Title: The dimensionality of biological diversity revisited.

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Abstract

Biodiversity can be represented by a variety of different dimensions (e.g. taxonomic diversity [operationalized mainly as species richness], functional diversity, phylogenetic diversity, genetic diversity). While the many different representations of biodiversity can lead to a more complete understanding of its variability across scales, they also lead to some degree of "fragmentation" of the concept, and do not provide insight into the intrinsic multidimensionality embedded in biodiversity. Developing a unified measure that integrates all the known dimensions of biodiversity is a theoretical solution for this problem; however, it remains an operationally utopian task. In this study we explore the concept of dimensionality of biological diversity and propose a way to integrate different dimensions. We define dimensionality of diversity as the number of dimensions needed to effectively describe biological diversity. We also provide an operational framework to quantify the concept and an example of the proposed framework using South American small mammal communities (cricetids and marsupials). Our results demonstrate that the taxonomic

dimension of diversity captures most of the variation among these communities across space, in detriment to the functional and phylogenetic dimensions of diversity. We conclude by highlighting the need for considering two components of dimensionality — the correlation among dimensions and variance — in the same framework.

Keywords: biodiversity metrics, communities, biodiversity measurement, correlation, variation.

Introduction

Biodiversity consists of the fundamental source of information that underlies all ecological studies, which justifies the efforts present in the agenda of ecological research to develop measures that properly operationalize the concept of biodiversity (Wilson 1989). This importance is reflected in the immensurable number of metrics that have appeared to date in an attempt to encompass all the variation in biodiversity. At the same time that the number of metrics to operationalize biodiversity grows and promotes the vast possibility of describing its different components, the same proliferation of metrics promotes what is best exemplified by the term coined by Hurlbert (1971) as the "non-concept of diversity".

Which components of diversity must diversity metrics (among those showing desirable statistical properties) represent in order to sufficiently express the variation underlying biodiversity? Searching for an answer to this question comprises the main goal of this article, and we believe that it must necessarily involve the adequate operationalization of a property of diversity named dimensionality (Lyashevska and Farnsworth 2012, Stevens and Tello 2014, Stevens and Gavilanez 2015). Dimensionality is a property of biodiversity that is related to the amount of information needed from different dimensions (e.g. taxonomic, functional or phylogenetic) to effectively describe its variation. Therefore, if the amount of information needed to effectively describe biodiversity comes from several different dimensions, the more dimensional it is (Stevens and Gavilanez 2015). Alternatively, if a single or

few dimensions provide the amount of information needed to effectively describe biodiversity, then the less dimensional it is. In summary, analyzing the dimensionality of biodiversity enables the assessment of how much information we need from different sources of variation to effectively describe what we call biodiversity (Stevens and Tello 2014).

Some approaches have already been proposed for quantifying the dimensionality of biodiversity. The most recent involves the calculation of Evenness of Eigenvalues (hereafter EE) (Stevens and Tello 2014). The rationale of this method is straightforward and understandable through the analogy colors (O. Lyashevska, non-published data). The great variety of colors can be summarized in only three basic axes: red, green and blue, known as the RGB system. These three colors comprise the minimum set of axes of variation able to capture the amount of information present in a pallet of colors (considering the basic color system). Calculating EE is like summarizing numerous colors (metrics of diversity) to a minimum set that effectively capture the most information (biodiversity). The higher the EE (the maximum value is 1), the more axes needed (more primary colors), the lower the EE, the fewer biodiversity measures needed (only a few primary colors).

Nonetheless, EE provides an incomplete picture for dimensionality of biodiversity. While this measure helps to understand how correlated the metrics are in a given set of communities, it is not able to reveal which dimensions contribute most to the observed dimensionality. This problem is illustrated in Figure 1. Circles and triangles represent two metacommunities for which two

metrics of diversity was calculated and plotted against each other (panel A). In one scenario, biodiversity measures are highly correlated with each other (HiC), while in the other scenario the same biodiversity measures minimally correlated with each other (LoC scenario). Thus, communities in HiC and LoC present low and high dimensionality (according to EE), respectively (panel B). However, in the scenario HiC we can note that the metric 2 for triangles has a much lower variance than metric 1 (high correlation and differential variation among metrics – HiC/DifV). In contrast, both metric 1 and metric 2 present similar variation for the circles (high correlation and similar variation among metrics – HiC/EqV). In other words, EE did not distinguish the differential contribution of the distinct metrics, since it relies only on the component of correlation among metrics. A similar situation is expressed by the LoC scenario, in which metric 1 has lower variation than metric 2 for triangle communities while variation does not differ between the two metrics for the circle communities (respectively, low correlation and differential variation [Lo/DifV] and low correlation and equal variation [Lo/EqV]).

Through EE we can not distinguish the amount of variation that each metric of diversity account to the entire metacommunity. A community can present high values of correlation for diversity metrics however each metric may account for a different amount of variation in the multidimensional space, thus, to characterize a sufficient portion of variation in biodiversity for these communities we must rely for more than one metric. This shed light to the problem of use only EE to operationalize the dimensionality concept.

