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Evolutionary and ecological process acting on rich  
community assemblage.

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## **Résumé**

Les communautés actuelles sont définies par des processus évolutifs et écologique agissant à différentes échelles temporelles et spatiales. Afin d'observer les potentiels effets confondants de ces processus sur l'assemblage des communautés, cette étude développe une approche top-down qui combine des mécanismes d'évolution de traits sur une phylogénie reconstruite (à partir des communautés d'arbres des néotropiques) avec différents filtres environnementaux. Nous observons les différentes signatures de ces processus au moyen d'un jeu de métriques de diversités taxonomiques, fonctionnelles et phylogénétiques. Les signatures seront décrites afin d'étudier les cas pour lesquels l'identification des processus n'est pas trivial dans l'assemblage des communautés.

## **Abstract**

Extant communities are shaped by both evolutionary and ecological processes acting at different time and spatial scales. To examine the potentially confounding effects of these processes on community assembly, we develop a top-down approach that combines mechanisms of trait evolution along a reconstructed phylogeny (based on extant neotropical tree communities) with environmental filtering. We examine the signatures of these eco-evolutionary processes on a set of taxonomic, functional and phylogenetic diversity metrics, and discuss cases where it is challenging to disentangle their effects of community assembly.

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# 1 Introduction

## 1.1 Ecological and Evolutionary perspectives of extant assemblages

Understanding how diversity patterns in extant communities are shaped by ecological and evolutionary processes remain a major challenge to date [1]. Whether and how a snapshot of biodiversity patterns can unambiguously reflect the signatures of many processes acting simultaneously at different spatial and temporal scales is still much debated [2, 3], although there have been attempts at bridging the gap between ecology and evolution [4, 5]. Community assembly can be viewed in a top-down perspective whereby species present in a regional pool go through a series of filters (dispersal limitation, environmental filtering, biotic interactions) to assemble in local communities [6]. It is assumed that the regional species pool and associated phenotypes represent a snapshot of an evolutionary heritage from which species assemble through local dynamics over recent and short enough time periods to neglect diversification events. However, the pool is constantly shaped by evolutionary dynamics that influences species regional abundances and biological attributes determined by the balance between speciation and extinction occurring over longer periods of time.

Recent studies have underlined the critical influence of the diversity of the species pool [7] in providing immigrants and called for a more mechanistic modelling approach that directly represents key processes shaping community assembly [8]. The ability of species to cross biogeographic borders and migrate to a given region can increase the phylogenetic diversity of the regional pool [9]. Also, phylogenetic diversity can increase with diversification rates, ie. the outcome of extinction and speciation, which depend on larger geological events [10]. However the question remains of how diversification and trait evolution contribute in conjunction with ecological processes to shaping extant community-level patterns.

Null models, permuting species or their attributes in local communities, are often used to evaluate whether assembly is random relatively to a fixed species pool (e.g.[11]). However, null models do not explicitly represent the processes shaping community assembly and regional diversity (since the pool is defined a priori). Phylogenies represent the evolutionary relationships between extant species and have been used to integrate evolutionary history and its underlying processes into ecology [12]. Phylogenetic approaches have proven useful to go further in understanding the processes shaping taxonomic and functional diversity in regional pools and

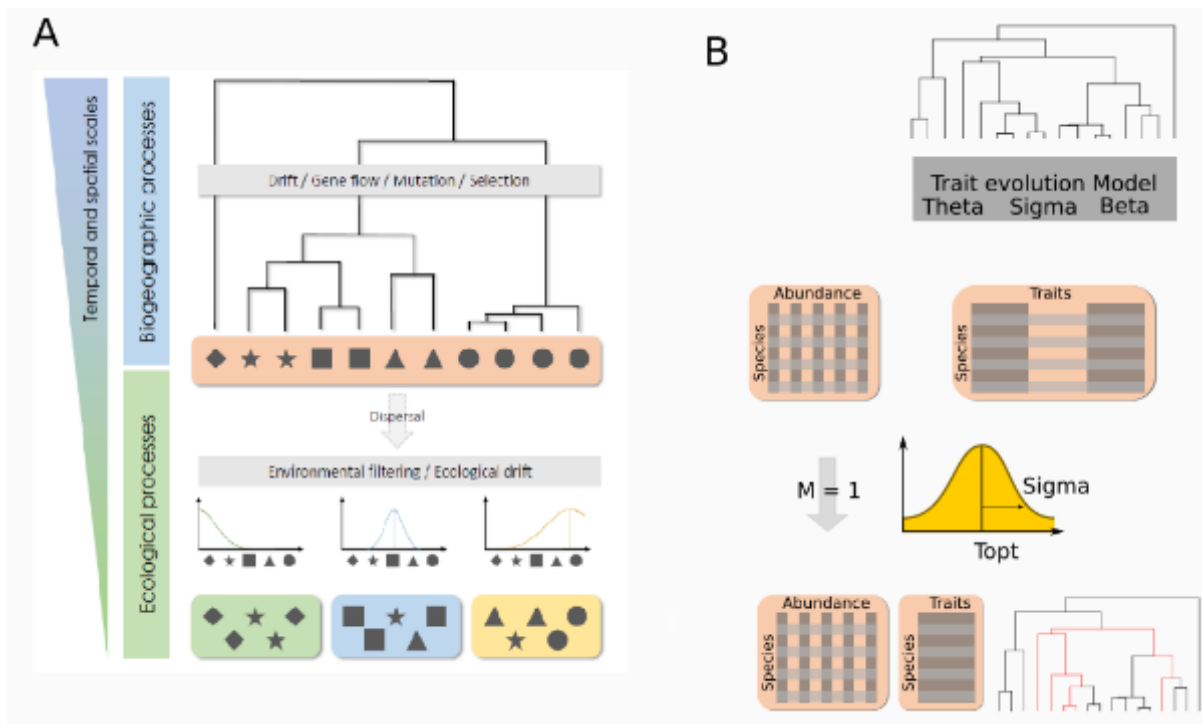
study the processes shaping community assembly. Overlaying trait and niche evolution onto reconstructed diversification dynamics offers a promising way forward to understand how evolutionary processes influence patterns of community assembly via how these affect the regional species pool [1].

