Title: Revisiting the dimensionality of biological diversity

Abstract

Biodiversity can be represented by a variety of different dimensions (e.g. functional diversity, phylogenetic diversity, genetic diversity and taxonomic diversity). While the many different representations of biodiversity can lead to a more complete description of communities, they also lead to a degree of 'fragmentation' of the biodiversity concept. Developing a unified measure that integrates all the dimensions of biodiversity is a theoretical solution for this problem, however, it remains an operationally utopian task. Alternatively, quantifying the dimensionality of biodiversity is a way to integrate the different dimensions of biological diversity. This concept is explored in the present study. We define the dimensionality of diversity as the number of different diversity metrics needed to effectively describe biodiversity. We provide a solution that joins the two components of dimensionality (correlation and the variation of each diversity metric) in the same framework, allowing us to quantify dimensionality. We show, through a simulation study, that considering the correlation among dimensions with the variation of each dimension offers important information that is neglected when only correlation information (the component used in the current methodology to measure dimensionality) is considered. We demonstrate how to apply the proposed framework by investigating the dimensionality of South American small mammal communities (cricetids and marsupials). Our example demonstrates that the taxonomic dimension of diversity captures most of the spatial variation among these communities. We conclude by highlighting the greater understanding of dimensionality that is obtained through this method, as well as the insights it provides into the importance of each diversity metric to the whole

biodiversity space, insights which can not be obtained through the current common method.

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 of ecological research to develop measures that properly operationalize its concept (Wilson 1989). These efforts are reflected in the immensurable number of diversity metrics that have appeared in an attempt to encompass all the variation in biodiversity. As the number of diversity metrics grows and promotes the description of the different dimensions of variation, the same proliferation promotes confusion around the definition of biodiversity, which was expressed well by Hurlbert (1971) in his seminal work on the "non-concept of diversity".

A possible way to resolve the confusion created from the many operational solutions (diversity metrics) of such a unique concept (biodiversity), exists in the search for a unifying diversity metric that encompass all the dimensions of variation that define biodiversity. However, consolidating the many dimensions represented by diversity metrics in a reliable way appears to be a utopian task. This consolidation can be achieved by investigating the relationships among the existing metrics, which essentially means assessing the dimensionality of biological diversity.

Dimensionality is an inherent characteristic of biological diversity that can be defined as the minimum set of diversity metrics needed to sufficiently describe the whole variation that is present at a given level of biological organization (e.g. populations and communities) (Lyashevska and Farnsworth 2010; Stevens and Gavilanez 2015). Which metrics of diversity must be used to sufficiently express the variation in a given community? What is the minimum set of metrics needed to characterize a community (Lyashevska and Farnsworth, 2010)? Do functional, phylogenetic and taxonomic diversity consist of independent dimensions of variation

when defining the diversity of communities? These questions that can be answered by quantifying the dimensionality of biological diversity. The search for answers to these questions leads to the development of statistical tools that are able to capture the level of redundancy (or correlation) in a set of diversity metrics calculated for communities. In this multidimensional context, ordination techniques offer the basic machinery to solve problems that involve multiple dimensions however, when considered on their own, they do not provide a global measure that indicates the dimensionality of a data set.

A sequence of recent publications by Stevens and Tello (2014), Stevens and Gavilanez (2015) and Stevens and Tello (2018) follows the investigation of the dimensionality of bat communities using an index called the Evenness of Eigenvalues (hereafter EE). This metric is obtained by applying a Principal Ordination Analysis (PCA) over a matrix of diversity metrics calculated for a set of communities (the calculation details are explained later in the methods section). The logic behind EE is that, if the diversity metrics used to characterize a given set of communities are very redundant, this indicates low dimensionality and produces low EE values. On the other hand if diversity metrics are completely orthogonal with each other, this indicates a high dimensionality and the EE value of the community will be high (close to 1).

The EE metric certainly accomplishes, in a simple and effective way, the operationalization of the correlation component presented in dimensionality. However it ignores the amount of variation, or importance, of each metric present in the multidimensional biodiversity space. Let´s suppose a situation in which diversity metrics are correlated, but each one accounts for similar amounts of variation in the total multidimensional biodiversity space. In this situation, despite the high

correlation among dimensions and the low dimensionality, according to the EE calculation, we will need to rely on a great number of diversity metrics in order to effectively represent the variation in biodiversity present in this set of communities. Wilsey et al (2005) was the first to quantify the amount of information that each metric accounted for in a multidimensional space, using a metric called Importance Values (hereafter IV, with detailed calculations presented in the methods section). Through this metric the authors accessed the variation component of dimensionality in communities.