In order to overcome the problem illustrated in Figure 1, that EE do not capture adequately the concept of dimensionality, a framework that combines measures that capture both the component of correlation among metrics and the component of variation among metrics must be used. The variation component could be operationalized by applying a measure called Importance Value (IV) (Willig and Hollander 1995, Wilsey et al. 2005). Importance Values allow the biodiversity measures that are most important in capturing the information of biodiversity contained in the entire set of metrics used to represent it to be recognized. In Figure 1C we illustrate how the IV can distinguish the different patterns of variation that metrics 1 and 2 present in metacommunities represented by circles and triangles. We expect that IV for circle communities present similar values for both metrics in both HiC and LoC scenarios, on the contrary, for triangle communities we expected that metric 1 present higher IV than metric 2 in HiC and lower values of IV in LoC.

Therefore, in this study, our aim is to propose a general framework to study the dimensionality of biodiversity by extending the investigation of dimensionality through the union of two different methods: EE and IV. The scenarios proposed in Figure 1 can be interpreted as a logical test to access if EE and IV can distinguish different patterns regarding the two components of dimensionality, that are correlation and variation in biodiversity metrics, thus, specifically, our objectives were to: 1) test, through numerical simulations, the theoretical expectations presented in Figure 1 regarding EE and IV to assess the dimensionality of communities; and 2) provide an empirical example of the

application of the measures of dimensionality with small mammal communities, showing how the information of the presented framework for dimensionality can be used.

Methods

Investigating the dimensionality of biodiversity: obtaining EE and IV

Our framework to investigate the dimensionality of biodiversity comprises by three steps. The first step is to calculate the matrix of biodiversity, hereafter called matrix **M** (*sensu* Ricotta 2005). In our work matrix **M** will be contain three metrics of diversity: a measure of functional diversity (FD [Petchey & Gaston, 2006)]), a measure of phylogenetic diversity (PD [Faith, 1992]) and richness. We choose these three metrics since they represent a sample of the metrics most used to represent, respectively, the functional, phylogenetic and taxonomic dimensions, and thus comprise the main accessed components of biological diversity in the ecological literature (Magurran 2011). Furthermore, the specific choices of metrics to compose the matrix **M** should not matter to the operationalization of dimensionality (for EE metric), as pointed out by Stevens and Tello (2018), who found that using different sets of diversity metrics to represent the same dimensions used here did not affect their results. The second step involves performing a Principal Component Analysis (PCA) of matrix **M**. As will be shown next, the standardization method applied to matrix **M** must differ between the calculation of EE and IV.

The third step is the calculation of the dimensionality metrics EE and IV. The first is calculated by applying Camargo's evenness index over the eigenvalues resulting from a PCA performed on a standardized matrix **M** (metrics scaled to a mean of zero and equal variance), following the same procedure used by Stevens and Gavilanez (2015). IV was calculated based on Wilsey et al., (2005), by using numerical elements provided by a PCA of matrix **M** standardized by the maximum values of each metric. This standardization was done to remove the effect of different units of each diversity metric without modify the original variation of the metrics. To obtain IV for each metric in matrix **M** we apply Equation 1 to components returned from the PCA, where IV_i represent the Importance Value for a given biodiversity metric, r^2_{ij} is the correlation of metric *i* with principal component *j* (PC_j) and R^2_j is the amount of variation that PC_j accounts for in ordination space.

$$IV_i = \sum r_{ij}^2 \times R_j^2 \qquad \text{Equation 1}$$

We calculate both EE and IV for metacommunities simulated according to the patterns of biodiversity metrics illustrated by the scenarios of Figure 1 (HiC/EqV], HiC/DifV, LoC/EqV and LoC/DifV) (but, for three biodiversity metrics instead of two). We are interested in whether EE can correctly detect the levels of redundancy in dimensions of diversity (high or low) and if IV can identify differences in the contribution of each dimension of diversity. The differences between IV must be lower in communities in which all metrics possess similar variation (HiC/EqV and LoC/EqV, represented by circle

communities in Figure 1) and greater in scenarios in which only one, or a few metrics, account for most of the variation in matrix **M** (HiC/DifV and LoC/DifV, represented by triangle communities in Figure 1). Furthermore, EE values must be equal in scenarios with equal and differential variation in metrics importance but differ between scenarios HiC and LoC. An illustration of the general framework to investigate dimensionality of diversity is presented in Figure 2.

Simulation methodology

To test the theoretical expectations about EE and IV in the measurement of dimensionality we simulated metacommunities according to a pattern-oriented procedure to achieve specific patterns of correlation and variation among metrics of biodiversity. We simulated scenarios that followed the patterns presented in Figure 1: HiC/EqV - biodiversity metrics that are highly correlated and with similar variation in dimensional space (illustrated in Fig.1A, HiC with circles); HiC/DifV - biodiversity metrics that are highly correlated but with variation among measures in multidimensional space being due to one dimension (illustrated in Fig. 1A with triangles).

To generate the communities in scenario HiC/EqV and HiC/DifV we followed a simulation procedure based on species distribution patterns expected by the species sorting model (Leibold et al. 2004). Under this model, species possess traits that allow them to persist in a community according to some availability of resources present along a gradient.

