Species Contribution to Beta Diversity (SCBD)				
Overall assessment (all sites)	Regional community composition	Diversity index (e.g. Shannon entropy, Simpson-Gini index), Total abundance, Total richness, Proportion of rare/abundant species			Average over all species: *AUC*, Kappa, F1-Score	Average over all species: *RMSE*, MAE, R2, Correlation *between predicted and observed values*
	Residual correlation matrix	Co-occurrence network analysis (e.g centrality, number of degrees)	Comparison with observed or reconstructed networks (expert-based or estimated e.g. based on trophic analyses) , using e.g. correlations, *residual correlation index (δ̂)*[6]			
	Trait-based regression coefficients	*Traits-environment response curves*, Heatmap of traits-environment coefficients	Qualitatively, based on literature and/or expert knowledge[7]			

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[1] All performance measures can theoretically be compared between models. For instance, we here measured differences between models using a measure of relative change in RMSE or AUC relative to the Bench model using Eq. 1. Other measures could be correlations between model predictions.

[2] See Ryo et al. (2021)

[3] To ease model comparison and interpretation, we propose to summarize the information contained in species response curves using the framework initially proposed by Rigal, Devictor, and Dakos (2020) for classifying species temporal trajectories based on their trend, acceleration, direction and velocity. Applied to regression coefficients, it allows to classify the response of species to each environmental variable into several shapes that are easy to interpret, to link with ecological theory, and to compare across models.

[4] For jSDM assessment, pairwise dissimilarities can be computed on the observed site-by-species matrix and on the predicted one. Comparing these values (e.g. through correlation analysis or simply through differences) will inform on how well the model reproduces/predict beta diversity patterns. Alternatively, pairwise dissimilarities can be computed between the observed taxa composition of a sample and its predicted one. These dissimilarities then become a metric to assess model performance based on species-composition predictions.

[5] For jSDMs comparisons, pairwise dissimilarities computed between the observed taxa composition of a sample and its predicted one can be compared across models (e.g. through correlations) to assess to what extent differences between predicted and observed taxa composition are congruent across different models. Alternatively, comparing correlations between pairwise dissimilarities computed on the observed site-by-species matrix and on the predicted one will inform on which model best predict beta diversity patterns.

[6] Species interaction networks can be reconstructed under certain conditions using the residual correlation matrices estimated by jSDM (see Momal, Robin, and Ambroise (2020)). The comparison between these reconstructed interaction networks and already known interaction networks (based on trophic data, experimental data, expert knowledge or qualitative information on species interactions) can serve as a means of model validation.

[7] Comparing modelled species trait-environment responses (e.g., signs, shape of response curves) with expected responses (e.g. from theory, experiments or expert knowledge) can also serve to validate qualitatively the models.

Results

Both MCMC convergence and effective sample size of the different *jSDMs* were satisfactory (see Appendix D).

Model Fit & Predictive power

Species level

Presence/absence models showed excellent explanatory power with mean AUCs above 0.9 on the train dataset, but lower predictive power with mean AUCs around 0.66 on the test set (Fig. S17). Both explanatory (mean AUC between 0.92 and 0.93) and predictive (mean AUC between 0.64 and 0.66) power were overall similar across models (fig. 2, Fig. S17). Within the target species assemblage, predictions improved for 41 species and worsened for 36 species (out of the 99 target species, which implies marginal changes for the remaining 22) in the *WhC* model relative to the benchmark. In comparison in the *Ph* or the *TrPh* models, predictions only improved for 26 and 27 species, respectively, and worsened for 49 and 48 species, respectively.

Abundance models also showed a satisfactory explanatory power with a mean RMSE close to nine for all models, given a mean abundance in the train dataset of 307.31 ± 583.58 (mean ± sd). Overall, all models underpredicted species abundances (Fig. S18-19). While explanatory power was similar across models, larger variations were observed for predictive power. The *Bench* model had a mean RMSE of 126.67 (for a mean abundance in the test dataset of 700.57 ± 818.66; Fig S17). The Ph model performed better (mean RMSE of 62.23; -50.87% compared to the *Bench*; Fig. S17) whereas the *TrPh* model did worse (mean RMSE of 139.21; +9.90%; Fig. S17). The best model was the *WhC* with a mean RMSE of 6.59 (-94.80% compared to the *Bench*, Fig. S17). Out of the 99 target species, the *WhC* model predictions improved for 57 species but declined for 15 species relative to the Bench. Conversely, performance gain for the *Ph* and *TrPh* models were poor relative to the Bench, as predictions improved for 38 and 31 species, respectively, but declined for 40 and 46 species, respectively.

