UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL

INSTITUTO DE BIOCIÊNCIAS

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

Tese de Doutorado

Diversidade biológica: problemas, soluções e novas propostas

Gabriel Nakamura de Souza

Porto Alegre, junho de 2019

Diversidade biológica: problemas, soluções e novas propostas

Gabriel Nakamura de Souza

Tese de Doutorado apresentada ao Programa de Pós-Graduação em Ecologia, do Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como parte dos requisitos para obtenção do título Doutor em Ciências com ênfase em Ecologia.

Orientador: Prof. Dr. Leandro Duarte

Comissão Examinadora
Prof. Dr. Tadeu de Siqueira Barros
Prof. Dr. Valério De Patta Pillar
Dr. Vanderlei Júlio Debastiani

Porto Alegre, junho de 2019

CIP - Catalogação na Publicação

Souza, Gabriel Nakamura de
Diversidade biológica: problemas, soluções e novas propostas / Gabriel Nakamura de Souza. -- 2019.
175 f.
Orientador: Leandro da Silva Duarte.

Tese (Doutorado) -- Universidade Federal do Rio Grande do Sul, Instituto de Biociências, Programa de Pós-Graduação em Ecologia, Porto Alegre, BR-RS, 2019.

1. Diversidade biológica. 2. Medidas de diversidade. 3. Métodos quantitativos. 4. Ecologia de comunidades. I. Duarte, Leandro da Silva, orient. II. Título.

Elaborada pelo Sistema de Geração Automática de Ficha Catalográfica da UFRGS com os dados fornecidos pelo(a) autor(a).

Dedico esta tese a minha batchan, Fumiko, o começo e o motivo de tudo

“All are, but parts of one stupendous whole…” Alexander Pope - Essay on Man

Agradecimentos

Expressar um sentimento complexo, formado por tantas dimensões, em um plano cartesiano encerrado nestas páginas, não é nada fácil. As ajudas que recebi foram das mais variadas formas. Sempre fico com o sentimento de que as palavras não são representações suficientes do quanto cada pessoa me ajudou ao longo destes 4 anos. Então, combinamos uma coisa, ao ler seu nome, pense em um grande abraço apertado que gostaria de te dar, e que vai muito além de um simples “obrigado” escrito numa página. Portanto, agradeço:

Ao meu orientador, Leandro Duarte, antes de tudo por ter me aceito como seu orientado, mesmo depois de uma tentativa terrível de pedido de orientação. Pela confiança e ensinamentos, que vão além das teorias e métodos científicos. Obrigado professor.

As mulheres da minha vida, Mãe, Tia Tscó, Tico, Mitsue. Sempre me ensinaram que o estudo e o conhecimento é o caminho. Especialmente a minha mãe, Marcia Nakamura, que pegaria um avião de onde estivesse para me salvar das piores dificuldades da vida.

À minha companheira Iara, que acredita na minha capacidade muito mais que eu mesmo e sempre tem o abraço que conforta quando a maré está brava, a palavra que provoca pra fazer pensar nos meus preconceitos mais arraigados e a suavidade forte que nem pedra. Obrigado por dividir a vida comigo.

Ao meu pai, Wagner, que me mostrou que nunca é tarde.

À Marina, que tanto me ajudou no início desta jornada.

Aos meus amigos “monstrinhos” Lucas e Thiago, apesar de não ter dado certo a Street Cavanhas, a amizade fica pra sempre.

À Dirleane, o ombro mais amigo desta Porto Alegre. Obrigado por atender ao meu chamado nos momentos mais difíceis, e mais alegres também.

Aos “sem floresta” (Crisla, Mari, Tais) que fizeram de alguns domingos um verdadeiro almoço em família.

À Fernanda e ao Luiz, que me receberam em Goiânia, me ofereceram um abrigo e bons momentos. Obrigado por me fazerem sentir tão bem, mesmo com dengue.

Ao José Alexandre Diniz-Filho e Lucas Jardim, que auxiliaram com discussões de várias ideias importantes para o desenvolvimento desta tese.

Aos amigos de laboratório, PPG, academia e vida. Jac, Berga, Vanderlei, Ricardo, André, Arthur, Murilo, Crisla, Tais, Mari, Bini. Obrigado pelas inúmeras conversas sobre a vida, universo e tudo mais.

Ao PPG Ecologia, por oferecer a estrutura necessária para o desenvolvimento desta tese.

A CAPES pela bolsa.

Resumo

A principal forma de se caracterizar a diversidade biológica é através da sua operacionalização por métricas de diversidade. Apesar da grande quantidade de métricas presentes na literatura, estas nos trazem apenas uma visão restrita das dimensões individuais da biodiversidade. Uma visão integrada, que relacione estas diferentes dimensões através de um mesmo arcabouço analítico ainda constitui uma lacuna na descrição da biodiversidade. Desta forma, surge a necessidade da integração destas métricas, de modo que possamos aproximar a forma como operacionalizamos (as partes) da maneira como a definimos biodiversidade (o todo). Portanto, nesta tese apresento, primeiramente, os problemas relacionados à caracterização da diversidade biológica, questionando se as métricas de diversidade estão sendo combinadas de maneira a otimizar a informação obtida da biodiversidade (Capítulo 1), de modo a considerar suas diferentes dimensões. Para tanto, realizamos uma revisão sistemática das métricas de diversidade utilizadas para caracterização de comunidades biológicas nos últimos 15 anos. Caracterizamos o padrão de utilização conjunta de métricas de diversidade e revelamos a predominância de um padrão redundante de utilização de métricas para a descrição da biodiversidade. Este problema, em conjunto com a identificação de falhas metodológicas nos métodos que visam a integração das métricas de diversidade, nos conduziu ao Capítulo 2. Nele desenvolvemos uma abordagem integrada para a avaliação da biodiversidade através de métricas de diversidade, que considera a complementariedade e a quantidade de variação que as métricas capturam da biodiversidade. Este arcabouço integrado está baseado na quantificação do conceito de dimensionalidade – a quantidade de dimensões necessárias para descrever efetivamente a biodiversidade através de métricas e quanto estas métricas são informativas. Desenvolvemos este arcabouço analítico através da união de dois métodos para quantificação da dimensionalidade

(Evenness of Eigenvalues e Importance Values) e mostramos que, quando utilizados em conjunto, a dimensionalidade pode ser descrita de maneira mais efetiva que por métodos propostos anteriormente. Por fim, apresentamos uma nova família de métricas para quantificação da diversidade beta que captura os componentes taxonômico, funcional e filogenético na variação da biodiversidade (Capítulo 3). Essas métricas foram obtidas a partir da extensão de um método existente restrito a quantificação de diversidade beta taxonômica. Além de mostrar a efetividade dessas novas métricas na representação de padrões, mostramos como podem descrever padrões na variação da diversidade gerados por processos ecológicos e evolutivos, bem como apontamos caminhos futuros sobre como podem integrar os diferentes componentes da variação da diversidade beta (Conclusões e direções futuras). De forma geral, este trabalho avança no campo da caracterização da diversidade biológica por apontar um problema recorrente nos estudos de biodiversidade e propor um arcabouço integrado baseado na quantificação da dimensionalidade da biodiversidade como solução para este e outros problemas envolvendo a integração de métricas de diversidade, possibilitando assim a mensuração de novos padrões de diversidade beta usando as novas medidas propostas.

Palavras-chave: métricas de diversidade, dimensionalidade, diversidade Beta, métodos quantitativos, cienciometria.

ABSTRACT

Diversity metrics consists in the main tool used for biodiversity quantification. Despite the great number of diversity metrics present in ecological literature, they bring only a limited picture based on individual dimensions of biodiversity. An integrated proposition that relates the different dimensions of biological diversity still lacks in the biodiversity investigation. It is time to seek for this integrated solution capable to approximate the way in which we operationalize biological diversity to the manner in which we define its concept. Therefore, in this work we present, firstly, the main problems related to biodiversity assessment, asking how diversity metrics are being used to describe biological diversity (Chapter 1). We offer a systematic review of diversity metrics used to characterize biological communities in the last 15 years. With this data we characterize the pattern of co-utilization of diversity metrics and revealed that the prevalent pattern is the joint use of redundant metrics to describe biodiversity. This problem, jointly with the identification of methodological issues in the available frameworks that propose an integration of diversity metrics, lead to the Chapter 2 of this work, in which we developed an integrated approach to relate diversity metrics considering both correlation and variation component of a concept know as dimensionality - the number of dimensions needed to effectively describe biodiversity through diversity metrics. We obtain this analytical framework by merging two different approaches used to quantify the dimensionality (Evenness of Eigenvalues and Importance Values), showing that, when used together, the dimensionality can be effectively describe, filling the gap presented in the previous methods. Finally, we presented a new family of beta diversity metrics that captures (Chapter 3) taxonomic, functional and phylogenetic dimensions of diversity. These metrics are obtained through a simple extension of an existing framework to taxonomic beta diversity. Besides to show the effectiveness of these metrics to reveal patterns of variation of functional, phylogenetic and taxonomic diversity we pointed for potential uses of these metrics to seek for an integrated framework for beta diversity (Conclusions and future directions). Our work moves forward in the field of diversity assessment by revealing a recurrent problem in biological characterization through diversity metrics, offering a solution for this problem, and more broadly, an unifying tool for dimensionality assessment. Besides we offer new possibilities for quantification of beta diversity considering its multiple dimensions.

Key-words: diversity metrics, dimensionality, Beta-diversity, quantitative methods, scientometric.

Sumário

Agradecimentos *5*

Resumo *7*

ABSTRACT *9*

Lista de Figuras *14*

Lista de Tabelas *17*

Lista de Equações *17*

Introdução Geral *19*

- **O paradoxo da diversidade biológica** 19
- **O modelo de Ricotta como solução para o paradoxo da diversidade** 21
- **Identificando problemas relacionados à operacionalização da biodiversidade** 22
- **Em busca de soluções** 23

Capítulo 1 – Identificando o problema *26*

- **Abstract** 27
- **Introduction** 28
- **Methods** 30
- **Results** 34
- **Discussion** 35
- **Conclusion and future direction towards an integrated analysis of biodiversity** 39
- **References** 40

Capítulo 2 – As soluções *44*

Abstract **45**

Introduction **46**

Material and Methods **50**

Investigating the dimensionality of biodiversity: obtaining EE and IV 50

Testing the assessment of the dimensionality of diversity using EE and IV.......... 52

Assessing the dimensionality of biodiversity in small mammal communities....... 56

Results **60**

Simulated data 60

Small mammal communities 62

Discussion **65**

Conclusion and future directions **69**

Capítulo 3 – Novas métricas ***74***

Introduction **76**

Methods **78**

Expanding the BD framework to include functional and phylogenetic dimensions of biodiversity **78**

A simulation-based evaluation of BD_{Phy} and BD_{Fun} as measures of phylogenetic and functional β-diversity 81

Empirical application: β-diversity of stream fish communities of a tropical river basin 84

Results **86**

Performance of metrics 86

Application of extended framework to stream fish communities.......................... 89

Discussion **91**

Concluding remarks and future directions **93**

References **95**

Considerações finais e conclusão ***99***

Direções futuras **100**

Dimensionalidade: indo além da descrição de padrões 101

Perspectivas práticas para a dimensionalidade 103

Expandindo as possibilidades para quantificação da diversidade Beta 104

REFERÊNCIAS BIBLIOGRÁFICAS **107**

ANEXOS E APÊNDICES ***111***

Apêndice introdução **111**

Apêndice capítulo 1 .... **112**

Appendix S2 – Bibliographic data 113

Apêndice capítulo 2 .... **144**

Appendix S1 – Simulation procedure 144

Appendix S2 – R functions for IV 147

Appendix S3 – Dimensionality function 153

Apêndice capítulo 3 .... **157**

Lista de Figuras

Capítulo 1

Figura 1. Flowchart indicating all steps necessary to obtain the pattern of diversity metrics use in community ecology literature. Step 1 consists in the assembling of matrix **M**, step 2 and 3 comprises, respectively, the calculation of the number of metrics co-occurrence and the calculation of an equivalence matrix used in step 4, that consists in apply a clustering method to obtain the groups of metrics and finally, tests the sharpness of each group by means of density calculation (step 5). The details of each step were presented in the methods section of the main text.

Figura 2. Dendrogram of diversity metrics reflecting the probability of their joint use in community ecology works realized in the last 13 years. Besides each cluster we report the values of density and the dimensions of biological diversity that the diversity metrics that assemble the clusters represent. Some items on the dendrogram represents a group of various metrics that were put together to simplify the analysis (e.g. Beta diversity indices reunite all beta diversity metrics, Similarity indexes reunite all similarity index that have only one occurrence in the sampled works). Abbreviations for diversity metrics are in Table S1 of Appendix 2 in supplementary material.

Capítulo 2

Figura 1. A) A set of communities described by two diversity metrics (Metric 1 and Metric 2) that are highly correlated. This pattern of correlation can be related to two diversity metrics that account for similar amounts of variation in the reduced biodiversity space (B, high redundancy), or be a situation in which one metric has disproportional importance for capturing variation in biodiversity space (C, low redundancy).

Figura 2. Schematic representation of simulated scenarios and expected outcomes for EE and IV. The abscissa represents the variation component of dimensionality. Metacommunities were simulated to show similar values of variation among metrics (lower left quadrant) or different values of variation among metrics (lower right quadrant), so that, respectively, similar and different IV values among diversity metrics are expected. The ordinate represents the correlation component of dimensionality. Metacommunities were simulated that had metrics with high (upper right panel) and low correlation, so that, respectively, low and high EE values are expected.

Figura 3. Bar plots showing IV and EE calculated for metacommunities simulated according different scenarios (HiC/EqV, HiC/DifV, LoC/EqV and LoC/DifV) using PD, FD and richness metrics in matrix **M**. For each of these scenarios situations were presented in which the metrics contribute similarly or unequally in biodiversity space (variation in ordinate axis) and are highly or lowly correlated (variation in abscissa axis).

Figura 4. IV profile for marsupial and cricetid mammal communities from South America calculated using matrix **M** containing eight diversity metrics. Bar height corresponds to the mean IV for each diversity metric while lines represent 95% confidence intervals, both calculated via a bootstrap procedure.

Figure 5. Values of EE and evenness of IV calculated for four different configurations of matrix **M**. Symbols represent mean values for each matrix configuration while lines represent confidence intervals. Bar graphics represent IV profiles calculated for matrix **M** with all metrics of diversity; functional metrics and richness; phylogenetic metrics and richness; and functional and phylogenetic metrics. Bars represent means while lines represent confidence intervals obtained via a bootstrap procedure applied to each matrix **M**.

Capítulo 3

Figura 1. Steps and numerical structures needed extend the BD framework for β-diversity. Solid boxes represent the original numerical structures presented in Legendre & De Cáceres (2013) to calculate BD, while dashed boxes comprise the matrices used in this paper to extend the original framework. The resemblance matrices $\mathbf{S_f}$ and $\mathbf{S_p}$ are necessary to obtain two matrices that describe communities by their trait (**X**) and phylogenetic (**P**) composition by means of fuzzy weighting. Distance matrices obtained from **P** and **X** are then used to obtain phylogenetic (PLCBD) or trait-based (XLCBD) measures of local contribution for beta diversity, respectively with the equations indicated in arrows.

Figura 2. Schematic representation of all simulation scenarios used to test the metrics proposed in this work. **W** represents a metacommunity that is generated by a simulation process, **P** and **X** represents functional and phylogenetic structure of metacommunity. When a given component of diversity presented variation in the metacommunity we assigned the number 1, on the contrary we attribute 0 in the table. The performance tested with each one of the scenarios (type I, power or both) is specified beside each scenario.

Figura 3. Map showing the distribution of LCBD, PLCBD and XLCBD values for fish communities of Ivinhema River Basin. Each point represents a combination of values of local contribution for the three dimensions. The redder the color the greater the uniqueness of a community regarding taxonomic composition; the greener the color the greater uniqueness regarding clade composition; the bluer the color the greater the uniqueness regarding functional composition. Communities that presented significant values for PLCBD and XLCBD for site and taxa shuffle are represented by points with, respectively, crossed circles and triangles.

Conclusões gerais

Figura 1. Representação esquemática de diferentes cenários envolvendo o arcabouço metodológico para avaliação da dimensionalidade. Cada letra no interior das caixas indica uma dimensão da biodiversidade (F, T e P – funcional, taxonômica e filogenética, respectivamente). Os gráficos de pontos ilustram o padrão de correlação entre as métricas, enquanto que as caixas ilustram a quantidade de variação que cada métrica de diversidade apresenta no espaço total da biodiversidade. O eixo da abscissa corresponde ao componente de correlação, enquanto a ordenada indica o componente de variação. O quadrante IV compreende o cenário de maior dimensionalidade por apresentar baixa correlação entre as métricas e cada métrica apresentar uma porção semelhante de variação do total. Por outro lado, o quadrante II apresenta a menor dimensionalidade. Ao lado de cada quadrante listamos possíveis fatores que podem gerar os padrões de dimensionalidade.

Lista de Tabelas

Capítulo 3

Tabela 1. Statistical performance — type I error (alpha 0.05) and power — of BD_{Fun} and BD_{Phy} and their components XLCBD and PLCBD, calculated with the distance-based approach.

Tabela S1. Statistical performance, type I error (alpha 0.05) and power of BD_{Fun}, BD_{Phy} and their components XLCBD and PLCBD calculated with raw data approach.

Lista de Equações

Capítulo 1

Equação 1. Equação utilizada para cálculo da matriz de equivalência.

Equação 2. Equação utilizada para obtenção da estatística de densidade de cada grupo formado na análise de agrupamento.

Capítulo 2

Equação 1. Equação para cálculo do índice de dimensionalidade EE.

Equação 2. Equação para cálculo do índice de dimensionalidade IV.

Equação 3. Equação do modelo linear que relaciona os valores de IV com as dimensões da diversidade biológica.

Capítulo 3

Equação 1. Equação utilizada para obtenção da soma dos quadrados totais presentes em uma matriz de distâncias.

Equação 2. Equação utilizada para obtenção do valor de BD a partir da soma dos quadrados totais.

Equação 3. Equação utilizada para obtenção da matrix **G**, utilizada para cálculo dos valores de soma dos quadrados a partir de uma matriz de distância.

Equação 4. Equação utilizada para obtenção da contribuição local de cada comunidade a partir de uma matriz de distância entre comunidades.

Introdução Geral

Nesta primeira seção exponho os principais fundamentos teóricos que conduziram as questões levantadas nesta tese e as respectivas soluções que desenvolvemos. Visto que a investigação científica parte de uma ideia ou conceito estabelecido (paradigma), questionando sua validade a partir da identificação de lacunas e propondo soluções que promovem o avanço do campo de conhecimento (Kuhn, 1962), iniciamos identificando o problema relacionado à mensuração da diversidade biológica por meio do uso de métricas de diversidade (Capítulo 1). A partir deste problema, em conjunto com outras inconsistências identificadas nos estudos que envolvem a quantificação do conceito denominado dimensionalidade da biodiversidade, que por sua vez é central para integração das diferentes métricas da diversidade, derivamos soluções metodológicas para sua resolução (Capítulo 2) bem como a proposição de novas métricas de diversidade que consideram a multidimensionalidade presente na biodiversidade. Finalizo apontando caminhos possíveis que podem ser trilhados a partir dos resultados apresentados neste estudo (Conclusão e direções futuras). Apesar de 3 capítulos distintos, apresentados no formato de artigos, todos têm como ponto de intersecção a operacionalização do conceito de biodiversidade através de métricas de diversidade. Portanto, inicio a contextualização teórica destacando o problema central que permeia todos os capítulos, denominado paradoxo da diversidade biológica.

O paradoxo da diversidade biológica

Em ecologia, a operacionalização do conceito de diversidade biológica usa métricas de diversidade. A utilização dessas métricas para quantificar aspectos referentes à biodiversidade corresponde a uma simplificação necessária e indispensável no processo de descrição de padrões da biodiversidade (Magurran and McGill, 2011), bem como no desenvolvimento de teorias ecológicas (e.g. Colwell, 2000). A simples contagem do número de espécies presentes em um determinado local, conhecido como riqueza de espécies, é o descritor mais utilizado para expressar a diversidade biológica, sendo que, historicamente muitas questões de grande importância relativas à distribuição da diversidade foram elucidadas (MacArthur e Wilson, 1967; Rahbek, 2005) a partir dessa representação da biodiversidade. A riqueza como descritor da biodiversidade tem tamanha aceitação que por muitas vezes encontramos ela sendo utilizada para expressar o próprio conceito de biodiversidade (Magurran, 2010). Porém, notavelmente a partir dos anos 90, outras formas de se quantificar a biodiversidade surgiram motivadas pelo reconhecimento de que a contagem do número de espécies se trata de um descritor incompleto da biodiversidade. Métricas que consideram outras características da diversidade biológica, como, por exemplo, o parentesco evolutivo entre as espécies ou a variação de características fenotípicas (Faith, 1992; Petchey and Gaston, 2006) surgem na literatura, ampliando assim a possibilidade de descrição da biodiversidade e evidenciando cada vez mais a necessidade de caracterização de suas múltiplas dimensões.