The simulation procedure starts with a phylogeny simulated by a birth-death processes (function *sim.bdtree* from package geiger [Harmon, Weir, Brock, Glor, & Challenger, 2008]) and a species, chosen by chance, to colonize the community and start the assembling procedure. The addition of species to the community is dependent on the species already present in that community. In one extreme of the gradient represented by communities that assemble the metacommunity, some communities will possess only species that are phylogenetically closely related to each other (the 10% most phylogenetically related species), with the phylogenetic restriction becoming less until the other extreme in which the communities will present species have the same probability of being selected to coexist (less selective conditions), creating a gradient of phylogenetic diversity in the metacommunity (a pattern expected by a process of phylogenetic habitat filtering, *sensu* Duarte [2011]). Specifically, in Scenario HiC/EqV, we simulate a trait that is continuously conserved over the phylogenetic tree (Paradis, 2012) (a trait that evolves accordingly to a Brownian model of evolution, using the function *rTraitCont* with the ρ [*rho*] parameter set to value of 3) with the number of species in each community increasing gradually (more phylogenetic filter, less species), creating a gradient in phylogenetic, functional and taxonomic diversity in a metacommunity that had high correlation and similar values of variation in diversity metrics. In Scenario HiC/ DifV we simulated a trait that evolves according to a stabilizing selection regime (Ornstein-Uhlebeck model with the strength of selection set by α parameter with a value of 0.8) that restricts trait variation to bet within an

optimal range (represented by θ [theta] with value of 0). This allowed us to we generate a metacommunity in which the metrics of diversity possess high correlation, but variation of FD is much lower than that of the metrics Richness and PD.

In Scenario LoC/ DifV, we simulated metacommunities according to the same rationale as for HiC Scenario. We start with a phylogeny and then generate traits following the same procedures described above, however, the trait was generated to possess low phylogenetic signal and the phylogenetic tree used to calculate PD for each community was modified to simulate a process of evolution in which most speciation occurs near the root (a star-like phylogeny). This procedure resulted in diversity metrics with low correlation, and low variability for PD and Richness, since we set the same number of species for all communities; most of the variation in this scenario is due to the FD metric. Finally, the Scenario LoC/EqV was simulated in a manner by which all species present in the phylogenetic tree had equal probability of being present in any community in the metacommunity (no phylogenetic habitat filtering acting on the assembly of the metacommunity). This procedure generated metacommunities with low correlation and similar variation in the diversity metrics.

We generated 999 metacommunities for each scenario described above (HiC/EqV; HiC/DifV; LoC/EqV and LoC/DifV). In all scenarios the metacommunities were composed of 50 communities, with each community possessing a minimum of 20 and a maximum of 200 species. The phylogenetic

filter was applied to act gradually through the communities by increasing by the order of 10% (i.e, start selecting only the 10% most phylogenetically related species, then the 20% most and so on until 90% of the most related species are selected. The details and an illustration of the simulation procedures and scenarios are presented in Supplementary Material S1.

Finally, to test the differences in importance of each dimension in each one of the scenarios presented above we used compare the IV values with a graphical tool called profile of importance (*sensu* Wilsey et al. 2005) and obtained F values from a linear model (Equation 2) that compare the IV of the three dimensions to test the magnitude of differences among dimensions of diversity for EqV and DifV scenarios.

Assessing dimensionality of biodiversity in small mammal communities

To illustrate the application of the dimensionality framework, we used a database of small mammal communities (marsupial and cricetid mammals) distributed throughout the South America continent. We consider the same three dimensions of diversity used in the simulation analysis (taxonomic, phylogenetic and functional, represented by Richness, PD and FD, respectively) to assemble matrix **M.** The EE and IV metrics were calculated as previously described in the section *Investigating the dimensionality of biodiversity: obtaining EE and IV,* although we used only the first axis of variation provided by the PCA of matrix **M** to calculate the IV metric.

We calculated EE using the procedures described by Stevens and Tello (2014) and Stevens and Gavilanez (2015), except we did not use a stop criterion for choosing axes derived from the PCA, since we were working with a matrix that possess only three dimensions, which is near the minimum needed to obtain any evenness metric.

We also compare the observed values of EE with a null distribution composed of 999 EE values generated according to two null models. The first null model randomizes a matrix of incidence of species preserving the differences in richness among sites, but shuffling species equiprobably (*sim3* function in *EcoSimR* package [Gotelli, 2000]). The second null model randomizes a matrix of incidence preserving both differences in species richness among sites and species frequency (*sim9* function in *EcoSimR* package). Null analysis of EE allows testing the null hypothesis that the observed EE do not differ from a given variation in species richness; in other words, failure to reject the null hypothesis means that the observed EEs can be explained by variation in richness among localities. We implemented a function named *dimensionality* to calculate EE from a matrix **M** with the possibility of choosing the evenness method that will be used in the calculation (the function can be accessed at https://github.com/GabrielNakamura/dimensionality_function).

To calculate IV for the metacommunities of small mammals we applied the R code for IV function, *ImportanceVal*, (the function can be accessed at https://github.com/GabrielNakamura/IV_function/blob/master/ImportanceVal.