We further investigated this gain in predictive power of the *WhC* model fitted to abundance data by examining the relationships between changes in predictive power and the occurrence or abundance of the species. On the test set, performance of the *WhC* model most improved relative to the *Bench* model for rare species (correlation with average species abundance: Kendall's $\tau = 0.12$,
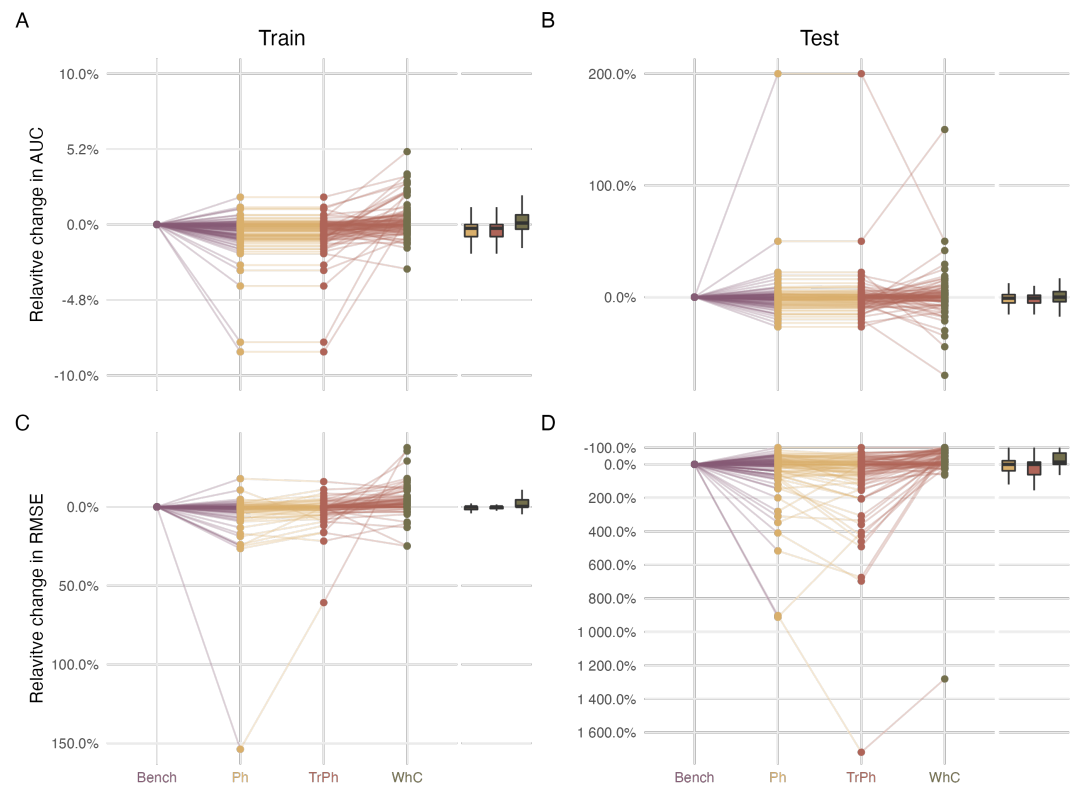
Figure 2. Change in explanatory and predictive power of three model structures (yellow for *Phylogeny* (*Ph*), red for *Traits and phylogeny* (*TrPh*), and green for *Whole community* (*WhC*) models) relative to the *Benchmark model* (*Bench*; purple). Changes are expressed as percentages relative to the benchmark fitted on presence/absence (top row) or abundance (bottom row) data. Points above the zero line indicate performance gain.