The common way to quantify dimensionality within the ecological literature (Stevens and Tello, 2015) provides an incomplete picture of the inherent characteristics of biodiversity, since it only relies on correlation and does not consider the variation component of the dimensionality concept. In Figure 1 we illustrate the problem associated with only considering the correlation component of dimensionality. Circles and triangles represent two metacommunities for which two diversity metrics (which could be imagined as functional diversity and phylogenetic diversity) were calculated and plotted against each other (panel A). In the first scenario diversity measures are highly correlated (HiC in Figure 1), while in the other scenario the same biodiversity measures are minimally correlated with each other (LoC in Figure 1). Thus, communities in scenarios HiC and LoC present low and high dimensionality, respectively, when calculated according to the EE (panel B). However, in scenario HiC we note that, for triangles, diversity metric 2 has a much lower variance than diversity metric 1 (high correlation but a different amount of variation among metrics – HiC/DifV). In contrast, both diversity metric 1 and diversity metric 2 present similar variation for the circles (high correlation and similar variation among metrics – HiC/EqV). Despite these different patterns, the EE cannot

distinguish the differential contribution of the two diversity metrics, since it only relies on the correlation component of dimensionality. A similar situation is expressed by the LoC scenario, in which metric 1 has a lower variation than metric 2 for triangle communities (low correlation and differential variation [Lo/DifV]), and variation does not differ between the two metrics for the circle communities (low correlation and equal variation [Lo/EqV]).

To overcome the problem illustrated in Figure 1, which is that the EE do not capture all the components that make up the concept of dimensionality, a framework that combines a measure that captures the correlation among metrics with the variation of each diversity metric must be used. Operationally, this implies combining the EE and IV measures into one framework which adequately characterizes the dimensionality of biodiversity. Despite the existence of these two metrics that are capable of measuring the two components of the dimensionality concept, they have so far only been used separately, providing a limited perspective of the dimensionality of biodiversity.

In this paper we propose an integrative framework for the dimensionality of biodiversity and provide the most well-rounded characterization of dimensionality to date. Within this framework we integrate the EE and IV metrics in order to conciliate the correlation and variation components of the dimensionality of diversity. We start by showing, through a simulation study, how using the EE and IV together can overcome the problem presented in Figure 1. Following this we present an empirical example of the investigation of dimensionality by applying the proposed framework of dimensionality to communities of small mammals (crycetids and marsupials).

Methods

Investigating the dimensionality of biodiversity: obtaining EE and IV

Our framework to investigate the dimensionality of biodiversity is comprised of three steps. The first step is to calculate the matrix of diversity metrics, hereafter called matrix **M** (*sensu* Ricotta 2005). Here matrix **M** will contain three metrics of diversity: a measure of functional diversity (FD [Petchey & Gaston, 2006)]), phylogenetic diversity (PD [Faith, 1992]) and richness. Despite our choices of these three metrics we highlight that the matrix **M** can be assembled with any other diversity metrics. We chose these three metrics since they are some of the most commonly used diversity metrics, representing the most frequently applied dimensions of biological diversity in the ecological literature (Magurran 2011). 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** prior to the PCA must differ between the calculation of EE and IV. The third step is the calculation of the dimensionality metrics EE and IV. We calculate EE using the Camargo´s evenness index:

$$EE = 1 - \left(\sum_{P}^{A(A-1)} |e_{ip} - e_{jp}|\right) \Big/ A \qquad \text{Equation 1}$$

Camargo's evenness index (Camargo 1983) was calculated Using the axes (A) and their respective eigenvalues (e_{ih} and e_{jh}), which were produced from a PCA (p) performed on a standardized matrix **M** in which metrics were scaled to have zero mean and equal variances. This is the procedure used by Stevens and Tello (2015). EE values range from 0 (low dimensionality) to 1 (high dimensionality). The greater the value of EE, the less correlated communities are in relation to the diversity metrics that characterize these communities. On the contrary, low EE values indicate that the diversity metrics that characterize the communities are highly correlated. IV was

calculated by modifying the method proposed by Wilsey et al., (2005), which uses a matrix (**M)** that has been standardized by the maximum values of each diversity metric. This standardization removes the effect that the different units of each diversity metric can have, without modifying their original variation. To obtain the IV of each diversity metrics in matrix **M** we apply Equation 2, in which IV_i represents the IV of the diversity metric, *i*, r^2_{ij} is the correlation of diversity metric *i* with PC*j*, and R^2_j is the amount of variation that PC_j accounts for in the ordination space.

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

PC varies from 1 to *j* and corresponds to the number of significant eigenvectors in the PCA, evaluated by Kaiser-Gutmann criterion. The greater the IV value the more variation the diversity metric accounts for in the multidimensional biodiversity space. IV values approach 1 when the diversity metric accounts for almost all variation and approach zero when the metric presents low values of variation.

Testing the assessment of the dimensionality of diversity using EE and IV

We calculated both EE and IV values for metacommunities simulated according to the patterns of diversity metrics illustrated in the scenarios presented in Figure 1 (HiC/EqV, HiC/DifV, LoC/EqV and LoC/DifV). They were calculated by using the matrix **M**, which was composed of three metrics: richness, PD and FD. An illustration of the general framework used to investigate the dimensionality of diversity is presented in Figure 2. Here, the matrix **M** is shown to have three dimensions, however it can be assembled by more than three dimensions and any other dimension of diversity can be used inside the framework presented in this work.