R). We used the Kaiser-Gutmann stop criterion and a bootstrap procedure to generate confidence intervals for the IV of each dimension. We made all the calculations with a standardized matrix **M** (scale to zero mean and unit variance in the case of EE and standardized by the maximum values of each metric for calculating IV for reasons were explained in the previous section). The bootstrapped IV was submitted to an Ordinary Least Square (OLS) linear model (Equation 2) to test the null hypothesis that IV do not differ among dimensions of diversity.

$$IV_i = \alpha + \beta * dimension_i + \varepsilon_i \qquad \text{Equation 2}$$

In Equation 1 IV_i represents the predicted value of IV for dimension *i*, resulting from the sum of the intercept α and the effect of the dimension *i* (β_i). ε_i represents the error term associated with residuals, that follows a gaussian distribution.

Results

Simulated data

Our simulation shows that EE and IV behave as we predicted according the scenarios tested. EE did not differ between scenarios HiC/DifV and HiC/EqV (Figure 1A). Relative to IV, HiC/DifV presented greater differences than the differences among IV of metrics in HiC/EqV, as expressed through the distribution of F values from the two scenarios (Figure 1C).

The results for scenarios LoC also behaved as we predicted, with EE not differing between LoC/DifV and LoC/EqV (Figure 2B), and IV having higher differences in the scenario that possessed different contributions (LoC/DifV)

than the scenario with similar contributions of dimensions (LoC/EqV), as can be seen in the boxplot D of Figure 2 through the magnitude of F values. Finally, comparing EE values between scenarios HiC and LoC shows greater values of EE in LoC than HiC, revealing the difference in the correlation component of dimensionality between the two scenarios.

Small mammal communities

Calculation of EE for the small mammal communities resulted in an observed value of 0.46. Figure 4 reveals that the correlation component of dimensionality, at least for the three dimensions analyzed (functional, phylogenetic and taxonomic), may be due to spatial gradients in species richness.

Following our proposed framework, the IV metric is illustrated in Figure 5 through what we call Importance Values profile (*sensu* Willig and Hollander, 1995). The analysis of IV showed that the taxonomic dimension, represented by richness, captures most of the variation component of dimensionality of diversity, with a value of 0.32, followed by the phylogenetic dimension (PD) with 0.29 and the functional dimension (FD) with 0.22. These values represent, respectively, 38%, 34% and 26% of the total variation in the significant axis selected for the IV analysis of matrix **M** (only the first axis was selected according to the Kaiser-Guttman criterion). Furthermore, the ANOVA model showed that IV differed significantly (F-value= 3.428; $p<0.05$), reinforcing the greater contribution of richness in capturing most of the variation in the dimensionality of communities of cricetids and marsupials.

Discussion

Our simulations clearly demonstrate the need to using EE and IV in a complementary manner, since a single value of EE can be found for communities possessing different rankings of importance of dimensions, as we demonstrated through simulated communities in scenarios of high and low correlations between metrics (HiC and LoC). The IV showed to be effective in quantifying and detecting the differences in the contribution of each dimension. Given these findings, our framework represents a step beyond the frameworks proposed by Stevens and Tello (2014 and 2018) and Stevens and Gavilanez (2015) in two ways. First, it allows accessing the variation component of dimensionality of diversity, and second by providing, as far as we know, the first formal statistical test to evaluate the behavior of EE and IV.

Despite the use of only three dimensions in the present work, the methods used here are highly flexible in the sense that we can use a matrix **M** that contains many more dimensions (Ricotta 2005). Therefore, in other words, we could represent diversity in a much more complete manner with metrics that capture other dimensions, such as the genomic dimension (*e.g.* Nei 1978), and so many others (*e.g*. Gotelli et al. 2012) that can be quantified and used to assess the dimensionality present in ecological communities. Including these dimensions will allow assessing the contribution of other metrics to capturing the information of communities and whether these metrics account for a complementary source of information relative to the phylogenetic, functional and taxonomic dimensions.

Our example using the dimensionality framework with small mammal communities showed that cricetids and marsupials possess low dimensionality and that the observed value can be explained by variation in the taxonomic dimension (represented by richness). These findings differ from those of Stevens and Gavilanez (2015), who found the dimensionality of bat communities to be significantly more dimensional than expected by null models (the same null models used in the present work), although the observed value was lower than that observed in the present study. This difference between the present study and that performed by Stevens and Gavilanez (2015), evidence that the correlation component of dimensionality of diversity can change depending on the taxonomic group being investigated and that the factors generating this correlation can also be differ.

Our results for IV with the small mammal communities were in contrast with the findings of Wilsey et al (2005) and Lyashevska and Farnsworth (2002), who concluded that richness to be of less importance than other diversity metrics. So, we have evidence indicating that the variation component of dimensionality, in addition to the correlation component, presents specific patterns depending on the taxonomic group being investigated, highlighting the need to understand the contingencies in the correlation and variation components of dimensionality of different communities.

Conclusion and future directions

The main take home message of the present study is an updated definition of the concept of dimensionality for ecological communities

(Stevens and Tello 2014) by including the variation component and operationalize it though EE and IV. Thus, an effective investigation of dimensionality must involve assessing both correlation and variation among metrics of diversity.