283 p-value < 0.05; Fig. S20). However, we found no patterns between change in RMSE relative to the

284 Bench model and proportion of presence (Kendall's $\tau\tau = 0.12$, p-value $= 0.09$; Fig S21).

285 Community level

286 In terms of alpha diversity, the *Bench*, the *Ph* and *TrPh* models fitted on abundance data all un-

287 derpredicted mean species richness of the train set by 4 species on average (-29.2% compared to

288 observed data; fig. 3). In contrast, the *WhC* model overpredicted mean richness by 11 species on

289 average (+80% compared with observed data). Similar results were found on the test dataset with

290 the *Bench*, *Ph* and *TrPh* models underpredicting richness by 5 species (-24.9 %) on average whereas

291 the *WhC* model overpredicted richness by 7 species (+35.8% compared with observed data). Similar

292 results were found for models fitted on presence/absence data (Fig. S22).

293   All models overall underpredicted mean total abundance relative to the train dataset (fig. 3),

294 by 153 individuals for the *Bench* model (-49.8% compared to observed data) and by 159 and 155

individuals (-51.7% and -50.4%) for the *Ph* and *TrPh* models, respectively. The *WhC* model only underpredicted total abundance by 22 individuals (-7.12% compared to observed data). Relative to the test dataset, the *Bench*, the *Ph* and the *TrPh* models overpredicted mean total abundance by 1642 (+234% compared to observations), 465 (+66.3%), and 1969 individuals (+281%), respectively. In contrast, the *WhC* model underpredicted mean total abundance of the test data samples by 404 individuals on average (-57.6%).

Mean beta diversity patterns in the train dataset were overall well captured by all models fitted on abundance or presence/absence data (fig. 3). Observed dissimilarities were slightly overpredicted by all abundance models: by 0.057 for the *Bench* (+7.3% compared with observed data), 0.050 for the *Ph* (+6.4%), 0.054 for the *TrPh* (+6.9%) and 0.070 for the *WhC* models (+8.9%). Differences for presence/absence models were of similar order but all models underpredicted mean pairwise dissimilarities between samples (Fig. S22). On the test dataset, beta diversity patterns were rather poorly captured by the models fitted on abundance data. The Bench model overpredicted the pairwise dissimilarities by 0.364 on average (+67.1% compared with observed data), the *Ph* model by 0.365 (+67.4%), the *TrPh* model by 0.375 (+69.1%) and the *WhC* model by 0.338 (+62.4%). Similar results were observed for presence/absence models with slightly smaller overpredictions (Fig. S22).