Beyond modelling efforts, an essential objective of many studies in ecology and evolution is to retrieve parameter values of natural mechanisms from an observed outcome, i.e. the inference or inverse problem [13]. However, attributing observed patterns to specific evolutionary or ecological mechanisms becomes difficult when confounding effects arise from the simultaneous and ambiguous effects of these multi-level processes [14].

Using complementary diversity metrics at both the regional and local scale can provide more insight into underlying mechanisms. The signature of taxonomic diversity and species relative abundances have been used to characterize the signature of neutral assembly processes and the influence of limited dispersion [4, 15]. However this aspect alone is often insufficient to identify the role of deterministic assembly processes such as species niche differences. Fitness differences between individuals resulting from differences in the adequacy of their biological attributes to their local environment affect the dynamics of species and the resulting diversity patterns [16, 17]. Trait-based approaches have been useful to study how niche dynamics shape ecological communities [18, 19]. In addition, phylogenetic approaches have allowed accounting for the evolutionary relationships between co-occurring taxa [20]. Under the hypothesis that closely-related species can be functionally similar due to evolutionary conservatism, phylogenetic relatedness can be used as an indicator of functional similarity [21]. Abiotic constraints on community membership are expected to result in phylogenetically-clustered communities where co-occurring species are highly related [20]. Yet subsequent studies have shown that similar patterns of community relatedness can emerge from distinct ecological processes such as biotic interactions acting on different traits with different evolutionary histories [22].

For instance, species relative abundances will fluctuate depending on niche dynamics affecting their traits because some species will benefit from higher performance in a given community. Also there are instances where phylogenetic diversity may be relevant to identify underlying ecological processes. It is therefore essential not only to identify the processes directly affecting each aspect of diversity, but also to evaluate to which extent confounding effects arise and hinder our ability to conduct robust inferences.

Here we propose to evaluate how community diversity patterns are shaped by eco-evolutionary dynamics using controlled settings to identify the respective contributions of (i) evolutionary heritage shaping the regional species pool and (ii) species niche differences. We argue that this integrated approach is essential to identify potential confounding effects between ecological and evolutionary processes on community assembly, and avoid bias in future analyses of empirical data. To this aim, we simulated different trait evolution models, from Brownian motion to Early and Late Burst along the phylogeny of neotropical trees of French Guiana (Molino *et al.* submitted). These traits were used by applying environmental filters to obtain different communities. These filters range from neutral assembly process to strong filters acting on the previously simulated traits. Communities thus simulated allow obtaining high local species richness consistent with the high diversity of tropical forests[21].



**FIGURE 1 – A : Conceptual schema of different scales and processes acting, top-down image.** In the top-down view, species traits evolve in relation with the evolutionary and biogeographic history of the pool. From this regional pool, species assemble into local communities through dispersion, filtering by local environmental conditions and interactions with other species. **B : Model pathway and associated parameters used in this study.** (i) At the regional pool level, we model trait evolution from the tree phylogeny of French Guiana. This evolution is based on a Brownian motion starting at the root value Theta, with Sigma controlling the amplitude of the motion. Beta controls for an exponential acceleration or deceleration of the motion through time, with the value 0 setting a classic Brownian motion. (ii) To simulate the community, the regional pool is filtered with a Gaussian function defined by Topt and Sigma. (iii) The final community is described by an abundance table, a trait table and a cropped phylogeny.

Regional pool		Community	
Aspect	Metric	Process	Pattern
Taxonomic diversity	Richness	Evolute heritage (biogeographic history, mass extinction)	Increase with spatial scale (size of the regional pool) Depend on the region selected [23]
	Simpson		
	Shannon		
Moments of trait distribution	Mean	Directive trait evolution	Depend on the ancestral trait value, direction of evolution, and mutations accumulation toward optimum
	Variance	Mutation and trait selection along time (motion of the trait)	Depend on the mutations accumulation through time
	skewness	Niche conservatism and phylogenetic topology link	Increase with higher dependence to phylogenetic tree [25] Increase with strong selection
	kurtosis		
Present pattern of evolution [26]	Faith's Phylogenetic diversity	Evolute heritage (biogeographic history, mass extinction)	Increase with age of the root and richness
	Mean Pairwise Distance	Rate of diversification through time	Increase with ancient diversification
	Mean Nearest Taxon Distance		Increase with recent diversification
Time dependant pattern	Epoch-specific Lineage Diversities [28]	Rate of diversification per period.	Increase with rate of diversification of the period.
			Dispersion toward the community and extinction [24], biotic and biotic selection.
			Selection with environmental filter or interactions with other species
			Environmental filter mean, with minor shift close to the pool border [8]
			Environmental filter sigma
			Increase close to the pool border [8] and with richness decrease
			Increase with lower niche conservatism or lower weak filter [27]
			Increase with evenness of species in the phylogeny
			Increase with clustering of species in the phylogeny
			Increase with strong filter on conservative traits