O surgimento de novas métricas para quantificação da biodiversidade é contínuo. Ao passo que sua representação através de diferentes métricas possibilitou um avanço em relação a capacidade de descrição de padrões de biodiversidade (Cianciaruso et al., 2009; Colzani et al., 2013; Faith, 1992; Webb et al., 2002), alguns autores defendem que a grande quantidade de métricas mais confunde que revela os aspectos importantes referentes a biodiversidade (Rousseau et al., 1999). O fundamento subjacente a esta afirmação baseia-se no fato de que, apesar de conhecermos cada vez mais formas de representar as diferentes partes da biodiversidade, este conhecimento acumulado não contribui na mesma proporção para uma compreensão do todo do qual fazem parte. Este fenômeno é aqui denominado como paradoxo da diversidade.

Uma analogia que ilustra de maneira clara o paradoxo da diversidade é o conto hindu dos homens e o elefante (Magurran and McGill, 2011). Quatro homens são vendados e colocados com um elefante à sua frente. Sem saber de que animal se trata lhes é pedido que descreva o que estão tocando. Para tanto, cada um pode tocar apenas uma parte do animal, resultando em respostas enviesadas pela parte do elefante em que cada homem tocou, de modo que nenhum dos homens entre em consenso sobre o animal a sua frente. No contexto dos estudos de biodiversidade os cientistas podem ser comparados aos homens vendados, que tocam apenas uma parte (métricas de diversidade) do elefante (biodiversidade), sem entrar em um consenso sobre o todo que estamos tentando descrever (Magurran and McGill, 2011).

A noção de que a biodiversidade é um conceito que apresenta múltiplas dimensões e, portanto devemos representá-lo através de diferentes métricas é consenso, porém, a questão que emerge dado o paradoxo da diversidade é: qual a melhor forma de combinar as diversas representações de diversidade biológica, de modo que possamos ter uma melhor descrição do todo (descobrir o elefante ao invés de suas partes individuais)? Uma solução utópica envolveria a simplificação da biodiversidade em uma única métrica que abarcasse todas suas fontes de variação. Seria a panaceia dos problemas envolvendo a biodiversidade e sua representação. Porém, entre o ideal utópico e a aproximação imperfeita, porém factível, ficamos com a segunda. Esta segunda opção envolve a integração das múltiplas fontes de variação da diversidade biológica representadas pelas métricas de diversidade. Neste contexto a proposta oferecida por Ricotta (2005), traz consigo o fundamento teórico e operacional necessário para o desenvolvimento metodológico desta abordagem integrada, e dado sua importância trataremos dela com mais detalhes na seção seguinte.

O modelo de Ricotta como solução para o paradoxo da diversidade

A par do problema gerado pelo paradoxo da diversidade, Ricotta (2005), em seu trabalho intitulado "Through the jungle of biological diversity" (Através da natureza da diversidade biológica), oferece uma definição operacional da biodiversidade para integrar as diferentes dimensões em um mesmo arcabouço analítico. Ricotta argumenta que, dada a grande discordância sobre sua verdadeira natureza, a biodiversidade pode ser definida como "um conjunto de medidas estatísticas utilizadas para quantificar diferentes aspectos da estrutura de comunidades". Esta definição serve como um modelo operacional que reúne em uma única estrutura numérica as diferentes formas de quantificação da biodiversidade, ou seja, se pudéssemos reunir todas as métricas de diversidade existentes, esta estrutura numérica seria a representação da própria biodiversidade. Denominamos esta estrutura como matriz **M**.

A matriz **M** trata-se da estrutura numérica central para o desenvolvimento de métodos integrados para análise da biodiversidade. Veremos nas seções posteriores, bem como nos artigos que ela representa a fonte de informação numérica da qual utilizamos para o desenvolvimento de métodos que visam relacionar as diferentes métricas de diversidade. Desta maneira, esta tese apresenta como proposta central métodos que extraem informações da biodiversidade que podem ser obtidas a partir do modelo operacional representado pela matriz **M**. Porém, como o título desta tese sugere, primeiramente revelamos os problemas associados à forma como a biodiversidade vem sendo caracterizada, ou melhor, como a matriz **M** vem sendo construída para representar a biodiversidade nos estudos de ecologia de comunidades.

Identificando problemas relacionados à operacionalização da biodiversidade

Utilizando o modelo operacional oferecido por Ricotta, poderíamos nos perguntar qual seria a combinação adequada de métricas que otimiza a informação presente na matriz **M**? É consenso na literatura que a integração de diferentes métricas de diversidade deve seguir um critério de complementariedade, ou seja, as métricas devem capturar porções complementares da informação presente na diversidade biológica (Lamb et al., 2009; Lyashevska e Farnsworth, 2012; Saito et al., 2015). Porém, o critério da complementariedade é realmente levado em consideração no momento que diferentes métricas são utilizadas em conjunto? Em outras palavras, os estudos que envolvem a descrição da biodiversidade o fazem com o intuito de maximizar a informação presente na matriz **M**? Caso não, podemos afirmar que os estudos que visam caracterizar a diversidade biológica estão subestimando a informação presente na diversidade biológica. Este é o questionamento que nos conduz ao Capítulo 1 desta tese. Apesar da importância da utilização do critério de complementariedade na decisão das métricas a serem utilizadas para caracterização da biodiversidade (Magurran, 2004), até o momento não há uma avaliação empírica para entender se este critério vem sendo aplicado. Portanto, apresentamos no Capítulo 1 a primeira avaliação empírica sobre o uso de métricas de diversidade para caracterização da biodiversidade, onde focamos, especificamente, na avaliação da maneira com que as métricas estão sendo combinadas nos estudos que visam a caracterização da diversidade biológica em nível de comunidades. Este estudo foi realizado a partir de uma revisão sistemática de trabalhos que caracterizaram a diversidade biológica em nível de comunidades usando métricas de diversidade. Com essa informação nos perguntamos: como as métricas são combinadas para a descrição da diversidade biológica? A resposta para esta questão nos revela um problema relacionado ao uso redundante de métricas de diversidade, e nos conduz ao Capítulo 2 desta tese.

Em busca de soluções

Os resultados encontrados no Capítulo 1 referentes ao uso redundante de métricas de diversidade, juntamente com a identificação de vieses existentes nas propostas para integração da diversidade biológica para resolução do paradoxo da diversidade, conduziu ao segundo capítulo, que consiste nas soluções propostas para tais problemas. Estas soluções foram obtidas a partir do desenvolvimento de um novo arcabouço analítico integrado que resolve vieses presentes em métodos anteriores (Stevens e Tello, 2014) referentes à mensuração da dimensionalidade da diversidade biológica.

A dimensionalidade corresponde a uma característica inerente da biodiversidade e pode ser definida como a quantidade mínima de informação necessária para descrever de maneira suficiente a biodiversidade. A dimensionalidade requer necessariamente uma visão integrada de biodiversidade, pois assume que as métricas de diversidade correspondem apenas a partes de informação de um todo. Consequentemente, a operacionalização da dimensionalidade passa pela integração das diferentes métricas de diversidade, que por sua vez pode ser obtida a partir da extração de informações presentes na matriz **M**. Métodos anteriores que propuseram a integração da biodiversidade visaram justamente a operacionalização da dimensionalidade (Wilsey et al., 2002, Stevens e Tello, 2014; Stevens e Gavilanez, 2015), porém, mostraremos no Capítulo 2 como o não reconhecimento de componentes importantes presentes na dimensionalidade pode conduzir a conclusões equivocadas sobre esta característica da biodiversidade (Tabela S1 mostra trabalhos que visaram a integração de métricas de diversidade a partir da matriz **M**). A partir da identificação dos componentes adequados para operacionalização da dimensionalidade, propusemos um novo arcabouço analítico que soluciona os problemas apresentados nos métodos anteriores para quantificação da dimensionalidade.

A busca por soluções que envolvem a descrição da biodiversidade em suas diferentes dimensões se estende ao Capítulo 3, onde desenvolvemos novas propostas para quantificação da diversidade Beta. Desta maneira, com o intuito de ampliar a gama de possibilidades de descrição da biodiversidade de modo a considerar a sua natureza multidimensional, no Capítulo 3 desta tese derivamos uma nova família de métricas de diversidade capazes de capturar efetivamente a variação presente em diferentes níveis de organização biológica (espécies, comunidades e metacomunidades) bem como dimensões da biodiversidade (taxonômica, funcional e filogenética). Para tanto utilizamos a junção de dois arcabouços estatísticos, o primeiro proposto por Legendre e De Cáceres (2013) para quantificação da diversidade Beta, com o método de ponderação por grupos difusos (Pillar et al. 2009). Demonstramos como a utilização destes dois métodos possibilita a obtenção de novas medidas de diversidade beta que carregam consigo as vantagens presentes no método proposto por Legendre e De Cáceres, considerando a multidimensionalidade da variação biológica.

Concluímos esta tese mostrando as novas possibilidades que os resultados alcançados abrem no caminho da integração dos diferentes componentes da diversidade, de modo a conciliar as diferentes métricas de diversidade com a visão holística necessária para uma melhor compreensão do conceito de diversidade biológica.

Capítulo 1 – Identificando o problema

Title: Patterns of diversity metric use in ecological literature: redundancy or complementarity in biodiversity assessment?

Gabriel Nakamura[1,2] and Leandro da Silva Duarte[2]

[1] – Email: gabriel.nakamura.souza@gmail.com; Orcid ID 0000-0002-5144-5312

[2] – Departamento de Ecologia, Universidade Federal do Rio Grande do Sul, CP 15007, Porto Alegre, RS 91501-970, Brazil.

Capítulo formatado na forma de artigo, seguindo as normas da revista Ecological Indicators.

Abstract

Diversity metrics comprises the main tool that community ecologists use to describe patterns related to biodiversity, test the process and mechanisms generating these patterns and support conservation actions. Biodiversity is inherently multidimensional, requiring different diversity metrics to encompass the variation present in its different dimensions. Many metrics are currently available, and it is desirable that the choice be guided by an objective criterion. The complementarity approach, which consists in the selection of metrics capturing different sources of variation in biodiversity, can guide this choice. However, despite effective, we do not know if the complementarity is really being used as a guide in the choice of diversity metrics. In this work we investigated to what extent diversity metrics have been used in a complementary or redundant manner. We performed a systematical review in community ecology literature published in the last 15 years to access the patterns of use of diversity metrics, specifically, to assess how the diversity metrics are combined to operationalize biodiversity concept. Based on the number of times that diversity metrics have to be used together in the same work, we performed a classification that represented groups of diversity metrics frequently used together. The classification method used in this work (called co-metric analysis) revealed a predominance of redundant use of diversity metrics in community ecology assessment. As a take-home message we highlight the need to a twist in the way that diversity metrics are combined to represent the variation in biological diversity, being guided by the complementary approach and by combining metrics that represent different dimensions of biological variation.

Key-words: biological measurement, biological diversity, co-word analysis, scientometric.

Introduction

Diversity metrics are the main tool used to characterize biodiversity at community level (Magurran, 2010), revealing ecological patterns (e.g. Safi et al. 2011) and supporting conservation decisions (e.g. Faith, 1992; Hidasi-Neto et al., 2013; Mazel et al., 2017). Since biological diversity is a multidimensional concept and each diversity metric provides a limited picture of one or few biodiversity dimensions, an effective characterization of biological diversity generally involves the use of multiples diversity metrics together in order to join the pieces in a satisfactory representation of the biodiversity (Wilson, 1997).

Biological diversity assessment is defined by Magurran (2011) as being a two-step process: the choice of the diversity metric to be used and the analysis of the distribution of this metric in space and/or time. Here we will focus on the first step, which is an important decision since the diversity metrics may express distinct information of biological diversity and, consequently, the insights gained in the characterization of ecological communities can be different depending on the metrics used. Ecological literature offers a myriad of diversity metrics that allows for the characterization of a number axes of variation in community composition (e.g. Faith 1990, Petchey and Gaston 2002, Botta-Dukat 2005, Laliberte et al. 2010, Jost and Chao, 2004; Presley et al., 2014) making the choice of diversity metrics not a trivial task. An objective criterion in the choose of diversity metrics is the complementarity approach, in which the rationale is based on the selection of diversity metrics capturing different portion of variation present at community level, in other words, the complementarity criterion implies in selecting diversity metrics that are not correlated.

Complementarity is a central concept in the design of conservation strategies, since it optimizes the amount of information to be protected of a taxonomic group in a given region (Daru et al. 2015; DeVictor et al. 2010; Saito et al. 2015). Since the level of correlation varies among diversity metrics, indicating that some of them describes redundant information and others are complementary (Lyashevska, 2010; Gallardo et al., 2011; Lamb et al., 2009), the use of complementary metrics are of pivotal interest in order to maximize the amount of information that can be acquired from biological communities For example, Saito et al. (2015) showed that integrating functional, phylogenetic and taxonomic metrics of diversity provides complementary information on biodiversity in monitoring programs. Daru et al. (2015) and Devictor et al. (2010) showed that, respectively, for trees and birds, functional, phylogenetic and taxonomic dimensions represents spatial mismatches, being an empirical evidence that a complementary approach must be adopted in order to capture the variation present in biodiversity at community level. Beyond the conservation perspective, Lyashevska and Farnsworth (2012) showed that biodiversity is best described when using a combination of metrics representing three dimensions of variation, being functional, taxonomic and phylogenetic. Consequently, the complementary approach has both practical and theoretical reasons to be adopt in the choice of diversity metrics.

Therefore, its clear that the complementary approach can be adopted as a guide in the first step of biological assessment, nevertheless, until now we have no empirical evidence of how frequent the complementary approach is adopted in ecological studies in community ecology after in view of the numerous diversity metrics. An empirical evaluation of how the choose of diversity metrics is being conducted is required, since it can evidence effectiveness biological diversity. Therefore, in this work we performed an investigation of the patterns of use of diversity metrics in ecological literature, specifically we evaluated if diversity metrics are being used in a redundant or complementary way to characterize biological diversity. If the authors are guided by a complementary principle in the choice of diversity metrics, we hypothesize that we must find a pattern of use of diversity metrics in which metrics that represent different dimensions of diversity will present higher chances of being used together than metrics that are redundant regarding the dimension that they express.

Methods

We performed a systematic search on the data-base of Web of Science. In this search we seek for studies of community ecology that measured biodiversity through diversity metrics. Since our objective was investigate the pattern of use of diversity metrics, we choose terms in order to make our search was the most inclusive as possible, covering the many different ways that biological diversity can be measured in community ecology studies. We use the search terms "community ecology" and "bio*diversity measurement", the asterisks in last search term indicating that the words were allowed for variations in its form (biological diversity measurement, biodiversity measurement and diversity measurement). This search was restricted to the years 2002 to 2015, since a great number of diversity metrics and its use becomes popular in its usage from 1990 (Magurran, 2005).

For each article that returned in the search we check to decide if the work would be included or not in our sample for further statistical analysis. First, we accessed the abstract to check if the article quantify a given dimension of diversity by means of any diversity metric, if so we checked if the article was empirical, discarding works that did not presented any empirical assessment of biological diversity (e.g. entirely theoretical, methodological, review or meta-analytical articles, as well as works that used only methods that accessed species composition). These filtering was applied to guarantee that sample included only empirical uses of diversity metrics independently of the studied taxonomic group or region.

The articles included in the sample, we assembled an incidence metric matrix (matrix **I**) of diversity metrics and their incidence in each article. Matrix **I** comprised the core numerical structure to our investigation of patterns of usage of diversity metrics in literature (step 1 in Figure 1).

Matrix **I**, was used as the numerical structure in which we applied a modified version of the co-word analysis used by Neff and Corley (2009). Neff and Corley´s analytical framework access the pattern of co-occurrence of key-words to reveal the main themes being investigated in a givel field of knowledge. Instead of using a matrix of key-words, as commonly used in scientometric analysis (Coulter, Monarch, & Konda, 2002), we used the framework of co-word analysis (Callon, Courtial, & Laville, 1991) by substituting the matrix of key-words by matrix **I**. Due to this difference, and to avoid the confusion among the original application of the method from that used in this work, we will refer to our analytical framework hereafter as co-metric analysis.

We grouped some metrics presented in matrix **I**, since they presented very similar information (e.g. richness estimators and rarefaction methods) or metrics that reflect composition (e.g. Beta diversity metrics) to reduce the number of metrics that had only one occurrence in the articles. For each metric pair we quantified the number of articles in which the two metrics co-occured (step 2 in Figure 1), resulting in a symmetrical matrix metrics referred here as matrix **C**. With matrix **C** we calculated the strength of association among diversity metrics based in its co-occurrence in the articles (Callon et al. 1991, Neff and Corley, 2009) obtaining the equivalence matrix (matrix **E**, obtained through step 3 in Figure 1).The equivalence values in matrix **E** were obtained using Equation 2, where E_{ij} represents the equivalence value among diversity metrics i and j, that was calculated by dividing the squared frequency of co-occurrence between metrics i and j by the total frequency of diversity metric *i* multiplied by total frequency of diversity metric *j* in all articles.

$$E_{ij} = {}^{c_{ij}}/_{c_i * c_j} \qquad \text{Equation 1}$$

The next step was a classification of metrics according to their co-occurrence in the articles. Therefore, we performed a cluster analysis using matrix **E** (step 4 in Figure 1). For cluster analysis we first used the square of Euclidean distance over matrix **E** and then apply Ward´s clustering algorithm (following the procedures in Neff and Corley 2009). We defined the number of groups in our diversity metric dendrogram by setting the level of cut off in a value that preserve groups with the mean number of diversity metrics similar to that used by the articles presented in our sample, which was of 2.12 mean metrics per study (standard deviation of ±1.10). We choose this procedure in order to prevent the assemble of groups that do not match realistic scenarios of use of diversity metrics (e.g. groups containing a great number of metrics), and then allows to interpret the co-occurrence of metrics in a reliable way.

Finally, to validate if the groups that we define in our diversity metric dendrogram and support further interpretations, we applied for each cluster the density index calculating according Equation 5 (He, 1999) (step 5 in Figure 1), where D_{cluster} is the density index for a given cluster in the dendrogram, E_{ij} is the equivalence value for metrics *i* and *j* and *n* the number of metrics present in a cluster. This index shows that a group with high value of density in relation to others presented a great evidence that the usage of one metric is generally accompanied by others that make up the same cluster.

$$D_{cluster} = {}^{\sum_{E1,1}^{Eij} E_{ij}} \Big/ {}_{\frac{n!}{[2!(n-2)!]}} \qquad \text{Equation 2}$$

We accessed if the use of diversity metrics has been made in a complementary or redundant manner by inspecting the dendrogram of diversity metrics association. By redundant or complementary we mean metrics that, respectively present, respectively, high and low correlation. We adopt as a theoretical reference to judge if a given diversity metric are redundant or not with others, the correlations and general conclusions presented in Lyashevska and Farnsworth´s (2012) work. As was already said before, Lyashevska and Farnsworth´s work presented general premises that allows to adopt their results as the baseline for our interpretation, indicating that a mixture of functional, phylogenetic and taxonomic metrics is the best set to represent biodiversity.

In Appendix 1 of supplementary material we provided the full list of articles in which we extract the data used to perform the co-metric analysis. Figure 1 represents a flowchart illustrating all steps used to obtain the pattern of metric co-occurrence. For a complete description of all metrics presented in matrix **I** used to perform cluster analysis see Supplementary material, Appendix 2, Table S1).

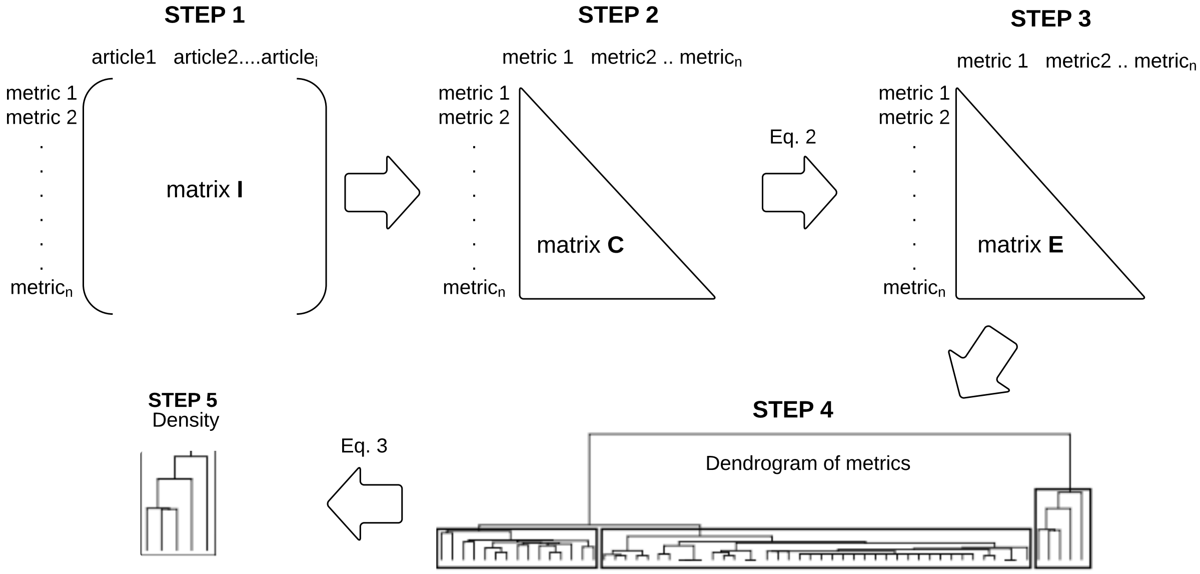


Figure 1: Flowchart indicating all steps necessary to obtain the pattern of diversity metrics co-occurence in community ecology literature. Step 1 consists in the assembling of

matrix **M**, step 2 and 3 comprises, respectively, the calculation of the number of metrics co-occurrence and the calculation of the equivalence matrix used in step 4, which consists in apply the clustering method to obtain the groups of metrics and finally, tests the sharpness of each group by means of density calculation (step 5). The details of each step were presented in the methods section of the main text.