Variance partitioning

The mean amount of total variance explained across the 99 polychaetes varied between 21 and 23% for models fitted with presence/absence data and between 18 and 30% for abundance-based models (Fig. S23). For all models, environmental variables, rather than random effects, accounted for most (more than 68% ± 18%; mean ± s.d.) of the explained variance (Fig. S24). However, a larger part of variance is explained by random effects in the *WhC* model compared to the other models, including the Bench (Fig. S24). Compared to the *Bench* model fitted with abundance data, the relative change in the part of variance explained by random effects across the 99 species decreased by 17.00% for the *Ph* model, 10.90% for the *TrPh* model and increased by 224% for the *WhC* model (fig. 4). Similar results with smaller relative changes were obtained across presence/absence models (fig. 4 ; Fig. S23-24).
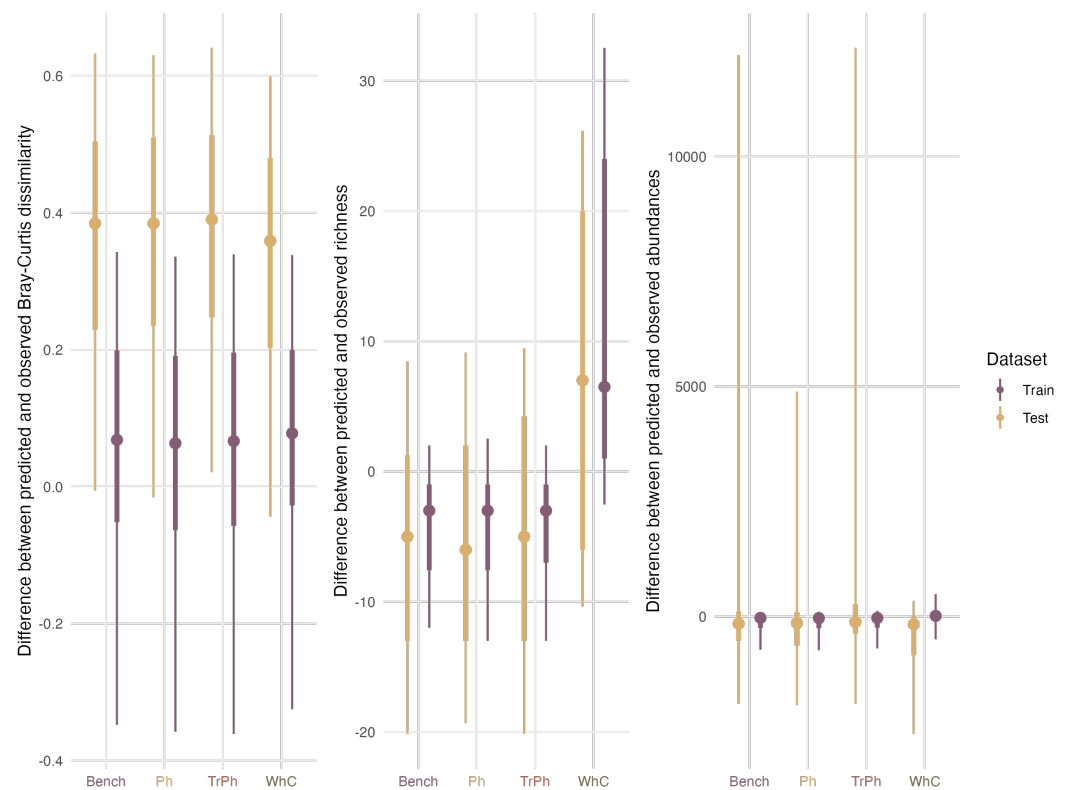
Figure 3. Comparison of model performances with regards to their ability to predict community structures when fitted with abundance data for the train (purple) and test (yellow) dataset. Left: differences in pairwise dissimilarities estimated on the observed and the predicted assemblages. Centre: differences in species richness between observed and predicted assemblages. Right: differences in total abundance between observed and predicted assemblages.
