



UNIL | Université de Lausanne

Faculté de biologie
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École de biologie

HOW IMPORTANT ARE BIOTIC INTERACTIONS IN PREDICTING THE REALIZED DISTRIBUTIONS OF SPECIES AND ASSEMBLAGES?

**Travail de Maîtrise universitaire ès Sciences en comportement, évolution et
conservation, spécialisation « écologie et évolution computationnelles »**

***Master Thesis of Science in Behaviour, Evolution and Conservation,
specialisation « Computational Ecology and Evolution »***

par

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Janvier 2019

ABSTRACT

Species Distribution Models (SDMs) are commonly used to understand and predict species distributions across space and time by combining information about the species occurrences and environment. However, biotic interactions are expected to be key drivers of species distributions, and the stress-gradient hypothesis predicts that their type and quantity may vary along an environmental stress-productivity gradient. Given that, the question whether biotic interactions should be included in SDMs has been risen. Models containing biotic predictors (as species presences/absences or biomass) and Joint Species Distribution Models (JSDMs), able to capture species associations, have been proposed to consider biotic interactions and their influence on species distribution across a landscape. Here, we used vegetation data from a mountain environment to investigate if species distribution predictions can be improved with SDMs including proxies for biotic interactions as predictors and JSDMs. Our results showed that JSDMs performed equally as the models containing only abiotic variables. The predictions slightly improved when biotic predictors were added for all models. In addition, we found variation in the amount of biotic interactions along the elevation gradient. All models performed better at sites of low species richness. Nevertheless, adding biotic interactions in our models only brought small improvements on predictions.

KEYWORDS: SDMs, JSDMs, stress-gradient hypothesis

RÉSUMÉ

Comprendre le fonctionnement de la distribution des espèces est un défi en écologie. Nous savons qu'une grande partie de ces distributions peut être expliquée par l'environnement. Néanmoins, les interactions entre espèces y jouent aussi un rôle majeur. Ces interactions peuvent varier en intensité ainsi qu'en nature. En effet, elles peuvent être négatives, lorsque deux espèces sont en compétition pour la même ressource, ou positives lorsque deux espèces s'apporte mutuellement un avantage. Une récente théorie a proposé l'hypothèse que la fréquence de ces interactions dépend de la quantité de stress à laquelle les espèces sont soumises : tendant à être plus négatives lorsque les conditions sont moins stressantes et plus positives lorsque les conditions sont difficiles. Aujourd'hui les modèles de distribution d'espèces (SDMs) sont utilisés afin de caractériser et prédire la distribution de ces dernières. Ces derniers utilisent principalement des paramètres environnementaux. Néanmoins, comme les interactions biotiques sont également importantes, de nouveaux modèles utilisant des mesures d'interactions biotiques comme prédicteurs ont été testés et d'autres capables d'intégrer ces interactions ont été développés. Nos résultats montrent que ces nouveaux modèles n'améliorent pas la précision des prédictions lorsqu'ils sont comparés aux modèles basés uniquement sur des paramètres abiotiques. Cette précision montre une augmentation minime lorsque des paramètres biotiques sont ajoutés comme prédicteurs dans nos modèles. Nous avons également observé une variation de la quantité des interactions biotiques en fonction de l'altitude. En conclusion, nous montrons que l'intégrations des interactions biotiques n'apporte que de petites améliorations avec nos données.

INTRODUCTION

Understanding the relationship between environment and species distribution has been a central issue in ecology since a long time (Humboldt & Bonpland, 1807; Austin, 2002). It is known that environmental conditions play a key role for species distributions. To study this matter, Species Distribution Models (SDMs) have been developed and are used to understand and predict species distributions (Guisan & Zimmermann, 2000). In addition, SDMs can also be used to predict species distributions under past and future conditions to assess the changes and potential challenges resulting from global environmental changes such as climate (Bakkenes *et al.*, 2002; Peterson *et al.*, 2002; Midgley *et al.*, 2003), land-use change (Faleiro *et al.*, 2013) and nitrogen deposition (Vries *et al.*, 2010) and to evaluate the invasive potential of a newly introduced species (Nyari *et al.*, 2006; Zimmermann *et al.*, 2010).

Classical SDMs are usually based on abiotic predictor variables representing environmental conditions. However, it is known that biotic interactions play a key role in shaping species distributions, and thus, may need to be accounted for when building models and making the predictions (Callaway *et al.*, 2002; Araújo & Luoto, 2007; Gotelli *et al.*, 2010). These interactions can be negative, such as competition, locally decreasing occurrences of species (Weiner *et al.*, 2001) or reducing fitness (Lovett Doust & Lovett Doust, 1990), or positive such as facilitation resulting in a beneficial effect for at least one species and no negative effect for the other (Stachowicz, 2001). This can lead to reduction of the abiotic stress by neighbouring species allowing them to survive in conditions where they could not grow alone (Bertness & Callaway, 1994; Bertness & Leonard, 1997; Cavieres & Badano, 2009). Surely, not all species affect each other, and many relationships are neutral. Finally, species traits can be an indicator of species' ability to compete and could thus, give hints about the nature and amount of the biotic interactions among species (Kunstler *et al.*, 2016). For instance, it has been demonstrated that species with higher leaf area tended to be more competitive in fertile environments (Fynn *et al.*, 2005).

In addition to species traits, environmental conditions of a site may influence the nature and amount of biotic interactions. This has been formalized as Stress-Gradient Hypothesis (SGH) which states that the frequency of negative biotic interactions (competition) is bigger in a low-stress environment, while in a high-stress environment, the interactions tend to shift to neutral and positive interactions (facilitation) (Maestre *et al.*, 2009). This theory is controversial, yet several studies have found supporting results (Cavieres & Badano, 2009; Meier *et al.*, 2011). For example, it has been shown that when looking at survival of species, biotic interactions change from competition to facilitation with the increasing abiotic stress and from negative to less negative when looking at the growth and reproduction instead of abundance or occurrences (He *et al.*, 2013). Further, it has been demonstrated that species interactions tends to shift from competition to facilitation with stress in a cold alpine environment (Callaway *et al.*, 2002) and along a salinity gradient (Bertness & Shumway, 1993). Nevertheless, several other studies found rejecting results in semi-arid environments (Maestre & Cortina, 2004; Liancourt *et al.*, 2005) suggesting that this hypothesis could not be applied to every type of stress gradient

(Maestre *et al.*, 2009) or that the data were not appropriate to test this hypothesis. In addition, a related hypothesis, the Species-Interactions Abiotic-Stress Hypothesis (SIASH), states that abiotic forces (e.g. minimum temperatures) define species range limits in stressful conditions while biotic forces (e.g. competition) set the species range limits in less challenging environments (Louthan *et al.*, 2015) (Figure 1). From the SIASH, we can also hypothesize that more negative biotic interactions occur at low elevation compared to high elevation. Indeed, more species will be able to cope with soft environmental conditions, leading to a higher species richness and number of competitors there, compared to harsh and stressful environment where a lower number of species have the appropriate adaptations (Liancourt *et al.*, 2005). Altogether, combining the two (related) hypothesis, one can expect that species occurrence at the sites with low abiotic stress are likely more defined by negative interactions, whereas at sites with high abiotic stress, species occurrences are more driven by abiotic environmental conditions and rather positive than negative interactions.

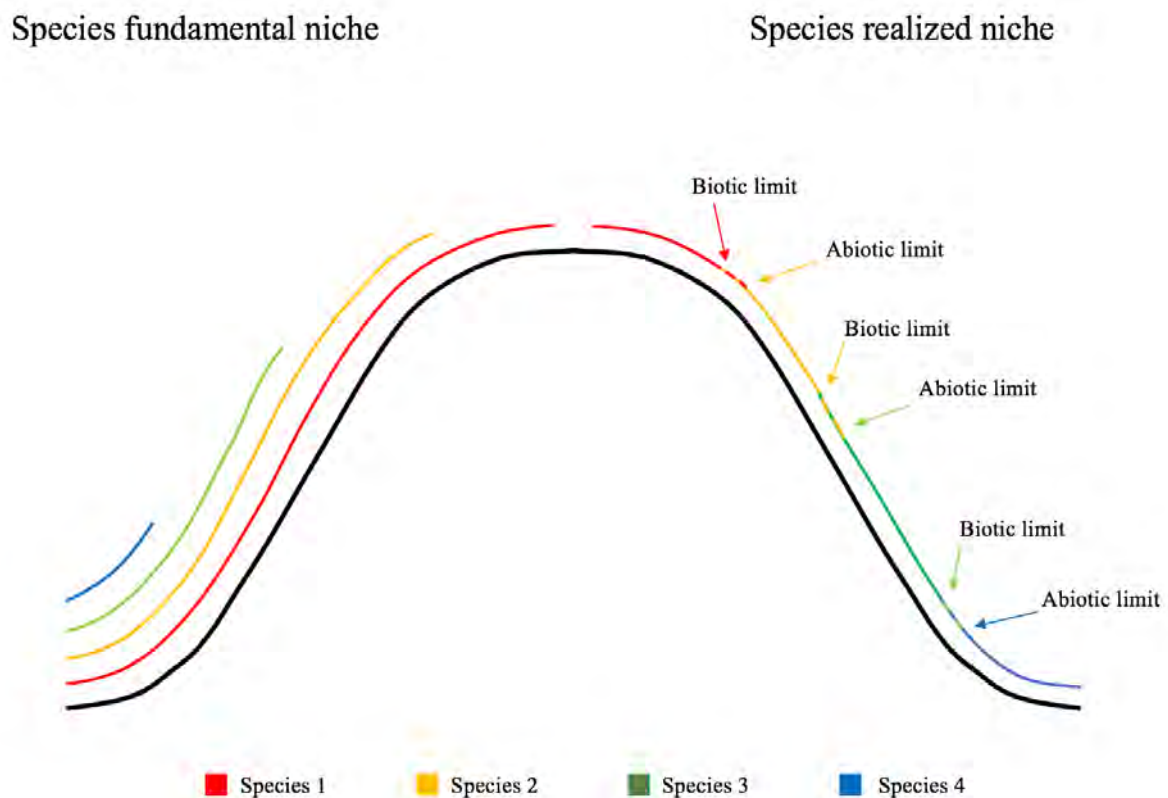


Figure 1: Visualization of the SIASH hypothesis (Louthan *et al.*, 2015); On the left: the hypothetical species fundamental niche, defined by the environmental conditions only. On the right, species realized niche, as subsets of the fundamental niche driven by the environmental conditions and the competition between species.

Because of the biotic interactions' importance in shaping species distribution, the question whether they should be taken into account in SDMs has been examined (Hubbell, 2001; Wisz *et al.*, 2013; Anderson, 2017). Several studies tried to include biotic interactions using other species as predictors to improve models' accuracy (Araújo & Luoto, 2007; Heikkinen *et al.*, 2007), but these represent a small proportion of unidirectional biotic interactions and does not take into account the effects and networks of all species (Kissling *et al.*, 2012; Harris, 2016).

Moreover, a single or few dominating, generally influential, species cannot be identified in all environments (Mod *et al.*, 2016a). Instead of single species, comprehensive measures such as site biomass have also been used and demonstrated to improve the models (Meier *et al.*, 2010), yet such information is rarely available, or is correlated with abiotic factors (such as NDVI and temperature in the northern hemisphere (Schultz & Halpert, 1993)). In order to improve the integration of biotic interactions in modelling, Joint Species Distribution Models (JSDMs) have recently been proposed (Pollock *et al.*, 2014), and numerous different models have been developed (Clark, Gelfand, Woodall, & Zhu, 2014; Clark, Nemergut, Seyednasrollah, Turner, & Zhang, 2017; Hui, 2016; Pollock *et al.*, 2014; Thorson *et al.*, 2015). JSDM have several new advantages: i) they build species-to-species association matrices; ii) some take into account species traits and phylogenetic correlations, and iii) some can help choosing suitable environmental predictors. Nevertheless, their capacity to increase accuracy of predictions is controverted as some studies showed improved results using them (Thorson *et al.*, 2015; Ovaskainen *et al.*, 2016; Tikhonov *et al.*, 2017), while others found no difference compared to classical SDMs (Copenhaver-Parry & Bell, 2018). In fact, it is possible that biotic interactions may not be necessary to include in the models, as the species occurrence data, used for model training represent the realized niche of species (Guisan & Zimmermann, 2000) and thus, the influence of biotic interactions could already be incorporated implicitly in the models.

To further examine the incorporation of biotic interactions in SDMs, the two aims of this thesis were: i) to investigate how well biotic interactions help in predicting species distributions; and ii) to quantify their effect on different species distribution models along a stress-gradient. In order to answer these, we used elevation to represent a stress-gradient, tried several modelling methods and used different explanative variables as proxy for the biotic interactions. We first assessed how much we can improve classical SDMs by incorporating occurrence of other species as a proxy for biotic interactions and how these compared to JSDMs. As biotic interactions are important for species distributions, we expected improvement in model performance, especially for less competitive species. Second, we examined if accuracy of model predictions varies along the elevation gradient. According to the SGH, we expected the improvement, and thus influence of biotic interactions, to be higher at low compared to higher elevations. Finally, two additional technical questions were investigated. First, we asked whether species distribution predictions could be improved when statistical interactions between the predictors are added in the models. And second, we tested if using species richness as a proxy for biotic interactions is more precise than using occurrences of specific species. As the analyses presented in this thesis are based on presence/absence information of species, identification of biotic interaction is based on species co-occurrences patterns. This means that for example, competition is identified if segregation of two species cannot be explained with abiotic variables only (i.e. one species locally excludes another from a suitable patch). Further, only the 100 most prevalent species of our study area were included, meaning that our results do not apply to the entire plants community.

MATERIAL AND METHODS

Analyses were carried out in three steps (Figure 2): pre-modelling, modelling and post-modelling, with all of the codes available here: <https://github.com/EleonoreLavanchy/Master>. During a pre-modelling phase, we chose species and environmental predictors to be included in the analyses. For modelling, species occurrences were modelled using the 80% of the available data and predicted against the remaining 20% (modelling phase) within each cross-validation round. Once the models were fitted, their predictions were compared to the observed species occurrences and the different models' performances were compared among species and sites in a post-modelling phase. The importance of statistical interactions among the predictors was assessed comparing the predictions built with and without them. Additionally, the SGH was tested by comparing the variance partitioning among 3 bands of elevation (Figure 2).