Results

Our search returned 1451 articles, resulting in 344 articles and 56 diversity metrics after the filtering procedure. The most frequent metric in our sample was richness, occuring in 204 articles. Only eight metrics presented more than 10 occurrences. We illustrate the patterns of use of diversity metrics based in its co-occurrence in community ecology articles in the dendrogram of Figure 4. A total of 11 groups of diversity metrics were identified, being three of them assembled by diversity metrics that represent only taxonomic dimension (Tax), three groups compounded exclusively by functional diversity metrics (Funct), two assembled by metrics that represent phylogenetic dimension (Phylo) and three mixed groups, two of them formed by a combination of phylogenetic and taxonomic diversity metrics (Phylo/Tax) and one of functional and phylogenetic diversity metrics (Funct/Phylo).

Regarding density, the clusters with the highest value were the encompassing metrics that access only taxonomic, phylogenetic and functional aspects of biodiversity, all of them with value of 1. The other groups had density values ranging from 0.55 to 0.07 and a mean value of 0.41 (standard deviation of ±0.32). A group formed by a combination of various diversity metrics were formed (Figure 2, upper part of the dendrogram), but it encompasses mainly diversity metrics that present only one or few occurrences (e.g. LIDAR index, phylogenetic and functional diversity metrics less used in the assessment of these two dimensions of diversity) as well as some composition metrics, that is not the focus of the present work (Beta diversity metrics and composition metrics as CWM).

Discussion

It is worth to highlight two aspects regarding the patterns of use of diversity metrics in biodiversity assessment: the redundant use of some diversity metrics and the small number of cases in which metrics of different dimensions of biodiversity are combined. As a general pattern, we observed that the complementary approach was not the major criterion guiding the choice of diversity metrics. Our findings imply that the first step in the biodiversity assessment, that consist in the choice of which metrics to use, can be compromised, with a general effect of underestimating biological variation presented at community level or an incomplete understanding of the possible mechanisms generating the variability in biological diversity (e.g. Cisneros et al., 2014).As a consequence of the redundant use of the diversity metrics, the second step in the process of biological assessment may also be affected, since the spatialization of biological information could not be revealing the possible variation in biodiversity or be biased through one or few dimension of biological diversity (Devictor et al., 2010; Meynard et al., 2011).

The problem involving the redundant assessment of biological diversity is notable for several metrics presented in our co-metric analysis. Particularly, we can stress the the groups formed by diversity metrics: Functional Dispersion, Functional Evenness, Functional Divergence and Functional Richness, that represents the functional dimension of biological diversity. Despite Mouchet et al. (2010) showed that, combining Functional Evenness, Functional Richness and Functional Divergence can capture complementary aspects regarding functional dimension, all of these index represent only functional dimension of biodiversity variation (Lyashevska and Farnsworth, 2012). Relative to the phylogenetic dimension, the redundant use of metrics was also notable in the co-metric analysis, in which we highlight the frequent use of phylogenetic diversity metrics NTI, NRI, MPD and MNPD, that generally present high values of correlation (Lyashevska and Farnsworth, 2002). Both NTI and NRI are indexes used by researchers to detect patterns of clustering or dispersion of evolutionary lineages in a community, and the sensitivity of their responses are dependent on the conservatism of traits of species pool being investigated and the dominant ecological force (Webb, Ackerly, McPeek, & Donoghue, 2002). So, in this case we also claim caution in the utilization of these metrics together, since they all capture the same dimension of variation of biological diversity. Shannon, Simpson, abundance and richness metrics are also cases that are frequently used togheter to assess taxonomic dimension of biodiversity and generally present redundant information. For example, Gallardo et al., (2011) showed that richness and Shannon captures redundant information for biodiversity presented in invertebrate assemblage. Similar conclusions were reached by Lyashevska and Farnsworth (2012), for marine benthic communities.

One fact that can explain the redundancy in the use of functional and phylogenetic diversity metrics is the facility in computation offered by some statistical packages, for example, for functional diversity metrics the statistical package “FD” (Laliberte et al., 2010) and “picante” (Kembel et al. 2010), both freely available in R software. Although the great number of functional and phylogenetic metrics available in literature, just a few were gathered in a unique statistical package, as in the case of the metrics cited above. This fact reminds us that, despite the ease in computation of these metrics, their joint used do not contribute to optimize the information presented in biological diversity, and, consequently our criteria to the choice of diversity metrics must be guided by other criteria than the facility of computation, for example by choosing metrics that, when used together optimize the amount of information obtained from communities.

Despite less frequent than redundant cases, it is worth noting that in the co-metric analysis some groups were formed with diversity metrics that represents different dimensions of biodiversity (based on Lyashevska and Farnsworth, 2010), being only three, in a total of 11 groups, that mixed two dimensions of biodiversity. This fact highlights that the number of studies that account together for the three main axes of variation necessary to effectively represent the multidimensional concept of biodiversity, highlighted by Lyashevska and Farnsworth (2012), are still the minority in empirical studies of community ecology. Consequently, much of what has been done so far in biological assessment underestimates the information of biological diversity.

Since the importance occupied by the "complementarity orientation" highlighted by conservation studies (Devictor et al., 2010; Saito et al., 2015; Mazel, Mooers, Riva, & Pennell, 2017b), the present work highlight the need to a change in the first step of biological assessment by guiding the choose of diversity metric by complementary. As demonstrated recently by Pavoine and Bonsall (2011), a combination of measures of phylogenetic, functional and genetic diversity have the potential to reveal ecological and historical factors that influence the structure of the communities and have important applicability for conservation actions. So, the consequences of proceeding with the widespread practice in use of metrics that account for only one aspect of biodiversity, go beyond the underestimation of total information presented in biological diversity manifested at community level, also limiting the advances in understanding the factors that drive the structure of communities (Cisneros et al., 2014).

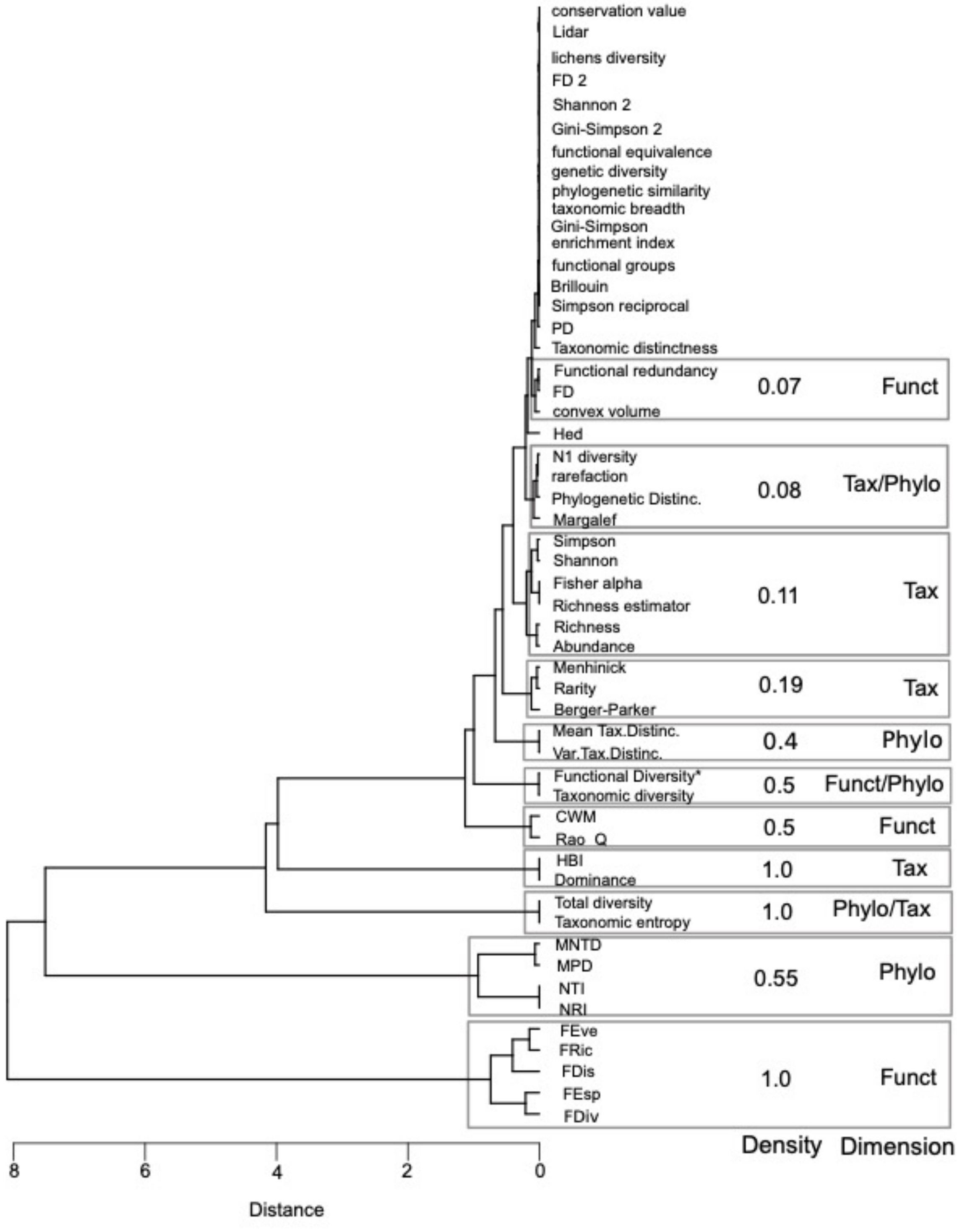


Figure 2: Dendrogram of diversity metrics reflecting the probability of their joint use in community ecology works realized in the last 13 years. Besides each cluster we report the values of density and the dimensions of biological diversity that the diversity metrics that assemble the clusters represent. Some items on the dendrogram represents a group of various metrics that were put together to simplify the analysis (e.g. Beta diversity indices reunite all beta diversity metrics, Similarity indexes reunite all similarity index that have only one occurrence in the sampled works). Abbreviations for diversity metrics are in Table S1 of Appendix 2 in supplementary material. Funct- Functional dimensions; Phylo- Phylogenetic dimension; Tax- Taxonomic dimension

Conclusion and future direction towards an integrated analysis of biodiversity

The recognition that redundancy is pervasive in community ecology studies point to the need of a change in the way at which diversity metrics are being used in ecological literature. As a take home message, we highlight the need to a “complementary orientation” when choosing diversity metrics that will be using in the characterization of biological diversity. We suggest that a starting point to the improvement on the biological accessment is to follow the conclusion reached in the work by Lyashevska and Farnsworth (2012), by combining in biodiversity assessment diversity metrics that encompass three dimensions of biological diversity: functional, phylogenetic and taxonomic.

References

Botta-Dukat, Z., 2005. Rao's quadratic entropy as a measure of functional diversity on mulitple traits. J. Veg. Sci. 16, 533–540.

Callon, M., Courtial, J.P., Laville, F., 1991. Co-word analysis as a tool for describing the network of interactions between basic and technological research: The case of polymer chemsitry. Scientometrics 22, 155–205. https://doi.org/10.1007/BF02019280

Cisneros, L.M., Burgio, K.R., Dreiss, L.M., Klingbeil, B.T., Patterson, B.D., Presley, S.J., Willig, M.R., 2014. Multiple dimensions of bat biodiversity along an extensive tropical elevational gradient. J. Anim. Ecol. https://doi.org/10.1111/1365-2656.12201

Coulter, N., Monarch, I., Konda, S., 2002. Software engineering as seen through its research literature: A study in co-word analysis. J. Am. Soc. Inf. Sci. 49, 1206–1223. https://doi.org/10.1002/(sici)1097-4571(1998)49:13<1206::aid-asi7>3.3.co;2-6

Daru, B.H., van der Bank, M., Davies, T.J., 2015. Spatial incongruence among hotspots and complementary areas of tree diversity in southern Africa. Divers. Distrib. 21, 769–780. https://doi.org/10.1111/ddi.12290

Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W., Mouquet, N., 2010. Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: The need for integrative conservation strategies in a changing world. Ecol. Lett. 13, 1030–1040. https://doi.org/10.1111/j.1461-0248.2010.01493.x

Faith, D.P., 1992. Conservation evaluation and phylogenetic diversity. Biol. Conserv. 61, 1–10. https://doi.org/10.1016/0006-3207(92)91201-3

Gallardo, B., Gascón, S., Quintana, X., Comín, F. a., 2011. How to choose a biodiversity indicator - Redundancy and complementarity of biodiversity metrics in a freshwater ecosystem. Ecol. Indic. 11, 1177–1184. https://doi.org/10.1016/j.ecolind.2010.12.019

He, Q., 1999. Knowledge Discovery Through Co-Word Analysis. Libr. Trends 48, 133–159. https://doi.org/x

Hidasi-Neto, J., Loyola, R.D., Cianciaruso, M.V., 2013. Conservation Actions Based on Red Lists Do Not Capture the Functional and Phylogenetic Diversity of Birds in Brazil. PLoS One 8. https://doi.org/10.1371/journal.pone.0073431

Jost, L., Chao, A., 2004. Diversity analysis : a fresh approach. Diversity.

Laliberte, E., Legendre, P., Ecology, S., January, N., 2010. A distance-based framework for measuring functional diversity from multiple traits A distance-based framework for measuring from multiple traits functional diversity. Ecology 91, 299–305. https://doi.org/10.1890/08-2244.1

Lamb, E.G., Bayne, E., Holloway, G., Schieck, J., Boutin, S., Herbers, J., Haughland, D.L., 2009. Indices for monitoring biodiversity change: Are some more effective than others? Ecol. Indic. 9, 432–444. https://doi.org/10.1016/j.ecolind.2008.06.001

Lyashevska, O., Farnsworth, K.D., 2012. How many dimensions of biodiversity do we need? Ecol. Indic. 18, 485–492. https://doi.org/10.1016/j.ecolind.2011.12.016

Magurran, A.E., McGill, B.J. (Eds.), 2011. Biological diversity frontiers in measurement and assessment. Oxford University Press.

Mazel, F., Mooers, A.O., Riva, G.V.D., Pennell, M.W., 2017a. Conserving Phylogenetic Diversity Can Be a Poor Strategy for Conserving Functional Diversity. Syst. Biol. 66, 1019–1027. https://doi.org/10.1093/sysbio/syx054

Mazel, F., Mooers, A.O., Riva, G.V.D., Pennell, M.W., 2017b. Conserving Phylogenetic Diversity Can Be a Poor Strategy for Conserving Functional Diversity. Syst. Biol. 66, 1019–1027. https://doi.org/10.1093/sysbio/syx054

Meynard, C.N., Devictor, V., Mouillot, D., Thuiller, W., Jiguet, F., Mouquet, N., 2011. Beyond taxonomic diversity patterns: How do α, β and γ components of bird functional and phylogenetic diversity respond to environmental gradients across France? Glob. Ecol. Biogeogr. 20, 893–903. https://doi.org/10.1111/j.1466-8238.2010.00647.x

Mouchet, M.A., Villéger, S., Mason, N.W.H., Mouillot, D., 2010. Functional diversity measures: An overview of their redundancy and their ability to discriminate community assembly rules. Funct. Ecol. 24, 867–876. https://doi.org/10.1111/j.1365-2435.2010.01695.x

Nakamura, G., Vicentin, W., Súarez, Y.R., 2017. Functional and phylogenetic dimensions are more important than the taxonomic dimension for capturing variation in stream fish communities. Austral Ecol. 1–11. https://doi.org/10.1111/aec.12529

Neff, M.W., Corley, E. a., 2009. 35 years and 160,000 articles: A bibliometric exploration of the evolution of ecology. Scientometrics 80, 657–682. https://doi.org/10.1007/s11192-008-2099-3

Pavoine, S., Bonsall, M.B., 2011. Measuring biodiversity to explain community assembly: A unified approach. Biol. Rev. 86, 792–812. https://doi.org/10.1111/j.1469-185X.2010.00171.x

Presley, S.J., Scheiner, S.M., Willig, M.R., 2014. Evaluation of an integrated framework for biodiversity with a new metric for functional dispersion. PLoS One 9. https://doi.org/10.1371/journal.pone.0105818

Purvis, A., Hector, A., 2000. Getting the measure of biodiversity. Nature 405, 212–219. https://doi.org/10.1038/35012221

Safi, K., Cianciaruso, M. V, Loyola, R.D., Brito, D., Armour-Marshall, K., Diniz-Filho, J.A.F., 2011. Understanding global patterns of mammalian functional and phylogenetic diversity. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 366, 2536–2544. https://doi.org/10.1098/rstb.2011.0024

Saito, V.S., Siqueira, T., Fonseca-Gessner, A.A., 2015. Should phylogenetic and functional diversity metrics compose macroinvertebrate multimetric indices for stream biomonitoring? Hydrobiologia 745, 167–179. https://doi.org/10.1007/s10750-014-2102-3

Webb, C.O., Ackerly, D.D., McPeek, M. a., Donoghue, M.J., 2002. Phylogenies and Community Ecology. Annu. Rev. Ecol. Syst. 33, 475–505. https://doi.org/10.1146/annurev.ecolsys.33.010802.150448

Wilson EO. 1997. A situação atual da diversidade biológica In: Wilson EO e Peter FM eds. Biodiversidade. Editora Nova Fronteira, Rio de Janeiro. 657 p

Capítulo 2 – As soluções

Title: Revisiting the dimensionality of biological diversity

Gabriel Nakamura de Souza[1,2], Larissa Oliveira Gonçalves[2] and Leandro da Silva Duarte[2].

[1] – Email: gabriel.nakamura.souza@gmail.com; Orcid ID orcid.org/0000-0002-5144-5312

[2] – Departamento de Ecologia, Universidade Federal do Rio Grande do Sul, CP 15007, Porto Alegre, RS 91501-970, Brazil.

Manuscrito submetido à revista Ecography

Abstract

Biodiversity can be represented by different dimensions. While many diversity metrics try to capture the variation of these dimensions they also lead to a 'fragmentation' of the concept of biodiversity itself. Developing a unified measure that integrates all the dimensions of biodiversity is a theoretical solution for this problem, however, it remains operationally impossible. Alternatively, understanding which dimensions better represent the biodiversity of a set of communities can be a reliable way to integrate the different diversity metrics. Therefore, to achieve a holistic understand of biological diversity, we explore the concept of dimensionality. We define dimensionality of diversity as the number of complementary components of biodiversity, represented by diversity metrics, needed to describe biodiversity in an unambiguously and effective way. We provide a solution that joins two components of dimensionality — correlation and the variation — operationalized through two metrics, respectively: Evenness of Eigenvalues (EE) and Importance Values (IV). Through simulation we show that considering EE and IV together can provide information that is neglected when only EE is considered. We demonstrate how to apply this framework by investigating the dimensionality of South American small mammal communities. Our example evidenced that, for some representations of biological diversity, more attention is needed in the choice of diversity metrics necessary to effectively characterize biodiversity. We conclude by highlighting that this integrated framework provides a better understanding of dimensionality than considering only the correlation component.

Keywords: biodiversity metrics, communities, biodiversity measurement, Importance Values, Evenness of Eigenvalues.

Introduction

Biodiversity encompasses all variation present in life, from genetic material to populations, communities and higher levels of biological organization like entire ecosystems (Wilson 1997). In addition to its broadness in scale and complexity, the central position of the concept of biodiversity in ecological studies justifies efforts to develop measures that properly operationalize the concept. These efforts are reflected in the immensurable number of diversity metrics that have appeared as attempts to encompass all the variation in biodiversity. However, although these diversity metrics allow the description of different dimensions, as the number of them increases the concept of biodiversity becomes operationalized in disparate ways that convey no precise information. This lack of consensus in operationalization of the concept of biodiversity led Hulrbert (1971) to propose the idea of the non-concept of species diversity, in which he advocated that the many metrics of biodiversity be summarized in only a few relevant ones that can be used to express adequately and unambiguously the concept of biodiversity.

Long since Hulrbert´s seminal work, there has been a pronounced increase in the number of metrics that quantify characteristics of biological diversity other than the traditional taxonomic-based metrics, revealing that patterns of diversity for some communities can be best described using other components of biological diversity, such as functional and phylogenetic components (Graham and Fine 2008, Cisneros et al. 2014). However, these findings are not consensual (e.g Lamb et al. 2009), since some phylogenetic and functional metrics can be strongly correlated with traditional metrics (Tucker and Cadotte 2013, Tucker et al. 2018), deepening the question of which metrics represent the fundamental components of biological diversity (Hulrbert, 1971). A theoretical approach to searching for fundamental variation in biodiversity is to integrate the many sources of information in a unique framework. This integration can be achieved by investigating the relationships among existing metrics. A previous work that proposed this integration based it on quantifying a characteristic of biodiversity known as dimensionality (Stevens and Tello 2014).