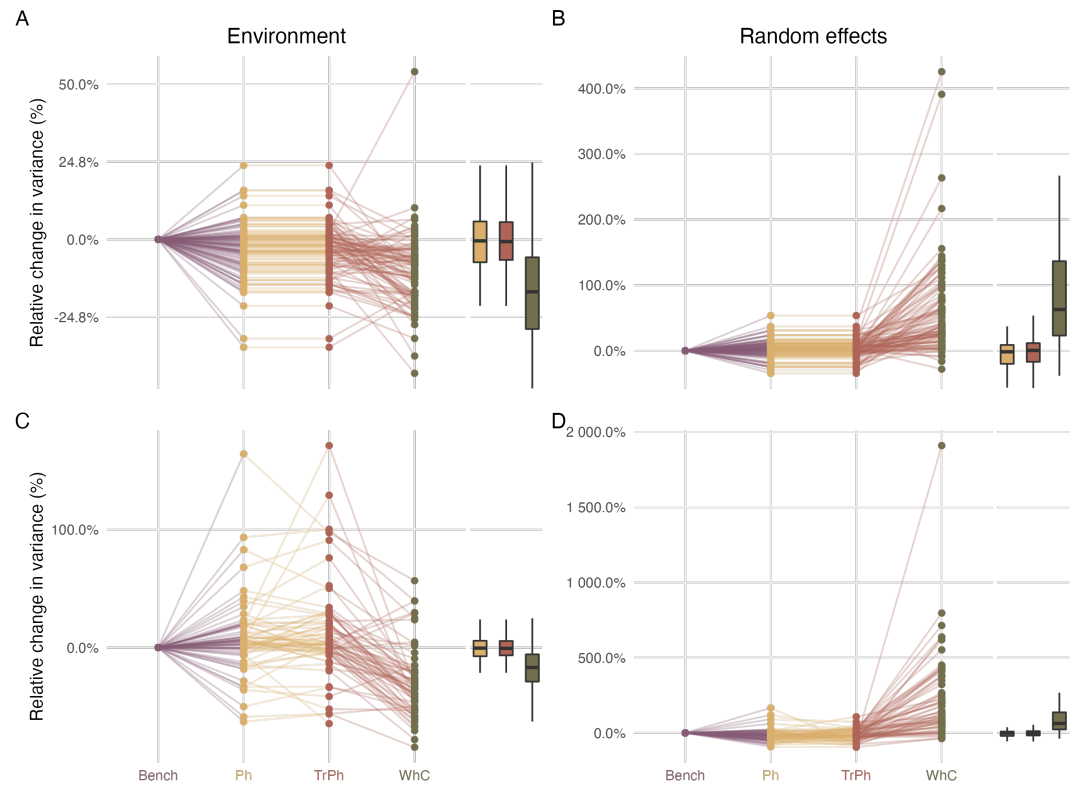
Figure 4. Change in explained variance related to environmental predictors (left column) and random effects (right column) for three alternative model structures (yellow for *Phylogeny* (*Ph*), red for *Traits and phylogeny* (*TrPh*), and green for *Whole community* (*WhC*) models) relative to the *Benchmark model* (*Bench*; purple). Percentage changes were computed relative to the *Benchmark model* fitted with presence/absence (top panels) or abundance (bottom panels) data. Positive values indicate an increase in the proportion of variance explained by the focal model compared to the *Benchmark model*. See Figure S23 and S24 for the raw percentages, expressed as percentages of explained variance or total amount of variance respectively.
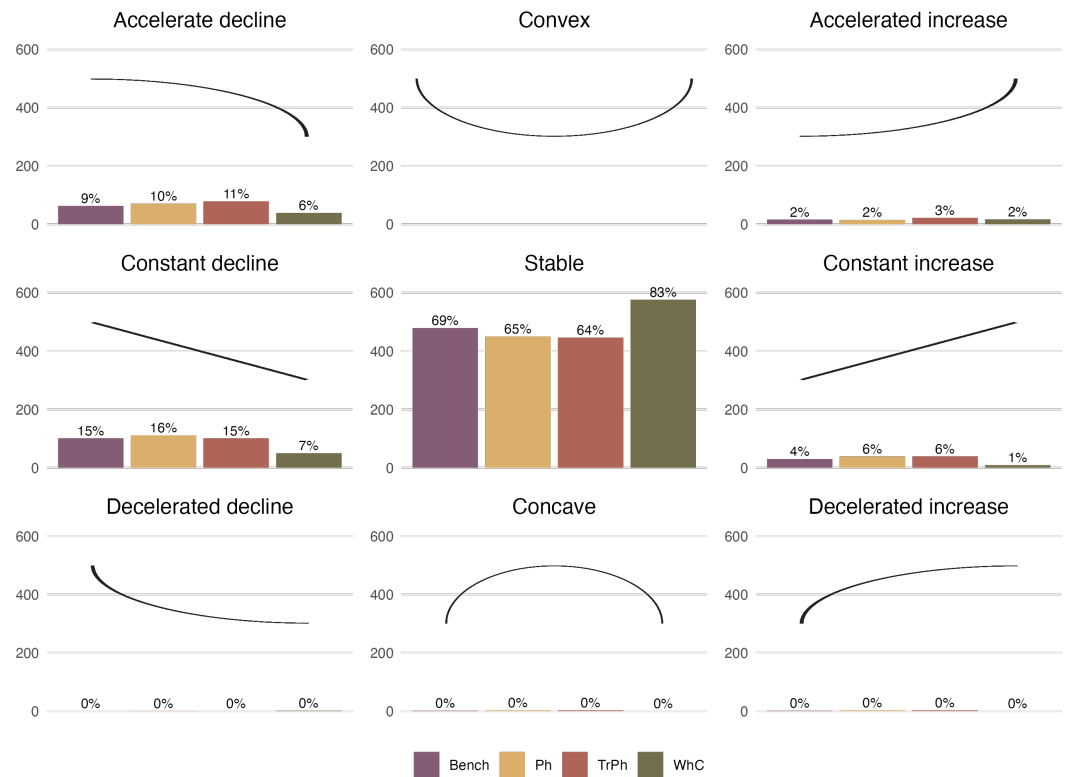
Figure 5. Number (y-axis) and proportion (computed across all coefficients for each model, as indicated above individual bars) of response curves (i.e. one for each species-predictor combination according to the typology (nine shapes highlighted by the black curve in each panel) defined by Rigal, Devictor, and Dakos (2020). Results are presented for the different model structures