Since the evidence presented in the literature is limited, and based only on specific groups of organisms, some questions still need to be addressed to render a more complete understanding and generalization of the role of some factors in explaining the dimensionality of ecological communities. For instance, we might wonder if some dimensions of diversity are consistently more informative than others in describing diversity patterns among different taxa, or if distinct factors (historical, evolutionary and/or ecological) generate higher or lower levels of dimensionality of diversity across communities in predictable ways.

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Figures captions

Figure 1: A) Relationships between two diversity metrics from two metacommunities – circles that represent the Equal Variation and triangles that represents Different Variation among biodiversity metrics. These metacommunities can present high correlation among metrics (HiC) and low correlation among metrics (LoC). B) Evenness of eigenvalues (EE). C) Importance Values (IV).

Figure 2: General framework to investigate dimensionality of diversity through the calculation of the metrics EE and IV. Starting with a set of communities, metrics of

diversity are calculated to assemble matrix **M** (step 1). A PCA of matrix **M** (step 2) is then performed and the measures of dimensionality of diversity calculated (step 3). Details for the calculation of IV and EE are provided in the text of the Methods section Investigating the dimensionality of biodiversity: obtaining EE and IV.

Figure 3: Profile of importance for IV and EE metric (bar plots A and B) calculated for simulated metacommunities according to scenarios HiC and LoC. For each of these scenarios we presented situations in which the metrics either had similar contributions or had different contributions to dimensionality (respectively EqV and DifV). Boxplots C and D represent the F-value distributions from linear models for scenarios HiC/DifV, HiC/EqV, LoC/DifV and LoC/EqV.

Figure 4: Histogram of null EEs. The dotted lines represent the 25% and 95% of the null distribution. The solid lines represent the observed EE, indicating that observed EE does not differ from the null models.

Figure 5: IV profile of communities of marsupial and cricetid mammals of South America. Bar height correspond to the observed IV for each dimension while the lines represent the 95% confidence intervals generated by a bootstrap procedure.