We were interested in determining whether EE values could correctly detect the levels of information redundancy present in matrix **M** (high or low), and if IV

values could identify differences in the contribution of each diversity metric to the multidimensional biodiversity space. To prove that EE and IV values can do these things, the following conditions must be met. EE values must not differ in scenarios with equal and differential variation (when comparing between scenarios HiC/EqV and HiC/DifV or LoC/EqV and LoC/DifV), but they can differ between highly correlated and poorly correlated scenarios (when comparing between scenarios HiC/EqV and LoC/EqV or HiC/DifV and LoC/DifV). The differences between the values of IV must be lower in communities in which all diversity metrics possess similar variation (Scenario HiC/EqV and LoC/EqV, represented by the circle communities in Figure 1) and they must be greater in scenarios in which only two diversity metric accounts for most of the variation in matrix **M** (Scenarios HiC/DifV and LoC/DifV, represented by the triangle communities in Figure 1).

Simulation methodology

Figure 1 represents the theoretical scenarios in which the performance of the EE and IV values were tested. We simulated metacommunities based on a pattern-oriented procedure, producing diversity metrics with patterns of correlation and variation that resembled the scenarios presented in Figure 1. In the HiC/EqV scenario the diversity metrics are highly correlated but have a similar variation in the dimensional space (illustrated in Fig.1A, HiC with circles). The HiC/DifV scenario presents diversity metrics that are highly correlated but vary in relation to the variation that each one account in the multidimensional space, which is mainly determined by two diversity metric. In these two scenarios we expect to obtain low values of EE (since the diversity metrics are very correlated), but we expect similar values of IV in the HiC/EqV scenario and different values of IV in the HiC/DiFV

scenario. In the HiC/DiFV scenario we expect two diversity metrics to have higher values than the other one of the diversity metrics.

The biological reasoning of the HiC/EqV and HiC/DifV scenarios followed a pattern that can be predicted by a species sorting model (Leibold et al. 2004). Within this model, species possess traits that allow them to persist in a community according to the availability of resources (represented along a gradient here). The simulation starts with a phylogeny that is simulated by a birth-death processes (function *sim.bdtree* from the package geiger [Harmon, Weir, Brock, Glor, & Challenger, 2008]) where a species, chosen randomly, colonizes the community and starts the assembling procedure. The addition of a species to the community depends on the species that are already present in that community. At one extreme of the gradient the communities will only contain species that are phylogenetically closely related to each other (the 10% of species that are the most phylogenetically related to each other), with the phylogenetic filter becoming less restrictive until at the other extreme the communities contain species that have the same probability of being selected to coexist (less selective conditions). This creates a phylogenetic diversity gradient in the metacommunity (a pattern expected by a process of phylogenetic habitat filtering, *sensu* Duarte [2011]).

In scenario HiC/EqV we simulated a trait that was continuously conserved over the phylogenetic tree (a trait that evolved according to a Brownian motion model of evolution, determined by using the function *rTraitCont* (Paradis, 2012) with the ρ [*rho*] parameter set to the value of 3), with the number of species in each community increasing gradually (less phylogenetic filter, more species). This created a gradient in phylogenetic, functional and taxonomic diversity in a metacommunity that contained high levels of 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 giving the α parameter a value of 0.8) that restricts trait variation to within an optimal range (represented by a θ [theta] value of 0). This allowed us to generate a metacommunity in which the diversity metrics are highly correlated, but the variation of FD is much lower than that of the richness and PD metrics since the traits that were used in the calculation of FD were restricted by the selection process.

In scenario LoC/DifV we start with a phylogeny and then generate traits following the same procedures described above for HiC/EqV scenario. However, the trait generated here to had a 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 of the speciation occurs near the root (a star-like phylogeny). This procedure resulted in poorly correlated diversity metrics since the relationship between phylogeny and traits was disrupted. Additionally, a low variability for PD and richness metrics was obtained since we set the simulations to produce communities with the same number of species. Consequently most of the variation in this scenario is due to the FD metric. Finally, scenario LoC/EqV was simulated in a manner by which all species present in the phylogenetic tree had an equal probability of being present in any community within the metacommunity (no phylogenetic habitat filtering acting on the assembly of the metacommunity). This procedure generated metacommunities with low correlation and similar amounts of variation for 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 set to act gradually through the communities, increasing by the order of 10% (*i.e*, start by selecting the top 10% of species that are the most phylogenetically related, followed by the top 20% and so on until 90% of the species have been selected from the pool). The details and an illustration of the simulation procedures and scenarios are presented in the Supplementary Material S1. Here we also describe the interactive module we produced to illustrate the simulation procedure used in this work.

Finally, we tested whether the EE and IV values met our expectations in the simulated communities. To analyze the EE values we checked if they were different in scenarios with low correlation and high correlation (scenarios HiC/DifV and HiC/EqV differing from LoC/EqV and LoC/DifV). To effectively capture dimensionality the EE metric must be higher in scenarios with low correlation than in scenarios that presented high correlation among diversity metrics. To test for differences among the IV values of each metric in the scenarios presented above we compared the IV values using a graphical tool called profile of importance (*sensu* Wilsey et al. 2005) and quantified the differences by calculating F values from a linear model (Equation 3). These values compare the IV of the three dimensions (PD, FD and richness) and test if the IV in the scenarios with differential variation in diversity metrics (scenarios HiC/DifV and LoC/DifV) presented greater differences than IV calculated for the scenarios that present similar variation in diversity metrics (scenarios HiC/EqV and LoC/EqV).