Dimensionality can be defined, at the community scale of biological organization, as the amount of information needed to effectively characterize the variation presented in a given biodiversity representation, by means of diversity metrics. Communities with high dimensionality require more dimensions to be effectively described than communities with low dimensionality (Stevens and Tello 2014). Quantifying the dimensionality of biodiversity currently involves searching for the degree of complementarity in spatial or temporal variation among multiple metrics of diversity, which is obtained mainly through a measure denominated Eveness of Eigenvalues (hereafter EE) (Stevens and Tello 2014).

Stevens and Tello´s EE metric is obtained by Principal Component Analysis (PCA) of a matrix of diversity metrics (hereafter matrix **M,** *sensu* Ricotta 2005) for a set of communities, and calculating an evenness metric for the eigenvalues of the axes that represent this fundamental biodiversity space. The logic behind EE is that, if the diversity metrics used to characterize communities have low complementarity, almost all of the fundamental variation in biodiversity will be concentered in a few axes, producing a low EE. On the other hand, if diversity metrics are completely complementary with each other (variation in biodiversity will be equally distributed among axes) the EE of the communities will be 1.

The EE metric represents, in a simple way, the degree of complementarity among the dimensions of biodiversity represented by diversity metrics, which comprises what we call here the correlation component of dimensionality (see also Tucker and Cadotte 2013, Lamb et al. 2006 for uses of correlation component). However, EE ignores another source of information in dimensionality — the amount of variation, or importance, that each diversity metric presents in fundamental biodiversity space. This comprises what we call here the variation component of dimensionality.

Suppose a situation in which diversity metrics are highly correlated (Figure 1 A) and each metric accounts for a similar amount of variation in fundamental biodiversity space (Figure 1B). This situation has low complementarity among dimensions of biodiversity and high redundancy in the amount of variation that each metric captures in fundamental biodiversity space (represented as the length of the arrows in 1B). Consequently, we could rely on any of these diversity metrics to effectively represent the variation in biodiversity of these communities. On the other hand, communities with low complementarity may present a situation in which one of the metrics captures almost all the variation in the fundamental biodiversity space (Metric 2 in Figure 1C), indicating low redundancy of metrics. Following the current approach to measuring dimensionality, EE would indicate similar patterns of dimensionality for communities in 1B and 1C. However, the choice of metric in 1C is of greater importance than in 1B, in which the metrics are highly redundant regarding the information captured. Therefore, considering only the correlation component does not provide enough evidence to support the decision of which diversity metrics to use to effectively characterize biological diversity for two communities with similar EE, because it disregards the variation component inherent to dimensionality.

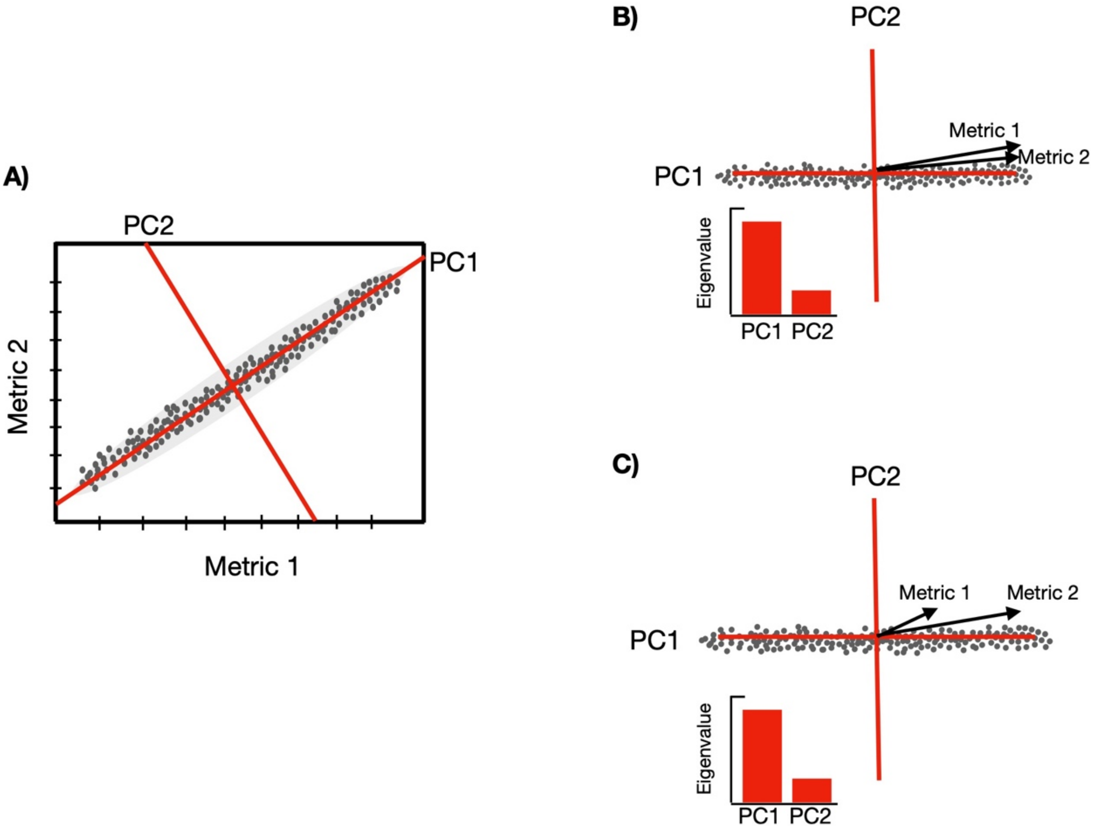


Figure 1: A) A set of communities described by two diversity metrics (Metric 1 and Metric 2) that are highly correlated. This pattern of correlation can be related to two diversity metrics that account for similar amounts of variation in the reduced biodiversity space (B, high redundancy), or be a situation in which one metric has disproportional importance for capturing variation in biodiversity space (C, low redundancy).

Finding a measure that captures the variation component of dimensionality is not an impediment for effectively characterizing dimensionality, since it can be operationalized by the metric Importance Values (hereafter IV) proposed by Wilsey et al. (2005). However, since the common way to quantify dimensionality (Stevens and Tello 2014) is limited to capturing only the correlation component, the development of a unified framework that combines both correlation and variation components would provide a way to better represent the dimensionality of biodiversity.

Therefore, our aim was to update the concept of dimensionality of biodiversity and its operationalization by integrating the correlation and variation components through EE and IV in a framework for quantification of dimensionality. To do this we show, through simulation, how EE and IV together can distinguish situations with different degrees of complementarity of dimensions of diversity and redundancy of information that each metric captures. We then present an empirical example of the investigation of dimensionality by applying the integrated framework to communities of small mammals (cricetids and marsupials). Specifically, we evaluated the level of complementarity and redundancy for different sets of diversity metrics used to describe the biodiversity of cricetids and marsupials, highlighting how the proposed dimensionality framework facilitates the first step of biological assessment — the choice of metrics to be used for characterizing biodiversity.

Material and Methods

Investigating the dimensionality of biodiversity: obtaining EE and IV

Our framework for investigating the dimensionality of biodiversity comprises three steps. The first step is to calculate matrix **M**, which, for the sake of simplicity, will contain three metrics of diversity for the simulation analysis: a measure of functional diversity (FD [Petchey & Gaston 2006)]), a measure of phylogenetic diversity (PD [Faith 1992]) and richness. We chose a simplistic approach with only three metrics since our objective with the simulation analysis was to focus on showing how IV can reveal patterns that are not detected by using only EE. We were more interested in the patterns of correlation and variation of diversity metrics in biodiversity space than the particularity of the metrics themselves. We present a more realistic exploration of the integrated framework in the section *Assessing the dimensionality of biodiversity in small mammal communities*.

The second step involves performing a PCA of matrix **M** using a standardized correlation matrix. 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 to calculate the dimensionality metrics EE and IV. We calculate EE using Camargo´s evenness index in Equation 1, following the original proposition of Stevens and Tello (2014):

$$EE = 1 - {(\sum_{P=1}^{A(A-1)/2} |e_{ip} - e_{jp}|)} \Big/ {A} \qquad \text{Equation 1}$$

Camargo's evenness index (Camargo 1993) is calculated using the axes (A) and their respective eigenvalues (e_{ih} and e_{jh}) from a PCA of the standardized matrix **M**, in which the metrics were scaled to have a mean of zero and equal variances. The higher the value of EE, the higher the complementarity the communities have in relation to the dimensions of biodiversity represented in matrix **M**. On the other hand, lower EE values indicate lower complementarity in the dimensions used to characterize the communities. IV is calculated according to the method proposed by Wilsey et al. (2005), using a matrix (**M**) standardized by the maximum values of each diversity metric. This standardization removes the effect that the different units of each diversity metric have, without modifying their original variation. To obtain IV for each diversity metric in matrix **M** we apply Equation 2, in which IV_i represents the IV of diversity metric i, r^2_{ij} is the squared correlation of diversity metric i with PC_j, and R^2_j is the amount of variation that PC_j accounts for in ordination space (biodiversity 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 the Kaiser-Gutmann criterion. The greater the IV the more variation the diversity metric accounts for in biodiversity space. IV approaches 1 when the diversity metric accounts for almost all the variation and approaches zero when the metric accounts for little variation. Sets of communities with highly uneven IV values for diversity metrics possess low redundancy in metric importance, while communities with highly even IV values possess high redundancy regarding the amount of information captured by each metric.

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

To assess the effectiveness of EE and IV in acquiring information regarding correlation and variation of dimensionality in matrix **M**, the following conditions must be met: (1) EE values must not differ for set of communites simulated in scenarios with the same level of correlation among diversity metrics, and must differ among communities that have different levels of correlation among diversity metrics; (2) for scenarios with low and high correlation, IV must be similar among metrics that have similar variation in biodiversity space (e.g. Figure 1B), and differ for scenarios in which variation in biodiversity space is mainly due to a single metric (e.g. situation represented Figure 1C, Metric 2 must have a higher IV than Metric 1). We evaluate whether EE and IV can recover these patterns by simulating communities with varying degrees of correlation and variation for each metric in biodiversity space obtained from matrix **M**.

The simulations were based on a pattern-oriented procedure, producing diversity metrics with patterns of correlation and variation that represent four scenarios with the following characteristics: In the HiC/EqV (High Correlation and Equal Variation) scenario the diversity metrics are highly correlated and have similar variation in biodiversity space. The HiC/DifV (High Correlation and Different Variation) scenario has diversity metrics that are highly correlated and vary in importance of each metric in biodiversity space. The LoC/EqV (Low Correlation and Equal Variation) scenario has diversity metrics with low correlation and similar importance in biodiversity space. Finally, the LoC/DifV (Low Correlation and Different Variation) scenario has diversity metrics with low correlation and dissimilar importance in biodiversity space.

We generate scenarios HiC/EqV and HiC/DifV by starting with a phylogeny that was simulated by a birth-death processes (function *sim.bdtree* from the package geiger [Harmon, Weir, Brock, Glor, & Challenger, 2008]) where a species, chosen randomly, initiates the procedure by colonizing a given community. Subsequent addition of species to the community depends on the species that are already present in that community. Communities at one extreme will only contain species that are phylogenetically closely related to each other (top 10%), with the phylogenetic filter becoming less restrictive until communities do not have any phylogenetic filter that restricts coexistence of species (least restrictive condition). Since we simulated a continuous trait that was conserved over the phylogenetic tree — evolved according to a Brownian motion model, using the function *rTraitCont* (Paradis et al. 2004) with the ρ [*rho*] parameter set to 3 — with the number of species in each community gradually increasing (less phylogenetic filter, more species), the procedure created a gradient of phylogenetic, functional and taxonomic diversity metrics. In order to generate differences in variation of the diversity metrics, in scenario HiC/ DifV we simulated a trait that evolves according to a regime of stabilizing selection (Ornstein-Uhlebeck model with the strength of selection set by the parameter α at 0.8) that restricts trait variation to within an optimal range (represented by a θ [theta] of 0). This allowed us to generate a set of communities in which the diversity metrics were highly correlated but variation of FD was much lower than that of richness and PD since the traits that were used in the calculation of FD were restricted by the selection process.

We generated the scenario LoC/DifV by following the same procedures described above for scenario HiC/EqV, however, the trait was simulated to have low phylogenetic signal and the phylogenetic tree used to calculate PD was modified to simulate a process of evolution in which most speciation occurs near the root (a star-like phylogeny). This procedure resulted in low correlation between PD and FD, since the relationship between phylogeny and traits was disrupted. Additionally, low variability for PD and richness metrics was obtained since we set the simulations to produce communities with the same number of species but with the phylogenetic filtering acting in community assembly. Consequently, most of the variation in this scenario is due to the FD metric. Finally, to generate scenario LoC/EqV we simulated communities in which all species in the phylogenetic tree had an equal probability of occurring in any community (no phylogenetic filtering acting on the assembly), and set the richness to be very similar for all communities. This procedure generated metacommunities with low correlation and similar amounts of variation for all diversity metrics.

We generated 999 sets of communities for each scenario described above, with the metacommunities of all scenarios being composed of 50 communities with a minimum of 20 and a maximum of 200 species. The phylogenetic filter was set to act gradually on the communities, increasing by the order of 10% (start by selecting the top 10% most phylogenetically similar species, followed by the top 20% and so on until 90% of the species have been selected from the pool). Details and an illustration of the simulation procedures and scenarios are presented in the supplementary material Appendix S1, along with a link to an interactive module that we produced to illustrate the simulation procedure used in this work.

Finally, we tested whether the values of EE and IV met our theoretical expectations. We checked if EE values differed between scenarios with low correlation and scenarios with high correlation (scenarios HiC/DifV and HiC/EqV versus scenarios LoC/EqV and LoC/DifV). To effectively capture the correlation component of dimensionality EE must be higher in scenarios with low correlation among diversity metrics than in scenarios with high correlation. To test for differences among IV values of each metric in the scenarios we used a graphical tool called profile of importance (Wilsey et al. 2005) and quantified differences in IV of each metric by calculating F values obtained from a linear model (Equation 3). F values allow the IV values of the three dimensions (PD, FD and richness) to be compared and to determine if the IV values of the DifV scenarios (scenarios HiC/DifV and LoC/DifV) differed more from each than did the IV values calculated for the EqV scenarios (scenarios HiC/EqV and LoC/EqV). The simulation scenarios and the theoretical expectations regarding EE and IV follow the schematic representation present in Figure 2.

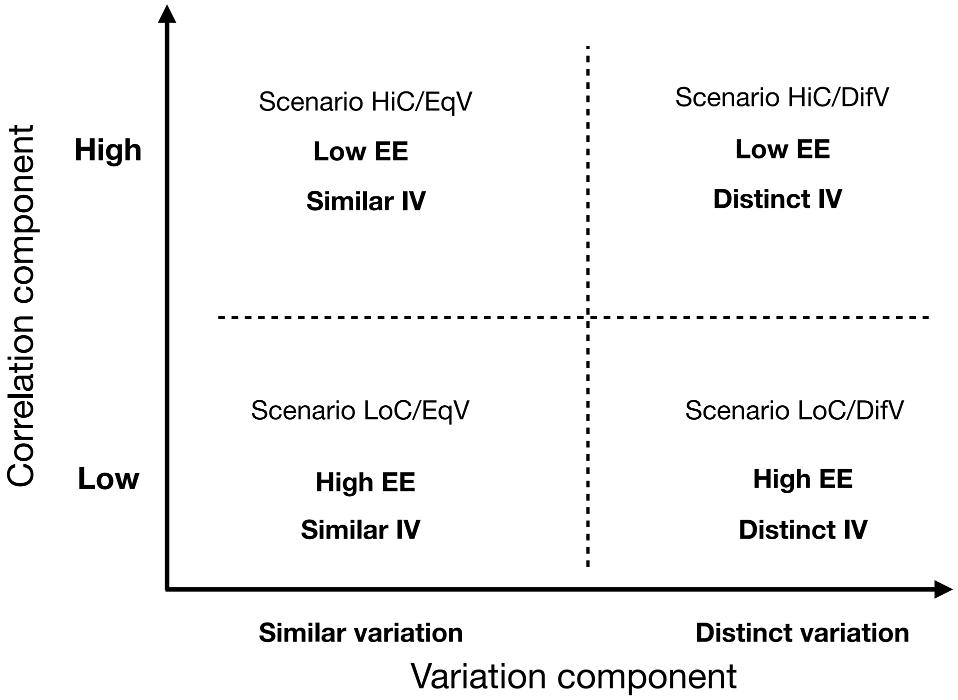


Figure 2: Schematic representation of simulated scenarios and expected outcomes for EE and IV. The abscissa represents the variation component of dimensionality. Metacommunities were simulated to show similar values of variation among metrics (lower left quadrant) or different values of variation among metrics (lower right quadrant), so that, respectively, similar and different IV values among diversity metrics are expected. The ordinate represents the correlation component of dimensionality. Metacommunities were simulated that had metrics with high (upper right panel) and low correlation, so that, respectively, low and high EE values are expected.

Assessing the dimensionality of biodiversity in small mammal communities

We illustrate the application of the dimensionality framework with a database of small mammal communities (marsupial and cricetid mammals) distributed throughout the South American continent. We constructed matrix M for these communities by calculating eight diversity metrics that represent different dimensions of taxonomic, functional and phylogenetic components of biological diversity. The choice of metrics was based on the works of Tucker et al. (2017) and Scheiner (2019), which together represent the most complete compilation and classification of metrics of taxonomic, functional (Scheiner, 2019) and phylogenetic diversity (Tucker et al. 2017). We chose at least one metric for each of the richness, divergence and regularity dimensions of the three components of biodiversity considered here. The taxonomic component was represented by richness; the functional component by FD (richness dimenson, Petchey and Gaston 2006b), FEve (regularity dimension) and FDiv (divergence dimension, Villéger et al. 2008); and the phylogenetic component by PD (richness dimension, Faith 1992), MNTD (divergence dimension, Webb et al., 2002), PSV (divergence dimension, Helmus et al., 2007) and PE_{ve} (regularity dimension, Villéger et al. 2014).

Traits used to calculate functional metrics comprised life-history attributes — weight, head-body length, diet and form of locomotion. Species were categorized according to their diet as insectivores, herbivores, granivores, omnivores, frugivores, piscivores, seed predators and leaf predators, and according to their modes of locomotion as terrestrial, semifossorial, semiaquatic, arboreal and scansorial. Some species were allocated to more than one diet and locomotion category. All calculated diversity metrics require a distance matrix or a functional dendrogram obtained from a distance matrix. Therefore, to obtain the functional distance matrix we used Gower distance (Pavoine et al. 2009) for traits that have different statistical characteristics (numerical and categorical).

The phylogenetic hypothesis used to calculate phylogenetic indices was obtained from the mammalian phylogenies of Bininda-Emonds et al. (2007) and

Fabre et al. (2012), the latter of which was used to improve the phylogenetic resolution to species level. Seven species present in our data were not included in the phylogeny Fabre et al. (2012), so we included these species as polytomies within their respective genera. Divergence times for our phylogeny were estimated in millions of years by equally distributing the ages of undated nodes, based on the know ages present in Bininda-Emonds et al. (2007) and Fabre et al. (2012), using the BLADJ algorithm of Phylocom software (Webb et al. 2008). The phylogenetic hypothesis and the original references compiled to assemble the community data used in this work are provided in Figure S2 and Table S1 of Appendix 2 of the supplementary material.

The metrics EE and IV were calculated as previously described, with the number of axes used in IV calculation being determined by the Kaiser-Gutmann stop criterion. We also compared the observed values of EE with a null distribution of 999 EE values generated by a null model that randomizes a species incidence matrix while preserving differences in richness among sites and mixing species frequency (performed with the *sim3* function from the *EcoSimR* package [Gotelli and Ellison 2013a]). Using this null model we tested the null hypothesis that observed EE values do not differ from expected EE values according to variation in richness. We implemented a function called *dimensionality* to calculate EE values from 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.

We calculated IV for the small-mammal metacommunities according to Equation 2, applying *ImportanceVal* — the R code for the IV function (the function can be accessed at https://github.com/GabrielNakamura/IV_function). We used the Kaiser-Gutmann stop criterion and a bootstrap procedure that re-sampled matrix **M** 999 times and recalculated

IV for each metric so that we generated confidence intervals for the IV value of each diversity metric. We performed all calculations with a standardized matrix **M** (scaled to a mean of zero and unit variance for the calculation of EE values and standardized by the maximum values of each metric for the calculation of IV values). Bootstrapped IV values were submitted to an Ordinary Least Square (OLS) linear model to test for differences in the importance of the components of diversity that assemble matrix **M**:

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

Equation 3 represents the effects parametrization model in which IV_i represents the predicted value of IV for the diversity metric i, β the effect of a given dimension over another and ε_i the error term associated with the residuals, which follow a Gaussian distribution. Each value of IV was classified as belonging to the phylogenetic (PD, PEve, PSV and mntd), the functional (FD, FDis and FDiv) or the taxonomic (richness) dimension. Through this model we aimed to determine if any of the components of diversity (functional, phylogenetic or taxonomic) captures a greater amount of information from biodiversity space. Additionally, we performed another linear OLS model using the same set of data but considering each metric as the explanatory variable, in order to assess differences in importance among diversity metrics. For both models we performed a Tukey test to assess pairwise differences in importance among dimensions and metrics.