TABLE 1 – *Aspects of diversity and relation between process and patterns. Patterns here are expected without standardisation.*

## 2 Material and Methods

We propose to benchmark a given set of simulated diversity metrics contrasted scenarios so as to characterize the signature of both evolutionary heritage and local assembly processes on observed patterns of diversity. Later we estimate using a cross-validation analysis whether such metrics can be used to faithfully estimate parameter values. This workflow has been done using R [29].

### 2.1 Phylogenetic information

The phylogeny used to simulate species regional abundances and their traits was reconstructed from French Guiana tree census data (Molino *et al.* submitted, [30]) regrouping every tropical tree species over 10cm in diameter (DBH). This taxonomic information was compared to an extended phylogeny based on the GBOTB tree using V.phylomaker [31]. The phylogeny was cropped for known species and missing species bound to higher taxonomic level branches. We used the third binding scenario because it binds the new tips on the middle of the branch, rather than binding to random or higher nodes. This is important to not underestimate or overestimate latter estimations of number of lineage at a given time. We obtained a dated ultrametric tree, rooted at -136 Ma comprised of 1816 tropical tree species.

### 2.2 Generating the regional pool from the phylogeny with trait evolution models

Species trait values were obtained by using the above-mentioned phylogeny as a back-bone to trait-evolution models provided in the mvMORPH package [32]. Three models of trait evolution were implemented, in which a single trait evolved from an ancestral value of 0. In the first model, traits evolved from their ancestral state following a pure Brownian motion (BM) with parameter sigma set to 3. In the second model, trait evolution exponentially decelerated with time (beta = -0.05) following an Early Burst model (EB). Finally, the third model used was a Late Burst (LB) model, in which trait evolution experienced exponential acceleration on the more recent branches (beta = 0.05). The different values of parameter beta were chosen to avoid extreme scenarios of trait evolution. For instance, a very low Brownian motion would



exacerbate the influence of the phylogenetic structure, or elseways, too great motion yields trait values from a normal distribution centered on the ancestral value. .

Before simulating community assembly, regional trait values were standardized to obtain a mean of 0 and a standard deviation of 1. This standardisation reflects the fact that in empirical dataset, the ancestral state at the regional scale is poorly known, and that we cannot detect whether (i) all the regional pool trait values have shifted to one side or (ii) evolved around the ancestral value. We then built the regional pool from which communities assemble through immigration and environmental filtering by uniformly sampling 200 individuals per species and their associated traits having evolved along the phylogeny.

### **2.3 Community simulations**

Communities were simulated using a coalescent-based simulation scheme whereby the establishment of immigrants from the regional species pool and survival of their descendants in the local community are determined by the correspondence of their trait values to a given environmental filtering function [33]. Environmental filtering was defined as a Gaussian distribution centered on an optimal trait value  $t_{opt}$  and with standard deviation  $\sigma$  (see Eq. 1). Simulated  $t_{opt}$  values ranged between extreme trait values in the regional species pool which filtered communities close or far from the mean trait value of the regional species pool. The parameter  $\sigma$  took multiple values (2, 1, 0.5, 0.2, 0.1, 0.05 and 0.02) to simulate cases where community assembly is almost neutral (large  $\sigma$  values) to cases of strong environmental filtering (small  $\sigma$  values). The migration parameter  $m$  was set to 1 for all simulated communities, thereby removing limited dispersal and excluding local extinctions due to ecological drift. Each community was composed of 200 individuals.

$$f(x) = e^{-\frac{(x-t_{opt})^2}{2\sigma^2}} \quad (1)$$

### **2.4 Patterns of taxonomic, functional and phylogenetic diversity**

Different diversity metrics were used to characterize multiple aspects of a given community. Taxonomic diversity was measured using species richness, Simpson's and Shannon's diversity

indexes, using the `vegan` package [34]. Functional diversity was characterized by Community Weighted Mean (CWM), variance (CWV), kurtosis (CWK) and skewness (CWS), using the `TAM` package [35]. Additionally, we used the `picante` package in R language to compute Phylogenetic diversity (PD), Mean pairwise distance (MPD) and Mean Nearest Taxon Distance (MNTD) [36], in order to characterize a snapshot of communities' phylogenetic diversity. In order to account for the influence of historical legacies on present community assembly, we implemented Epoch-specific Lineage Diversities (ELD) [37] in R language. The code will be available within an R package to allow for the complete workflow to be ran. The phylogeny is thus subdivided into multiple periods, for which the log of the difference in the number of lineages per period is computed. In our case we chose seven time periods (165-126 Ma; 126-100 Ma; 100-66 Ma; 66-33.9 Ma; 33.9-23 Ma; 23-5.3 Ma 5.3-present Ma) as these have been shown to be linked to important past geological and biological events (as in [37]). ELD should reflect whether extant communities carry the signature of ancient or more recent diversification events based on the dynamics of their trait evolution.