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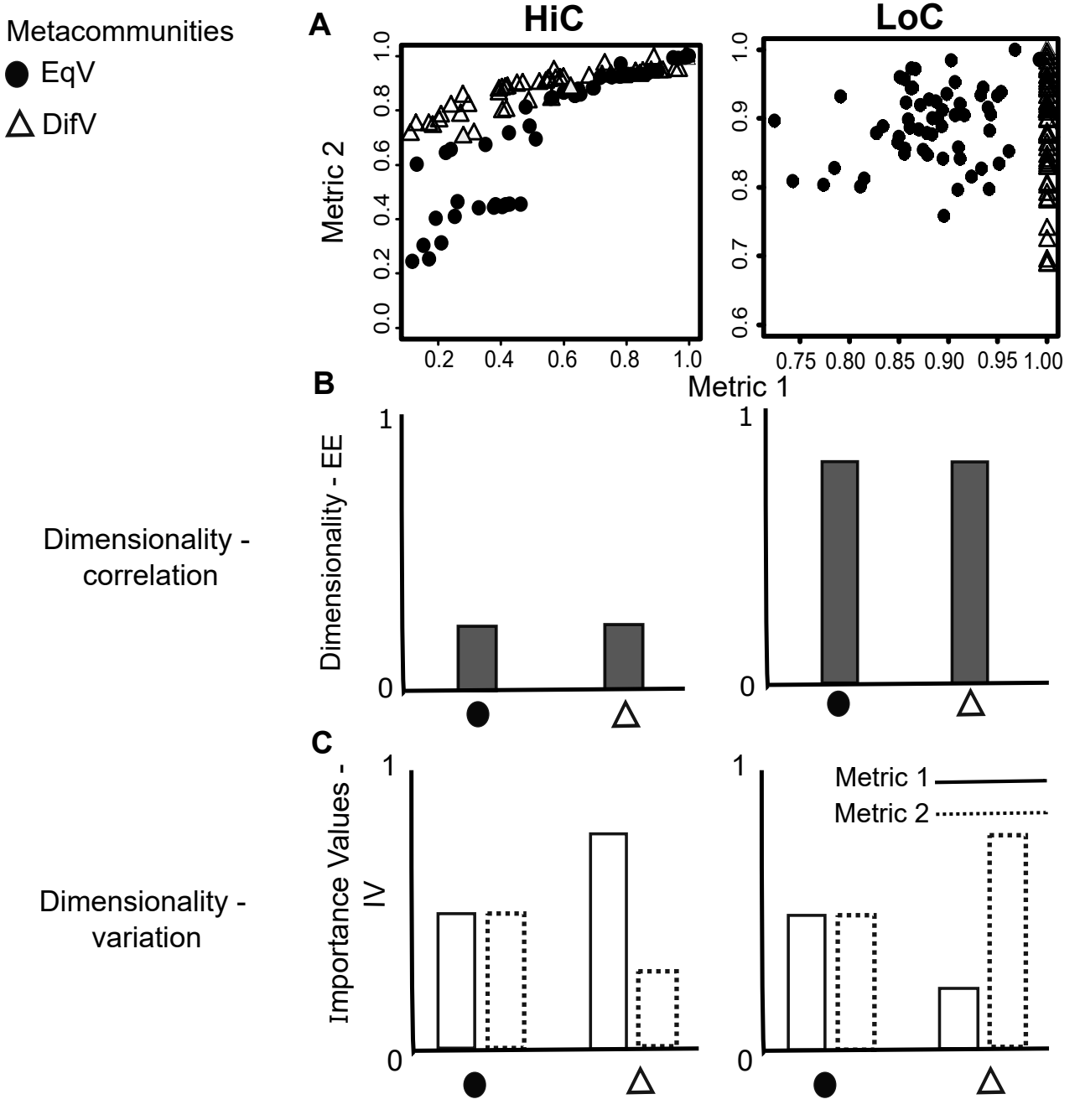
Metacommunities
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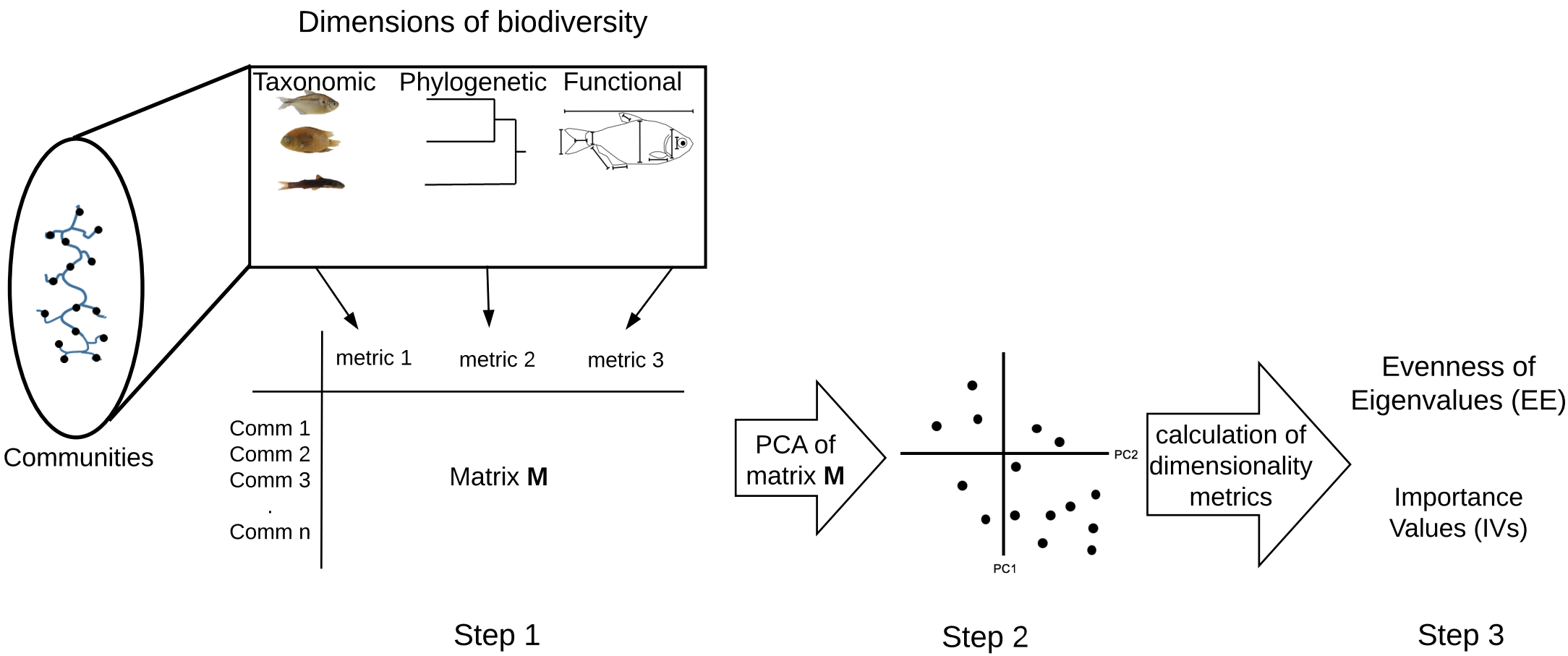
Dimensionality - variation
Metric 1
Metric 2