The dimensionality framework was applied to four different configurations of matrix **M**: all metrics; a combination of phylogenetic metrics and richness; a combination of functional metrics and richness; and a combination of functional and phylogenetic metrics. We performed these analyses to show how dimensionality can change depending on the components of diversity used in matrix **M**, and what the implications of different values of EE and different similarities among metrics IV (represented as Camargo´s evenness of IV metrics) are on the choice of diversity metrics to be used to represent the biodiversity. For these analysis we also computed EE as the mean value calculated from a bootstrap procedure equivalent to that used for the IV metric, in order to generate confidence intervals.

Results

Simulated data

Our simulation revealed that EE and IV, when used together, acquire information regarding two aspects of dimensionality: correlation among metrics and the variation that each metric accounts for in biodiversity space. This complementary information that IV brings to the analysis of dimensionality is evidenced in Figure 3. Thus, different patterns of redundancy in information captured by the metrics can be obtained for a given level of correlation, with greater differences among IV values in scenarios HiC/DifV and LoC/DifV (right side of Figure 3) than in HiC/EqV and LoC/EqV (left side of Figure 3).

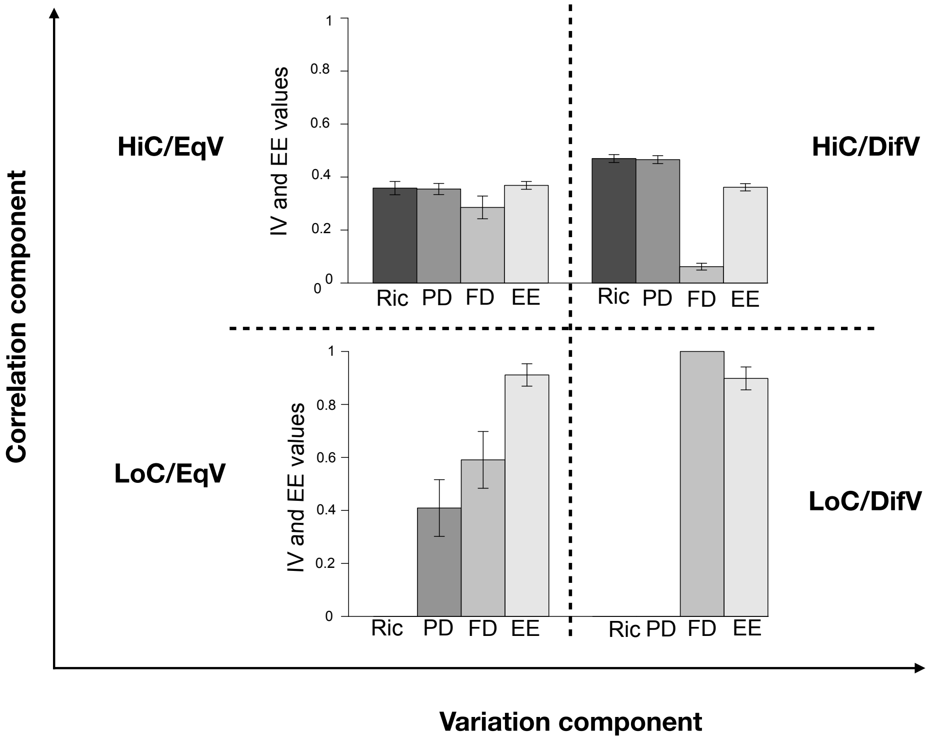


Figure 3: Bar plots showing IV and EE calculated for metacommunities simulated according different scenarios (HiC/EqV, HiC/DifV, LoC/EqV and LoC/DifV) using PD, FD and richness metrics in matrix **M**. For each of these scenarios situations were presented in which the metrics contribute similarly or unequally in biodiversity space (variation in ordinate axis) and are highly or lowly correlated (variation in abscissa axis).

The differences in EE between scenarios of high and low correlation (Figure 1, comparison between EE of upper and lower graphics), but not between scenarios of different and equal variation (Figure 1, comparison between EE bars in the same row) support our argument that this metric captures only the correlation component of dimensionality.

The ability of IV to capture the degree of redundancy in biodiversity information of the metrics was clear mainly for the HiC/DifV scenario, in which the attribute used to generate communities exhibited low variation (OU model) and, consequently, the FD metric presented lower IV than richness and PD metrics. It is worth noting that differences among the IV of metrics was greater in scenario LoC/EqV than in scenario HiC/EqV (Figure 1, lower right graphic), since it is not possible to obtain high redundancy in metric information (indicated by similar IV values among metrics) along with high values of complementarity (indicated by high EE). High redundancy in the importance of metrics is only possible for communities with low EE (low complementarity of dimensions), as demonstrated by scenario HiC/EqV. The magnitude of the differences in IV among metrics for each scenario is shown in Figure S3 of Appendix S3 of the supplementary material.

Small mammal communities

We obtained a moderate value for complementarity for the small mammal communities, as indicated by an EE of 0.49 for matrix **M** calculated with all eight diversity metrics. The correlation component of dimensionality, at least for the three analyzed components of diversity (functional, phylogenetic and taxonomic), may be a consequence of spatial gradients of species richness, as evidenced by comparing observed EE with that expected by the null model distribution of EE (Figure S4 in Appendix 3 of the supplementary material).

Only two axes of the PCA were significant according Kaiser-Guttman criterion (representing 70% of all the variation in matrix **M**), and composed the fundamental biodiversity space in which IV was calculated. Observed IV values for the eight diversity metrics ranged from 0.19 for PSV (27% of all the variation in biodiversity space) to 0.003 to FDiv (0.3% of all the variation in biodiversity space). Bootstrap means and confidence intervals for IV for all metrics are illustrated in Figure 4 through the IV profile (*sensu*

Willig and Hollander 1995), evidencing PSV as the metric capturing most of the variation in biodiversity space, followed by richness.

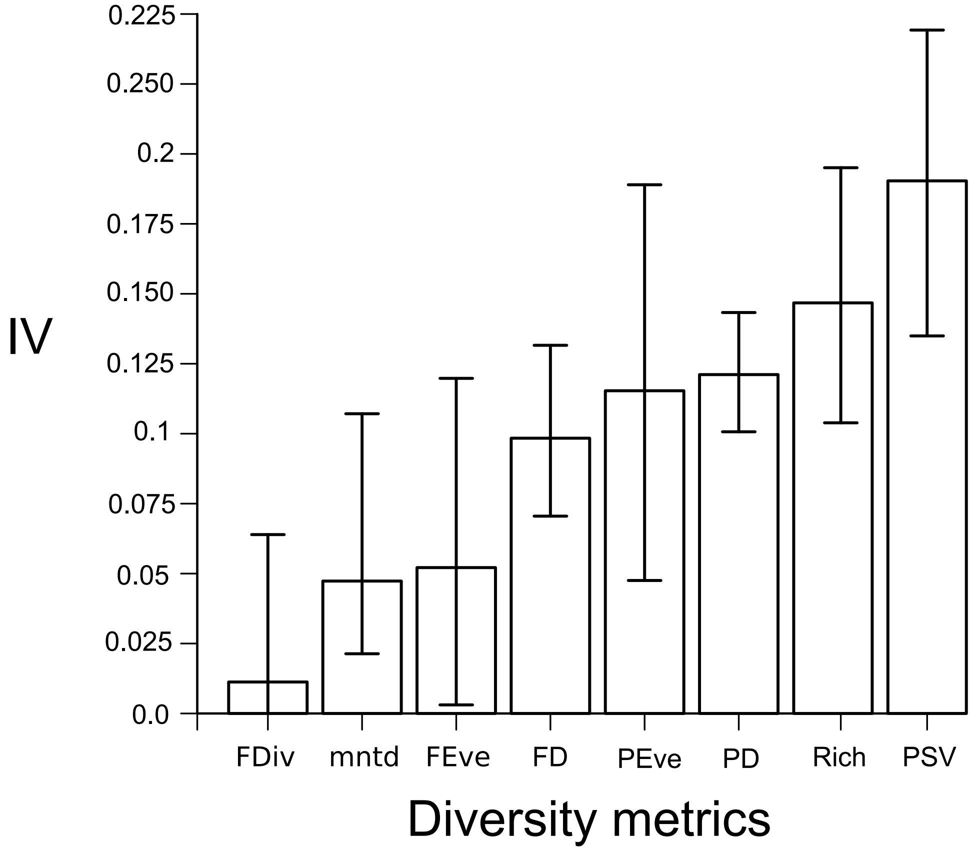


Figure 4: IV profile for marsupial and cricetid mammal communities from South America calculated using matrix **M** containing eight diversity metrics. Bar height corresponds to the mean IV for each diversity metric while lines represent 95% confidence intervals, both calculated via a bootstrap procedure.

The linear OLS model showed significant variation in IV among diversity metrics (F-value= 3.428; $p<0.05$), while the Tukey test revealed that the greatest difference in importance was between taxonomic and functional components of biodiversity followed by the difference between phylogenetic and functional components (difference between observed means of 0.092 and 0.064, respectively; Figure S5 of Appendix 3). This finding highlights the importance of considering the taxonomic and phylogenetic dimensions in characterizing the biodiversity of communities of cricetids and marsupials.

Analysis of dimensionality for matrix **M** containing functional metrics and richness had the highest complementarity (highest EE) and lowest redundancy in metric importance (biodiversity representation with similar values of IV, as indicated by a lower evenness of IV than obtained for other sets of metrics) (Figure 5). PSV was the metric that captured the most information in matrix **M** containing phylogenetic metrics and richness (30% of all the variation in biodiversity space) and phylogenetic and functional metrics (31% of all the variation in biodiversity space), as well as for matrix **M** containing all metrics (24% and of all the variation in biodiversity space). For matrix **M** that considered only functional metrics and richness, richness captured most of variation (47% of all the variation in biodiversity space). Despite the high variability, as indicated by the confidence intervals of IV and EE evenness , it is worth noting that IV evenness remains constant for different mean values of EE, with the greatest IV evenness being for the set of metrics that had the lowest EE value (matrix **M** with phylogenetic metrics and richness).

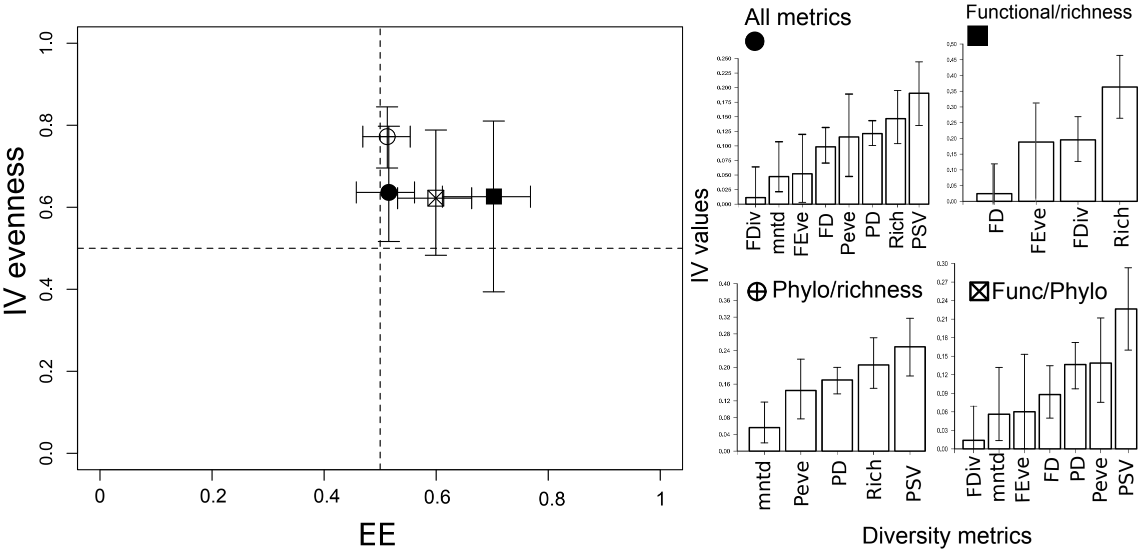


Figure 5: Values of EE and evenness of IV calculated for four different configurations of matrix **M**. Symbols represent mean values for each matrix configuration while lines represent confidence intervals. Bar graphics represent IV profiles calculated for matrix **M** with all metrics of diversity; functional metrics and richness; phylogenetic metrics and richness; and functional and phylogenetic metrics. Bars represent means while lines represent confidence intervals obtained via a bootstrap procedure applied to each matrix **M**.

Discussion

Our results with simulated data evidence the need for a dimensionality framework that integrates both EE and IV in order to effectively characterize dimensionality by considering its two components —correlation and variation in biodiversity space. Operationalizing these two components through EE and IV reveals their complementarity (by means of EE) and, given some level of complementarity, the degree of redundancy in information captured by the metrics used to express these dimensions (through IV). Therefore, our proposed dimensionality framework represents a step beyond the current approach to operationalizing dimensionality, as proposed by Stevens and Tello (2014) by distinguishing the degree of redundancy in information that each diversity metric captures.

Our integrated dimensionality framework joins other propositions in helping to choose metrics for the biological characterization of communities. We are aware that the main guide for choosing diversity metrics must be the objectives of the work. However, regardless of the objective, it is desirable to use diversity metrics that encompass complementary components of biological diversity and account for a satisfactory amount of the information present in the biodiversity component being investigated (Ricotta 2005b). In this respect, Saito et al. (2015) showed that phylogenetic, functional and traditional taxonomic indices present complementary information and should be used to adequately characterize and monitor biodiversity of stream macroinvertebrate communities. Ouchi-Melo et al. (2018) performed an integrated assessment to identify areas of conservation interest in the Cerrado biome, and evidenced the importance of considering traditional together with functional and phylogenetic metrics. Although both of these works considered the complementarity component by accounting for correlation among metrics, they did not account for redundancy in the amount of variation that each metric captures in biodiversity space, thus facing the same problem presented by using the EE metric alone. The dimensionality framework presented here, therefore, represents the most general and complete framework to date for guiding researchers in their choice of metrics to be used for biological assessment by considering both complementarity among biological dimensions and the amount of information that metrics can capture.

It is worth pointing out that the dimensionality of diversity can be investigated at any spatial and temporal scale, and using any configuration of matrix **M**. Even for works that focus on only one component of biodiversity, the investigation of dimensionality can be important for knowing which aspects of biodiversity are worthy of being included in biological assessment. Tucker et al. (2017) identified three complementary components of the phylogenetic component: richness, divergence and regularity. Thus, research focused on phylogenetic diversity can address whether these three components are complementary dimensions in the analyzed communities and which metrics are the most important to measure in order to best represent variation in these dimensions. As we showed in our empirical example with small mammal communities, dimensionality will depend on the representation of biological diversity used in matrix **M**, which influences practical decisions regarding which metrics are the most important for characterizing biodiversity.

At least for the cricetid and marsupial communities analyzed here, characterizing diversity through functional and taxonomic components requires great care in the choice of diversity metrics to be used. This is because this situation has the highest complementarity regarding diversity dimensions (highest EE value), indicating the need to rely on different components of diversity to effectively describe biodiversity, and a moderate level of redundancy in metrics, indicating that some metrics account for disproportionately more information than others. In this example, richness accounted for more information than the other metrics, but consideration of other components that represent functional information is also important for effectively characterizing biological diversity. This functional component can be represented by FDiv or FEve, which are very redundant in information. On the other hand, if the characterization of small mammal communities was focused on phylogenetic and taxonomic components, the choice of metrics to be used would require less caution since complementarity among dimensions is lower and redundancy of information is greater, indicating that all the metrics capture similar amounts of information of biodiversity space.

When considering matrix **M** with all eight diversity metrics, applying the dimensionality framework to small mammal communities revealed that cricetids and marsupials possess intermediate to low levels of complementarity (mean EE of 0.51 ±0.025). Together with low complementarity, low levels of redundancy among the metrics was found when considering the three components of biodiversity together (mean IV evenness of 0.63 ±0.082). Consequently, we suggest that the choice of diversity metrics to effectively represent these communities must encompass the three components of diversity — choosing the PSV metric, which accounts for the highest IV, and two other complementary metrics to represent taxonomic (richness) and functional components (FD that has the highest IV among functional metrics, as shown in Figure 6).

The patterns of IV values for small mammal communities contrasted with the findings of Wilsey et al. (2005) and Lyashevska and Farnsworth (2012), who concluded that richness was the least important diversity metric for representing variation in community structure (grassland and marine benthic communities, respectively). Although we did not considered abundance-based metrics, as these studies did, we point out that patterns of complementarity and redundancy can differ depending on the taxonomic group being investigated and the metrics being used (as already emphasized by our empirical application of the IV framework with different configurations of matrix **M**). This finding highlights the need to understand contingencies in the correlation and variation components of the dimensionality of different communities.

We only used metrics that capture three sources of information from biodiversity (phylogenetic, functional and taxonomic), since they are the main assessed components of diversity and represent important metrics for capturing different dimensions of these components (Tucker et al. 2017). Despite the limited number of metrics presented in this work, the dimensionality framework used here is highly flexible in the sense that it can be applied to 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 components such as genomic (*e.g.* Nei 1978), proteomic (*e.g.* Gotelli et al. 2013b) or any other dimension that can be quantified.

Conclusion and future directions

This work represents an upgrade of the operationalization of the concept of dimensionality presented by previous works. We demonstrate that including the correlation component of dimensionality with the variation component, through the use of EE and IV, in the same framework more effectively characterizes the dimensionality of biodiversity.

Besides conceptual and operational advances, the dimensionality framework proposed here provides evidence regarding practical situations in which the choice of diversity metrics is more critical for effectively characterizing biodiversity. The use of this dimensionality framework can help identify these different situations and assist in choosing metrics.

Since the evidence presented in the literature regarding characterization of dimensionality is limited (Lyashevska and Farnsworth 2012, Stevens and Tello 2014, 2018, Stevens and Gavilanez 2015), 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, one 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 predictably higher or lower levels of dimensionality across communities.

Acknowledgements

The authors thank W Ulrich, VD Pillar, V Debastiani and one anonymous review for invaluable suggestions in previous versions of the manuscript, and E Wild and E Bradley for proof-reading the English. GN received a PhD. Fellowship from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES). Research activities of LDSD was supported by Conselho Nacional de Pesquisa (CNPq) Productivity fellowships. GN and LDSD are members of the Instituto Nacional de Ciência e Tecnologia (INCT) in Ecology, Evolution and Biodiversity Conservation, supported by MCTIC/CNPq (proc. 465610/2014-5) and FAPEG.

References

Bininda-Emonds, O. R. P. et al. 2007. The delayed rise of present-day mammals. - Nature 446: 507–512.

Camargo, J. A. 1993. Must Dominance Increase with the Number of Subordinate Species in Competitive Interactions? - J. Theor. Biol. 161: 537–542.

Cisneros, L. M. et al. 2014. Multiple dimensions of bat biodiversity along an extensive tropical elevational gradient. - J. Anim. Ecol. in press.

Fabre, P. et al. 2012. Open Access A glimpse on the pattern of rodent diversification : a phylogenetic approach. in press.

Faith, D. P. 1992. Conservation evaluation and phylogenetic diversity. - Biol. Conserv. 61: 1–10.

Gotelli, N. 2000. Null Model Analysis of Species Co-occurrence Patterns. - Ecology 81: 2606–2621.

Gotelli, N. J. et al. 2012. Environmental proteomics, biodiversity statistics and food-web structure. - Trends Ecol. Evol. 27: 436–442.

Graham, C. H. and Fine, P. V. A. 2008. Phylogenetic beta diversity : linking ecological and evolutionary processes across space in time. in press.

Harmon, L. J. et al. 2008. GEIGER: Investigating evolutionary radiations. - Bioinformatics 24: 129–131.

Helmus, M. R. et al. 2007. Phylogenetic Measures of Biodiversity. - Am. Nat. 169: E68–E83.

Hollander, R. R. and Willig, M. R. 1995. Secondary sexual dimorphism and phylogenetic constraints in bats: a multivariate approach. - J. Mammal. 76: 981–992.

Lamb, E. G. et al. 2009. Indices for monitoring biodiversity change: Are some more effective than others? - Ecol. Indic. 9: 432–444.

Lyashevska, O. and Farnsworth, K. D. 2012. How many dimensions of biodiversity do we need? - Ecol. Indic. 18: 485–492.

Nei, M. 1978. Estimation of Average Heterozygosity and. - Genetics 89: 583–590.

Ouchi-Melo, L. S. et al. 2018. Integrating phylogenetic and functional biodiversity facets to guide conservation: a case study using anurans in a global biodiversity hotspot. - Biodivers. Conserv. 27: 3247–3266.

Paradis, E. et al. 2004. APE: Analyses of phylogenetics and evolution in R language. - Bioinformatics 20: 289–290.

Pavoine, S. et al. 2009. On the challenge of treating various types of variables: Application for improving the measurement of functional diversity. - Oikos 118:

391–402.

Petchey, O. L. and Gaston, K. J. 2006a. Functional diversity: Back to basics and looking forward. - Ecol. Lett. 9: 741–758.

Petchey, O. L. and Gaston, K. J. 2006b. Functional diversity: back to basics and looking forward. - Ecol. Lett. 9: 741–758.