Functional and phylogenetic diversity metrics were computed with or without standardisation using null models that reattribute species identity from the pool in each community (249 permutations, due to limits in computation time). This resampling affect both trait values and species places in the phylogenetic tree without modification of the community richness and species local abundances

Given the considered metrics, we expect different signatures to emerge with the simulated processes of interest as referenced in Table 1.1. The expected patterns are detailed in this table, but briefly, the richness increases with larger filters ( $\sigma$ ), as well as CWV. CWM will be driven by the  $\text{topt}$  value. For the phylogenetic metrics, they are expected to be more influenced by the trait evolution model. Lastly, in order to even out the weight given to each metric and reduce their dimension we resumed all the above-mentioned diversity metrics using a multi-factorial analysis (MFA) implemented using the `FactoMineR` package [38].

## 2.5 Cross-validations

We assessed whether the signature carried by these different metrics was sufficient to faithfully infer our model's parameter values. This was assessed by generating a large number of datasets from the simulated parameter values and using Approximate Bayesian Computation (ABC) me-

thods to retrieve the true parameter values, following a “leave-one-out” procedure [39]. We used a subset of 100 randomly selected simulations in which both trait evolution and environmental filtering parameters varied and used the abc package [40], to compare the summary statistics of the selected simulations to those of others from the sample. We then plotted the true parameter value for each simulation against its estimated value, with a 5% tolerance, thereby indicating the reliability of the parameter estimations, for a given set of metrics. This cross-validation was done to compare functional (CWM, CWV, CWK, CWS) and phylogenetic (PD, MPD, MNTD) metrics and their ability to retrieve the two environmental parameters sigma and topt.

## **3 Results**

### **3.1 Taxonomic, functional and phylogenetic diversity patterns**

We simulated a total of 1431 communities using every combination of environmental filtering parameters (topt and sigma) and the three trait evolution models (BM, EB, and LB). The resulting diversity metrics and how these relate to the simulated trait evolution models and environmental filtering parameters are shown in Figure 2.

#### **3.1.1 At the regional scale (species pool)**

Regional trait distributions differed between models of trait evolution in terms of range and kurtosis. Both with the BM and LB trait evolution models, regional trait distributions had higher kurtosis than with the EB model, for which the traits are more dependent on the phylogeny structure. The LB model differed from the BM model as it led to a wider range of trait values, that we expected in the Table 1.1. We suppose that in the LB model, the combinations of acceleration of the trait evolution and an increasing number of lineage improve the range of trait values (Figure 2 **A**)

#### **3.1.2 At the local scale (communities)**

As expected, community diversity changed according to the parameters (topt and sigma) used to simulate environmental filtering (Figure 2 **B**). Species richness increased with increasing sigma,