Assessing the 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 American continent. We considered the same three diversity

metrics used to assemble the matrix **M** in the simulation analysis (richness, PD and FD,)**.** The EE and IV metrics were calculated as previously described in the section 'Investigating the dimensionality of biodiversity: obtaining EE and IV', although we only used the first axis of variation provided by the PCA of matrix **M** to calculate the IV metric, since this was the only axis that was significant according to the Kaiser-Gutmann stop criterion.

We also compared the observed values of EE with a null distribution composed of 999 EE values, generated by two null models. The first null model randomizes a species incidence matrix while preserving the differences in richness among sites but mixing species frequency (performed with the *sim3* function from the *EcoSimR* package [Gotelli, 2000]). The second null model randomizes an incidence matrix while preserving both differences in species richness among sites and species frequency (*sim9* function in *EcoSimR* package). We tested the null hypothesis that the observed EE values do not differ from EE expected by variation in richness values. We implemented a function called *dimensionality* to calculate the EE values from the matrix **M**. The function allows the user to choose the evenness method that will be used in the calculation. It 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 the 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 value of each diversity metric. We performed all the calculations with a standardized matrix **M** (scaled to zero mean and unit variance for the calculation of EE values and standardized by the maximum values of each metric

for the calculation of IV values. Explanations were provided in the previous section). The bootstrapped IV values were submitted to an Ordinary Least Square (OLS) linear model:

$$IV_i = \alpha + \beta * dimension_i + \varepsilon_i \quad , \qquad \text{Equation 3}$$

where IV_i represents the predicted value of IV for the diversity metric i (the sum of the intercept α and the effect of the dimension i (β_i)), and ε_i represents the error term associated with the residuals, which follow a gaussian distribution. This tests the null hypothesis that IV values do not differ among the dimensions of diversity.

Results

Simulated data

Our simulation shows that EE and IV behave as we predicted, according the scenarios tested. EE correctly captured the correlation component of dimensionality, evidenced by the higher values presented in the LoC/DifV and LoC/EqV than in the HiC/DifV and HiC/EqV scenarios. The IV metric also behaved as we expected; showing greater differences among IV values in scenarios where the variation in the multidimensional biodiversity space was only affected by two or one metric (PD and richness in HiC/DifV and FD in LoC/DifV). This result was evidenced in Figure 3 C and D, with much greater F-values in the HiC/DifV and LoC/DifV scenario (indicating greater differences in contribution) than in the HiC/EqV and LoC/EqV scenario.

Small mammal communities

Calculation of the EE value for the small mammal communities produced 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 a consequence of the spatial gradients of species richness.

IV values for the three diversity metrics were illustrated in Figure 5 through the Importance Values profile (*sensu* Willig and Hollander, 1995). Analysis of the IV values showed that richness represents most of the variation in the biodiversity space (composed of the three diversity metrics), with an importance value of 0.32. The phylogenetic dimension (PD) represents the second largest quantity of variation, with a value of 0.29, and the functional dimension (FD) represents the smallest quantity with a value of 0.22. These values represent, respectively, 38%, 34% and 26% of the total variation along 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 quantity of variation that is represented by richness in the dimensionality of the communities of cricetids and marsupials.

Discussion

Our simulation results demonstrate that it is necessary to use EE and IV values in a complementary manner, since a similar value of EE can be found for communities presenting diversity metrics with different levels of importance. Given this finding, our framework represents a step beyond the method proposed by Stevens and Tello (2014) to quantify the dimensionality of diversity. Additionally, our work promotes an integration of different tools already used to quantify separate aspects of dimensionality in a single and comprehensive framework. Finally, we provide the first results (to our knowledge) showing the effectiveness of using EE and IV values to capture patterns of the dimensionality of biodiversity.

Despite only using 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, we could represent diversity in a much more complete manner, with metrics that capture other quantifiable dimensions such

as the genomic dimension (*e.g.* Nei 1978) and many others (*e.g*. Gotelli et al. 2012). Including other dimensions would allow the contributions of these other metrics to biodiversity to be assessed, and the complementary or redundant nature of these metrics, in relation to the phylogenetic, functional and taxonomic dimensions, could be discovered.

Our application of the dimensionality framework to small mammal communities showed that cricetids and marsupials possess low dimensionality and that the observed value of EE can be explained by the variation in the taxonomic dimension (represented by richness). These findings differ from those of Stevens and Gavilanez (2015), who found the EE of bat communities to be significantly higher than expected by null models (the same null models used in the present work), although their observed EE value is lower than the observed value of the present study. The difference between the present study and the study of Stevens and Gavilanez (2015) is evidence that the correlation component of the dimensionality of diversity can change depending on the taxonomic group being investigated.

IV values for small mammal communities contrasted the findings of Wilsey et al (2005) and Lyashevska and Farnsworth (2002), who concluded that richness was the least important diversity metric representing the variation in the structure of communities (grassland and marine benthic communities). Therefore we have evidence that the variation component of dimensionality, in addition to the correlation component, can present specific patterns depending on the taxonomic group being investigated. This highlights the need to understand the contingencies in the correlation and variation components of the dimensionality of different communities.