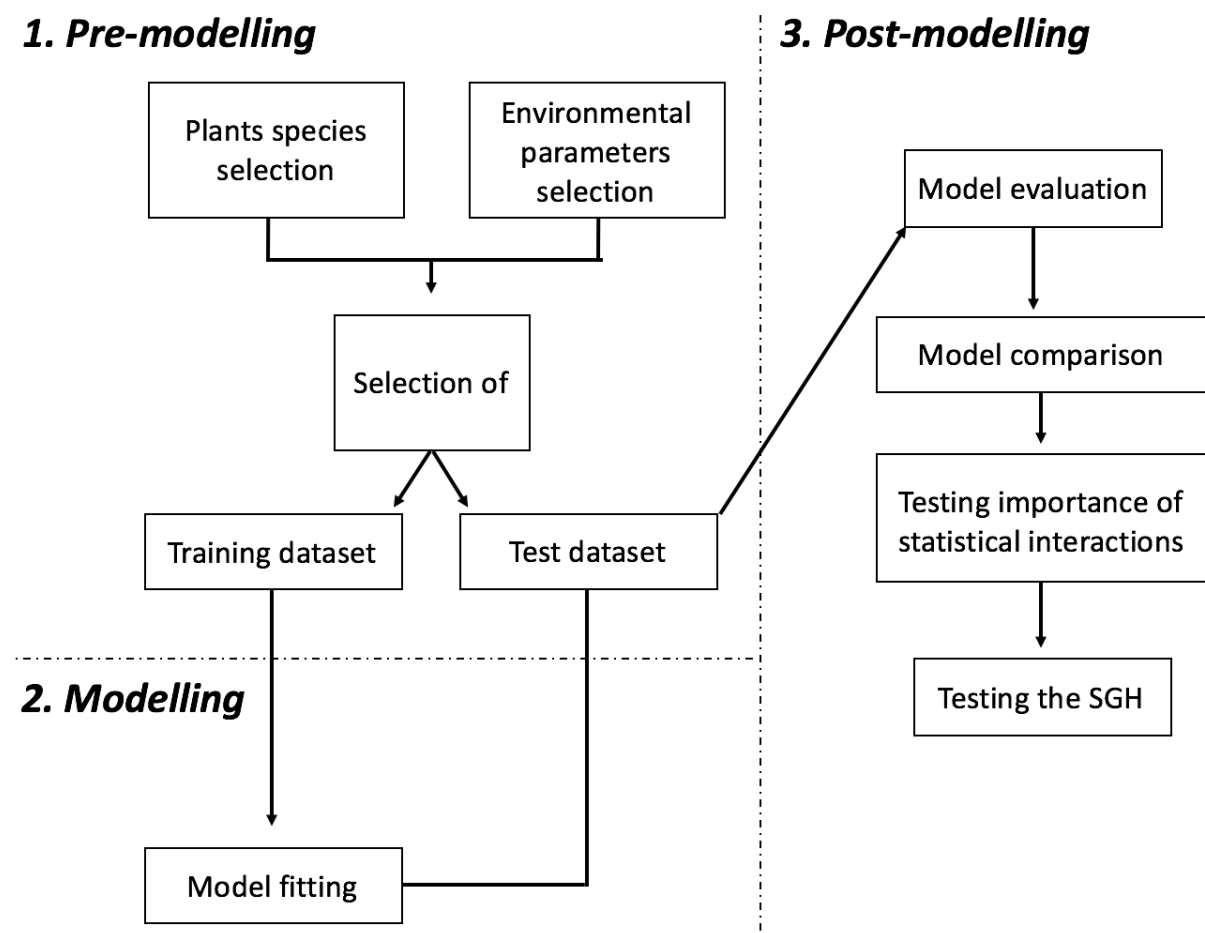


Figure 2: Framework of the study. **1. Pre-modelling phase**, where the plants species and the environmental variables to include in the models were selected. In addition, the sites were divided in training and evaluating datasets. **2. Modelling phase**, where the models were fitted on the 80% of the data and predictions were done against the 20% of remaining data. **3. Post-modelling phase**, where the models' predictions were evaluated by comparisons with the observed species occurrences. The performances were compared among the different models. Finally, the importance of statistical interactions and the SGH were investigated.

Study area

The study was conducted in the Western Swiss Alps and covers all the Alpine areas of cantons of Vaud (ca. 700 km²; center point: 46°22' N; 7°2' E). This mountainous area is a priority area for the University of Lausanne and for its new mountain center (CIRM: Centre Interdisciplinaire sur les Régions de Montagnes), and is also a priority conservation area for the WWF and ProNatura for instance (<http://www.leregional.ch/N67958/la-position-du-wwf-et-de-pro-natura-en-detail.html>). occurrence of vascular plant species were surveyed from 911 open vegetation sites (size 4 m²) by following a random-stratified sampling design considering elevation, slope and aspect as strata (Hirzel & Guisan, 2002). The minimum distance between the sites was set to 200 m to avoid spatial auto-correlation (Dubuis *et al.*, 2011). Elevation of the sites ranges from 418.8 m to 3101.4 m (Figure 3).

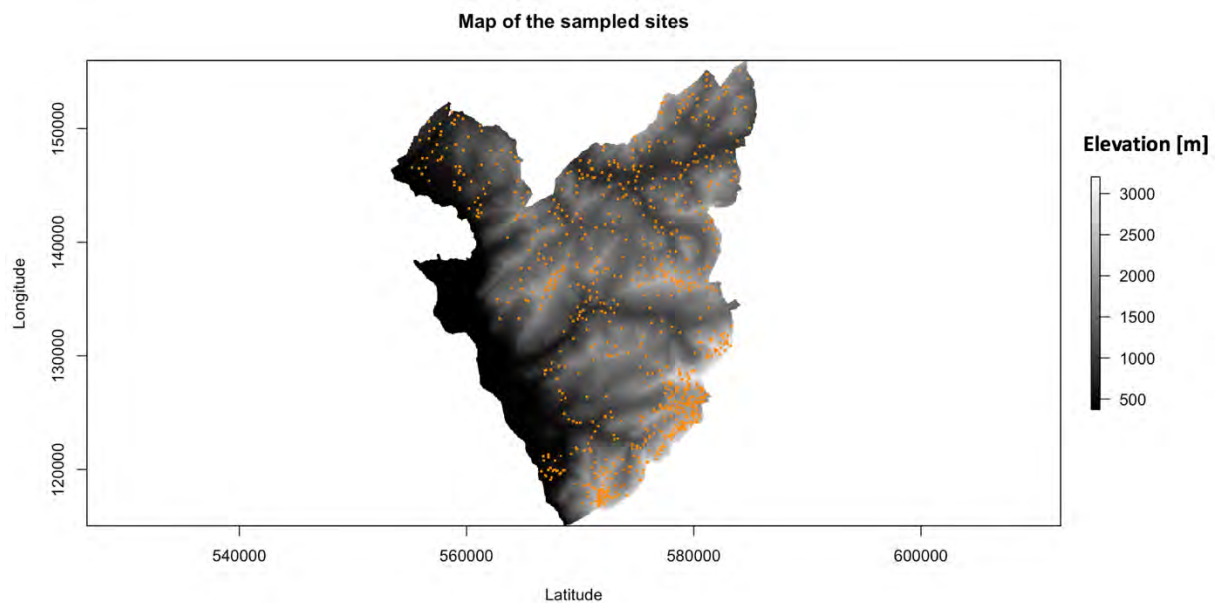


Figure 3: Map of the sampled sites, represented with orange dots, and their elevation. Geographic coordinates are provided in Swiss coordinate system (LV03).

Pre-modelling

Plant species selection

Out of 900 plant species recorded across the sites, the 100 most represented (with a minimum of 70 occurrences across sites) were chosen for the analyses. Only 100 species with a minimum prevalence were used to reduce the number of species modelled in order to decrease the analytical time and to ensure confidential parameter estimates, while still being able to incorporate the influential environmental predictors without overparameterizing the models (Merow *et al.*, 2014)(see the list of plants species and their prevalence in Figure S1 in Appendix). This study thus concerns the most prevalent open-habitat plant species in our study area.

Environmental predictors selection

Out of 93 available environmental predictors, (representing temperature, precipitation, evapotranspiration, topography, etc.), five were selected to build the models: growing season precipitation sum, mean temperature of growing season, growing season potential solar radiation, pH and slope. The growing season ranges from May to September.

These parameters were chosen to cover the main ecological dimensions of plants (temperature, water availability, light, nutrients, topography)(Mod *et al.*, 2016b). A principal component analysis (PCA) was additionally performed in order to select the parameters explaining the greatest proportion of variance in environmental conditions of the sites and to avoid highly correlated parameters (correlation table in the Appendix, Table S1). Among the selected variables, the only correlation above 0.7 was between temperature and precipitation with a value of 0.822. However, we still decided to keep both variables because they are of a high ecological importance.

The first and second order parameters (i.e. including squared terms) were used in the models for all five predictors according to the output of an analysis summarizing the parameters used in the best model for each plant species (*glmulti* function on R from the *glmulti* package (Calcagno & Mazancourt, 2010); see *glmulti* table results in Appendix, Table S2). Statistical interactions were not considered here because they were not yet implemented in the HMSC package (see modelling section).

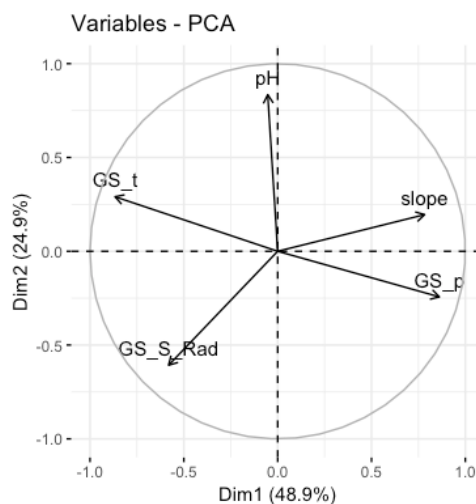


Figure 2 : PCA circle of the selected environmental predictors. *GS_t* represents the growing season temperature, *GS_p* the growing season precipitations and *GS_S_Rad* the growing season solar radiations.

All parameters were scaled (mean = 0 and standard deviation = 1) prior to analyses following recommendations of the *HMSC* package developers (see *HMSC* manual; https://www.helsinki.fi/sites/default/files/atoms/files/hmsc_manual_0.pdf).

Cross-validation

A random stratified cross-validation was used to determine which sites were used for model training or for model evaluation. Within each 200 m band of elevation, 80% of the sites were randomly sampled in the training dataset while the remaining 20% were assigned to the evaluating dataset. The highest elevation band was 400 m due to the small number of sites available at the highest elevations. This procedure was repeated 10 times to choose for each run different sites in the training and test datasets as it ensures that each site was selected seven to eight times for the training and two to three times for the evaluation.

Modelling

To investigate the performance of traditional SDMs and JSDMs along with their differences, we applied GLMs (Generalized Linear Model) and HMSC (Hierarchical Modelling of Species Communities), respectively. Different models were built with both approaches, including and excluding biotic components for all 100 species. Predictions were then evaluated across species and sites by comparing observed and predicted occurrences using several evaluation metrics (refer to M&M page 11, post-modelling section).

SDM models

GLM was chosen as the HMSC is based on it (Ovaskainen *et al.*, 2016). We used two abiotic and two biotic GLMs.

The first biotic model (*Biotic GLM1*) contained the occurrence (as presences and absences) of the three species with the highest sum of absolute residual correlation as calculated by the function *corRandomEff* in *HMSC* package (*Lolium perenne*, *Lotus corniculatus* and *Holcus lanatus*; Matrix of the residual correlation in Appendix) as biotic predictors in addition to the environmental variables. According to co-occurrences among species (independently of the abiotic environment), these species are expected to be strongly associated with other species and thus, might potentially affect their distributions (Pollock *et al.*, 2014). In order to keep same number of predictors in both abiotic and biotic models, the first abiotic model (*Abiotic GLM1*) contained the same predictors as the *Biotic GLM1* but the presences and absences of the biotic predictors were randomized among the sites, yet still retaining the same number of presences and absences for each plant species. Therefore, only the abiotic predictors should be expected to explain part of the variance in the *Abiotic GLM1*.

In addition to the five environmental predictors, the second biotic model (*Biotic GLM2*) used the presences and absences of the three most prevalent plant species in the dataset (le Roux *et al.*, 2014) (*Festuca rubra*, *Trifolium pratense* and *Antoxanthum odoratum* with respectively 434, 421 and 384 presences) as a high prevalence is likely to be correlated with competitiveness. The last model (*Abiotic GLM2*) is like the *Abiotic GLM1*: the same biotic predictors than in *Biotic GLM2* but randomized.

JSDM models

The package *HMSC* (*Hierarchical Modelling of Species Communities*) (Ovaskainen *et al.*, 2017) was used to build JSDMs as it allows the spatial predictions of species probability of occurrence under novel environmental realm and set of occurring species (“conditional predictions in new area”).

HMSC is a framework for modelling and analysing community data. Variance within the data is first attributed among environmental predictors and the remaining non-explained variance (i.e. residuals) is then associated with latent variables implemented in the model. Species-to-species matrices are built in order to capture the species association (i.e. potential biotic interactions) based on residual correlation representing co-presence, co-absences, or presence-absence repeated patterns not explained by the abiotic predictors (Ovaskainen *et al.*, 2016, 2017).

The first model (*Abiotic HMSC*) makes no conditional predictions making it a purely abiotic model (i.e. in theory comparable to the Abiotic GLMs). The second model (*Biotic HMSC*) makes predictions of each species conditional to the presence of all other species in the evaluation sites, making it a model aiming to account for biotic interactions. This last model contained latent variables in order to attempt to explain additional variance not explained by the abiotic predictors (see R help files of the package: <https://github.com/guiblanchet/HMSC>). To facilitate the latent variables in models, two random factors were incorporated to group sites among which the species associations were to be resolved. The first random factor contained the same value for all sites as they were sampled with the same method. The second one contained one value according to the elevation of a site. Sites at low elevation (i.e. with an elevation below the median elevation of the sampled sites) (from 400m to 1819m) received a value of 2 and the sites at high elevation (from 1819 to 3100m) received a value of 3. The latter random factor was done in accordance to the SGH; i.e. the nature of biotic interactions may vary along a stress gradient (here elevation).

Post-modelling

The mean predicted probability of occurrences within the 10 cross-validation runs was recorded for each plant species at each evaluation site, and then compared to observed occurrences in order to evaluate the models. Model performance per species was evaluated using four metrics. The first one was the $Tjur - R^2$ (Tjur, 2012) which ranges from 0 to 1. Additionally, Maximum True Skill Statistics (Max TSS) and Maximum Kappa (Max Kappa, based on Cohen’s kappa (Cohen, 1960)) were used, both from the *ecospat* package in R (Di Cola *et al.*, 2017) and ranging from -1 to 1, where 1 indicates perfect predictions and 0 not better than random. Finally, we used AUC from the *AUC* package, ranging from 0 to 1, with 1 indicating perfect predictions and 0.5 not better than random. Model performance per site was evaluated with Community AUC (implementing *AUC R*-package) and Maximum Sørensen Index (Max Sørensen), originally from (Sørensen, 1948) but calculated in a similar way as the Max Kappa and Max

TSS (see Scherrer et al. in prep.). The AUC and Max Sørensen metrics range from 0 to 1. Repeated measures ANOVA and post-hoc Tukey tests were used to assess if the performances of the models differed. Then the models' performances were examined across species and sites and relative to their properties. More specifically, we tested whether the best modelling technique per species is dependent on species prevalence and species' Specific Leaf Area (SLA; the ratio of leaf area to dry mass calculated by Dubuis et al., 2013), and whether the best modelling technique per site is dependent on elevation and observed species richness. For these, Wilcoxon rank-sum tests were used.