Dimensions of biodiversity
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Communities
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calculation of dimensionality metrics
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Step 1
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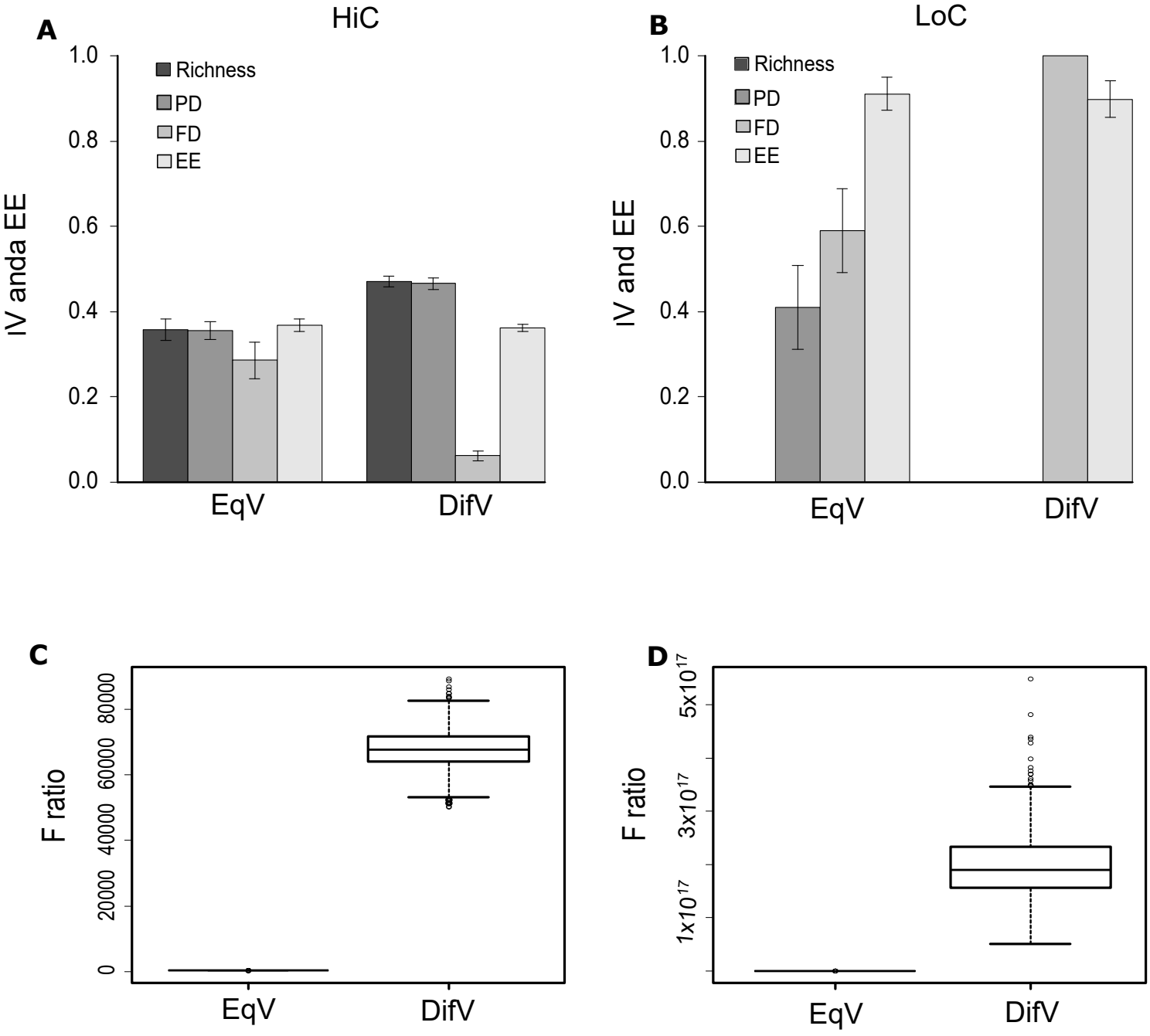