Conclusion and future directions

This work provides an update of the definition of the concept of dimensionality presented by previous works. We demonstrate how to include the variation components of dimensionality, through the use of EE and IV values, in the same framework. 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 provide a more complete understanding and generalization of the role that some factors play in the dimensionality of ecological communities. For instance, we might wonder if some dimensions of diversity are consistently more informative than others when describing diversity patterns among different taxa, or if distinct factors (historical, evolutionary and/or ecological) generate predictable higher or lower levels of diversity dimensionality across communities.

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Figure captions

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

Figure 2: General framework used to investigate the 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** is then performed (step 2) and the dimensionality measures of diversity are calculated (step 3). Details about 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 of the IV and EE metrics (bar plots A and B), calculated for simulated metacommunities according to the simulated scenarios. For each of these scenarios we presented situations in which the metrics either contributed similarly or contributed unequally to dimensionality (respectively HiC/EqV, LoC/EqV and HiC/DifV, LoC/DifV). Boxplots C and D represent the F-value distributions from linear models for scenarios HiC/DifV, HiC/EqV, LoC/DifV and LoC/EqV, evidencing the difference in contribution of one or two diversity metrics in scenarios HiC/DifV and LoC/DifV.

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

Figure 5: IV profile of marsupial and cricetid mammal communities from South America. Bar height corresponds to the observed IV for each diversity metric while the lines represent the 95% confidence intervals, generated by a bootstrap analysis.