Variance partitioning

In order to assess the magnitude of species association captured by the latent variables, we computed a variance partitioning among the different predictors of both HMSC models (*Abiotic HMSC* and *Biotic HMSC*) using the *variPart* function of the *HMSC* package.

To test the SGH, we also applied a variance partitioning along the elevation gradient (comparing low elevation [418.8m → 1479.4m], mid elevation [1479.4m → 2040.5m] and high elevation [2040.7m → 3101.4m]) by fitting separate HMSC models for the three subsets of data. This was done in order to see if the proportion of the variance explained by the latent variables vary depending on elevation.

Assessing interactions between predictors

In addition to previous analyses, we built Random Forest (RF) models to see if models' predictions can be improved by adding statistical interactions among the predictors (automatically incorporated in RF). Two RFs were built: the first with the most prevalent species as predictors (*Random Forest 2*) for comparison with *Biotic GLM2* as it was on average the best model per species (see Results), and the second RF (*Random Forest 2*) with the species having the highest sum of absolute residual correlation as calculated by the function *corRandomEff* in *HMSC* package (*Random Forest 1*) to compare it to *Biotic GML1* as it was the best model per site.

Additionally, the species richness per site was used as a predictor to see if using another proxy of biotic interaction was more efficient than adding presences and absences of some species. With this, we built two different models: one GLM (*Biotic GLM SR*) and one RF (*Random Forest SR*). Finally, we tested which models was predicting the more accurately species richness. The predicted species was calculated as the sum of the predicted probabilities of occurrence of species as proposed by Calabrese *et al.*, (2014).

RESULTS

Species occurrences as a proxy for biotic interactions

Models performances per species

Generally, the four metrics measuring model performance per species indicate some, yet small, differences among the different models with *Biotic GLMs* being the most performant ones (repeated Measures ANOVA: $T_{jur} - R^2$: Df = 5, Sum of Squares = 0.02756, Mean of Squares = 0.055115, F-value = 199.19, Adjusted P-value (Bonferroni correction) < 0.001. Max TSS: Df = 5, Sum of Squares = 0.0450, Mean of Squares = 0.009004, F-value = 31.467, Adjusted P-value (Bonferroni correction) < 0.001. Max Kappa: Df = 5, Sum of Squares = 0.1005, Mean of Squares = 0.020102, F-value = 47.12, Adjusted P-value (Bonferroni correction) < 0.001. AUC: Df = 5, Sum of Squares = 0.02460, Mean of Squares = 0.0049203, F-value = 69.213, Adjusted P-value (Bonferroni correction) < 0.001, detailed analyses and Post-hoc Tukey tests available in Appendix Table S4). According to $T_{jur} - R^2$, the models' performances are divided in three groups (shown in decreasing order of performances): the *Biotic GLMs* (with mean $T_{jur} - R^2$ of 0.299 ± 0.127 for *Biotic GLM1* and 0.305 ± 0.128 for *Biotic GLM2* compared to 0.249 ± 0.121 for *Abiotic HMSC* which has the lowest value), the *Abiotic GLMs* and finally the *HMSCs models* (Figure 3A, detailed values for all models in table S3 in Appendix). The differences are small but significant among these groups and non-significant within the groups (Table S4 in Appendix). The three remaining metrics, Max TSS, Max Kappa and AUC showed the similar order in models' performance. For these three metrics, the models are divided in two groups: one containing both the *HMSCs models* and the *Abiotic GLMs* and one containing the *Biotic GLMs* (with mean Max TSS of 0.582 ± 0.106 for *Biotic GLM1* and 0.588 ± 0.108 for *Biotic GLM2* compared to 0.565 ± 0.110 for *Abiotic GLM2* which has the lowest value; mean Max Kappa of 0.439 ± 0.134 for *Biotic GLM1* and 0.447 ± 0.130 for *Biotic GLM2* compared to 0.414 ± 0.135 for *Abiotic GLM1* which has the lowest value; mean AUC of 0.853 ± 0.055 for *Biotic GLM1* and 0.855 ± 0.056 for *Biotic GLM2* compared to 0.839 ± 0.059 for *Abiotic GLM2* which has the lowest value)(Figure 3BCD, values for all models in Table S3 in Appendix). Altogether, the difference in model performances is small but significant comparing the *Biotic GLMs*, which are on average the best models, and the others (Figure 4 and Table S4 in Appendix).

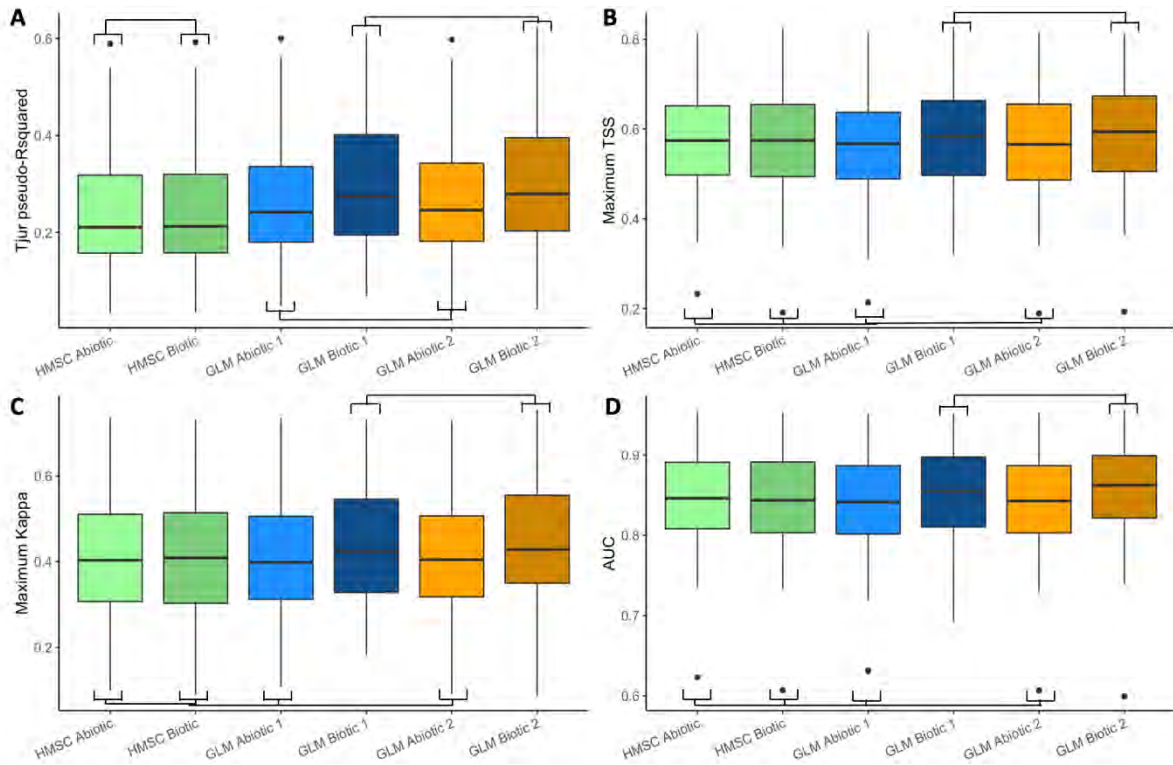


Figure 4: Model performance per species according to four metrics. **A.** Tjur – R^2 . **B.** Max TSS. **C.** Max Kappa. **D.** AUC. Boxes span from 1st to 3rd quantile, with median marked in-between with a black line. Whiskers span from “1st quantile - 1.5 x box height” to “3rd quantile + 1.5 x box height”. Black brackets connect the groups with non-significant comparisons according to repeated-measures Anova and Tukey post-hoc tests. Complete pairwise comparisons in Table S4 in supplementary materials.

Models performances per sites

The two metrics measuring model performance per site indicate some, yet very small and mainly non-significant, differences among the different models (repeated measures ANOVA, Community AUC: Df = 5, Sum of Squares = 0.043, Mean of Squares = 0.008648, F-value = 24.95, Adjusted P-value (Bonferroni correction) < 0.001. Max Sørensen: Df = 5, Sum of Squares = 0.108, Mean of Squares = 0.021690, F-value = 12.131, Adjusted P-value (Bonferroni correction) < 0.001, detailed analyses and Post-hoc Tukey tests available in Appendix Table S6). Biotic GLMs have the highest mean Community AUC (respectively 0.869 ± 0.090 for *Biotic GLM1* and 0.867 ± 0.093 for *Biotic GLM2* compared for instance to the lowest value 0.861 ± 0.096 for *Abiotic GLM1*, values for all models in Table S5 in Appendix), yet the difference to other models is more often significant for *Biotic GLM1* (Figure 5A and Table S6 in Appendix). According to the Max Sørensen, the models form two groups. As before, one with the *Abiotic GLMs* and the *HMSC* and one with the *Biotic GLMs* (0.682 ± 0.195 for *Biotic GLM1* and 0.678 ± 0.194 for *Biotic GLM2* compared to the lowest value 0.669 ± 0.200 for *Abiotic GLM2*, values for all models in table S5 in Appendix). However, as for the Community AUC, the *Biotic GLM2* is not significantly higher than the *HMSC models*, and *Biotic GLM1* shows slightly higher performances compared to the other models (Figure 5B and Table S6 in Appendix).

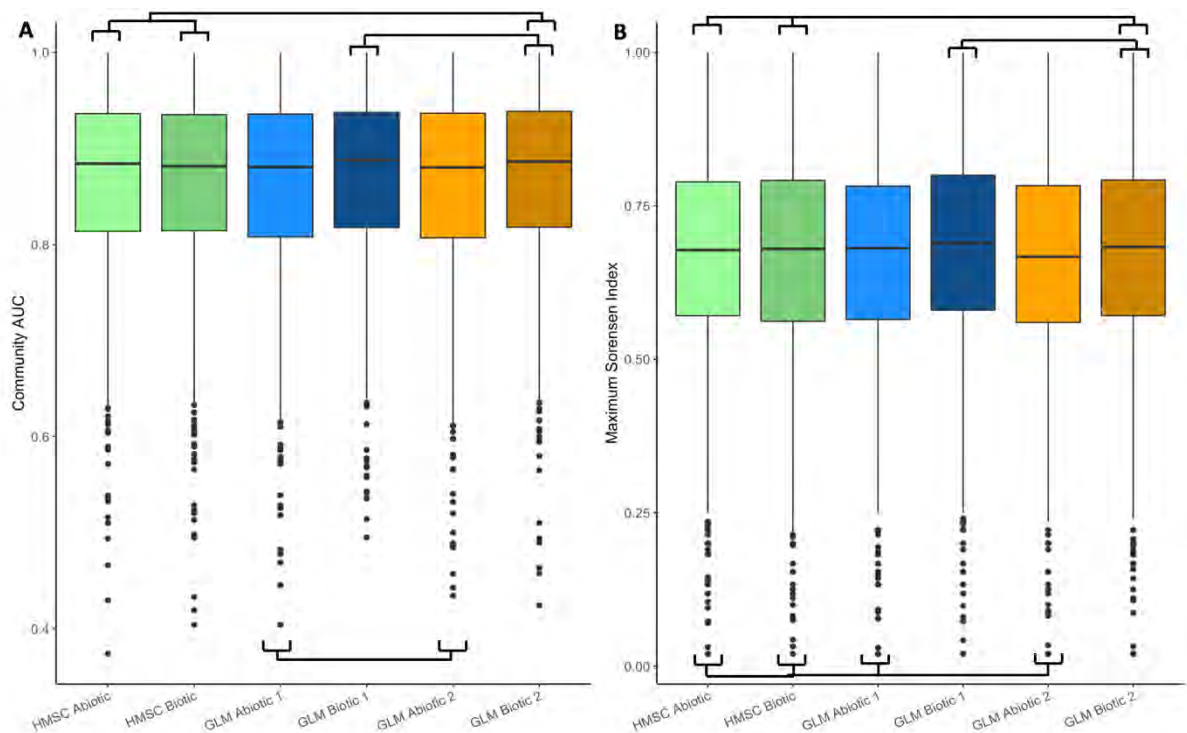


Figure 5: Models performances per sites according to two different metrics. **A.** Community AUC **B.** Maximum Sørensen Index. Boxes span from 1st to 3rd quantile, with median marked in-between with a black line. Whiskers span from “1st quantile - 1.5 x box height” to “3rd quantile + 1.5 x box height”. Black brackets connect the groups with non-significant comparisons according to repeated-measures Anova and Tukey post-hoc tests. Complete pairwise comparisons in Table S6 in supplementary materials.

Variance partitioning between an abiotic and a biotic model

Variance partitioning of HMSC models demonstrates that variance explained by the biotic interactions (i.e. latent variables) is small compared to the proportion explained by the environmental predictors (0.045% on average between all the species) (Figure 6).

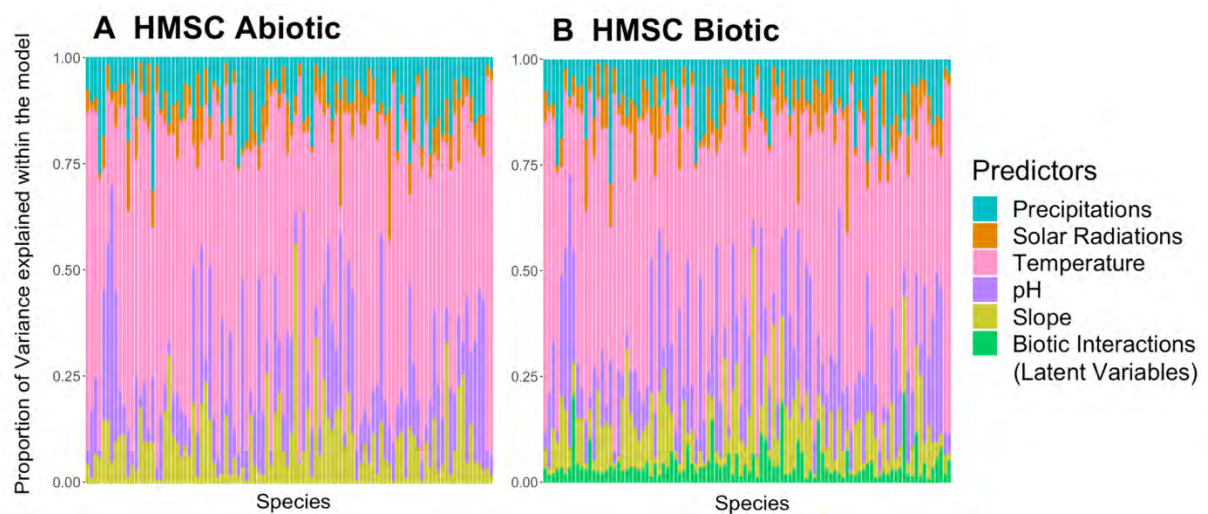


Figure 6: Variance partitioning among the predictors. Each vertical bar represents a species, ordered from 1 to 100. Names corresponding to the numbers can be found in the Appendix A: Abiotic HMSC; B: Biotic HMSC.