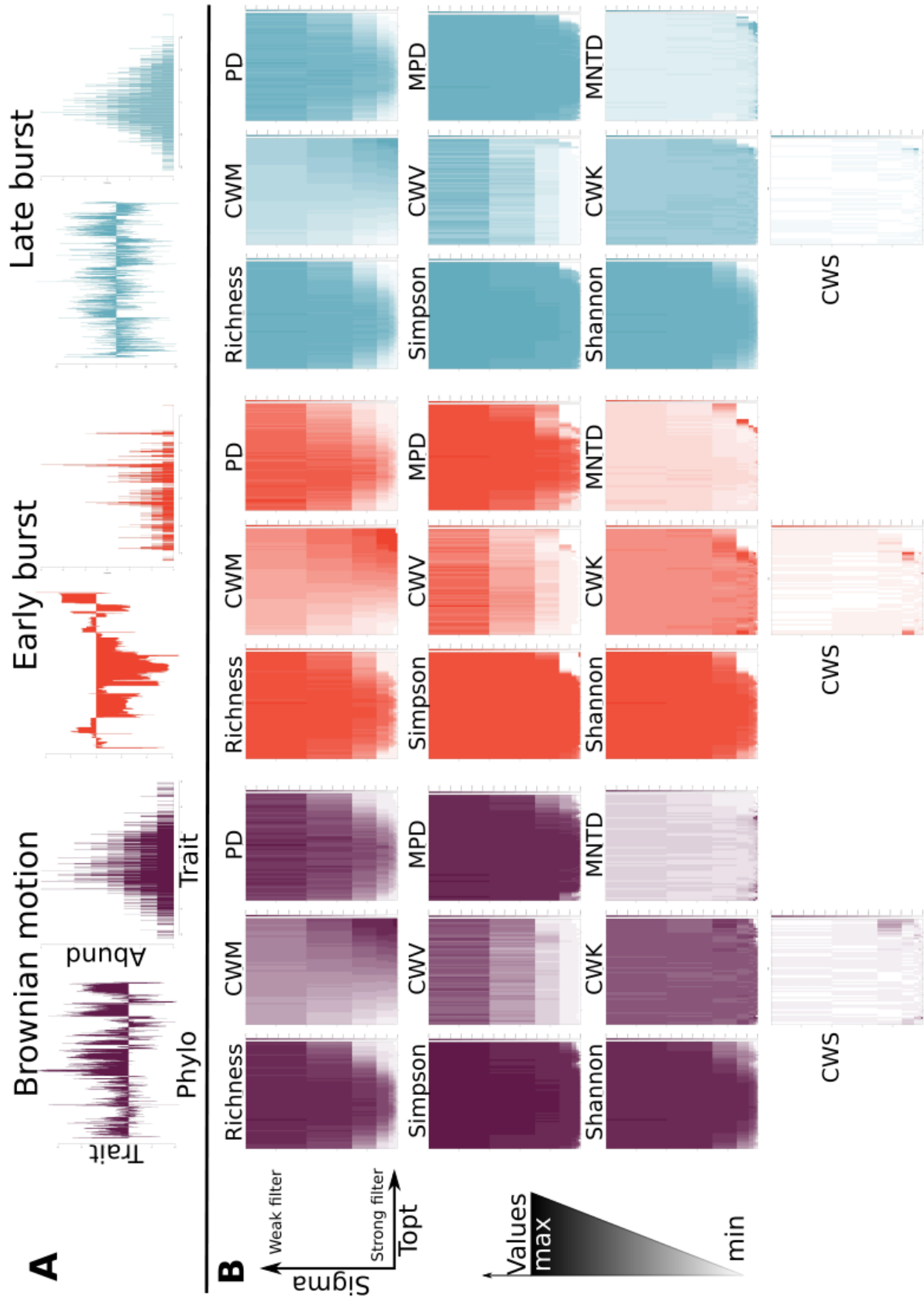


FIGURE 2 – *Gradients of every unstandardised metric along topt and sigma. A* represent the distribution of traits values along the phylogeny and its histogram for the three trait evolution models. *B* represent the gradients of values along topt and sigma parameters of the environmental filter. For every model, the columns regroup in this order the taxonomic metrics, functional metrics and phylogenetic metrics.

i.e. when tending towards more neutral assembly. This was reflected in increasing in CWV with increasing sigma : more species with loosely adequate - and therefore more variable - traits were included during community assembly, causing CWV to increase. Species richness also increased when environmental filtering was centered on an optimal value close to the mean trait value in the regional pool. This effect was weakened with a species pool generated under the EB model. CWS and CWK showed a similar signal in communities highly filtered away from the pool trait mean, which correspond to border effect at the extremes of pool trait range. This pattern is more visible with the EB model.

Phylogenetic diversity showed the same pattern as species richness. Communities resulting from weaker filter had a greater MPD value, whereas resulting for strong filters with topt distant from the pool trait mean show an increased MNTD. These observations depend also on the trait evolution model : a stronger Brownian motion at recent period (LB model and BM model) show higher MPD values for communities not filtered on the pool trait mean.

Finally we note that there are no strong differences between the different models of trait evolution, suggesting that the environmental filter is the main process affecting communities for the trait model considered here.

### **3.2 Multi-factorial analysis**

The multi factorial analysis shows simulated communities describing two main axes, representing 29.9 and 24.2 % of the variance in the range of models. Further axes show rapid loss in percentage variance with 11.5 % only. Phylogenetic metrics are defining the first axis, with MPD and MNTD opposed to recent ELD periods values. The second axe is defined by taxonomic metrics. The functional metrics are not particularly well described by these two axes, with CWK and CWS mostly contributing to the third axis, Adding the filter parameters to the MFA plot, sigma appears linked to taxonomic metrics, while topt looks correlated with CWM on the fourth axis.

The BM communities are halfway between EB and LB communities, as expected by the method we use for trait evolution. Differences in community grouping occurs with respect to the filter parameters. The communities filtered near the trait pool mean are grouped in the upper right corner, despite very different sigma on the filter. In contrast, communities with filters applied

away from the pool mean are more dispersed in the MFA space.

### **3.3 Cross validation**

Cross validation showed different results for functional and phylogenetic metrics when estimating the environmental filter parameters. Estimation of both  $\sigma$  and  $\text{topt}$  was accurate with functional metrics. In contrast, estimation based on phylogenetic metrics was sensibly less good, and better for  $\sigma$ . This precision however could depend on the evolution model of the traits, because we can observe that different trait models achieve better cross validation on specific parameters. BM model have smaller prediction error for the  $\sigma$  and the EB model for the  $\text{topt}$ . For the second one, this could be the result of traits more correlated with the phylogeny and therefore a better link between the phylogenetic information of the community and the species that can pass through the filter.

## **4 Discussion**

We addressed how combining taxonomic, functional and phylogenetic metrics allowed better grasping the signatures of entangled evolutionary and community assembly processes. We found that the different metrics yield complementary information.

### **4.1 Metrics**

For the single, non-standardised metrics (Figure 2), we found that as expected in table 1, taxonomic and phylogenetic (PD) diversity is impacted by the phylogenetic filter, mainly by the  $\sigma$  value. These metrics showed some redundancy in their response to modeled processes. By contrast, functional metrics showed different signals that allowed us to retrieve the functional filter parameters  $\text{topt}$  and  $\sigma$  with CWM and CWV respectively, in line with previous works [17]. CWK and CWS also confirmed previous results about border effects of the regional pool, with strong filters close to the pool range limits [8].