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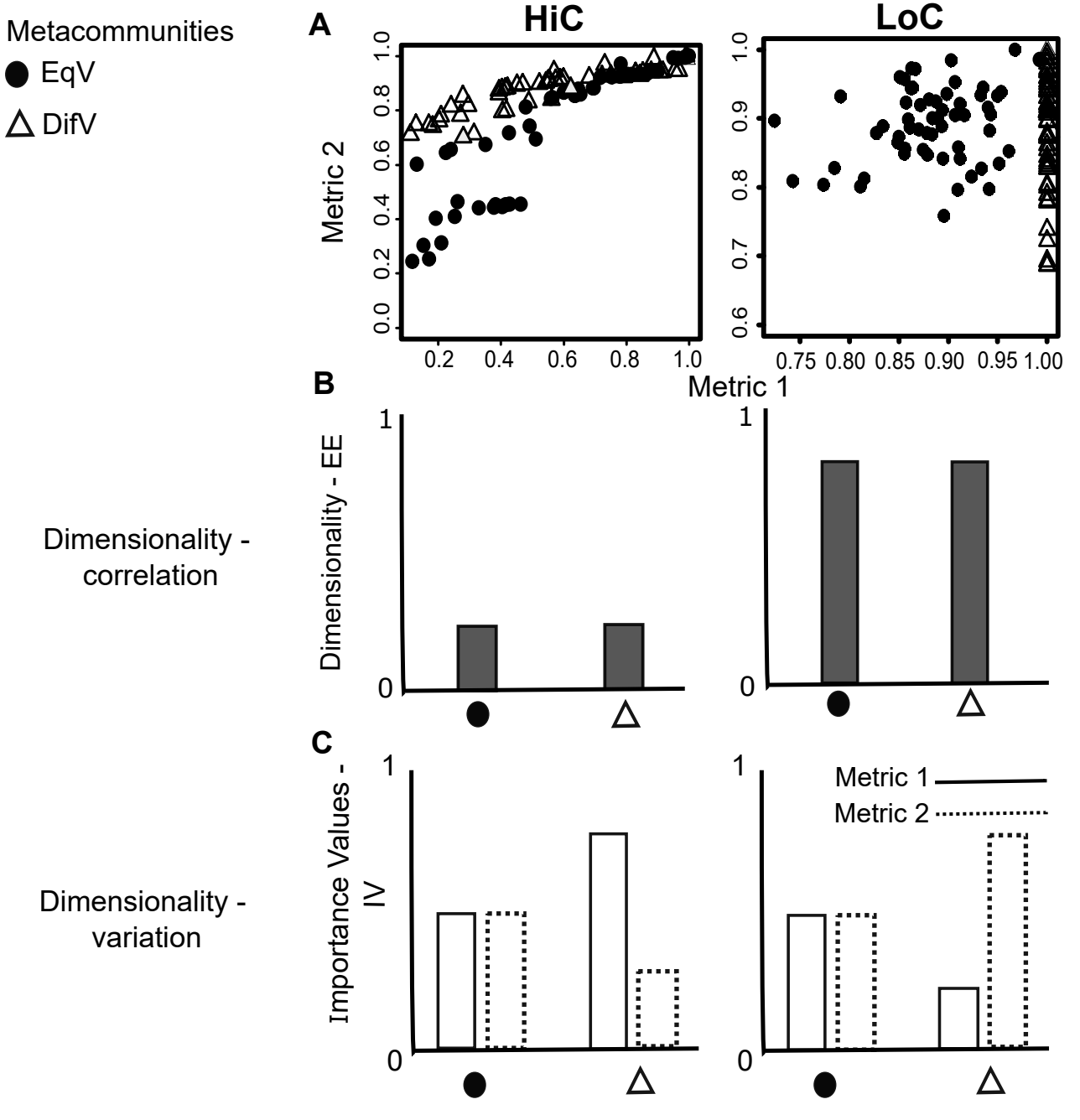
Metacommunities
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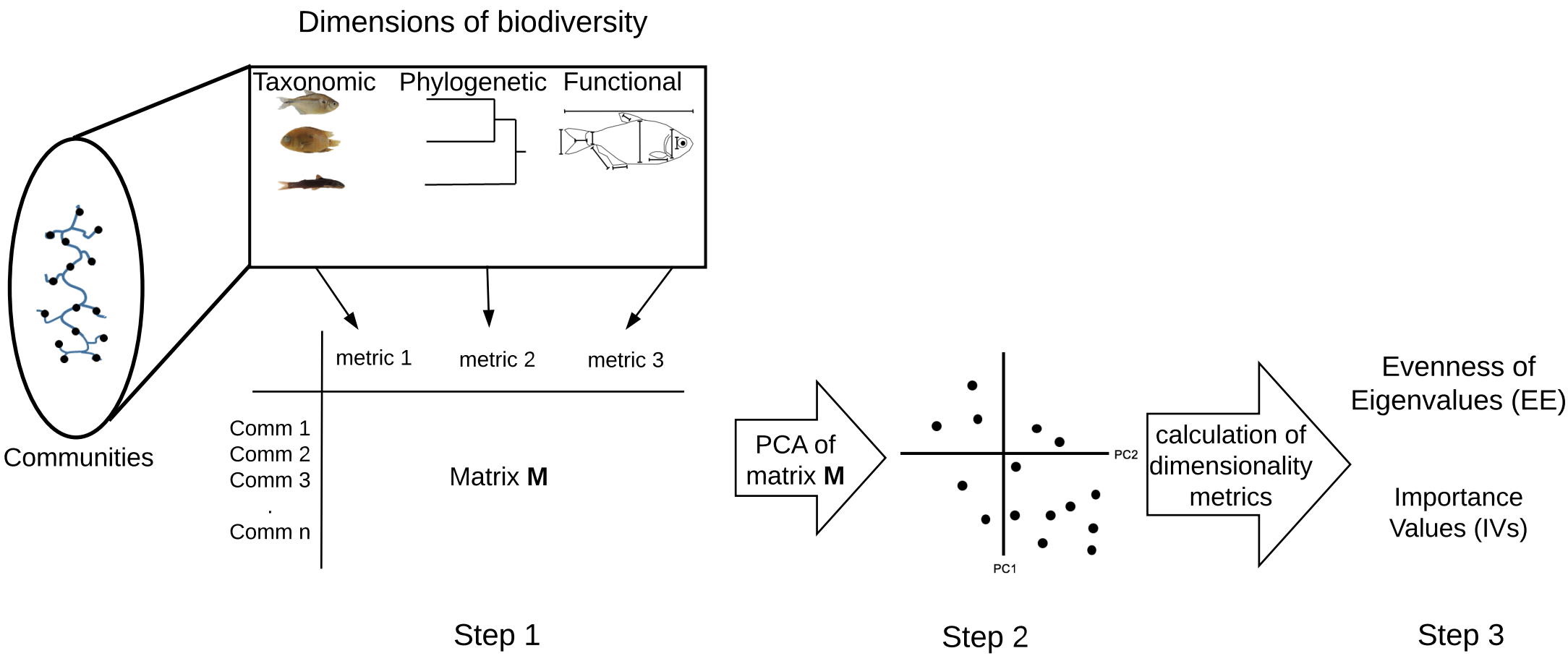