Ricotta, C. 2005a. Through the jungle of biological diversity. - Acta Biotheor.: 29–38.

Ricotta, C. 2005b. Through the jungle of biological diversity. - Acta Biotheor. 53: 29–38.

Saito, V. S. et al. 2015. Should phylogenetic and functional diversity metrics compose macroinvertebrate multimetric indices for stream biomonitoring? - Hydrobiologia 745: 167–179.

Scheiner, S. M. 2019. A compilation of and typology for abundance-, phylogenetic-and functional-based diversity metrics. - bioRxiv: 1–29.

Stevens, R. D. and Tello, J. S. 2014. On the measurement of dimensionality of biodiversity. - Glob. Ecol. Biogeogr.: n/a-n/a.

Stevens, R. D. and Gavilanez, M. M. 2015. Dimensionality of community structure: phylogenetic, morphological and functional perspectives along biodiversity and environmental gradients. - Ecography (Cop.). 38: 861–875.

Stevens, R. D. and Tello, J. S. 2018. A latitudinal gradient in dimensionality of biodiversity. - Ecography (Cop.).: 1–11.

Tucker, C. M. and Cadotte, M. W. 2013. Unifying measures of biodiversity: understanding when richness and phylogenetic diversity should be congruent. - Divers. Distrib. 19: 845–854.

Tucker, C. M. et al. 2017. A guide to phylogenetic metrics for conservation, community ecology and macroecology. - Biol. Rev. 92: 698–715.

Tucker, C. M. et al. 2018. On the relationship between phylogenetic diversity and trait diversity. - Ecology 99: 1473–1479.

Villéger, S. et al. 2008. New Multidimensional Functional Diversity Indices for a Multifaceted Framework in Functional Ecology Published by : Ecological Society of America content in a trusted digital archive. - Ecology 89: 2290–2301.

Villéger, S. et al. 2014. New Multidimensional Functional Diversity Indices for a Multifaceted Framework in Functional Ecology Published by : Ecological Society of America content in a trusted digital archive . We use information technology and tools to increase productivity and f. 89: 2290–2301.

Webb, C. O. et al. 2002. Phylogenies and Community Ecology. - Annu. Rev. Ecol. Syst. 33: 475–505.

Webb, C. O. et al. 2008. Phylocom: Software for the analysis of phylogenetic community structure and trait evolution. - Bioinformatics 24: 2098–2100.

Wilsey, B. J. et al. 2005. Relationships among indices suggest that richness is an incomplete surrogate for grassland biodiversity. - Ecology 86: 1178–1184.

Wilson EO (1997) A situação atual da diversidade biológica In: Wilson EO & Peter FM (eds) Biodiversidade. Editora Nova Fronteira, 657p, Rio de Janeiro.

Capítulo 3 – Novas métricas

A multifaceted approach to analyzing taxonomic, functional and phylogenetic β-diversity

Running title: A multifaceted approach to β-diversity

Gabriel Nakamura*[1], Wagner Vicentin[2], Yzel Rondon Súarez[3] and Leandro Duarte[1].

[1]Departamento de Ecologia, Universidade Federal do Rio Grande do Sul, Av. Bento Gonçalves 9500, CP 15007, Porto Alegre RS 91501-970, Brazil.

[2]Universidade Federal de Mato Grosso do Sul, Campo Grande, Brazil.

[3]Centro Integrado de Análise e Monitoramento Ambiental (CInAM), Universidade Estadual de Mato Grosso do Sul, Dourados, Brasil.

*e-mail for correspondence: gabriel.nakamura.souza@gmail.com

Abstract

Ecological literature offers a myriad of methods for quantifying β-diversity. One such methods is determining BD_{total} (BD), which, unlike other methods, can be decomposed into meaningful components that indicate how unique a community is regarding its composition (local contribution) and how unique a species is regarding its occurrence in the metacommunity (species contribution). Despite this advantage, the original formulation of the BD metric only assesses taxonomic variation and neglects other important dimensions of biodiversity. We expanded the original formulation of BD to capture variation in the functional and phylogenetic dimensions of a metacommunity by computing two new metrics — BD_{Fun} and BD_{Phy} — as well as their respective components that represent the local and species contribution. We tested the statistical performance of these new metrics for capturing variation in functional and phylogenetic composition through simulated metacommunities and illustrated the potential use of these new metrics by analyzing β-diversity of stream fish communities. Our results demonstrated that BD_{Phy} and BD_{Fun} have acceptable type I error and great power to detect the effect of deep evolutionary relationships and attributes mediating patterns of β-diversity. The empirical example illustrates how BD_{Phy} and BD_{Fun} reveal complementary aspects of β-diversity relative to the original BD metric. These new metrics can be used to identify local communities that are of conservation importance because they represent unique functional, phylogenetic and taxonomic compositions. We conclude that BD_{Phy} and BD_{Fun} are important tools for providing complementary information in the investigation of the structure of metacommunities.

Key-words: functional beta diversity, phylogenetic β-diversity, fuzzy sets, local contribution to beta diversity, statistical performance.

Introduction

Since Whitaker's seminal paper (Whittaker 1960), many measures and definitions have been proposed to refer to and operationalize β-diversity. Despite the diversity of mathematical formulations and propositions to operationalize this concept (Anderson et al. 2011 for a review), at the core of any β-diversity metric is the notion that it has the purpose of capturing patterns of variation in community composition (Legendre et al. 2005), which in turn can be used to describe ecological patterns that can shed light on the processes and mechanisms that affect the distribution of species in space and time (Baselga 2010).

Among the plethora of methods to measure β-diversity is the framework called BD_{total} (hereafter only BD) proposed by Legendre & De Cáceres (2013), which deserves special attention due to its computational simplicity and the meaningful components that can be extracted from it. Among the advantages of this method we stress its mathematical independence (the ability to compute β-diversity independently of computing alpha and gama diversity) (Ellisson 2010), as well as the possibility to decompose the total variation present in a metacommunity matrix it into two components: Local Contribution to Beta Diversity (LCBD), which indicates the portion of total variation accounted for by an individual sample/community in a metacommunity, and Species Contribution to Beta Diversity (SCBD), which indicates the contribution of individual species to total BD. Whereas BD can be interpreted as a general measure of β-diversity for a metacommunity, LCBD and SCBD represent, respectivelly, how unique communities and species are in that metacommunity (Legendre and De Cáceres, 2013).

Despite the advantages of the BD framework and its components for revealing ecological patterns in community structure (e.g. Li et al. 2019; Yao et al. 2019), it does not consider variation from other dimensions of biodiversity that could shed light on evolutionary and ecological patterns of species distributions across communities. It is known that traditional taxonomic metrics of β-diversity combined with functional and phylogenetic measures can shed light on the balance between environmental and evolutionary factors affecting the composition of communities (Graham and Fine 2008; Pillar et al. 2009; Pillar and Duarte 2010; Duarte et al. 2016; Safi et al., 2011). Among the practical advantages of considering variation in different dimensions of biodiversity is the possibility of identifying sites that concentrate functional, phylogenetic and taxonomic diversity as being of special interest for conservation proposes (Devictor et al. 2010). Consequently, statistical tools capable of characterizing variation in different components of biological diversity are needed for improving our understanding of factors acting on the structure of metacommunities.

Therefore, in order to join the advantages of the BD framework with the possibility of capturing other components of variation in biological diversity, we show herein how BD can be extended to produce β-diversity metrics that represent phylogenetic and functional dimensions of diversity, while preserving all the advantages of the original BD framework. Specifically, our goals were to: (1) expand the BD framework by deriving two new metrics called BD_{Phy} and BD_{Fun} and their respective components of local and species contributions to β-diversity; (2) test the performance of BD_{Phy}, BD_{Fun} and their local components in capturing variation in metacommunity composition and community uniqueness mediated by the functional and phylogenetic relationship among species; and (3) show how these metrics can be used together to reveal patterns of variation in metacommunities by using as an example a data base for a tropical stream fish metacommunity.

Methods

Expanding the BD framework to include functional and phylogenetic dimensions of biodiversity.

There are two ways to compute BD: directly from a matrix of species composition per site, or from a distance matrix calculated from a species composition matrix using an adequate dissimilarity index. For the sake of simplicity, we will demonstrate how BD can be extended using only the procedure involving distance matrices.

Given a matrix **W** describing *i* sites (rows) by *j* species (columns), the first step consists of redescribing the species occurrence matrix **W** to represent the clade and trait distribution of species across communities (Pillar & Duarte, 2010; Duarte et al., 2016). The redescription of matrix **W** to obtain the two new matrices starts by computing phylogenetic and trait resemblance matrices, $\mathbf{S_p}$ and $\mathbf{S_f}$, based on, phylogenetic tree and species traits, respectively, as shown in Figure 1. The matrices $\mathbf{S_p}$ and $\mathbf{S_f}$ are standardized by their column totals and multiplied by the transposition of matrix **W** (steps 2.1 and 3.1 in Figure 1) to obtain matrix **P** that represents phylogenetic composition and matrix **X** that represents the functional composition of communities. Computing the square root of Bray-Curtis distance for **P** and **X** we obtain, respectively, $\mathbf{D_P}$ and $\mathbf{D_f}$ (steps 2.2 and 3.2 in Figure 1), which describes pairwise distances (D_{hi}) among communities (n) regarding clade and functional composition. These two distance matrices can be used to obtain the total sum of squares ($\mathrm{SS_{total}}$) through Equation 1 and $\mathrm{BD_{Phy}}$ and $\mathrm{BD_{Fun}}$ by applying Equation 2.

$$SStotal = \frac{1}{n}\sum_{h=1}^{n-1}\sum_{i=h+1}^{n}\mathbf{Dp}_{hi}^{2} or\ \mathbf{Df}_{hi}^{2} \qquad \text{Equation 1}$$

$$BD_{\mathrm{Phy}}\ or\ BD_{Fun} = \frac{SS_{total}}{n-1} = Var(\mathbf{P} \text{ or } \mathbf{X}) \quad \text{Equation 2}$$

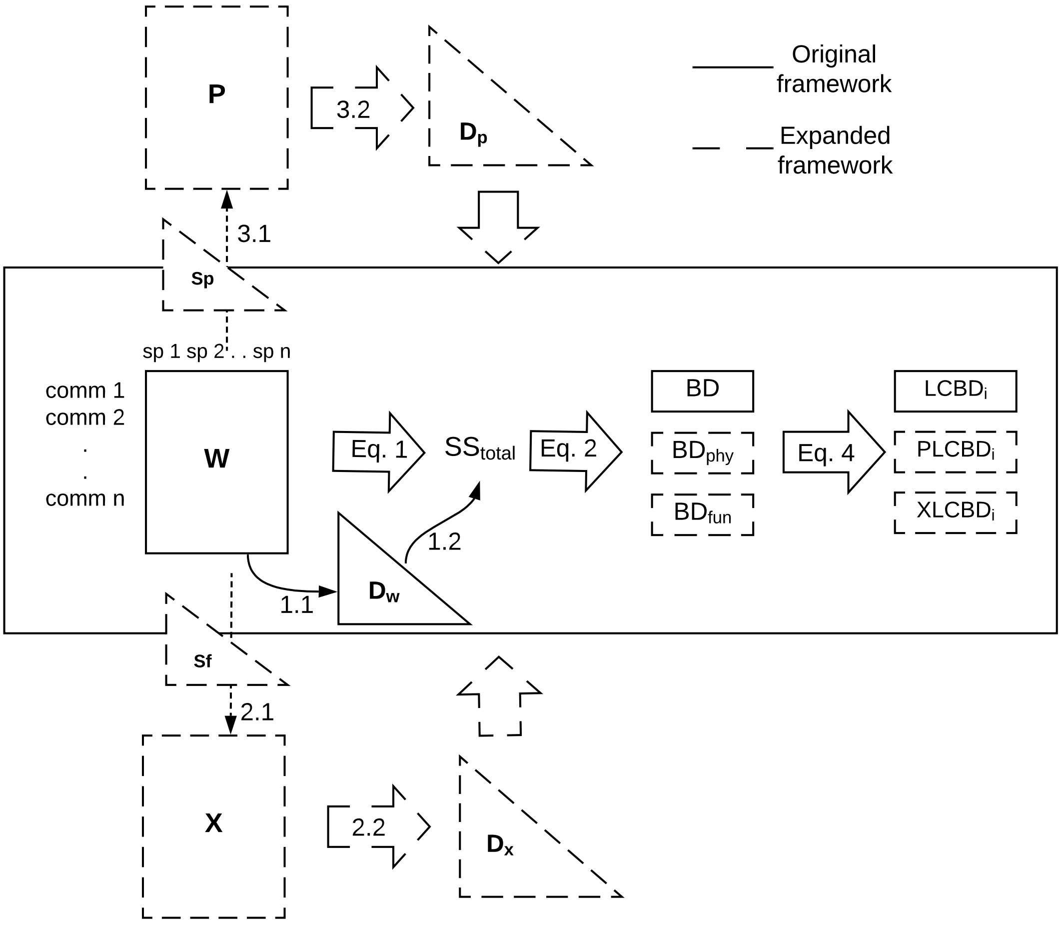


Figure 1: Steps and numerical structures needed extend the BD framework for β-diversity. Solid boxes represent the original numerical structures presented in Legendre & De Cáceres (2013) to calculate BD, while dashed boxes comprise the matrices used in this paper to extend the original framework. The resemblance matrices $\mathbf{S}_\mathbf{f}$ and $\mathbf{S}_\mathbf{p}$ are necessary to obtain two matrices that describe communities by their trait (**X**) and phylogenetic (**P**) composition by means of fuzzy weighting. Distance matrices obtained from **P** and **X** are then used to obtain phylogenetic (PLCBD) or trait-based (XLCBD) measures of local contribution for beta diversity, respectively with the equations indicated in arrows.

The components that represents the phylogenetic and functional local contributions of each community, PLCBD and XLCBD respectively, can be obtained by using the algebra of principal coordinate analysis by computing matrix **A** $(-0.5 * D_{hi}^2)$ and centering it to obtain matrix **G** through Equation 3. In equation 3, 1 is a vector of ones and 1' its transposition.

$$G = (I - \frac{11'}{n})A(I - \frac{11'}{n}) \qquad \text{Equation 3}$$

The diagonal elements of matrix **G** are SS_i values. Thus, dividing each value in the diagonal of **G** by SS_{total} we can obtain a measure that indicates the proportion that each sample unit accounts for of the total variation presented in **P** or **X** (PLCBD and XLCBD, respectively) (Equation 4).

$$PLCBD_i \ or \ XLCBD_i = diag(G)/SS_{total} \qquad \text{Equation 4}$$

More details on how to decompose BD into its components are provided by Legendre and De Cáceres (2013). The contribution of each species to total β-diversity can only be obtained when using calculations directly on matrices **P** and **X**. Thus, we show here only the components of BD_{Phy} and BD_{Fun} associated with the local contribution of communities. Both PLCBD and XLCBD, like LCBD, can be interpreted as measures of community uniqueness regarding clade and functional composition, respectively. Appendix S1 of the Supplementary Material shows how the BD framework can be extended by directly using matrices **P** and **X** to obtain BD_{Phy} and BD_{Fun}, respectively, and all of their components (raw data approach). Figure S1 of the Supplementary Material illustrates how XLCBD and PLCBD can be interpreted using a simple example of a hypothetical metacommunity.

A simulation-based evaluation of BD_{Phy} and BD_{Fun} as measures of phylogenetic and functional β-diversity

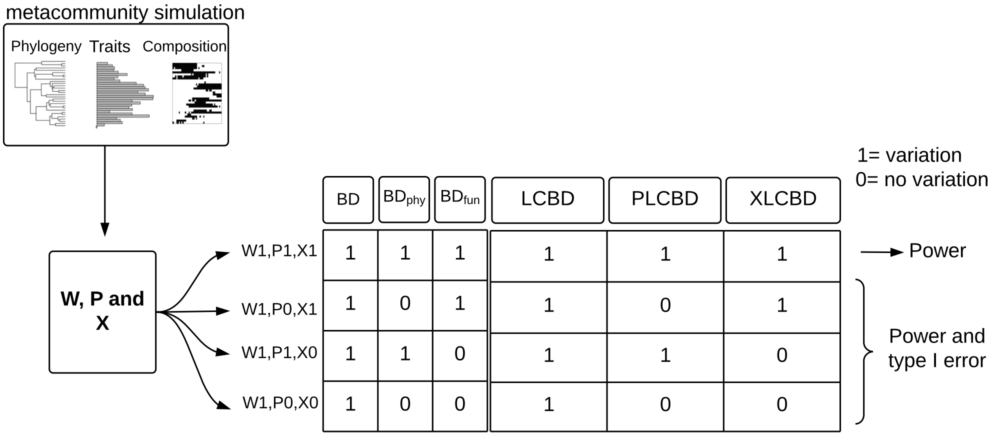
We performed a set of simulations to assess the performance of BD_{Phy}, BD_{Fun} and their respective components, PLCBD and XLCBD, in capturing variation in phylogenetic and functional structure of metacommunities. The simulation procedure is based on the protocol proposed by Peres-Neto et al. (2012) (see also Minchin, 1987 for the original simulation approach), and allows the integration of phylogenetic relationships, species traits, species composition and environmental gradients in different ways to determine if the distribution of attributes of species and clades across communities mediate variation in metacommunity composition in a simulated environmental gradient. The procedure starts with a simulation of a phylogenetic tree and species traits. The presence of a species in a community is determined by a probability function that corresponds to a match between a species trait value and a simulated environmental value for each community.

We simulated four scenarios to test the performance (type I error and power) of the new metrics obtained using the expanded framework for β-diversity: (1) metacommunities in which phylogenetic and functional composition are responsible for variation in metacommunity composition (scenario W1,P1,X1); (2) metacommunities in which only clade composition is responsible for variation in metacommunity composition (scenario W1,P1,X0); (3) metacommunities in which only functional composition is responsible for variation in metacommunity composition (scenario W1,P0,X1); and, finally, (4) metacommunities in which neither clade distribution nor functional composition are responsible for variation in metacommunity composition (scenario W1,P0,X0).

To generate metacommunities according to scenario W1,P1,X1, we simulated a phylogenetic tree in which species presented traits with high phylogenetic signal, so that both trait and phylogenetic composition will vary across the metacommunity. In scenario W1,P1,X0, metacommunities were assembled from a phylogenetic tree in which species traits have phylogenetic signal, however, the trait used to calculate BD_{Fun} and XLCBD was not the same as the one used to assemble the metacommunity, thus, phylogenetic composition must show variation across the metacommunity, but not functional composition. In scenario W1,P0,X1, the metacommunities were assembled from a phylogenetic tree in which species did not present traits with phylogenetic signal, thus, functional composition will vary across the metacommunity, but not phylogenetic composition. Finally, in scenario W1,P0,X0, the metacommunities were assembled from a phylogenetic tree in which species traits did not present phylogenetic signal and the trait used to calculate BD_{Fun} and XLCBD was not the same as the one used to assemble the metacommunities, thus, neither functional nor distribution of clades were responsible for variation in composition across the metacommunity.

All metacommunities were simulated to possess 50 communities with species selected from a pool of 200. The simulation procedure was repeated 999 times for each scenario. Type I error and power for BD_{Fun}, BD_{Phy}, PLCBD and XLCBD were calculated by counting the number of times that the null hypothesis was rejected in each round of the simulation procedure. Each round consisted of: (1) simulating the phylogenetic tree, species traits and metacommunities; (2) calculating BD_{Phy}, BD_{Fun} and the local components PLCBD and XLCBD; (3) running a null model that deconstructs the original phylogenetic and functional relationships among species (taxa shuffle null model, Kembel et al., 2013) and recalculating BD_{Phy}, BD_{Fun}, PLCBD and XLCBD; (4) repeating step 3 three 999 times to assemble a null distribution of metrics; and (5) comparing the observed values of BD_{Phy} and BD_{Fun} with the null distributions of BD_{Phy} and BD_{Fun} using $\alpha = 0.05$ as the nominal error to reject the null hypothesis. To test the performance of the metrics of local contribution, in step 4 we also obtained a F statistic from a linear model that related observed PLCBD and XLCBD with the environmental gradient used in the simulation and compared observed F with a null F distribution obtained from a linear model that relates the null PLCBD and null XLCBD with the environmental gradient. We compared the null F distribution with the observed F, also using the nominal $\alpha = 0.05$ to reject the null hypothesis (illustration of performance analysis is shown in Figure S3 of Appendix 2). More details on simulation procedures, models and theoretical expectations regarding PLCBD and XLCBD are presented in Appendix S2.

A summary of the four scenarios used to test the performance of the metrics proposed in this work is provided in Figure 2. Dimensions that presented variation in metacommunity composition in the simulation process are represented by the number one, while dimensions that did not mediate variation in the simulation process of the metacommunity are represented by a zero. Figure 2 also summarizes which scenarios were used to test power and which were used to test type I error. We did not perform tests of the original BD and LCBD since the statistical behaviors of these metrics were previously tested by Legendre and De Cáceres (2013). For more details about the simulation procedure and methods to obtain F values (models used to assess the performance of PLCBD and XLCBD) see Appendix S2 in Supplementary Material. We also tested the performance of all metrics proposed in this work using the raw data approach (Supplementary material).