Species niche estimated

For abundance models, the large majority (>60%) of flat response curves indicated a lack of meaningful species-environment relationships (fig. 5). This proportion reached 83% for the *WhC* model. The prevalence of flat relationships did not appear to be related to convergence issues (Fig. S15-16) or to be driven by a specific covariate (Fig. S25). Convex or concave response curves were rare in abundance models. Significant relationships primarily included constant or accelerated declines, representing approximately 10% and 15% of response curves in the *Bench*, *TrPh*, and *Ph* models (fig. 5). In the *WhC* model, these percentages decreased to 7% and 6%, respectively (fig. 5). Similar findings were observed for presence/absence models (Fig. S26; Fig. S27).

Both abundance and presence/absence *TrPh* models (which include species functional traits) reveal some meaningful trait-environment relationships between the first fuzzy-PCA axis and the seven environmental predictors. This suggests that the occurrence of certain traits is likely favored

334 (or hindered) under certain environmental conditions (Fig. S28). For instance, mobile predatory

335 species showed larger declines in abundance as fetch increases than sessile suspensivores (Fig.

336 S28). Moreover, increase in organic matter concentration and decrease in current velocities were

337 associated with higher abundances of suspensive feeders.

Exploring the residual correlation

339 Residual species-species correlations were compared between the *Bench* model and the *WhC*

340 model, only for the 99 target species, using both presence/absence (Fig S29) and abundance data

341 (fig. 6). We only focus this comparison on the *WhC* model (rather than other models) because

342 of its higher predictive performance and higher proportion of explained variance by random

343 effects (fig. 4). Residual correlations estimated from both models were highly correlated, both for

344 presence/absence and abundance data (fig. 6 and Fig. S29). However, agreement between models

345 varied across different random effects from a moderate correlation between residuals associated

346 with the Habitat random effects ($R^2 = 0.57$) or with the Site random effects ($R^2 = 0.64$), to a high

347 correlation between residuals related to the Year random effects ($R^2 = 0.95$). The δ index main

348 modal distribution, which is centered on zero, confirms an overall agreement between residual

349 correlations estimated from both models in relation to the Year random effects with a marginal

350 proportion of sign changes (0.45% of sign changes related to correlation greater than 0.25; fig. 6 B)

351 only related to low species-species residual correlations (<0.25; fig. 6 A and Fig. S29). In contrast,

352 the δ index highlights inconsistencies in both magnitude and signs changes between residuals

353 associated with the Habitat and the Site (12.2% and 9.11% of sign changes related to correlation

354 greater than 0.25) random effects. Similar results were obtained for presence/absence models (Fig.

355 S29).

Discussion

357 Case studies in community ecology typically rely on partial and heterogeneous observations (Pol-

358 lock, O'Connor, et al. 2020) but also on incomplete knowledge of target species ecological features

359 (e.g. traits, phylogeny; Tyler et al. (2012)). This study investigated how *jSDM* performance varies

360 depending on the type of information included (i.e. phylogeny, traits or data on non-target species)

361 using a multi-assessment framework (spanning interpretability, inference and prediction, for both