Species characteristics

According to Max Kappa, 89 % of species are best predicted by a biotic model versus 11 % by an abiotic model. Mean prevalence of the species for which a biotic model is the best (157.843 ± 87.063) is higher than the prevalence of the species for which abiotic model is the best (116.182 ± 56.798), whereas mean SLA of the species for which an abiotic model is the best (23.729 ± 9.060) is higher than mean SLA of the species for which a biotic model is the best (21.642 ± 9.725) (Figure 7). However, none of these differences are significant according to the Wilcoxon rank-sum tests (Prevalence: $W = 659$, Adjusted P-value (Bonferroni correction) = 0.12522; SLA: $W = 384$, Adjusted P-value (Bonferroni correction) = 0.4944).

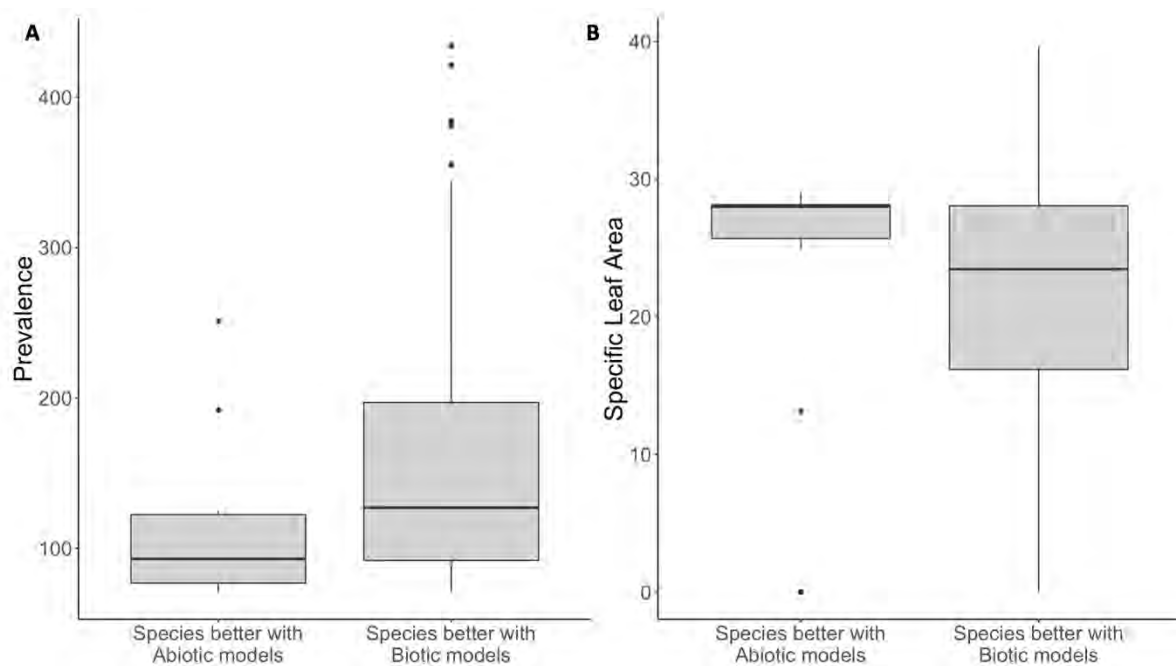


Figure 7: Characteristics of species the best predicted with a biotic or abiotic model. **A: Prevalence.** Wilcoxon rank-sum test **B: Leaf Area.** Wilcoxon rank-sum test.

Site characteristics

Out of the 76 % of sites for which only one model category (biotic or abiotic) appears as the best, 69% are better predicted with a biotic model and 31% with an abiotic model. Site's elevation and observed species richness are higher in these 69% of sites (mean elevation: 1663.566 ± 485.668 ; mean species richness: 20.160 ± 9.415) compared to the 31% others (mean elevation: 1595.692 ± 561.538 ; mean species richness: 19.344 ± 10.146) (Figure 8). These differences are however not significant using the Wilcoxon rank-sum tests (elevation: $W = 54158$, Adjusted P-value (Bonferroni correction) = 0.3718; species richness: $W = 53207$, Adjusted P-value (Bonferroni correction) = 0.7042).

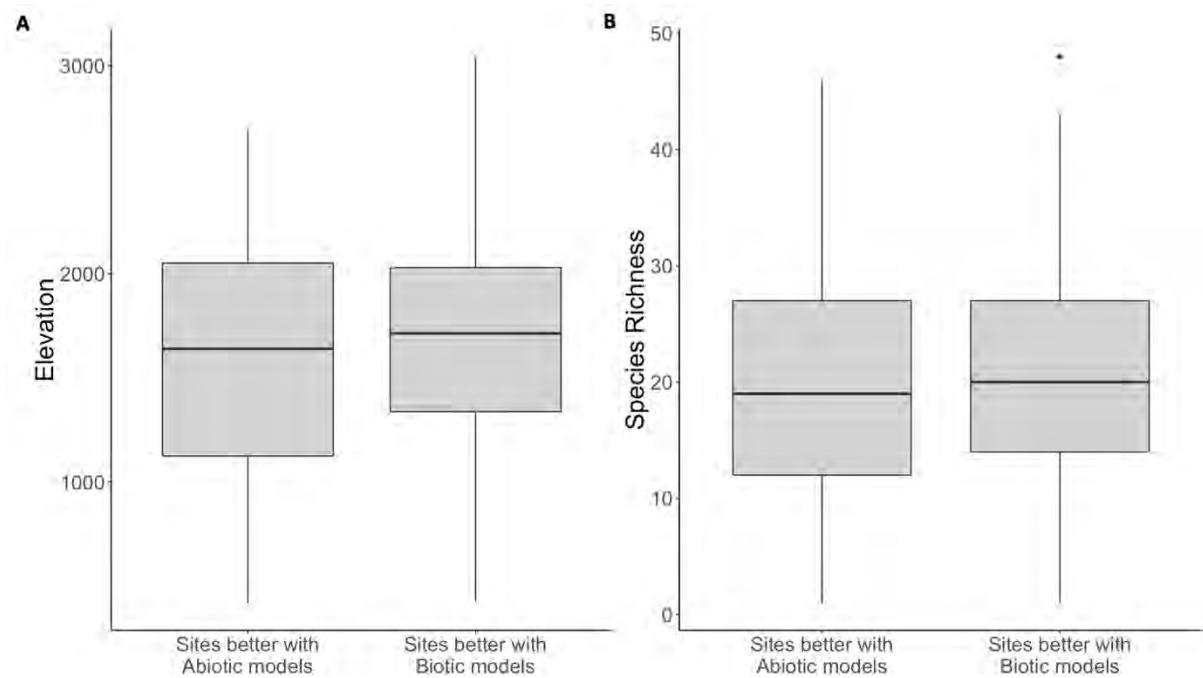


Figure 8: Similarities between sites better with Biotic models compared to Abiotic models. **A: Elevation.** Wilcoxon rank-sum test. **B: Species Richness.** Wilcoxon rank-sum test.

Biotic interactions variation along elevation (SGH)

Models performances along the elevation gradient

Along the elevation gradient, all models perform almost equally well, and better when the species richness is lower (repeated measure ANOVA, Models: Df = 5, Sum of Squares = 0.108, Mean of Squares = 0.02169, F-value = 0.5584, P-value = 0.732, Elevation: Df = 1, Sum of Squares = 0.508, Mean of Squares = 0.50819, F-value = 13.0828, P-value < 0.001) (Figure 9).

Variance partitioning

Variance partitioning based on HMSC along the elevational gradient (i.e. the three separate models with sites from the three elevation bands) shows that the variance explained by the latent variables is significantly higher at low and mid elevation compared to high elevation (repeated measures ANOVA, Elevation: Df = 2, Sum of Squares = 0.095476, Mean Sum of Squares = 0.046638, F-value = 34.4730, P-value < 0.001, Species :Df = 99, Sum of Squares = 0.181183, Mean Sum of Squares = 0.00183, F-value = 1.3202, P-value = 0.05104, Post-hoc Tukey range's test, Low-High Elevation: difference = 0.040 Lower = 0.028, Upper = 0.05, Adjusted P-value < 0.001; Mid-High Elevation: difference = 0.035, Lower = 0.022, Upper = 0.047, Adjusted P-value < 0.001; Mid-Low Elevation : difference = -0.005, Lower = -0.018, Upper = 0.007, Adjusted P-value = 0.558). Additionally, the importance of abiotic predictors varies along elevation. Temperature has the biggest importance at low elevation but is replaced by pH and slope at mid elevation, while precipitations seems to be driving species distributions at high altitudes (Figure 10).

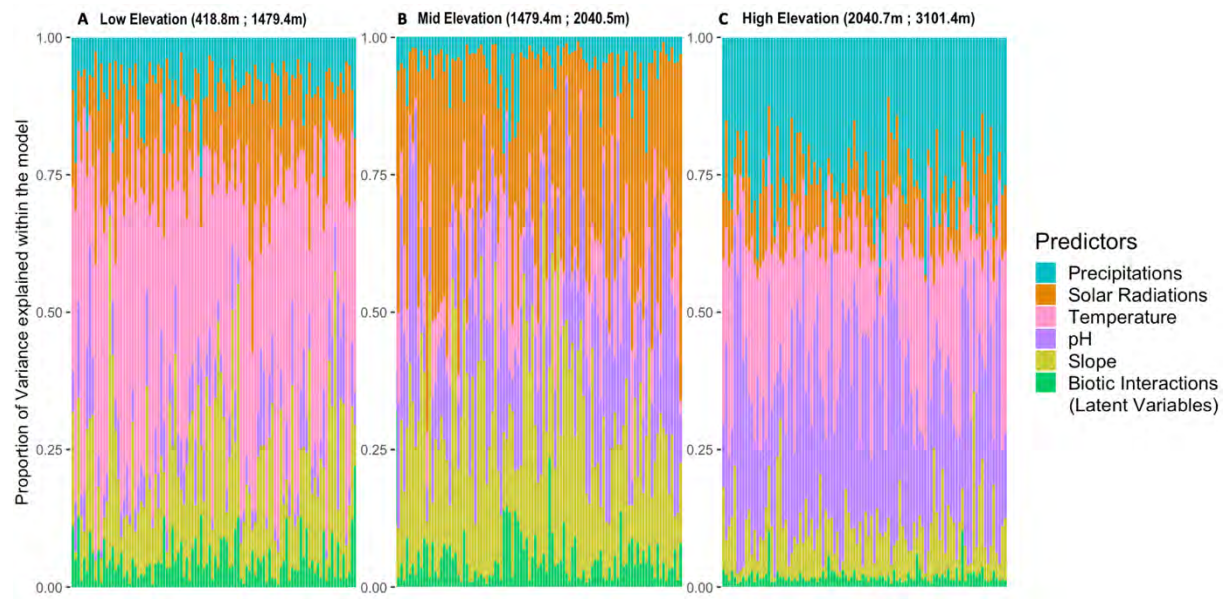


Figure 10: Variance partitioning along the elevation gradient. **A:** Low elevation (418.8m $\rightarrow$ 1479.4m). **B:** Mid elevation (1479.4m $\rightarrow$ 2040.5m). **C:** High elevation (2040.7m $\rightarrow$ 3101.4m).

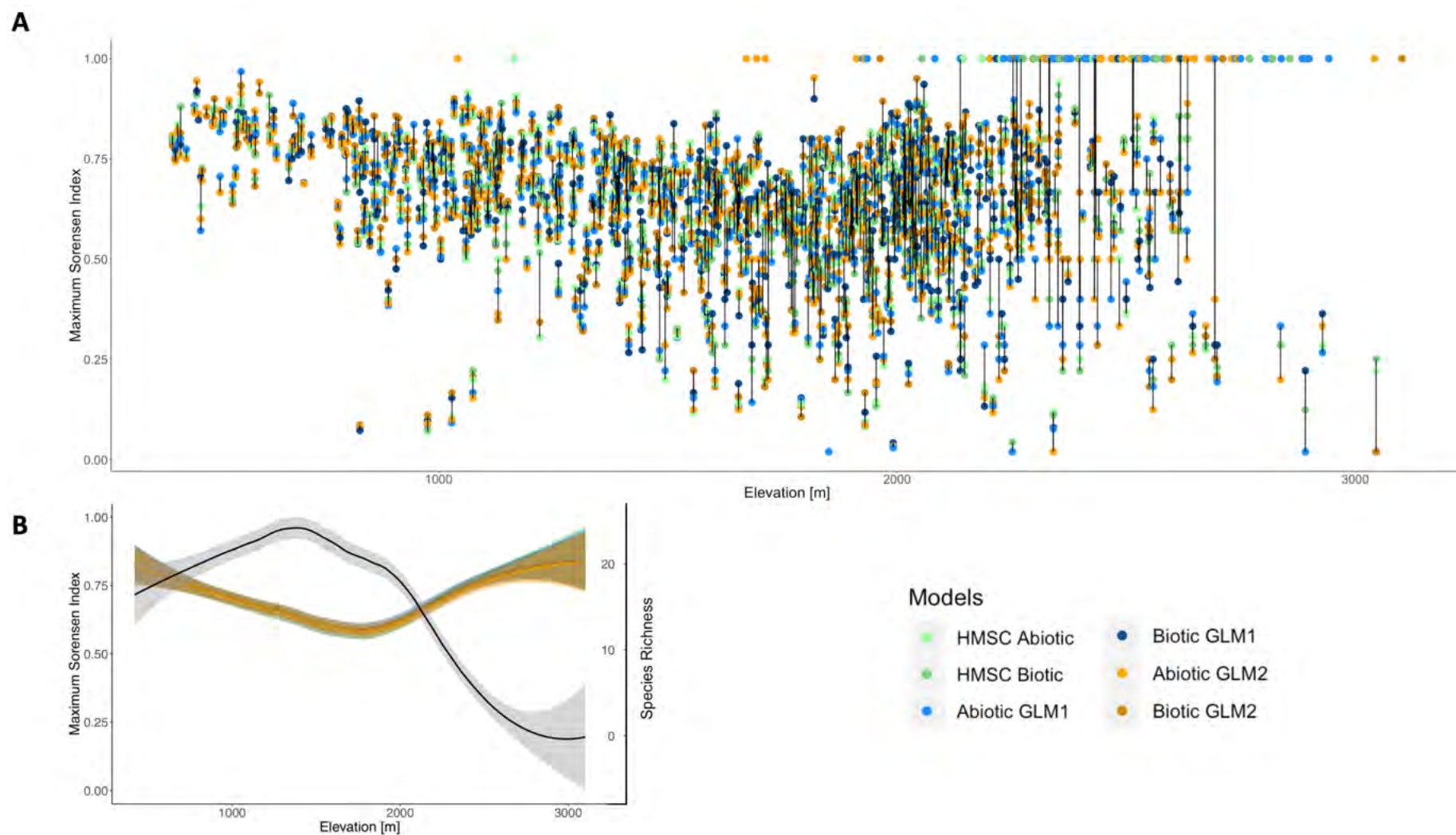


Figure 9: Models' performance along the elevational gradient. **A: Max Sørensen:** each site based on the six models are indicated by dots. Dots representing same sites are bound together by a black line. **B: Local polynomial regression curves of models' performances** (assessed with the Maximum Sørensen Index) with the standard error, in black: **Local polynomial regression curve of the observed species richness** with the standard error.