	BD	BD$_{phy}$	BD$_{fun}$	LCBD	PLCBD	XLCBD
W1,P1,X1	1	1	1	1	1	1
W1,P0,X1	1	0	1	1	0	1
W1,P1,X0	1	1	0	1	1	0
W1,P0,X0	1	0	0	1	0	0

Figure 2: Schematic representation of all simulation scenarios used to test the metrics proposed in this work. **W** represents a metacommunity that is generated by a simulation process, **P** and **X** represents functional and phylogenetic structure of metacommunity. When a given component of diversity presented variation in the metacommunity we assigned the number 1, on the contrary we attribute 0 in the table. The performance tested with each one of the scenarios (type I, power or both) is specified beside each scenario.

Empirical application: β-diversity of stream fish communities of a tropical river basin

We illustrate how the new metrics proposed here can be used by calculating BD$_{Phy}$, BD$_{Fun}$, PLCBD and XLCBD for tropical stream fish communities located in Brazil. This data comprises a sample of a metacommunity with 173 sites located in the Ivinhema River Basin, which is the main tributary of the Paraná River in the western part of the Paraná River Basin, one of the largest basins in South America. Each site corresponded to a stretch of approximately 100 meters in length and was sampled with the aid of an 80 x

120-cm rectangular sieve with a mesh size of 2mm. Electrofishing was also used at some sites.

We calculated BD, BD_{Phy}, BD_{Fun} and their local components, LCBD, PLCBD and XLCBD, for the 173 sampled sites. The BD metric was calculated using an incidence matrix standardized by the total occurrence of species in a community and subjected to a chord transformation. This standardization was done in order to keep BD, BD_{Phy} and BD_{Fun} on the same scale of variation. We assessed the significance of these metrics using two null models: site shuffle and taxa shuffle. Site shuffle randomizes species occurrence in the metacommunity by shuffling the lines of matrix **W**, with the rejection of the site shuffle null model ($\alpha \leq 0.05$) indicating that the composition of the community differs from that expected by chance. The taxa shuffle null model randomizes the tips of the phylogeny and functional dendrogram and uses these randomized structures to calculate, respectively, matrices **P** and **X**. The rejection of taxa shuffle indicates that the uniqueness of a community is also due to deep evolutionary relationships among the species or their functional attributes.

We performed a correlation analysis among LCBD, PLCBD and XLCBD using Pearson's correlation index, which allowed us to assess which dimensions serve as a proxy to indicate the local contribution of other dimensions. Finally, we represent the three quantities of local contribution spatially through an RGB plot to show how these three components can be used together to identify sites of high importance regarding uniqueness. To generate the RGB plot we first standardize LCBD, PLCBD and XLCBD to vary between 0-250 and attribute to each combination of the three metrics a color in the gradient of RGB system. The redder the color the greater the uniqueness of a community regarding taxonomic composition; the greener the color the greater uniqueness regarding clade composition; the bluer the color the greater the uniqueness regarding functional composition. We also calculated how much each species contributed to β-diversity of Ivinhema River Basin regarding taxonomic (SCBD), phylogenetic (PSCBD) and functional (XSCBD) components (Appendix S4).

More details regarding the sampling design, the phylogenetic hypothesis and traits of the fish metacommunity used to calculate the metrics are provided in Nakamura et al. (2017) and Appendix S4. In Appendix S5 in Supplementary Material we provide the R function used to calculate all the metrics proposed in this work and for testing their significance according to the taxa shuffle null model (Kembel et al. 2013). We suggest that the distance metric to be used for the two metrics proposed here be the square root of Bray-Curtis index, which produces a maximum value of 0.5 for BD_{Phy} and BD_{Fun} for communities with completely different compositions. For the raw data procedure, we suggest the use of chord transformation of matrices **P** and **X** prior to the calculation of BD_{Phy} and BD_{Fun} metrics, which will produce values ranging from 0 to 1.

Results

Performance of metrics

We present here only the results of the simulation analysis for metrics calculated with the distance-based approach, while the results for the raw data approach are provided in Table S1 of Appendix S3 in Supplementary Material. 0 shows the statistical performance (rejection rate, type I error and power) for BD_{Phy}, BD_{Fun}, PLCBD and XLCBD, and the mean R^2 of the linear models relating the simulated environmental gradient to the metrics PLCBD and XLCBD, calculated for the four simulated scenarios. Both BD_{Phy} and BD_{Fun} had acceptable type I error values for all scenarios, with BD_{Phy} having a value of 0.05 for both W1,P0,X0 and W1,P0,X1, and BD_{Fun} presenting a probability of 0.04 for both W1,P0,X0, and W1,P1,X0. Similar results were found for the raw data approach, in which

BD_{Phy} had values of 0.04 and 0.05 in scenarios W1,X0,P0 and W1,X1,P1, respectively, whereas BD_{Fun} had values of 0.05 for both W1,X0,P0 and W1,X0,P1(Table S1 of Appendix S3 in Supplementary Material). Both BD_{Phy} and BD_{Fun} presented high values for power for all scenarios tested (ranging from 0.99 to 1).

PLCBD had a type I error rate of 0.04 in both W1,P0,X0 and W1,P0,X1, whereas XLCBD had type I error rates of 0.04 and 0.05 for W1,P0,X0 and W1,P1,X0, respectively. Both PLCBD and XLCBD had high rates of power ranging from 0.66 to 1. The lowest power value was obtained for PLCBD in scenario W1,P1,X1 for both the distance-based and raw data approaches (0.66 for both).

Table 1: Statistical performance — type I error (alpha 0.05) and power — of BD_{Fun} and BD_{Phy} and their components XLCBD and PLCBD, calculated with the distance-based approach.

Scenario	BD_{Phy}	BD_{Fun}	PLCBD					XLCBD				
	Rejection rate	Rejection rate	Mean R^2	TI site	TI taxa	Pw site	Pw taxa	Mean R^2	TI site	TI taxa	Pw site	Pw taxa
W1,P0,X0	0.05	0.04	0.54±0.18	0.98	0.04	-	-	0.25±0.15	0.84	0.04	-	-
W1,P1,X0	0.99	0.04	0.83±0.20	-	-	0.99	0.85	0.26±0.20	0.72	0.05	-	-
W1,P0,X1	0.05	1	0.54±0.17	0.98	0.04	-	-	0.90±0.05	-	-	1	0.99
W1,P1,X1	0.99	1	0.59±0.14	-	-	0.99	0.66	0.64±0.10	-	-	1	0.96

Scenario - scenarios used to simulate metacommunities. The meaning of each scenario is explained in the Methods section of the main text; TI site = type I error for site shuffle procedure; TI taxa = type I error for taxa shuffle procedure; Pw site = statistical power for site shuffle procedure; Pw taxa = statistical power for taxa shuffle procedure.

Application of extended framework to stream fish communities.

BD, BD_{Phy} and BD_{Fun} presented values of, respectively, 0.38, 0.09 and 0.01 for the stream fish metacommunity of Ivinhema River Basin. BD_{Fun} and BD_{Phy} did not differ significantly from expected values of the taxa shuffle null model (p-values > 0.05). The contribution of local communities ranged from 0.003 to 0.009 for LCBD and 0.002 to 0.02 for both PLCBD and XLCBD. Regarding uniqueness in composition, 23 communities presented significant values for the site shuffle null model for LCBD, 26 for PLCBD and 45 for XLCBD. Of the 26 significant values for PLCBD, 11 were also significant for taxa shuffle, indicating the effects of deep evolutionary relationships in phylogenetic uniqueness of these communities. For XLCBD, 15 communities (from the 45 that presented significant p-values for site shuffle) presented significant values for the taxa shuffle null model. Communities that presented significant values for PLCBD and XLCBD for site and taxa shuffle are represented in Figure 3 by, respectively, crossed circles and triangles.

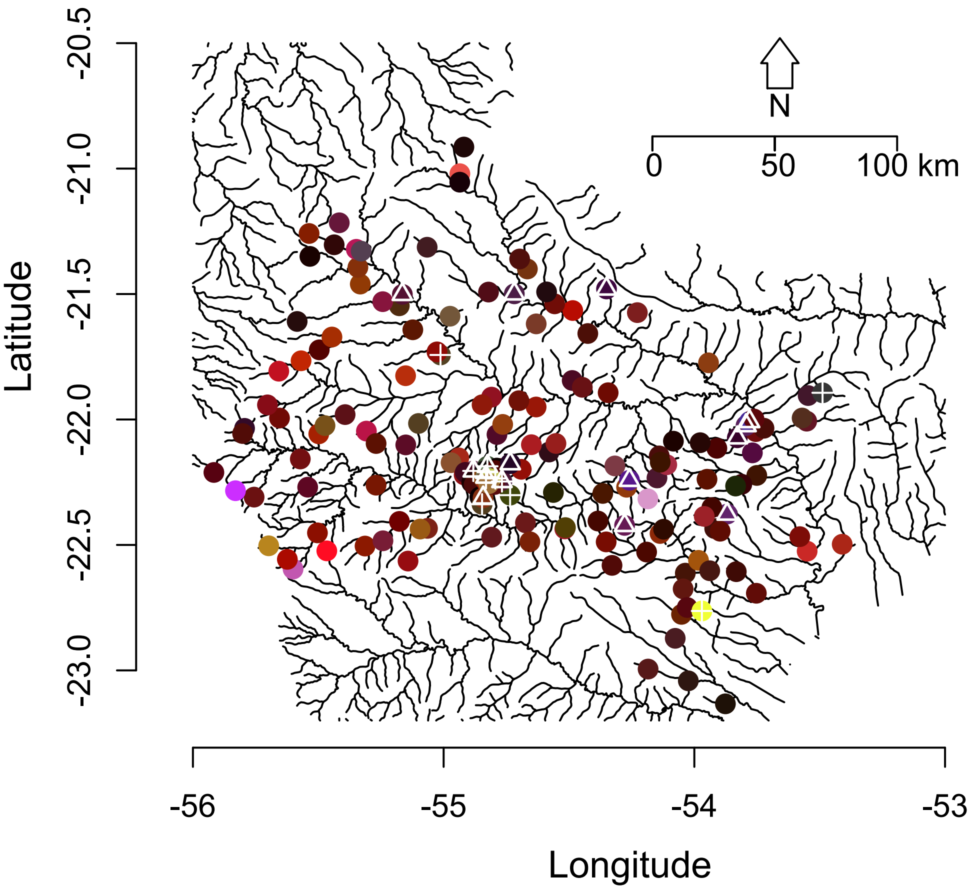


Figure 3: Map showing the distribution of LCBD, PLCBD and XLCBD values for fish communities of Ivinhema River Basin. Each point represents a combination of values of local contribution for the three dimensions. The redder the color the greater the uniqueness of a community regarding taxonomic composition; the greener the color the greater uniqueness regarding clade composition; the bluer the color the greater the uniqueness regarding functional composition. Communities that presented significant values for PLCBD and XLCBD for site and taxa shuffle are represented by points with, respectively, crossed circles and triangles.

All local components presented low correlation among each other, with the highest correlation found being for LCBD and PLCBD (ρ= 0.46; p-value < 0.001). This lack of correspondence among components of local contribution can also be noted in Figure 3. Figure 3 shows a predominance of a combination of low values for PLCBD, XLCBD and PLCBD (circles with black color), indicating the predominance of communities with low uniqueness. Only a few communities presented high values for at least one component, with LCBD being the component with more communities with high uniqueness regarding taxonomic composition (represented by red circles). The presence of high values for two components is even more rare among the communities analyzed, indicating that is very rare for the communities of Ivinhema River Basin to host unique species, clades or species that present very distinct attributes. In Appendix S4 we also show the contribution of each species for Beta diversity of metacommunity.

Discussion

We demonstrated that the BD framework proposed by Legendre and De Cáceres (2013) can be effectively extended to accommodate other components of biodiversity. The extension presented here incorporates the advantages of the original BD framework (decomposition into meaningful components of local and species contributions) while at the same time effectively assessing β-diversity for phylogenetic and functional dimensions of biodiversity, as shown by the performance analysis of the metrics.

As far as we are aware, the extension proposed in this work is the most general in literature, since other propositions that seek to expand Legendre and De Cáceres´ framework lack some important characteristics presented in the original proposition. Shooner et al. (2018) proposed a phylogenetic informed LCBD (also named as PLCBD) by using a phylogenetic distance matrix containing PhyloSor values (Bryant et al. 2009) for calculating LCBD. Since the use of a phylogenetic distance matrix among sites only allows BD to be decomposed into the local contribution component, it is not possible to obtain the portion of BD that accounts for species contribution to the total variation of the metacommunity (SCBD component). The use of the fuzzy weighting method together with Legendre and De Cáceres´ equations allows phylogenetic and functional informed BD and all of its components to be derived, since the calculations can be made using both distance and raw data approaches (using directly matrix **P** or **X**). Besides the generality presented in our extension, we also highlight its flexibility, to obtaining new β-diversity measures that capture other dimensions of biological diversity. For example, a matrix containing genetic distances among species can be used in fuzzy-weight transformation to obtain the genetic composition of sites (e.g. see Duarte et al., 2018), which in turn can be used to compute a genetic informed BD measure and its components. Therefore, the method presented here can be viewed as a unified approach that allows the derivation of a family of β-diversity metrics with the same mathematical characteristics yet encompassing different components of biological diversity.

The new local component metrics, PLCBD and XLCBD, can provide interesting tools to address questions in the investigation of patterns of organization of metacommunities. PLCBD can be used to identify patterns of variation present in the phylogenetic structure of metacommunities related to sites that host clades with unique evolutionary history. This information can be useful to test hypothesis that seek to understand how the degree of phylogenetic uniqueness of sites is related to environmental or historical factors (Graham & Fine, 2008; Leibold et al, 2010). Other methods, like PCPS (Duarte, 2011), can also be used to identify distinct sites regarding phylogenetic composition (heuristically, accompanied by an ordination procedure), however, PLCBD offers a more direct assessment of community uniqueness together with hypothesis testing to evaluate the role of species composition and deep evolutionary relationships in generating observed patterns of phylogenetic uniqueness (through site and taxa shuffle null models).

Regarding practical applications of PLCBD and XLCBD, we highlight their utility for conservation purposes by identifying sites that deserve special attention due to uniqueness in species composition, evolutionary history and functional attributes. In this way they serve as complementary measures for studies that use local uniqueness based solely from a taxonomic perspective (e.g. Landeiro et al. 2018). An integrative approach that addresses multiple dimensions of variation in biological diversity can be used to identify areas of congruence or mismatches in the distribution of biological diversity, which can influence decisions made in conservation plans to preserve regional biotas (Devictor et al. 2010; Meynard et al. 2011).

Our empirical example using a stream fish metacommunity illustrates how to link patterns of variation in β-diversity related to taxonomic, phylogenetic and functional diversity. Our findings complement those of Súarez et al (2011), by evidencing that the processes influencing the distribution of species in the upper Ivinhema River Basin are mainly mediated by variation in species composition and contemporary environmental factors, with the deep evolutionary history of the species having less impact on the structure of this metacommunity. By mapping LCBD, PLCBD and XLCBD we can see that only a few sites possess unique compositions of species, clades and attributes. Our multifaceted approach for beta diversity illustrates how these three metrics can be used together to help identify areas of special conservation interest (e.g., Devictor et al. 2010; Landeiro et al. 2018). The lack of a spatial pattern in local contribution indicates that the communities have very similar importance for the maintenance of the entire β-diversity of the Ivinhema River Basin.

Concluding remarks and future directions

We move forward in the operationalization of β-diversity patterns by presenting a simple way to extend the BD framework in order to derive effective phylogenetic and functional β-diversity measures. The methods used in this work to extend the original framework are general enough to be used as a basis to obtain other metrics that can represent other dimensions of biological diversity while at the same time preserve the unique advantages presented in the original BD framework.

Authors' contributions

GN and LD conceived the idea, performed the analysis and wrote manuscript. WV and YRS collected the data for stream fish communities and species traits, and constructed the phylogenetic hypothesis used in this study.

Acknowledgements

Research of LD and GN was conducted in the context of the National Institute for Science and Technology (INCT) in Ecology, Evolution and Biodiversity Conservation, supported by MCTIC/CNPq (proc. 465610/2014-5) and FAPEG (proc. 201810267000023). Research activities of LD was supported by a CNPq Productivity Fellowship (grant 307527/2018-2).

References

Anderson MJ, Crist TO, Chase JM, et al (2011) Navigating the multiple meanings of beta diversity: A roadmap for the practicing ecologist. Ecol Lett 14:19–28. doi: 10.1111/j.1461-0248.2010.01552.x

Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. Glob Ecol Biogeogr 19:134–143. doi: 10.1111/j.1466-8238.2009.00490.x

Bryant JA, Lamanna C, Morlon H, et al (2009) Microbes on mountainsides: Contrasting elevational patterns of bacterial and plant diversity. Light Evol 2:127–148. doi: 10.17226/12501

Devictor V, Mouillot D, Meynard C, et al (2010) Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: The need for integrative conservation strategies in a changing world. Ecol Lett 13:1030–1040. doi: 10.1111/j.1461-0248.2010.01493.x

Duarte LDS (2011) Phylogenetic habitat filtering influences forest nucleation in grasslands. Oikos 120:208–215. doi: 10.1111/j.1600-0706.2010.18898.x

Duarte LDS, Debastiani VJ, Freitas AVL, Pillar VD (2016) Dissecting phylogenetic fuzzy weighting: theory and application in metacommunity phylogenetics. Methods Ecol Evol 7:937–946. doi: 10.1111/2041-210X.12547

Duarte LDS, Lima J de S, Maestri R, et al (2018) HaploVectors: an integrative analytical tool for phylogeography. 1–21. doi: https://doi.org/10.1101/330761

Ellisson AM (2010) Partitioning diversity. Ecology 91:1988–1992. doi: 10.1890/09-1692.1

Graham CH, Fine PVA (2008) Phylogenetic beta diversity : linking ecological and evolutionary processes across space in time. doi: 10.1111/j.1461-0248.2008.01256.x

Kembel ASW, Ackerly DD, Blomberg SP, et al (2013) Package ‘ picante ’

Landeiro VL, Franz B, Heino J, et al (2018) Species-poor and low-lying sites are more ecologically unique in a hyperdiverse Amazon region: Evidence from multiple taxonomic groups. Divers Distrib 1–12. doi: 10.1111/ddi.12734

Legendre P, Borcard D, Peres-Neto P (2005) Analyzing Beta Diversity: Partitioning the spatial variation of community composition data. Ecol Monogr 75:435–450

Legendre P, De Cáceres M (2013) Beta diversity as the variance of community data: Dissimilarity coefficients and partitioning. Ecol Lett 16:951–963. doi: 10.1111/ele.12141

Leibold MA, Economo EP, Peres-Neto P (2010) Metacommunity phylogenetics: Separating the roles of environmental filters and historical biogeography. Ecol Lett 13:1290–1299. doi: 10.1111/j.1461-0248.2010.01523.x

Li K, Liao M, Ni J, et al (2019) Treeline composition and biodiversity change on the southeastern Tibetan Plateau during the past millennium, inferred from a high-resolution alpine pollen record. Quat Sci Rev 206:44–55. doi: 10.1016/j.quascirev.2018.12.029

Meynard CN, Devictor V, Mouillot D, et al (2011) Beyond taxonomic diversity patterns: How do α, β and γ components of bird functional and phylogenetic diversity respond to environmental gradients across France? Glob Ecol Biogeogr 20:893–903. doi: 10.1111/j.1466-8238.2010.00647.x

Minchin PR (1987) Simulation of Multidimensional Community Patterns : Towards a Comprehensive Model. Vegetatio 71:145–156. doi: 10.1007/BF00039167

Nakamura G, Vicentin W, Súarez YR (2017) Functional and phylogenetic dimensions are more important than the taxonomic dimension for capturing variation in stream fish communities. Austral Ecol 1–11. doi: 10.1111/aec.12529

Peres-Neto P-R, Leibold M, Dray S (2012) Assessing the effects of spatial contingency and environmental filtering on metacommunity phylogenetics. Ecology 93:14–30. doi: 10.1890/11-0494.1

Pillar VD, Duarte LDS (2010) A framework for metacommunity analysis of phylogenetic structure. Ecol Lett 13:587–596. doi: 10.1111/j.1461-0248.2010.01456.x

Pillar VD, Duarte LDS, Sosinski EE, Joner F (2009) Discriminating trait-convergence and trait-divergence assembly patterns in ecological community gradients. J Veg Sci 20:334–348. doi: 10.1111/j.1654-1103.2009.05666.x

Safi K, Cianciaruso M V, Loyola RD, et al (2011) Understanding global patterns of mammalian functional and phylogenetic diversity. Philos Trans R Soc Lond B Biol Sci 366:2536–2544. doi: 10.1098/rstb.2011.0024

Shooner S, Davies TJ, Saikia P, et al (2018) Phylogenetic diversity patterns in Himalayan forests reveal evidence for environmental filtering of distinct lineages. Ecosphere 9:. doi: 10.1002/ecs2.2157

Whittaker RH (1960) Vegetation of the Siskiyou montains, Oregon and California. Ecol Monogr 30:279–338

Yao J, Zhang C, De Cáceres M, et al (2019) Variation in compositional and structural components of community assemblage and its determinants. J Veg Sci 30:257–268. doi: 10.1111/jvs.1270

Considerações finais e conclusão

Neste trabalho contribuímos em três principais aspectos relacionados ao estudo da biodiversidade. Primeiro, identificando um problema presente no primeiro passo para caracterização da biodiversidade, que consiste na escolha das métricas (Magurran, 2004; Magurran and McGill, 2011). Ao contrário das recomendações que apontam para o uso de métricas complementares (e.g. Lamb et al., 2009; Lyashevska and Farnsworth, 2012), mostramos no Capítulo 1 o predomínio da utilização de métricas redundantes para caracterização da biodiversidade em comunidades biológicas. A utilização de métricas redundantes pode, na prática, resultar na subestimação da informação presente nas comunidades (Farnsworth et al., 2012), sendo necessária uma mudança na forma em que métricas de diversidade são escolhidas, prezando por aquelas que capturam porções complementares da biodiversidade.