Dimensions of biodiversity
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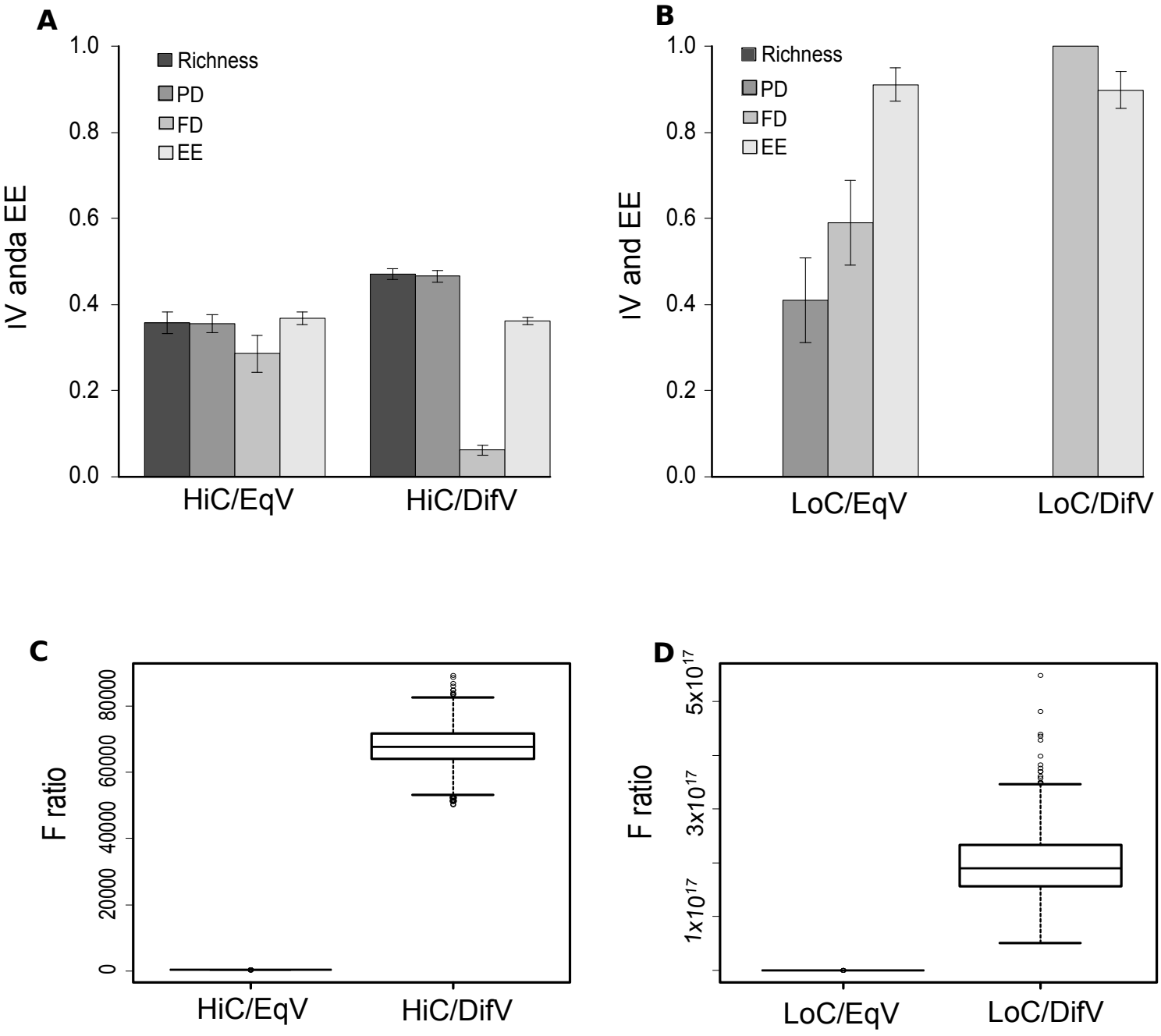
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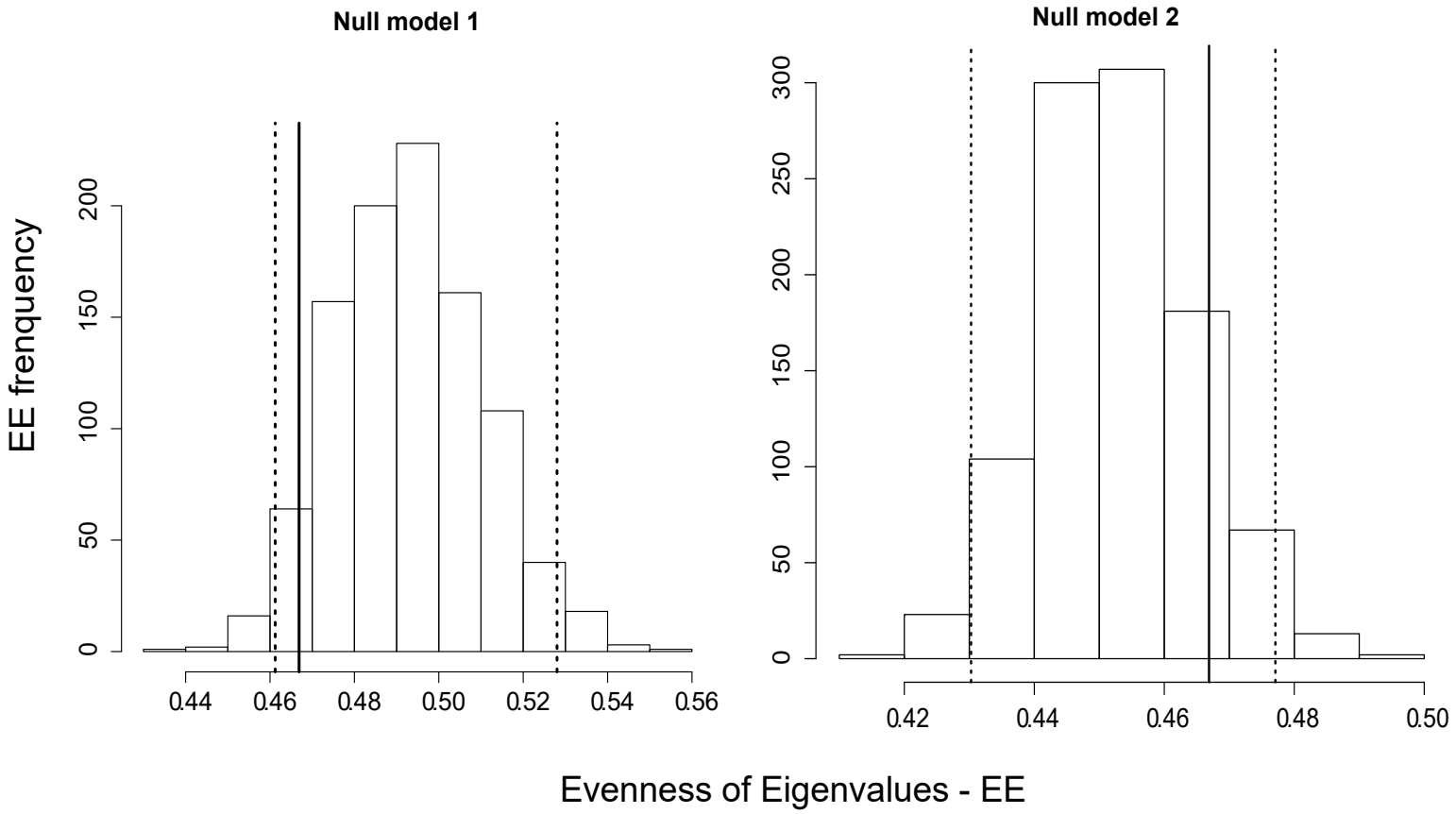