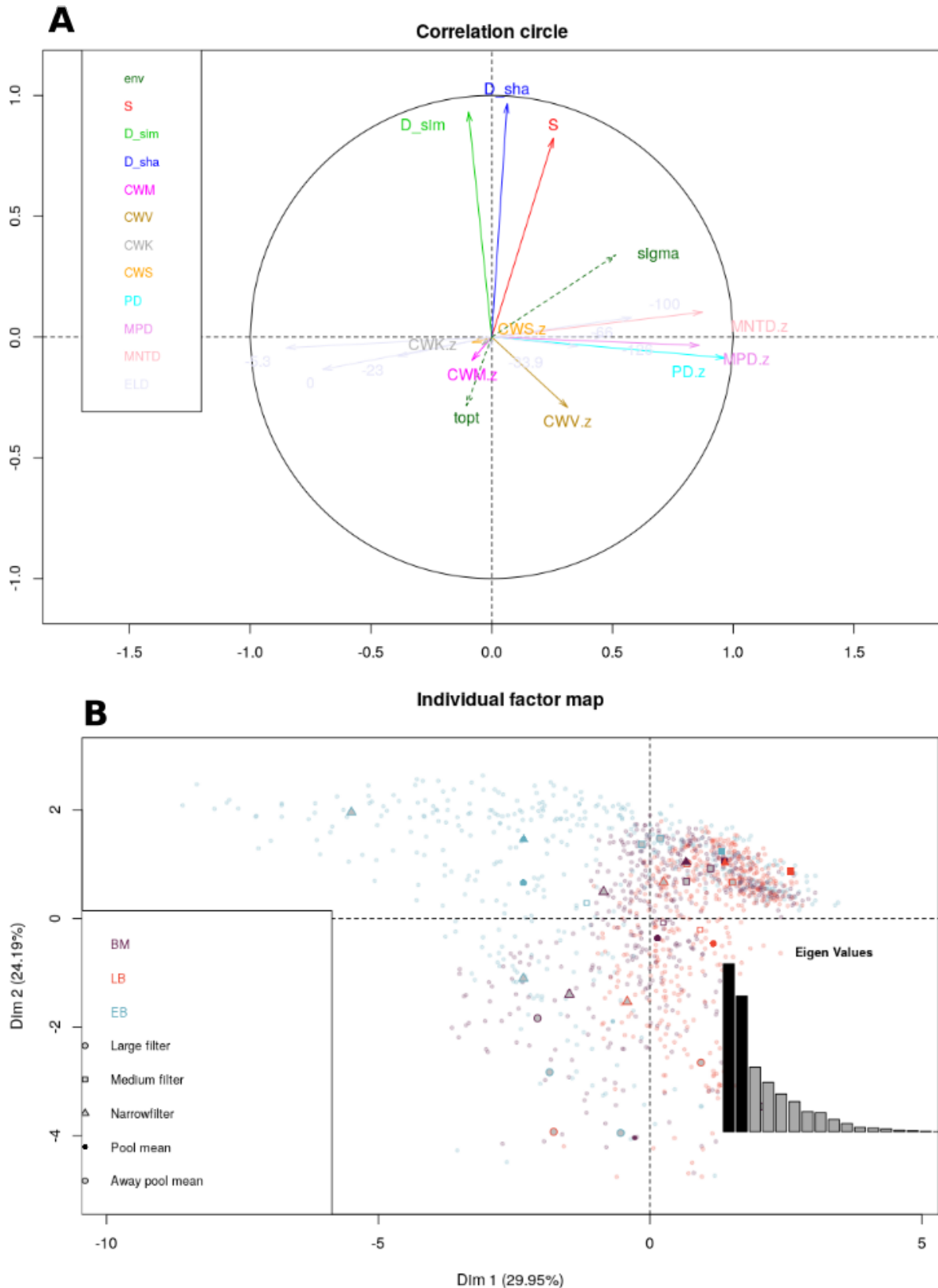


FIGURE 3 – *Result from the multi-factorial analysis for the two first axes with standardised metrics on the communities.* The MFA was done with *mvMORPH* package, using one group per metrics except the ELD that were grouped together. The communities were standardised by resampling species attribution in the pool and conserving community abundances. For the correlation circle, the environmental filter parameters are plotted but were not used in axe in the axe building.