Species richness as a proxy for biotic interactions and statistical interactions on models' performances,

RF models (*Random Forest 1* and *Random Forest 2*) are compared to *Biotic GLM2* when looking at per species metrics and to *Biotic GLM1* when looking at per sites metrics as they are the best models when using species occurrences as proxy for biotic interactions. Species richness is used as a proxy for biotic interactions and implemented in both GLM and RF methods. The $Tjur - R^2$ metric is left out of these analyses because the *PseudoR2* function in R is not implemented for RF models.

Models performances per species

There are small yet significant differences among the models (repeated measures ANOVA, Max TSS: Df = 3, Sum of Squares = 0.1447, Mean of Squares = 0.048237, F-value = 39.385, Adjusted P-value (Bonferroni correction) < 0.001. Max Kappa: Df = 3, Sum of Squares = 0.2128, Mean of Squares = 0.070941, F-value = 46.638, Adjusted P-value (Bonferroni correction) < 0.001. AUC: Df = 3, Sum of Squares 0.04905, Mean of Squares = 0.0163505, F-value = 45.574, Adjusted P-value (Bonferroni correction) < 0.001, detailed analyses and Post-hoc Tukey tests available in Appendix Table S7). For all metrics, best models per species are *Biotic GLM SR* and *Random Forest SR* (mean Max TSS: 0.626 ± 0.096 for *Biotic GLM SR* and 0.632 ± 0.089 for *Random Forest SR*; mean Max Kappa: 0.492 ± 0.125 for *Biotic GLM SR* and 0.499 ± 0.117 for *Random Forest SR*; mean AUC: 0.878 ± 0.047 for *Biotic GLM SR* and 0.881 ± 0.041 for *Random Forest SR*). These two models are significantly different from *Biotic GLM2* and *Random Forest 2* (mean Max TSS: 0.594 ± 0.093 ; Max Kappa: 0.453 ± 0.124 ; mean AUC: 0.861 ± 0.046 for *Random Forest 2*) (Figure 11 and Table S7).

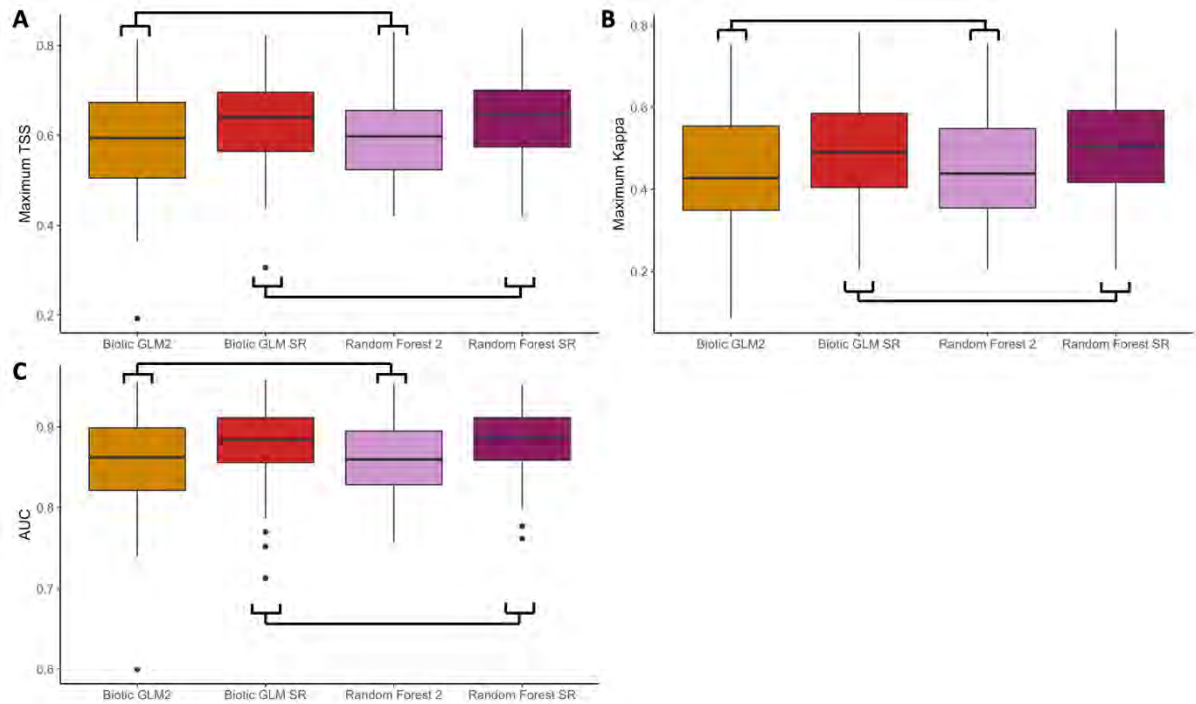


Figure 11: Model performance per species according to three metrics. **A.** Max TSS. **B.** Max Kappa. **C.** AUC. Boxes span from 1st to 3rd quantile, with median marked in-between with a black line. Whiskers span from “1th quantile - 1.5 x box height” to “3th quantile + 1.5 x box height”. Black brackets connect the groups with non-significant comparisons according to Repeated-measures Anova and Tukey post-hoc tests. Complete pairwise comparisons in Table S7 in supplementary materials.

Models performances per sites

Based on the evaluation per sites, there are no significant differences in Community AUC between the four models (repeated measures ANOVA, Df = 3, Sum of Squares = 0.0023, Mean of Squares = 0.000760, F-value = 0.8355, Adjusted P-value (Bonferroni correction) = 0.9484, detailed analyses and Post-hoc Tukey tests available in Appendix Table S8). The mean was 0.869 ± 0.090 for *Biotic GLM1*, 0.870 ± 0.094 for *Biotic GLM SR*, 0.870 ± 0.093 for *Random Forest 1* and 0.872 ± 0.095 for *Random Forest SR*, and the *Random Forest SR* has slightly and significantly higher Max Sørensen than the three other models (Repeated measures ANOVAs: Df = 3, Sum of Squares = 0.165, Mean of Squares = 0.055113, F-value = 11.646, Adjusted P-value (Bonferroni correction) < 0.001, detailed analyses and Post-hoc Tukey tests available in Appendix Table S8). The mean was 0.682 ± 0.195 for *Biotic GLM1*, 0.686 ± 0.195 for *Biotic GLM SR*, 0.687 ± 0.190 for *Random Forest 1* and 0.700 ± 0.189 for *Random Forest SR*) (Figure 12 and table S8).

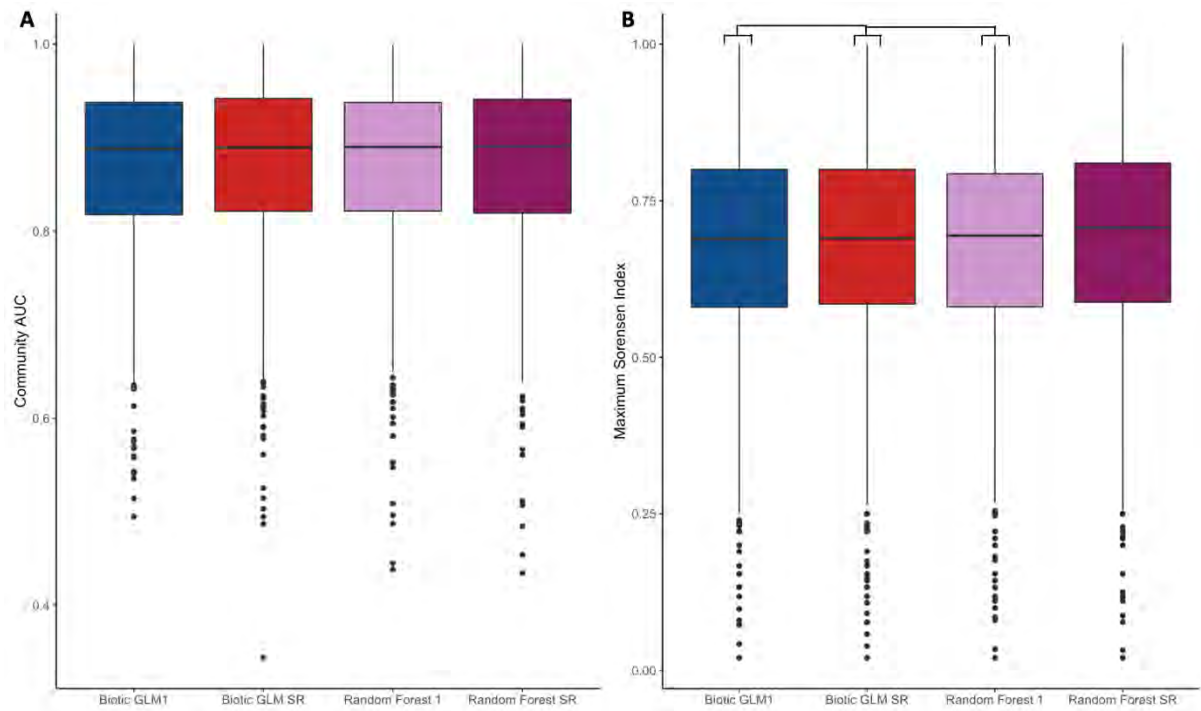


Figure 12: Models performances per sites according to two different metrics. **A.** Community AUC. **B.** Max Sørensen. Black brackets represent Non-Significant comparisons. Complete pairwise comparisons (from repeated measures ANOVAs) in Table S8 in supplementary materials.

Along the elevational gradient, the Max Sørensen of RF models and GLMs at low and mid elevation are comparable and even if RFs performances are higher at high elevation, the difference is not significant (repeated measures ANOVA, Models: Df = 3, Sum of Squares = 0.165, Mean of Squares = 0.05511, F-value = 1.504, P-value = 0.2121, Elevation: Df = 1, Sum of Squares = 0.974, Mean of Squares = 0.97508, F-value = 26.5363, P-value < 0.001) (Figure 13).

RF models are better at predicting the observed species richness compared to GLMs, independently of the proxy used for biotic interactions and especially when the species richness is high (above 21 species) (Figure 14).

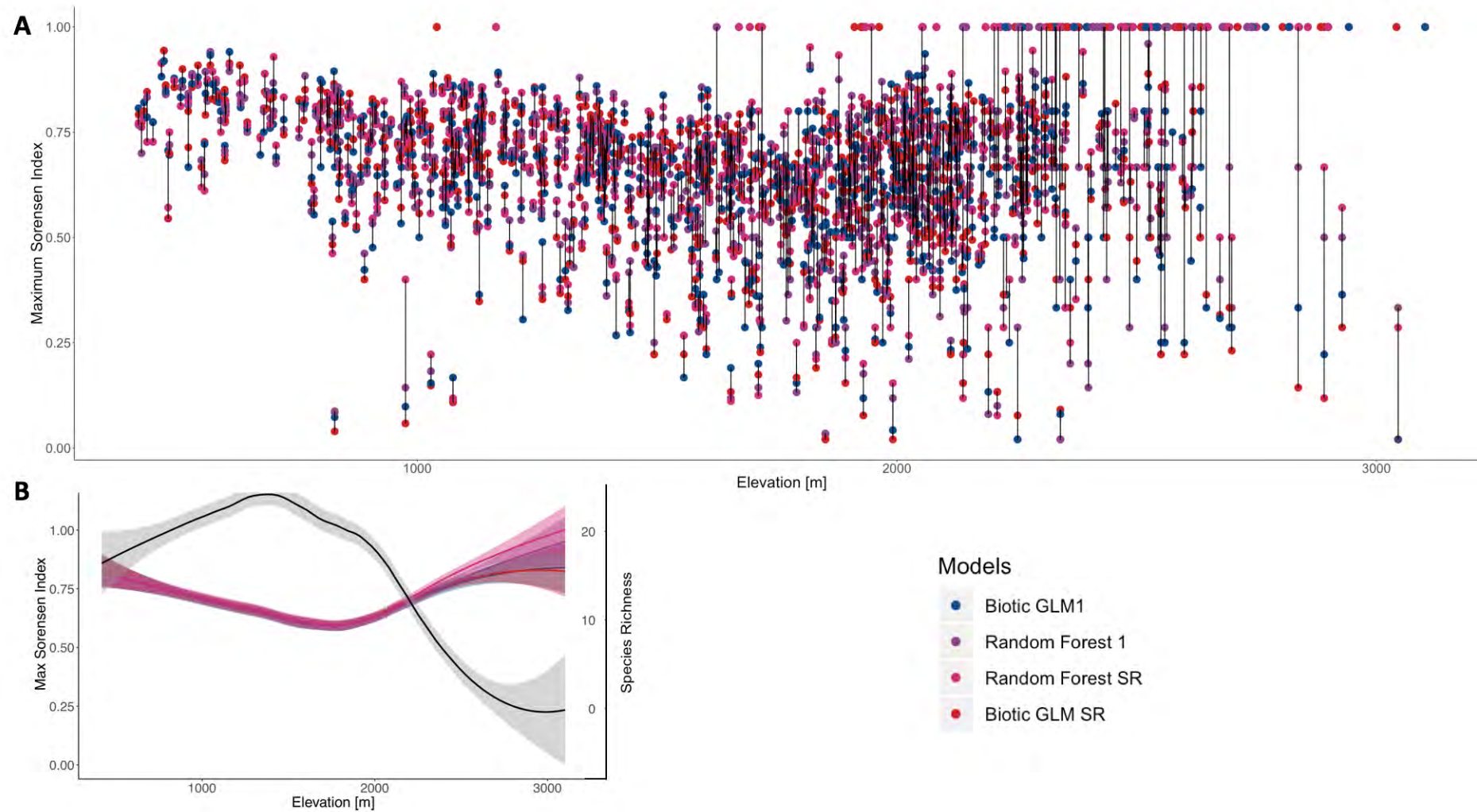


Figure 13: Models' performance along the elevational gradient. **A: Max Sørensen:** each site based on the four models are indicated by dots. Dots representing same sites are bound together by a black line. **B: Local polynomial regression curves of models' performances** (assessed with the Maximum Sørensen Index) with the standard error, in black: **Local polynomial regression curve of the observed species richness** with the standard error.