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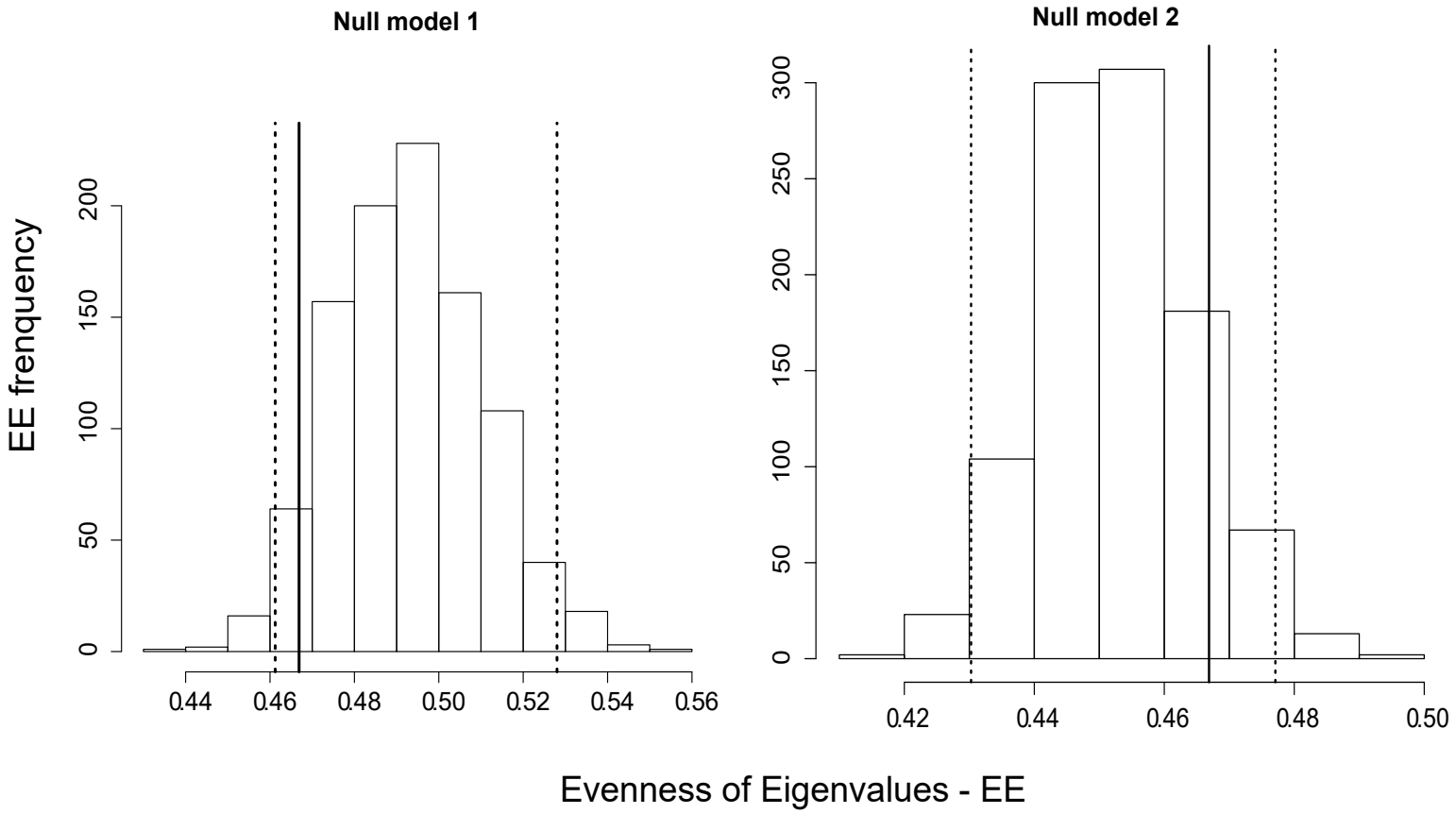
Null model 1
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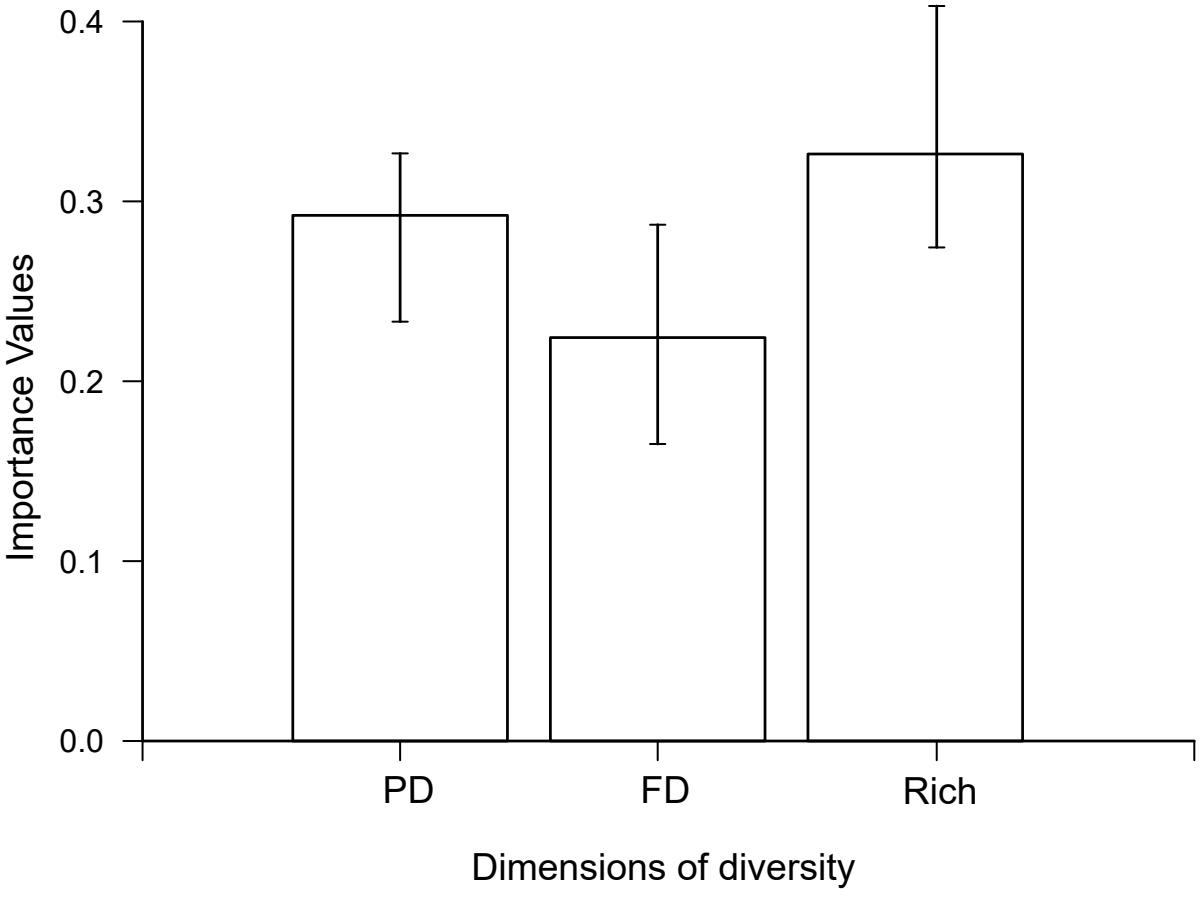
Evenness of Eigenvalues - EE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