362 species- and community-level metrics, Table 1) enabling a thorough evaluation of model perfor-
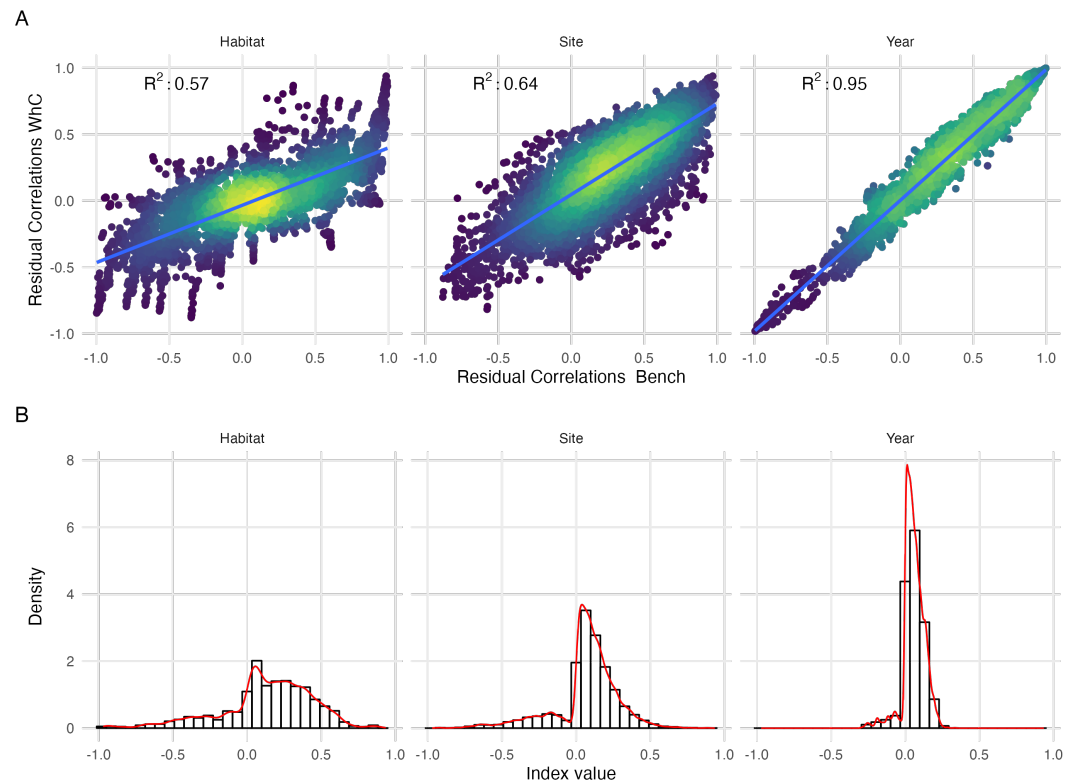
Figure 6. (A) Comparison of residual species-species correlations associated with the three random effects estimated by the *Whole Community Model* (*WhC*; y-axis) and the *Benchmark model* (*Bench*; x-axis) fitted on abundance data. The colour scale highlights the density of points in each scatter plot. (B) Distribution of the δ index characterizing change in sign (negative values indicate sign change) and magnitude (higher absolute values indicate higher numerical difference) between residual correlations estimated by the *WhC* model and the *Bench* model adjusted with abundance data for the three random effects (Habitat, Site, Year).

mance.

We found that *jSDMs*' performance, in particular predictive power of abundance models at the species level, mostly increased when including information related to the 179 non-target species sampled alongside with the 99 polychaetes of interest. However, improvement in species-level predictions does not directly translate into enhanced performance at the community level. The *WhC* model did not improve estimates of beta diversity or total abundance relative to the other models and largely overpredicted species richness, as previously suggested (Zurell, Pollock, and Thuiller 2018). Given *HMSC* hierarchical structure (Poggiato et al. 2021), inclusion of monitoring data related to other species likely improves model performance for the target assemblage by capturing relevant drivers that are not explicitly considered. For instance, it can help describe target species' realized niches by accounting for ecological processes related to environmental conditions (including trait-mediated responses) or biotic interactions that are not explicitly captured otherwise (Ovaskainen, Tikhonov, Norberg, et al. 2017). In our case, main differences between residual correlations estimated by the *Benchmark model* and the *Whole community* model relate to spatial random effects (i.e. site and habitat). In contrast, the temporal random effect yielded similar residual co-occurrences in both models. This suggests that including non-target species in our case, mostly helped capture spatial variability in species associations across sites and habitats.

Importantly, while we show that including non-target species can improve predictive performance, in particular for rare species, benefits of accounting for non-target species might vary depending on robustness of non-target species monitoring data (e.g. detection issues), their role within the ecosystem (e.g. engineer species are likely more influential on local communities than rare transient species), or processes shaping the target assemblage (if influence of abiotic factors dominates, then adding other species will have marginal consequences on model performance). While the list of additional species to consider can be prioritized based on existing knowledge in well-studied ecosystems, such information is often unavailable. Furthermore, a specific investigation, that might rely on simulated datasets to overcome limitations related to real world datasets (DiRenzo, Hanks, and Miller 2022), would be required to determine specific criteria, as well as optimal number of non-target species to include. While species communities and assemblages are largely defined arbitrarily (Stroud et al. 2015), a systematic assessment of *jSDM* performance as increasing the number and types (for instance based on their functional or trophic roles) of non-target species would be valuable to optimise model performance for the species of management interests.