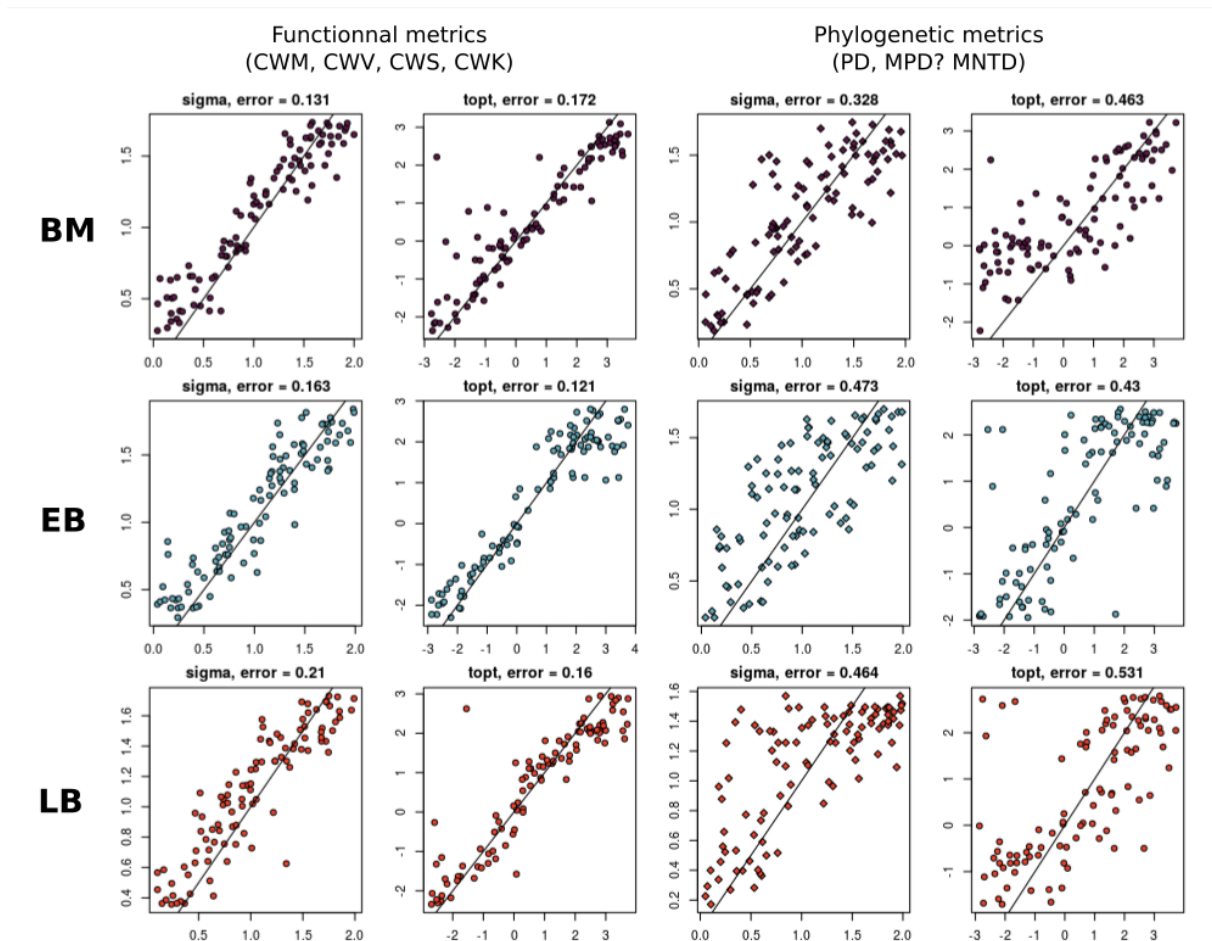


FIGURE 4 – *Cross validation on unstandardised metrics of communities. The cross validation was done with the cv4abc function of the abc package, fixing a tolerance to 5% with the rejection method on 100 values.*



## 4.2 MFA

The two main MFA axes mainly related to taxonomic and phylogenetic aspects of communities, respectively. This could be due to the fact that the three trait evolution models show similar patterns in functional metrics. Both taxonomic and phylogenetic aspects depend on Sigma, even though the parameter should be primarily correlated with CWV. The traits models are nonetheless partially separated on the first axis with phylogenetic metrics, showing that through environmental filters, we can detect small differences between functionally confounded trait evolution. This is contrasting with the absence of participation of the functional metrics to the first axis.

Nethertheless, the MFA shows unexpected results that call for further investigations. MNTD and recent ELD values are opposed on the first axis while we expected MNTD to be correlated with recent periods. The relation between the single phylogenetic metrics and the time decomposition metric could be caused by asymmetric representation of the phylogenetic information : the while the single metrics represent means, the ELD decompose the diversity in the tree depth in periods. Hence, this periods dont have the same length and are shorter in recent times. This difference in length could modify the decomposition signal and different periods and trees must be studied to check if this is the cause of the relation noted here, and in which range this affect future utilisation of the ELD metric.

## 4.3 Cross-Validation

The cross validation showed similar results for functional metrics to previous study [33]. However, we detected that phylogenetic metrics are less effective than functional metrics to estimate environmental filters. Consistent with our expectation, sigma could be estimated because phylogenetic metrics depend on the distance between species, that is directly linked with the number of species as shown in Figure 2. This is a direct relation because by adding a new species to the community, the phylogenetic tree has a new branch, and therefore more distance. Further analysis are needed to understand to what extent different metrics can improve this result, in particular by exploring cross validation on each metric at a time or other combination of the present metrics. If phylogenetic metrics can not easily estimate environmental filters, they could be useful to estimate the trait evolution models, either at the community or the regional pool

level, by adding the trait evolution model parameters.

Every metric used here evaluates diversity in a local community. Because communities with the same trait model come from the same pool, we could use beta diversity metrics to evaluate similarities or turnover in diversity between communities. Combining alpha and beta diversity metrics could further help disentangling confounding effects between ecological and evolutionary processes and add information to identify the trait evolution model [3].

## 5 Perspective

This study described communities with snapshot information, whereas species assemblages are dynamic through time. Integrating diversity patterns dynamics could help us define interaction of ecological mechanisms with species characteristics, as environmental filters and dispersion have a temporal dimension. [41].