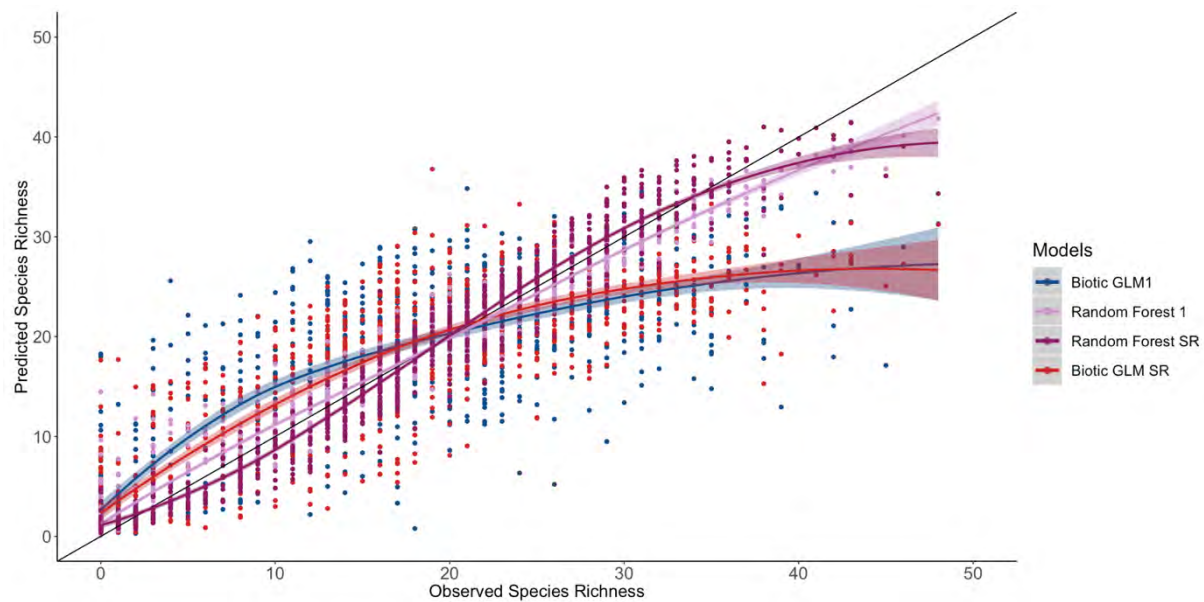


Figure 14: Predicted species Richness compared to observed species richness according to four modelling methods. Perfect species richness prediction is represented with a black line.

DISCUSSION

Our results showed that including a measure of biotic interactions among the predictors leads, on average, to a small improvement of the models' performances. In addition, JSDMs showed the same predictions accuracy compared to abiotic models. All of the models' performances were correlated with the species richness per site and performed better at low and high elevation, i.e. at sites of low species richness. The variance partitioning along the elevation gradient also revealed a difference between low and mid versus high elevation.

Model performance of abiotic and biotic models with other species occurrences as proxy for biotic interactions

Differences in model performance were minor, yet biotic models more often performed better than abiotic models. Considering the species, model performance of both *Biotic GLMs* was significantly higher than the other models, even though the differences were small and are not likely to change considerably the results when performing ecological studies (Figure 4 and 5). When looking at the evaluation metrics across sites, only the biotic GLM containing the three species with the highest sum of absolute residual correlation (*Biotic GLM1*) significantly differed from the other models but once more, the difference was almost negligible. Significant result was mainly because of the high statistical power (100 species and 911 sites). The small improvements in predictions observed in biotic models compared to abiotic ones could be explained by the size of the sites. Indeed 4 m² sites could be large enough to allow competitors to occur in same sites without contact and thus without measurable competition (Scherrer *et al.*, 2019). Moreover, using the species cover (abundance) instead of just presences/absences could have led to better results (Meier *et al.*, 2010) but here no such data was available. Nevertheless,

adding a species as predictor is not the most optimal way of taking into account biotic interactions as it only allows unidirectional interactions between the species (Kissling *et al.*, 2012) and because different species have different competitors (Mod *et al.*, 2016) and all cannot be taken into account as supplementary predictors.

Both JSDMs (*HMSC*) models gave the same performances as the *Abiotic GLMs*, suggesting that their GLM fundamentals were correct and there was no problem in the basic structure of the model. Given that they had the same performances according to the used evaluation metrics also implied that the biotic JSDM (*Biotic HMSC*) failed to improve the models and thus to capture/apply biotic interactions here. This hypothesis is supported by the variance partitioning (Figure 6) where it is possible to see that the proportion of the variance explained by the biotic interactions (latent variables) was comparatively small. This is congruent with a previous study that showed that biotic interactions have a lower importance on species distribution compared to environmental predictors in alpine plants (D'Amen *et al.*, 2018). Those results are also congruent with previous studies where it has been demonstrated that JSDMs do not really improve species distributions predictions (Copenhaver-Parry & Bell, 2018).

Furthermore, this low proportion of explanative power of latent variables could also be due to the complexity of the data, and in this case the model might not be able to extract or transfer to predictions reliable information about co-occurrences patterns. Thus, JSDM could better work when a lower number of species is involved (as used e.g. in Hui, 2016; Ovaskainen *et al.*, 2017). In addition, models' parameters (such as priors and latent variables values) could, in theory, influence the output, but in practice we tried different of them and the biotic JSDM (*Biotic HMSC*) performances did not change (results not shown). Finally, co-occurrences of species used in the latent variables of the JSDM can be due to different things than biotic interactions, such as shared niche, phylogenetic history and common migration patterns (Dormann *et al.*, 2018). However, we must be careful as another study showed that the importance of biotic interactions in shaping a species distribution can be misleadingly attributed to the environment using SDMs (Godsoe *et al.*, 2017).

Species characteristics and best modelling method

Leaf area has been shown to be a trait correlated with higher competitiveness (Fynn *et al.*, 2005; Kunstler *et al.*, 2016), and prevalent species are likely to over-compete the less prevalent species (le Roux *et al.*, 2014). Consequently, we expected that the distribution of the species with lower leaf area and prevalence would be better predicted with biotic models as their ranges should be limited by other species. This was supported as those species better predicted by biotic model had on average a higher prevalence and a larger specific leaf area (Figure 7). However, none of the species characteristics were found to be significantly different between the best modelling techniques. This could be explained as we had only 11 species for which the predictions were better using an abiotic model versus 89 with a biotic model. Hence, we could lack power to detect such difference. Besides, we selected only the 100 most prevalent species

and thus removing rarest species of our study area from the analyses could have affected the analyses and derived interpretations (about the prevalence for instance).

Sites characteristics and best modelling method

According to the SGH, elevation can have an influence on models' performances (Callaway *et al.*, 2002). Thus, we decided to focus on elevation to compare biotic and abiotic models' performances. In addition, we decided to concentrate on species richness as it was correlated with models' performances as observed in Figure 9 and shown in Pottier *et al.*, (2013). We expected that sites with a higher number of species should contain more biotic interactions and thus be better predicted with biotic models. No different characteristics between sites better predicted with abiotic or biotic models were found either. 400 sites were better predicted with biotic models but in this case the 74 sites with higher prediction accuracy with an abiotic model should be enough to have a sufficient statistical power. Elevation did not seem to make any difference among the models but as we excluded the rarest species (occurring at the highest elevations), many sites at high elevation appeared as empty in our analyses and all models were performing equally at predicting realized absences. Thus, considering less prevalent species could bring better and more reliable results. We did not detect any difference between the two modelling techniques (biotic or abiotic) and species richness but as seen in Figure 9 and in Pottier *et al.*, (2013), all models were affected by the species richness: the higher it was the lower were the models' performances. This might be due to the metrics used to assess models' performances. Indeed, their calculation depends on sites species richness and their results are thus, likely influenced by it (Wolda, 1981).

We demonstrated that all models performed worst at mid elevation, but this is likely affected by the species richness per sites (Pottier *et al.*, 2013). At this elevation with higher species richness, we expected biotic models to perform better as they should take into account the biotic interactions, but this was not the case.

Looking at the variance partitioning of the biotic JSDM (*Biotic HMSC*) along the elevation gradient (Figure 10), we showed that the proportion of variance explained by the biotic interactions (latent variables), was smaller at high elevation compared to low and mid elevations. This could support the SGH, showing that with our data, more biotic interactions occur at low/mid elevation, probably representing competition, and that those interactions tend to shift towards neutral at high elevations (Maestre *et al.*, 2009). Although we must be careful with the interpretation of this output since several sites at higher elevation were empty and most sites had lower species richness, and thus, biotic interactions could not occur and be captured by the models.

We also observed that the proportion of variance explained by each abiotic predictor varied along space (elevation)(Figure 10). At low elevation, temperature seemed to be the main driver of the species distribution. This result could be explained because plants at lower elevation are used to good climatic conditions and thus are less resistant to changes compared to plants at

higher elevation that have adapted to resist wider range of temperature. At mid elevation, pH, slope and solar radiations had a bigger importance while at high elevation solar radiation was replaced by precipitations. Light availability importance at mid elevation could be due to topography and surrounding mountains. At low elevation, the slope does not vary as it is mostly flat and thus, it is logical that its effect was relatively higher at mid and high elevation. At high elevation, the main driver seemed to be precipitation which at those altitudes probably represent snow. Snow is known to be an important parameter for high altitude plants (Niittynen & Luoto, 2018). For instance, snow cover can be a very effective protector against freezing, wind and winter desiccation (Sakai & Larcher, 1987).

Species richness as a proxy for biotic interactions and including statistical interactions using Random Forest

Considering per species performances, models with the species richness as predictor (independently of the base model GLM or RF) seemed to be the best of the tested models here (Figure 11). This was congruent with some previous results showing that using site's characteristics such as biomass can improve the models (as applied in Meier et al., 2010) and that RFs and GLMs can have the same accuracy in predictions (Syphard & Franklin, 2009). Once again, the difference was small but still a little bit higher compared to the first tested proxy for biotic interactions (other species distributions).

Per sites, we saw no difference between the models. Even if *Random Forest SR* was significantly higher than the other models using the Max Sørensen, the difference was minimal (Figure 12).

When we looked at the models' performances along the elevation gradient (Figure 13), even if the difference was not significant, we could see that both RFs were performing slightly better at high elevation. This may be because statistical interactions allowed to change a predictor's effect according to another predictors (Guisan & Zimmermann, 2000), and because RFs allowed more flexible response curves of the explanative variables. For example, at low and mid elevations, the biotic interactions should be in general negative (following the SGH) while it tends to shift towards facilitation at high elevation (Bertness & Callaway, 1994; Callaway *et al.*, 2002; Maestre *et al.*, 2009; D'Amen *et al.*, 2018). Including the statistical interactions may help the model to change the effect of other species along the elevation gradient (negative at low and mid elevation and positive at high elevation).

Finally, we looked at which models were closer to the realized SR when predicting species distributions. The RFs were the most performant ones irrespectively of their predictors (i.e. species richness or species occurrences) probably for the same reasons as stated before (statistical interactions and flexible response curves) (Figure 14). Nevertheless, adding biotic interactions as predictor(s) did not seem to improve the calculation of species richness. This result was not congruent with a previous study where adding biotic interactions as predictor led to a better estimation of species richness (Mod *et al.*, 2015). This may be due to the fact that,

unless in the latter study, in our data we did not have clear dominant species competing with the other species (Mod *et al.*, 2016a).

Altogether, while we cannot show that using other proxies for biotic interactions should not influence the predictions, incorporating biotic interactions as predictors in the models may not be necessary. Indeed, what the models captured was already the realized niche, and thus the biotic interactions, such as competitive exclusion, were already taken into account (Guisan & Zimmermann, 2000). In some particular cases, when for example one species dominates strongly the landscape, taking its distribution or cover into account can highly improve the results (Pellissier *et al.*, 2010). Another example is modelling the distribution of an invasive beetle species where including its host greatly improved the models (Simões & Peterson, 2018).

However, it is important to keep in mind that the improvements (even if small) of the biotic models (here biotic GLMs and RFs) could be due to the fact that these new predictors (here species occurrences or species richness) could represent an environmental dimension not covered by the used abiotic predictors (Kissling *et al.*, 2012; Warton *et al.*, 2015). We also have to acknowledge that the best modelling method depends on the data, such as geographical properties of the modelled species (prevalence, local or widespread etc.)(Elith & Graham, 2009; Marmion *et al.*, 2009; Aguirre-Gutiérrez *et al.*, 2013).

CONCLUSION

Using other species occurrences as a proxy for biotic interactions did not lead to great improvement of the models. We could not find strong evidence to support or reject the SGH but found that models performances per sites are negatively correlated with species richness. In addition, more complex RFs were performing slightly better at estimating species richness and high elevation predictions with our data. Finally, using species richness as a predictor led to better results than using other species occurrences. To conclude, with our data, adding species occurrence or richness as a proxy for biotic interactions did not improve the models. However, it does not mean that biotic interactions would not influence the species distribution, yet their inclusion in models did not appear necessary with the used proxies. As mentioned above, further work could imply redoing the analyses but without discarding the less prevalent species in order to cover the entire species community of the study area.

ACKNOWLEDGMENTS

I want to thank my master thesis director: Prof. Antoine Guisan for his precious help and review of this manuscript. A very big thanks to my supervisor: Dr Heidi Mod who proposed the project, helped me thorough this entire year, reviewed my manuscript and was always available and kind. I also want to thank Jérôme Goudet for his help during my statistical analyses. A special thanks to Daniel Scherrer, who kindly provided me with the function calculating the Maximum Sørensen Index on R and to let me have access to his non-published yet paper.