jSDMs have already been used to model the distribution of a wide variety of species ranging

from micro-organisms (Minard et al. 2019) to megafauna (Brimacombe, Bodner, and Fortin 2021)

inhabiting many different ecosystems. Here, while we studied assemblages associated with two

specific coastal habitats, i.e. seagrass and sand, that have original characteristics as they are located

at the land-sea interface (Boyé, Thiébaut, et al. 2019), our case study reflects typical aspects of

applied ecological research. These include issues related to data limitation and availability but

also typical features of ecological communities (e.g. prevalence of rare and transient species;

Magurran and Henderson (2003)) ; Snell Taylor et al. (2018)). Valuable insights on trait-environment

relationships are scarce in our study, which reflects how contributions of functional ecology in *jSDMs*

are likely limited by trait data quality and availability (Tyler et al. 2012; Juan et al. 2022). For instance,

we found an interaction between trophic modalities (i.e. microphagous versus macrophagous diet)

and fetch (Fig. S15), indicating that organisms that filter on small particles are less likely to occur in

wave-exposed sites where high levels of sediment resuspension can block their filtering systems

(Manning, Peterson, and Bishop 2014). Yet, the limited number of informative trait-environment

relationships or species-environment relationships either suggest that neutral processes may shape

polychaete assemblages (Boyé, Thiébaut, et al. 2019); or rather highlight a mismatch between trait

data, environmental data, and the ecological processes at play (Juan et al. 2022). For instance,

environmental variables only capture mean climatological conditions, but fail to quantify variability

in the coastal environment, such as extreme events and seasonal or annual variability. Likewise, the

list of available fuzzy-coded traits only partially captures species capacity to adapt to environmental

variability (Juan et al. 2022). Thus, effectiveness of inclusion of traits in *jSDMs* is likely to be limited,

or to rely on effort to collect relevant trait information. In our case, while including traits does not

improve model predictive power, it somehow enhances our understanding of species responses

along environmental gradients. Hence, if the goal is not prediction but inference (Tredennick et al.

2021), including traits and proxies of phylogeny can facilitate *jSDM* interpretation.

This paper lays out an original framework to systematically compare multiple facets of alternative

jSDM formulations (i.e. including phylogeny, traits or additional species) on model interpretability,

explanatory and predictive power (Table 1). Using a set of complementary metrics, we specifically

assess performance of alternative model formulations fitted to presence-absence or abundance

data at the species and community levels. Our framework goes beyond existing guidelines proposed

to assess the performance of *jSDM* fitted on presence-absence data (Wilkinson et al. 2021) or that

focus on the predictive power of abundance-based models (e.g. Waldock et al. (2022)). It specifically compares the performance (both explanatory and predictive) and interpretability of alternative models' formulations accounting for the multiple and high-dimensional components that are typical of *jSDMs*, namely: (1) species and community level predictions including alpha and beta diversity metrics and ranking of predictions according to species prevalence/abundance; (2) species-environment relationships where we transposed the framework initially developed for time series by Rigal, Devictor, and Dakos (2020) into an effective tool to classify response curves according to 9 categories across high numbers of species (e.g. 99 in our case study); (3) trait-environment relationships; and (4) residual species-species correlations associated with random effects thanks to a new index that summarizes both changes in the sign and magnitude of the residual correlations.

Overall, our results provide new insights into the most appropriate strategies for *jSDM* fitting, according to modelling objectives (Tredennick et al. 2021) and available data. While the four models considered had similar explanatory power, adding extra information to standard *jSDMs* that only consider abiotic predictors can prove useful in cases. For instance, adding monitoring data for other non-target species can substantially increase model predictive power by modifying inferred species-environment relationships and residual correlation matrices. Similarly, adding traits or phylogeny can improve model interpretability. Future studies will be key to consolidate our findings on simulated case studies (Zurell, Berger, et al. 2010; DiRenzo, Hanks, and Miller 2022), or across contrasted ecosystems, for instance dominated either by environmental filtering, or by competitive processes. Generalizing this approach across ecosystems will further help prioritize data collection effort on the long term. For this purpose, we recommend using a multi-model inference framework similar to the one used in this study to systematically assess trade-offs associated with alternative jSDMs formulations.

Author Contributions

MPM conceived the project with inputs from CV, AB, MC. CV analysed data and led manuscript write-up. All authors had significant inputs to the manuscript and approved this final version.

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