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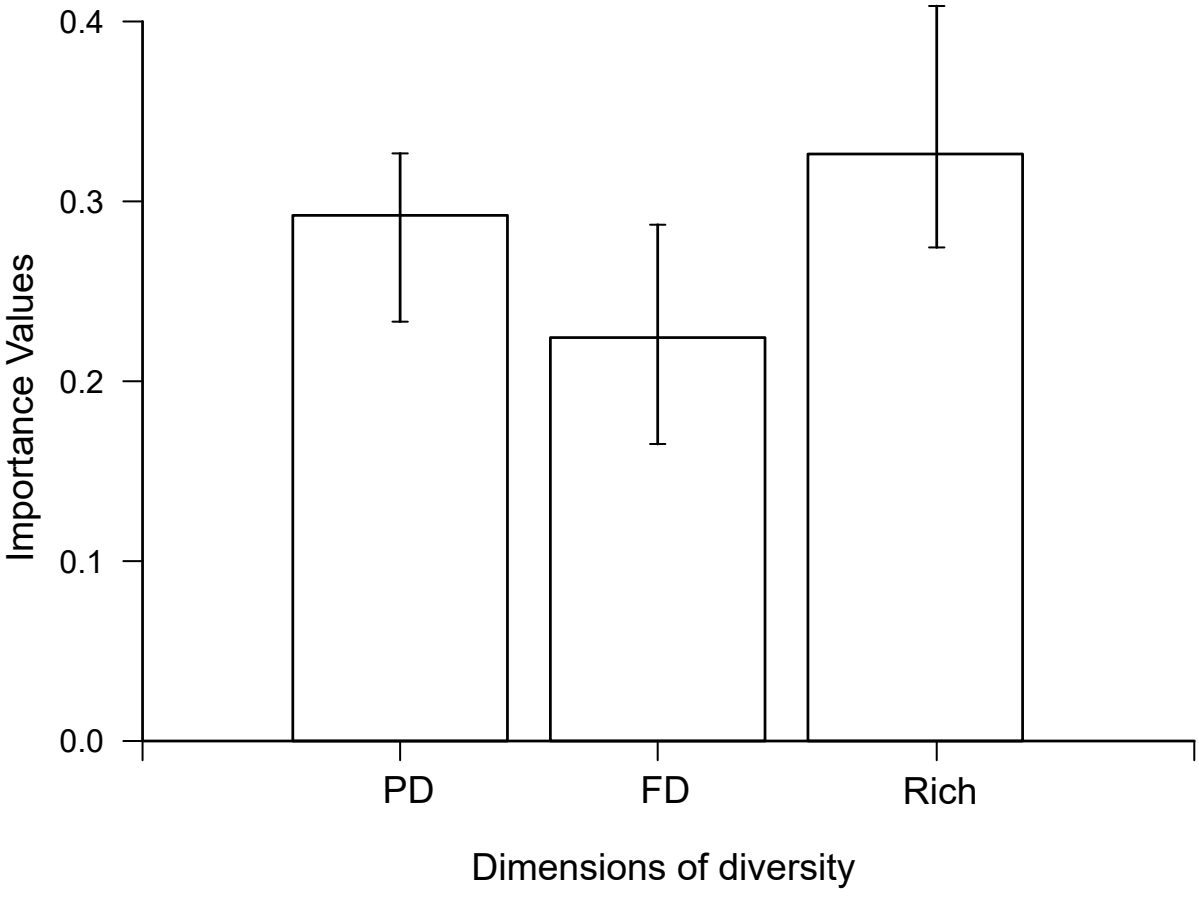
0.50
Evenness of Eigenvalues - EE


0.4
0.3
0.2
0.1
0.0
Importance Values
PD
FD
Rich
Dimensions of diversity