Second modality fixed in our models was the absence of feedback from the communities to the regional pool. This feature of our model sets the regional pool to be static, which only allows us to assemble independent communities. Despite being useful when monitoring the consequences of precise processes, this decouple spatial and temporal scales. However, one can consider that the selection shaping the communities through the assembly processes can influence the pool with migration of new species locally formed by speciation into a larger space scale [42].

Finally, further analysis could be done on the through-time decomposition. We briefly used the epoch-specific lineage diversity, which decomposes the richness of communities across periods of the phylogenies. Studies have already developed methods to decompose trait variance among the nodes of the phylogeny [43]. Decomposing trait variance by period could produce information used as ELD in the present study. However the periods can heavily influence the results and do not take into account the phylogenetic uncertainty about node datation [44]. Establishing a method to set periods for decomposing the historical dimension of the regional pool or communities offers a new challenge.

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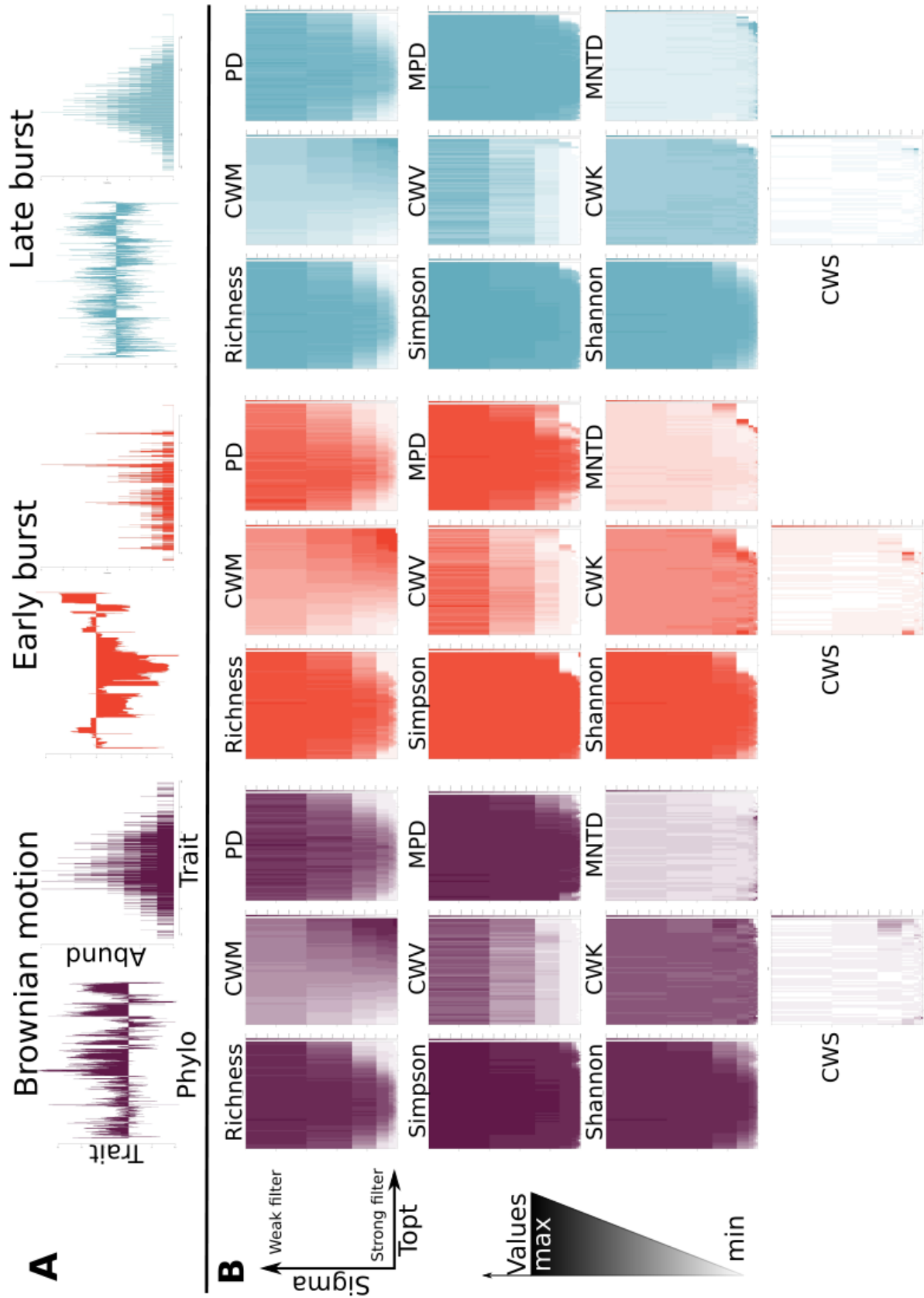
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Annexe 1 – *Gradients of every standardised metric along topt and sigma*. **A** represent the distribution of traits values along the phylogeny and its histogram for the three trait evolution models. **B** represent the gradients of values along  $\text{topt}$  and  $\sigma$  parameters of the environmental filter. For every model, the columns regroup in this order the taxonomic metrics, functional metrics and phylogenetic metrics. The standardisation was made by resampling 249 times the species attribution to the abundance in the pool.