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APPENDIX

Plant species

1. *Achillea millefolium*
2. *Agrostis capillaris*
3. *Ajuga reptans*
4. *Alchemilla conjuncta*
5. *Alchemilla vulgaris*
6. *Alchemilla xanthochlora*
7. *Anthoxanthum odoratum*
8. *Anthyllis vulneraria*
9. *Aposeris foetida*
10. *Arrhenatherum elatius*
11. *Aster bellidiastrum*
12. *Astrantia major*
13. *Bartsia alpina*
14. *Brachypodium pinnatum*
15. *Briza media*
16. *Bromus erectus*
17. *Campanula cochleariifolia*
18. *Campanula rhomboidalis*
19. *Campanula scheuchzeri*
20. *Carduus defloratus*
21. *Carex ferruginea*
22. *Carex flacca*
23. *Carex pallescens*
24. *Carex sempervirens*
25. *Carlina acaulis* subsp. *caulescens*
26. *Carum carvi*
27. *Cerastium fontanum*
28. *Chaerophyllum hirsutum*
29. *Crepis aurea*
30. *Crepis pyrenaica*
31. *Crocus albiflorus*
32. *Cynosurus cristatus*
33. *Dactylis glomerata*
34. *Deschampsia cespitosa*
35. *Euphorbia cyparissias*
36. *Euphrasia minima*
37. *Festuca pratensis*
38. *Festuca quadriflora*
39. *Festuca rubra*
40. *Festuca violacea*
41. *Galium album*
42. *Galium anisophyllum*
43. *Gentiana campestris*
44. *Geranium sylvaticum*
45. *Helianthemum nummularium*
46. *Heracleum sphondylium*
47. *Hieracium lactucella*
48. *Hieracium murorum*
49. *Holcus lanatus*
50. *Homogyne alpina*
51. *Hypericum maculatum*
52. *Knautia dipsacifolia*
53. *Lathyrus pratensis*
54. *Leontodon hispidus*
55. *Leucanthemum vulgare*
56. *Ligusticum mutellina*
57. *Linum catharticum*
58. *Lolium perenne*
59. *Lotus corniculatus*
60. *Nardus stricta*
61. *Phleum rhaeticum*
62. *Phyteuma orbiculare*
63. *Phyteuma spicatum*
64. *Pimpinella major*
65. *Plantago alpina*
66. *Plantago atrata*
67. *Plantago lanceolata*
68. *Plantago media*
69. *Poa alpina*
70. *Poa pratensis*
71. *Poa trivialis*
72. *Polygonum viviparum*
73. *Potentilla aurea*
74. *Potentilla erecta*
75. *Primula elatior*
76. *Prunella vulgaris*
77. *Pulsatilla alpina*
78. *Ranunculus acris*
79. *Ranunculus montanus*
80. *Ranunculus nemorosus*
81. *Rhinanthus alectorolophus*
82. *Rumex acetosa*
83. *Salix retusa*
84. *Sanguisorba minor*
85. *Saxifraga aizoides*
86. *Scabiosa lucida*
87. *Selaginella selaginoides*
88. *Sesleria caerulea*
89. *Silene vulgaris*
90. *Soldanella alpina*
91. *Taraxacum officinale*
92. *Thymus praecox* subsp. *polytrichus*
93. *Thymus pulegioides*
94. *Trifolium pratense*
95. *Trifolium repens*
96. *Trisetum flavescens*
97. *Trollius europaeus*
98. *Vaccinium myrtillus*
99. *Veronica chamaedrys*
100. *Vicia sepium*

Species occurrences

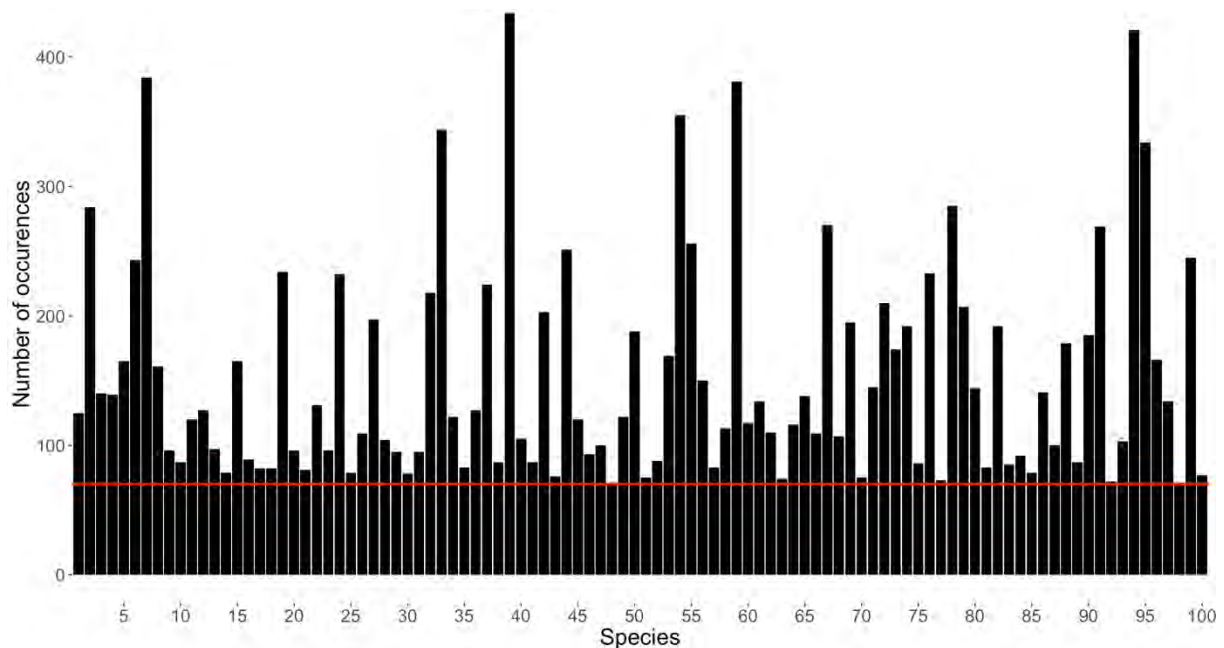


Figure S1: Total number of occurrences for each selected species. Species numbers correspond to species names in Appendix p°32. Red line represents the minimum occurrences selected (70).

Environmental predictors selection (detailed)

Temperature is an important ecological variable for plants, but many temperatures measures were available (growing degree day, bioclim11, etc.). The Growing season temperature was chosen because of the PCA results (better loadings scores). Besides, temperature is better than elevation as it is more transferable to other areas as temperature changes in same elevation comparing different areas.

Water availability is also a very important parameter for plants' ecology. The best parameter has been estimated to be soil moisture (Mod *et al.*, 2016b), unfortunately not available in our area, thus precipitation in the growing season have been chosen (better loadings scores in the PCA).

Light availability is another important parameter for plants' ecology. Here Growing Season Solar radiations (daily potential incoming sunshine radiation [without taking into account clouds or trees]) has been chosen (better loadings scores in the PCA).

Soil quality and composition is another important dimension of plants' ecology. Two parameters were available: pH and Carbon quantity. PH have been selected because in the PCA results Carbon quantity was highly correlated with precipitations.

Finally, slope have been chosen as the slope, e.g. combined with precipitation can be used to assess water availability in the soil as water tends to flow down.

Correlation of environmental variables

Table S1: Correlation of environmental parameters, *Spearman correlation tests*. Precipitations – Solar radiations: $t = -305.79$, $Df = 1155200$, $p\text{-value} < 0.001$; Temperature – Solar radiations: $t = 283.4$, $Df = 1155200$, $p\text{-value} < 0.001$; pH – Solar radiations: $t = -253.91$, $Df = 1155200$, $p\text{-value} < 0.001$; Slope – Solar radiations: $t = -630.49$, $Df = 1155200$, $p\text{-value} < 0.001$; Precipitations – Temperature: $t = -1552.5$, $Df = 1155200$, $p\text{-value} < 0.001$; Precipitations – pH: $t = -102.89$, $Df = 1155200$, $p\text{-value} < 0.001$; Precipitations – Slope: $t = 576.5$, $Df = 1155200$, $p\text{-value} < 0.001$; Temperature – pH: $t = 161.4$, $Df = 1155200$, $p\text{-value} < 0.001$; Temperature – Slope: $t = -616.8$, $Df = 1155200$, $p\text{-value} < 0.001$; pH – Slope: $t = 0.79618$, $Df = 1155200$, $p\text{-value} = 0.4259$.

	Solar Radiations	Precipitations	Temperature	pH	slope
Solar Radiations		- 0.274	0.255	- 0.230	- 0.506
Precipitations			- 0.822	- 0.095	0.473
Temperature				0.149	- 0.498
pH					0.001
slope					

glmulti table results

Number of species for which a variable appeared in the best model (i.e. the model with the lowest AIC value)

Table S2: Number of times a predictor was chosen for the best GLM without statistical interactions. Maximum is 100 times for all the plants species. GS states for Growing Season and _2 for the second order parameters.

Parameters	Number of occurrences
pH 1 st order	85
slope 1 st order	91
GS temperature 1 st order	79
GS precipitations 1 st order	96
GS Solar radiations 1 st order	74
pH 2 nd order	74
slope 2 nd order	68
GS temperature 2 nd order	52
GS precipitations 2 nd order	91
GS solar radiations 2 nd order	60

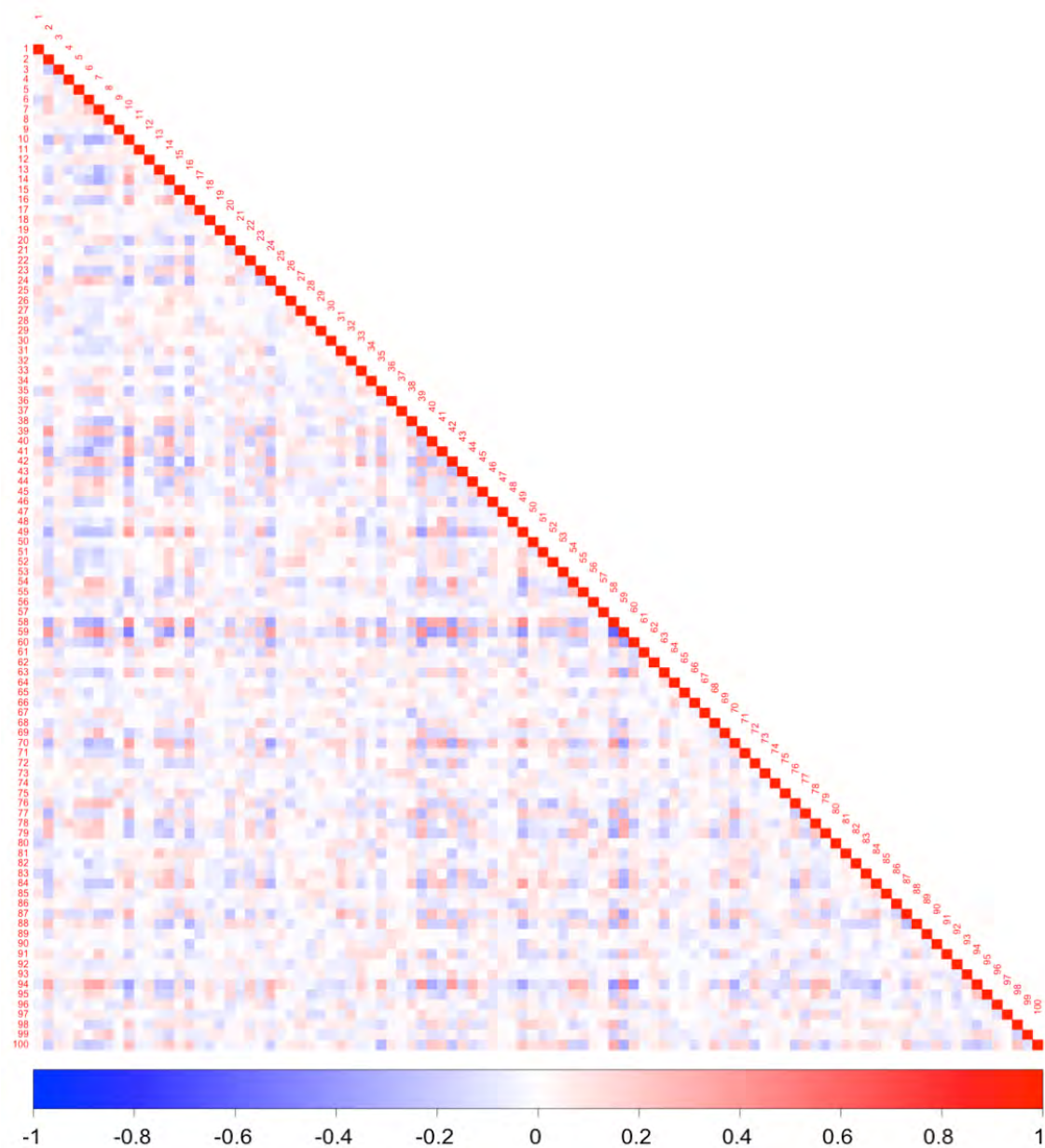
Matrix of the residual correlation

Figure S2: Matrix correlation of residuals of presences-absences of plants species. Red squares represent positive correlations, white ones no correlation and blue ones are negative correlations. The number represent plants species (corresponding names in Appendix p°32).

Table S3 per species metrics values*Table S3: detailed values of mean and standard deviation for all metrics and models.*

Metrics	Model	Mean	Standard deviation
<i>Tjur – R²</i>	<i>Abiotic HMSC</i>	0.249	0.121
	<i>Biotic HMSC</i>	0.251	0.121
	<i>GLM Abiotic 1</i>	0.273	0.121
	<i>GLM Biotic 1</i>	0.274	0.122
	<i>GLM Abiotic 2</i>	0.299	0.127
	<i>GLM Biotic 2</i>	0.305	0.128
Max TSS	<i>Abiotic HMSC</i>	0.571	0.108
	<i>Biotic HMSC</i>	0.569	0.110
	<i>GLM Abiotic 1</i>	0.566	0.108
	<i>GLM Biotic 1</i>	0.582	0.106
	<i>GLM Abiotic 2</i>	0.565	0.110
	<i>GLM Biotic 2</i>	0.588	0.108
Max Kappa	<i>Abiotic HMSC</i>	0.418	0.134
	<i>Biotic HMSC</i>	0.417	0.135
	<i>GLM Abiotic 1</i>	0.414	0.135
	<i>GLM Biotic 1</i>	0.439	0.134
	<i>GLM Abiotic 2</i>	0.141	0.134
	<i>GLM Biotic 2</i>	0.447	0.130
AUC	<i>Abiotic HMSC</i>	0.843	0.057
	<i>Biotic HMSC</i>	0.842	0.058
	<i>GLM Abiotic 1</i>	0.839	0.058
	<i>GLM Biotic 1</i>	0.853	0.055
	<i>GLM Abiotic 2</i>	0.839	0.059
	<i>GLM Biotic 2</i>	0.855	0.056

Table S4 per species repeated measures ANOVA and post-hoc Tukey tests

Table S4: Post-hoc Tukey range's tests, P-values adjusted with Bonferroni correction. Significant differences are bolded.

Previous Repeated Measures ANOVA: $T_{jur} - R^2$: Models: Df = 5, Sum of Squares = 0.02756, Mean of Squares = 0.055115, F-value = 199.19, Adjusted P-value (Bonferroni correction) < 0.001. Species: Df = 99, Sum of Squares = 8.9245, Mean of Squares = 0.090146, F-value = 325.80, Adjusted P-value (Bonferroni correction) < 0.001.

Maximum TSS: Models: Df = 5, Sum of Squares = 0.0450, Mean of Squares = 0.009004, F-value = 31.467, Adjusted P-value (Bonferroni correction) < 0.001. Species: Df = 99, Sum of Squares = 6.8554, Mean of Squares = 0.069246, F-value = 242.002, Adjusted P-value (Bonferroni correction) < 0.001.

Maximum Kappa: Models: Df = 5, Sum of Squares = 0.1005, Mean of Squares 0.020102, F-value = 47.12, Adjusted P-value (Bonferroni correction) < 0.001. Species: Df = 99, Sum of Squares 10.3672, Mean of Squares = 0.104719, F-value = 245.47, Adjusted P-value (Bonferroni correction) < 0.001.

AUC: Models: Df = 5, Sum of Squares = 0.02460, Mean of Squares = 0.0049203, F-value = 69.213, Adjusted P-value (Bonferroni correction) < 0.001. Species: Df = 99, Sum of Squares 1.90556, Mean of Squares = 0.0192481, F-value = 270.759, Adjusted P-value (Bonferroni correction) < 0.001.

Metrics	Comparison	Difference	Lower	Upper	Adjusted P-value
$T_{jur} - R^2$	Biotic HMSC – Abiotic HMSC	0.002	-0.005	0.008	1.000
	Abiotic GLM1 – Abiotic HMSC	0.024	0.018	0.031	<0.001
	Biotic GLM1 – Abiotic HMSC	0.050	0.044	0.057	<0.001
	Abiotic GLM2 – Abiotic HMSC	0.025	0.019	0.032	<0.001
	Biotic GLM2 – Abiotic HMSC	0.056	0.049	0.063	<0.001
	Abiotic GLM1 – Biotic HMSC	0.023	0.016	0.029	<0.001
	Biotic GLM1 – Biotic HMSC	0.049	0.042	0.055	<0.001
	Abiotic GLM2 – Biotic HMSC	0.024	0.017	0.030	<0.001
	Biotic GLM2 – Biotic HMSC	0.054	0.048	0.061	<0.001
	Biotic GLM1 – Abiotic GLM1	0.026	0.019	0.033	<0.001
	Abiotic GLM2 – Abiotic GLM1	0.001	-0.006	0.008	1.000
	Biotic GLM2 – Abiotic GLM1	0.032	0.025	0.038	<0.001
	Abiotic GLM2 – Biotic GLM1	-0.025	-0.032	-0.018	<0.001
	Biotic GLM2 – Biotic GLM1	0.006	-0.001	0.012	0.592
	Biotic GLM2 – Abiotic GLM2	0.031	0.024	0.037	<0.001
Max TSS	Biotic HMSC – Abiotic HMSC	-0.002	-0.009	0.005	1.000
	Abiotic GLM1 – Abiotic HMSC	-0.005	-0.012	0.002	1.000
	Biotic GLM1 – Abiotic HMSC	0.012	0.005	0.018	<0.001
	Abiotic GLM2 – Abiotic HMSC	-0.005	-0.012	0.002	0.908
	Biotic GLM2 – Abiotic HMSC	0.018	0.011	0.025	<0.001
	Abiotic GLM1 – Biotic HMSC	-0.003	-0.010	0.004	1.000
	Biotic GLM1 – Biotic HMSC	0.013	0.007	0.020	<0.001
	Abiotic GLM2 – Biotic HMSC	-0.003	-0.010	0.003	1.000
	Biotic GLM2 – Biotic HMSC	0.020	0.013	0.026	<0.001
	Biotic GLM1 – Abiotic GLM1	0.016	0.009	0.023	<0.001
	Abiotic GLM2 – Abiotic GLM1	-0.001	-0.007	0.006	1.000
	Biotic GLM2 – Abiotic GLM1	0.022	0.016	0.029	<0.001
	Abiotic GLM2 – Biotic GLM1	-0.017	-0.024	-0.010	<0.001
	Biotic GLM2 – Biotic GLM1	0.006	-0.001	0.013	0.410
	Biotic GLM2 – Abiotic GLM2	0.023	0.016	0.030	<0.001
Max Kappa	Biotic HMSC – Abiotic HMSC	-0.001	-0.010	0.007	1.000
	Abiotic GLM1 – Abiotic HMSC	-0.005	-0.013	0.004	1.000
	Biotic GLM1 – Abiotic HMSC	0.020	0.012	0.029	<0.001
	Abiotic GLM2 – Abiotic HMSC	-0.004	-0.012	0.004	1.000
	Biotic GLM2 – Abiotic HMSC	0.028	0.020	0.037	<0.001
	Abiotic GLM1 – Biotic HMSC	-0.003	-0.011	0.005	1.000
	Biotic GLM1 – Biotic HMSC	0.022	0.013	0.030	<0.001
	Abiotic GLM2 – Biotic HMSC	-0.002	-0.011	0.006	1.000
	Biotic GLM2 – Biotic HMSC	0.030	0.022	0.038	<0.001
	Biotic GLM1 – Abiotic GLM1	0.025	0.016	0.033	<0.001
	Abiotic GLM2 – Abiotic GLM1	0.001	-0.008	0.009	1.000
	Biotic GLM2 – Abiotic GLM1	0.033	0.025	0.041	<0.001

AUC	Abiotic GLM2 – Biotic GLM1	-0.024	-0.032	-0.016	<0.001
	Biotic GLM2 – Biotic GLM1	0.008	0.000	0.017	0.226
	Biotic GLM2 – Abiotic GLM2	0.032	0.024	0.041	<0.001
	Biotic HMSC – Abiotic HMSC	-0.001	-0.004	0.002	1.000
	Abiotic GLM1 – Abiotic HMSC	-0.003	-0.007	0.000	0.241
	Biotic GLM1 – Abiotic HMSC	0.010	0.007	0.013	<0.001
	Abiotic GLM2 – Abiotic HMSC	-0.003	-0.007	0.000	0.377
	Biotic GLM2 – Abiotic HMSC	0.013	0.009	0.016	<0.001
	Abiotic GLM1 – Biotic HMSC	-0.002	-0.006	0.001	1.000
	Biotic GLM1 – Biotic HMSC	0.011	0.008	0.014	<0.001
	Abiotic GLM2 – Biotic HMSC	-0.002	-0.006	0.001	1.000
	Biotic GLM2 – Biotic HMSC	0.014	0.010	0.017	<0.001
	Biotic GLM1 – Abiotic GLM1	0.013	0.010	0.017	<0.001
	Abiotic GLM2 – Abiotic GLM1	0.000	-0.003	0.004	1.000
	Biotic GLM2 – Abiotic GLM1	0.016	0.013	0.020	<0.001
	Abiotic GLM2 – Biotic GLM1	-0.013	-0.017	-0.010	<0.001
	Biotic GLM2 – Biotic GLM1	0.003	-0.001	0.006	0.797
	Biotic GLM2 – Abiotic GLM2	0.016	0.012	0.019	<0.001

Table S5 per plots metrics values

Table S5: detailed values of mean and standard deviation for all metrics and models.

Metrics	Model	Mean	Standard deviation
Community AUC	<i>Abiotic HMSC</i>	0.865	0.095
	<i>Biotic HMSC</i>	0.865	0.096
	<i>GLM Abiotic 1</i>	0.861	0.096
	<i>GLM Biotic 1</i>	0.869	0.090
	<i>GLM Abiotic 2</i>	0.861	0.097
	<i>GLM Biotic 2</i>	0.867	0.093
Max Sørensen	<i>Abiotic HMSC</i>	0.674	0.198
	<i>Biotic HMSC</i>	0.673	0.198
	<i>GLM Abiotic 1</i>	0.670	0.199
	<i>GLM Biotic 1</i>	0.682	0.195
	<i>GLM Abiotic 2</i>	0.669	0.200
	<i>GLM Biotic 2</i>	0.678	0.194

Table S6 per plots repeated measures ANOVA and post-hoc Tukey tests

Table S6: Post-hoc Tukey range's tests, P-values adjusted with Bonferroni correction.

Previous Repeated measures ANOVA: Community AUC: Models: Df = 5, Sum of Squares = 0.043, Mean of Squares = 0.008648, F-value = 24.95, Adjusted P-value (Bonferroni correction) < 0.001. Sites: Df = 812, Sum of Squares = 42.207, Mean of Squares = 0.051979, F-value = 149.96, Adjusted P-value (Bonferroni correction) < 0.001.

Maximum Sørensen Index: Models: Df = 5, Sum of Squares = 0.108, Mean of Squares = 0.021690, F-value = 12.131, Adjusted P-value (Bonferroni correction) < 0.001. Sites: Df = 910, Sum of Squares = 204.422, Mean of Squares = 0.224639, F-value = 125.636, Adjusted P-value (Bonferroni correction) < 0.001.

Metrics	Comparison	Difference	Lower	Upper	Adjusted P-value
Community AUC	Biotic HMSC – Abiotic HMSC	-0.001	-0.003	0.002	1.000
	Abiotic GLM1 – Abiotic HMSC	-0.004	-0.007	-0.002	<0.001
	Biotic GLM1 – Abiotic HMSC	0.004	0.001	0.007	<0.001
	Abiotic GLM2 – Abiotic HMSC	-0.004	-0.007	-0.002	<0.001
	Biotic GLM2 – Abiotic HMSC	0.002	-0.001	0.004	0.660
	Abiotic GLM1 – Biotic HMSC	-0.004	-0.006	-0.001	0.004
	Biotic GLM1 – Biotic HMSC	0.005	0.002	0.007	<0.001
	Abiotic GLM2 – Biotic HMSC	-0.004	-0.006	-0.001	0.004
	Biotic GLM2 – Biotic HMSC	0.003	0.000	0.005	0.137
	Biotic GLM1 – Abiotic GLM1	0.008	0.006	0.011	<0.001
	Abiotic GLM2 – Abiotic GLM1	0.000	-0.003	0.003	1.000
	Biotic GLM2 – Abiotic GLM1	0.006	0.003	0.009	<0.001
	Abiotic GLM2 – Biotic GLM1	-0.008	-0.011	-0.006	<0.001
	Biotic GLM2 – Biotic GLM1	-0.002	-0.005	0.000	0.363
	Biotic GLM2 – Abiotic GLM2	0.006	0.003	0.009	<0.001
Max Sørensen	Biotic HMSC – Abiotic HMSC	-0.001	-0.007	0.005	1.000
	Abiotic GLM1 – Abiotic HMSC	-0.004	-0.010	0.002	0.664
	Biotic GLM1 – Abiotic HMSC	0.008	0.002	0.013	0.004
	Abiotic GLM2 – Abiotic HMSC	-0.006	-0.011	0.000	0.090
	Biotic GLM2 – Abiotic HMSC	0.004	-0.002	0.009	0.956
	Abiotic GLM1 – Biotic HMSC	-0.003	-0.009	0.003	1.000
	Biotic GLM1 – Biotic HMSC	0.008	0.003	0.014	<0.001
	Abiotic GLM2 – Biotic HMSC	-0.005	-0.010	0.001	0.283
	Biotic GLM2 – Biotic HMSC	0.004	-0.001	0.010	0.460
	Biotic GLM1 – Abiotic GLM1	0.012	0.006	0.017	<0.001
	Abiotic GLM2 – Abiotic GLM1	-0.002	-0.007	0.004	1.000
	Biotic GLM2 – Abiotic GLM1	0.008	0.002	0.013	0.004
	Abiotic GLM2 – Biotic GLM1	-0.013	-0.019	-0.008	<0.001
	Biotic GLM2 – Biotic GLM1	-0.004	-0.010	0.002	0.638
	Biotic GLM2 – Abiotic GLM2	0.009	0.004	0.015	<0.001

Table S7 Additional Analyses per species models comparisons

Table S7: Post-hoc Tukey range's tests, P-values adjusted with Bonferroni correction.

Previous Repeated measures ANOVA: Maximum TSS: Models: Df = 3, Sum of Squares = 0.1447, Mean of Squares = 0.048237, F-value = 39.385, Adjusted P-value (Bonferroni correction) < 0.001. **Species:** Df = 99, Sum of Squares = 3.3241, Mean of Squares = 0.033576, F-value = 27.415, Adjusted P-value (Bonferroni correction) < 0.001.

Maximum Kappa: Models: Df = 3, Sum of Squares = 0.2128, Mean of Squares = 0.070941, F-value = 46.638, Adjusted P-value (Bonferroni correction) < 0.001. **Species:** Df = 99, Sum of Squares = 5.6309, Mean of Squares = 0.056878, F-value = 37.393, Adjusted P-value (Bonferroni correction) < 0.001.

AUC: Models: Df = 3, Sum of Squares = 0.04905, Mean of Squares = 0.0163505, F-value = 45.574, Adjusted P-value (Bonferroni correction) < 0.001. **Species:** Df = 99, Sum of Squares = 0.80693, Mean of Squares = 0.0081508, F-value = 22.719, Adjusted P-value (Bonferroni correction) < 0.001.

Metrics	Comparison	Difference	Lower	Upper	Adjusted P-value
Max TSS	Biotic GLM SR – Biotic GLM 2	0.038	0.025	0.051	< 0.001
	Random Forest 2 – Biotic GLM 2	0.006	-0.007	0.019	1.000
	Random Forest SR – Biotic GLM 2	0.043	0.030	0.056	< 0.001
	Random Forest 2 – Biotic GLM SR	-0.032	-0.045	-0.019	< 0.001
	Random Forest SR – Biotic GLM SR	0.005	-0.008	0.018	1.000
	Random Forest SR – Random Forest 2	0.037	0.025	0.050	< 0.001
Max Kappa	Biotic GLM SR – Biotic GLM 2	0.045	0.031	0.060	< 0.001
	Random Forest 2 – Biotic GLM 2	0.006	-0.008	0.020	1.000
	Random Forest SR – Biotic GLM 2	0.052	0.038	0.066	< 0.001
	Random Forest 2 – Biotic GLM SR	-0.039	-0.054	-0.025	< 0.001
	Random Forest SR – Biotic GLM SR	0.007	-0.008	0.021	1.000
	Random Forest SR – Random Forest 2	0.046	0.032	0.060	< 0.001
AUC	Biotic GLM SR – Biotic GLM 2	0.023	0.016	0.030	< 0.001
	Random Forest 2 – Biotic GLM 2	0.005	-0.002	0.012	0.586
	Random Forest SR – Biotic GLM 2	0.026	0.019	0.033	< 0.001
	Random Forest 2 – Biotic GLM SR	-0.018	-0.025	-0.011	< 0.001
	Random Forest SR – Biotic GLM SR	0.003	-0.004	0.010	1.000
	Random Forest SR – Random Forest 2	0.021	0.014	0.027	< 0.001

Table S8 Additional Analyses per sites models' comparisons

Table S8: Post-hoc Tukey range's tests, P-values adjusted with Bonferroni correction.

Previous Repeated measures ANOVA: Community AUC: Models: Df = 3, Sum of Squares = 0.0023, Mean of Squares = 0.000760, F-value = 0.8355, Adjusted P-value (Bonferroni correction) 0.9484. **Sites:** Df = 812, Sum of Squares = 25.9088, Mean of Squares = 0.031907, F-value = 35.0735, Adjusted P-value (Bonferroni correction) < 0.001. As the ANOVA per models was not significant, not post-hoc Tukey range's test was performed.

Maximum Kappa: Models: Df = 3, Sum of Squares = 0.165, Mean of Squares = 0.055113, F-value = 11.646, Adjusted P-value (Bonferroni correction) < 0.001. **Sites:** Df = 910, Sum of Squares = 121.633, Mean of Squares = 0.133663, F-value = 28.244, Adjusted P-value (Bonferroni correction) < 0.001.

Metrics	Comparison	Difference	Lower	Upper	Adjusted P-value
Max Sørensen	Biotic GLM SR – Biotic GLM 2	0.004	-0.004	0.012	1.000
	Random Forest 2 – Biotic GLM 2	0.005	-0.003	0.013	0.889
	Random Forest SR – Biotic GLM 2	0.018	0.010	0.026	< 0.001
	Random Forest 2 – Biotic GLM SR	0.001	-0.008	0.009	1.000
	Random Forest SR – Biotic GLM SR	0.014	0.006	0.022	< 0.001
	Random Forest SR – Random Forest 2	0.013	0.005	0.021	< 0.001