A segunda contribuição consiste na ampliação do modelo conceitual e operacional utilizado para quantificação da dimensionalidade da biodiversidade. Revelamos que para uma quantificação efetiva da dimensionalidade, é necessário considerar dois aspectos: a correlação entre as métricas de diversidade bem como a variação que cada uma delas apresenta no espaço multidimensional que caracteriza a biodiversidade. Apesar dos avanços pioneiros de Wilsey et al. (2005) seguidos por Lyashevska e Farnsworth (2012) e mais recentemente por Stevens e Gavilanez (2015) e Stevens e Tello (2018, 2014), nenhum destes autores promove uma união entre o componente de correlação e de variação para uma quantificação efetiva da dimensionalidade biológica. Portanto, promovemos a unificação dos métodos para quantificação da dimensionalidade, de modo que nossa proposta avança tanto no aspecto teórico sobre o conceito de dimensionalidade (agora composta por correlação e variação) como no aspecto operacional (através do arcabouço analítico composto pela obtenção de EE e IV). O novo arcabouço para mensuração da dimensionalidade possibilita a resolução do paradoxo da diversidade, visto que possibilita a identificação das dimensões importantes para capturar a variação da biodiversidade através das métricas de diversidade.

Por fim, propomos novas formas de quantificação da diversidade ao desenvolvermos uma família de métricas capazes de capturar padrões de diversidade Beta taxonômica, funcional e filogenética de metacomunidades. Estendemos as vantagens presentes no arcabouço analítico de Legendre e De Cáceres (2013) (p.ex. independência matemática da diversidade alpha, decomposição da variação total em componentes) com auxílio dos métodos de grupos difusos (Duarte et al., 2016; Pillar and Duarte, 2010; Zadeh, 1965) para obter métricas de diversidade beta que podem revelar padrões de variação na biodiversidade não contemplados na proposta original de Legendre e De Cáceres (2013). As novas métricas obtidas possibilitam, por exemplo, a quantificação da importância de locais em uma metacomunidade para manutenção da composição funcional, filogenética e taxonômica destas metacomunidades. Outra inovação é a possibilidade de obtenção de valores que indiquem a importância das espécies para a manutenção da variação presente na metacomunidade, que por sua vez também pode ser quantificada considerando as dimensões funcional, filogenético e taxonômica da diversidade Beta.

Direções futuras

Nesta seção destaco possibilidades de estudos que podem ser desenvolvidos a partir dos avanços teóricos e metodológicos obtidos nesta tese. Primeiramente ressalto a necessidade da busca por modelos mecanísticos capazes de relacionar fatores ecológicos e evolutivos com padrões de dimensionalidade de comunidades biológicas, que podem ser obtidos a partir do método proposto no Capítulo 2. Em seguida apresento caminhos para derivação de outras métricas de diversidade beta utilizando o arcabouço metodológico proposto no Capítulo 3 desta tese.

Dimensionalidade: indo além da descrição de padrões

O estudo realizado por Tucker e Cadotte (2013) propõe uma unificação entre medidas de diversidade, porém se restringe a comparação de apenas duas dimensões: riqueza e diversidade filogenética. Apesar de revelar como fatores ecológicos (representados por autocorrelação espacial) e evolutivos (representado por diversificação recente ou profunda e balanço da filogenia) podem influenciar na correlação entre estas dimensões, defendemos que um arcabouço analítico capaz de unificar as métricas de diversidade de maneira efetiva deve abranger outras dimensões da diversidade bem como a utilizar métodos de quantificação da dimensionalidade que abranjam não só o componente de correlação, mas também o componente de variação, tal como demonstrado no Capítulo 2 desta tese.

Aliando a investigação de fatores ecológicos e evolutivos (incluindo modelos de evolução de atributos) tal como realizada por Tucker e Cadotte (2013), através dos métodos de dimensionalidade aqui propostos podemos compreender como tais fatores moldam os padrões de biodiversidade e dimensionalidade. A Figura 1 apresenta possíveis cenários de dimensionalidade considerando os componentes levados em consideração no Capítulo 2, além de possíveis fatores que podem gerar tais cenários de dimensionalidade.

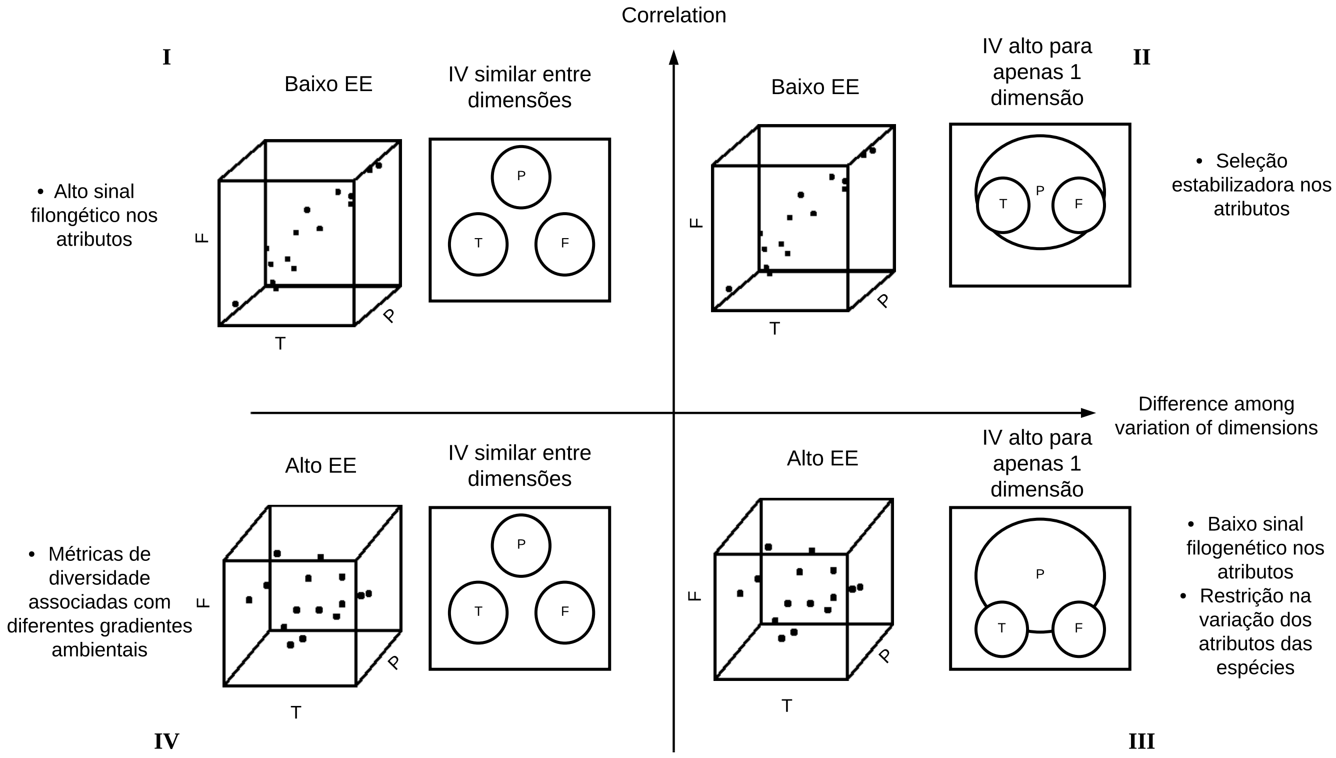


Figura 1: Representação esquemática de diferentes cenários envolvendo o arcabouço metodológico para avaliação da dimensionalidade. Cada letra no interior das caixas indica uma dimensão da biodiversidade (F, T e P – funcional, taxonômica e filogenética, respectivamente). Os gráficos de pontos ilustram o padrão de correlação entre as métricas, enquanto que as caixas ilustram a quantidade de variação que cada métrica de diversidade apresenta no espaço total da biodiversidade. O eixo da abscissa corresponde ao componente de correlação, enquanto a ordenada indica o componente de variação. O quadrante IV compreende o cenário de maior dimensionalidade por apresentar baixa correlação entre as métricas e cada métrica apresentar uma porção semelhante de variação do total. Por outro lado, o quadrante II apresenta a menor dimensionalidade. Ao lado de cada quadrante listamos possíveis fatores que podem gerar os padrões de dimensionalidade.

Os quatro padrões de dimensionalidade apresentados na Figura 1 representam apenas uma amostra das possíveis combinações que os componentes de correlação e variação podem apresentar, oferecendo um ponto de partida para levantarmos possíveis fatores capazes de gerar tais padrões. Por exemplo, o cenário presente no quadrante IV é esperado quando diferentes dimensões da diversidade estão associadas com diferentes fatores ambientais (e.g. Safi et al., 2011), consequentemente, uma alta dimensionalidade na biodiversidade também estaria acompanhada por uma alta dimensionalidade nas características ambientais (Stevens and Tello, 2018). Esta situação pode ser evidenciada através de altos valores de EE e IV semelhante entre as métricas de diversidade utilizadas. A situação oposta, de baixa dimensionalidade, ilustrada pelo cenário II, pode corresponder a uma situação em que as diferentes dimensões da diversidade sejam influenciadas pelos mesmos fatores (possível resultado de alta correlação espacial fatores ambientais) (Tucker e Cadotte, 2014), em conjunto com processos evolutivos de seleção estabilizadora dos atributos, restringindo a variação da diversidade funcional e taxonômica em uma amplitude restrita da variação filogenética (Diniz-Filho, 2004). Nesta situação esperamos valores baixos de EE (alta correlação entre as métricas) e valores de IV mais altos para métricas que indiquem diversidade filogenética em relação a métricas que reflitam a dimensão funcional.

Perspectivas práticas para a dimensionalidade

Como já foi destacado nas seções anteriores, o primeiro passo no processo de caracterização da biodiversidade consiste na decisão de quais métricas de diversidade serão utilizadas. Porém, raramente sabemos a priori quais destas métricas são os melhores descritores da biodiversidade contida no sistema que estamos investigando. A análise da literatura nos mostra que é comum a opção por métricas que apresentem vantagens práticas de quantificação, são intuitivas ou ainda historicamente bem estabelecidas, por exemplo a riqueza de espécies (Purvis and Hector, 2000), mesmo não correspondendo as mais efetivas na descrição da biodiversidade (Lyashevska e Farnsworth, 2012; Wilsey et al., 2005). Desta maneira, de que forma podemos garantir que as métricas escolhidas para caracterização da diversidade biológica capturam de maneira efetiva a informação presente na comunidade? Ou, quanta variação é perdida quando utilizado um dado conjunto de métricas e não outras? A resposta para tais questões deve passar por uma escolha de métricas que possibilita, de maneira objetiva, quantificar os ganhos e perdas ao decidir por um conjunto de métricas de diversidade em detrimento de outras. Neste sentido, o arcabouço analítico proposto no Capítulo 2 pode servir para sustentar decisões que envolvem a escolha de métricas de diversidade, visto que possibilita quantificar diretamente o conjunto mínimo de dimensões necessárias para descrever de forma efetiva a diversidade (EE) bem como quantificar a importância de cada métrica de diversidade para capturar a informação nela contida (IV).

Partindo do conhecimento prévio de que a biodiversidade pode ser representa por três dimensões de variação (Lyashevska e Farnsworth, 2012), um conjunto de métricas que representem cada uma destas três dimensões pode ser elencado, e a partir de subconjuntos de métricas (diferentes matrizes **M**) podemos quantificar tanto o componente de correlação (representado por EE) e variação (representada por IV) destas, buscando por valores que minimizam a correlação entre métricas (valores altos de EE) e maximizam a variação de cada métrica no espaço multidimensional (que pode ser representado pela equitabilidade de valores de IV entre as métricas).

Expandindo as possibilidades para quantificação da diversidade Beta

A nova família de métricas de diversidade Beta proposta no Capítulo 3, além de possibilitar a mensuração de aspectos da variação da biodiversidade em diferentes escalas (espécies, unidades amostrais e metacomunidades) e em diferentes dimensões da diversidade (funcional, filogenético e taxonômico), abre caminho para a estruturação de um arcabouço analítico capaz de integrar diferentes dimensões de variação da diversidade Beta. Visto que as métricas apresentadas no Capítulo 3 (BD_{Phy}, BD_{Fun}) são obtidas a partir de uma simples modificação da matriz de distância utilizada para ponderação da matriz de composição de espécies, podemos utilizar uma matriz de similaridade que caracterize outras dimensões de variação da biodiversidade que não foram contempladas em nosso estudo. Por exemplo, Duarte et al. (2018) demonstra como uma matriz que descreve a similaridade genética entre populações pode ser obtida a partir da informação proveniente de redes de haplótipos ou polimorfismo de base única (SNPs). Esta matriz de similaridade poderia ser utilizada no arcabouço metodológico presente na Figura 1 do Capítulo 3 para obtenção da variação genética presente em metapopulações/metacomunidades. Portanto, a flexibilidade do arcabouço analítico proposto no Capítulo 3 pode ser facilmente estendido para obtenção de medidas de diversidade beta que capturem outras dimensões da biodiversidade.

REFERÊNCIAS BIBLIOGRÁFICAS

Cianciaruso, M.V., Silva, I.A., Batalha, M.A., 2009. Diversidades filogenética e funcional: novas abordagens para a Ecologia de comunidades. Biota Neotrop. 9, 93–103. https://doi.org/10.1590/S1676-06032009000300008

Colwell, R., 2000. The mid-domain effect: geometric constraints on the geography of species richness. Trends Ecol. Evol. 15, 70–76. https://doi.org/10.1086/382056

Colzani, E., Siqueira, T., Suriano, M.T., Roque, F.O., 2013. Responses of aquatic insect functional diversity to landscape changes in Atlantic forest. Biotropica 45, 343–350. https://doi.org/10.1111/btp.12022

Diniz-Filho, J.A.F., 2004. Phylogenetic diversity and conservation priorities under distinct models of phenotypic evolution. Conserv. Biol. 18, 698–704. https://doi.org/10.1111/j.1523-1739.2004.00260.x

Duarte, L.D.S., Debastiani, V.J., Freitas, A.V.L., Pillar, V.D., 2016. Dissecting phylogenetic fuzzy weighting: theory and application in metacommunity phylogenetics. Methods Ecol. Evol. 7, 937–946. https://doi.org/10.1111/2041-210X.12547

Duarte, L.D.S., Lima, J. de S., Maestri, R., Debastiani, V., Collevatti, R.G., 2018. HaploVectors: an integrative analytical tool for phylogeography 1–21. https://doi.org/https://doi.org/10.1101/330761

Faith, D.P., 1992. Conservation evaluation and phylogenetic diversity. Biol. Conserv. 61, 1–10. https://doi.org/10.1016/0006-3207(92)91201-3

Farnsworth, K.D., Lyashevska, O., Fung, T., 2012. Functional complexity: The source of value in biodiversity. Ecol. Complex. 11, 46–52. https://doi.org/10.1016/j.ecocom.2012.02.001

Lamb, E.G., Bayne, E., Holloway, G., Schieck, J., Boutin, S., Herbers, J., Haughland, D.L., 2009. Indices for monitoring biodiversity change: Are some more effective than others? Ecol. Indic. 9, 432–444. https://doi.org/10.1016/j.ecolind.2008.06.001

Legendre, P., Borcard, D., Peres-Neto, P., 2005. Analyzing Beta Diversity: Partitioning the spatial variation of community composition data. Ecol. Monogr. 75, 435–450.

Legendre, P., De Cáceres, M., 2013. Beta diversity as the variance of community data: Dissimilarity coefficients and partitioning. Ecol. Lett. 16, 951–963. https://doi.org/10.1111/ele.12141

Legendre, P., De Cáceres, M., 2013. Beta diversity as the variance of community data: Dissimilarity coefficients and partitioning. Ecol. Lett. 16, 951–963. https://doi.org/10.1111/ele.12141

Lyashevska, O., Farnsworth, K.D., 2012. How many dimensions of biodiversity do we need? Ecol. Indic. 18, 485–492. https://doi.org/10.1016/j.ecolind.2011.12.016

Magurran, A.E., 2004. Measuring biological diversity.

Magurran, A.E., McGill, B.J. (Eds.), 2011. Biological diversity frontiers in measurement and assessment. Oxford University Press.

Ouchi-Melo, L.S., Meynard, C.N., Gonçalves-Souza, T., de Cerqueira Rossa-Feres, D., 2018. Integrating phylogenetic and functional biodiversity facets to guide conservation: a case study using anurans in a global biodiversity hotspot. Biodivers. Conserv. 27, 3247–3266. https://doi.org/10.1007/s10531-018-1600-4

Petchey, O.L., Gaston, K.J., 2006. Functional diversity: Back to basics and looking forward. Ecol. Lett. 9, 741–758. https://doi.org/10.1111/j.1461-0248.2006.00924.x

Pillar, V.D., Duarte, L.D.S., 2010. A framework for metacommunity analysis of phylogenetic structure. Ecol. Lett. 13, 587–596. https://doi.org/10.1111/j.1461-0248.2010.01456.x

Purvis, A., Hector, A., 2000. Getting the measure of biodiversity. Nature 405, 212.

Rahbek, C., 2005. The role of spatial scale and the perception of large-scale species-richness patterns. Ecol. Lett. 8, 224–239. https://doi.org/10.1111/j.1461-0248.2004.00701.x

Ricotta, C., 2005. Through the jungle of biological diversity. Acta Biotheor. 53, 29–38. https://doi.org/10.1007/s10441-005-7001-6

Rousseau, R., Van Hecke, P., Nijssen, D., Bogaert, J., 1999. The relationship between diversity profiles, evenness and species richness based on partial ordering. Environ. Ecol. Stat. 6, 211–223. https://doi.org/10.1023/A:1009626406418

Safi, K., Cianciaruso, M. V, Loyola, R.D., Brito, D., Armour-Marshall, K., Diniz-Filho, J.A.F., 2011. Understanding global patterns of mammalian functional and phylogenetic diversity. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 366, 2536–2544. https://doi.org/10.1098/rstb.2011.0024

Saito, V.S., Siqueira, T., Fonseca-Gessner, A.A., 2015. Should phylogenetic and functional diversity metrics compose macroinvertebrate multimetric indices for stream biomonitoring? Hydrobiologia 745, 167–179. https://doi.org/10.1007/s10750-014-2102-3

Stevens, R.D., Gavilanez, M.M., 2015. Dimensionality of community structure: phylogenetic, morphological and functional perspectives along biodiversity and environmental gradients. Ecography (Cop.). 38, 861–875. https://doi.org/10.1111/ecog.00847

Stevens, R.D., Tello, J.S., 2014. On the measurement of dimensionality of biodiversity. Glob. Ecol. Biogeogr. n/a-n/a. https://doi.org/10.1111/geb.12192

Stevens, R.D., Tello, J.S., 2018. A latitudinal gradient in dimensionality of biodiversity. Ecography (Cop.). 1–11. https://doi.org/10.1111/ecog.03654

Tucker, C.M., Cadotte, M.W., 2013. Unifying measures of biodiversity: understanding when richness and phylogenetic diversity should be congruent. Divers. Distrib. 19, 845–854. https://doi.org/10.1111/ddi.12087

Webb, C.O., Ackerly, D.D., McPeek, M. a., Donoghue, M.J., 2002. Phylogenies and Community Ecology. Annu. Rev. Ecol. Syst. 33, 475–505. https://doi.org/10.1146/annurev.ecolsys.33.010802.150448

Wilsey, B.J., Chalcraft, D.R., Bowles, C.M., Willig, M.R., 2005. Relationships among indices suggest that richness is an incomplete surrogate for grassland biodiversity. Ecology 86, 1178–1184. https://doi.org/10.1890/04-0394

Zadeh, L. a., 1965. Fuzzy sets. Inf. Control 8, 338–353. https://doi.org/10.1016/S0019-9958(65)90241-X

ANEXOS E APÊNDICES

Apêndice introdução

Tabela S1: Estudos que utilizaram uma abordagem integrada para investigação da biodiversidade utilizando o modelo operacional de Ricotta.

Estudo	Grupo biológico	Relação entre as métricas investigadas por:
Stevens and Tello (2014)	morcegos	Correlação (EE)
Stevens and Gavillanez (2015)		Correlação (EE)
Wilsey et al. (2005)	Vegetação campestre	Variação (IV)
Lyashevska and Farnsworth (2012)	Comunidades bênticas	Correlação e variação
Naeem et al. (2016)	plantas	
Stevens and Tello (2018)	morcegos	Correlação
Tucker and Cadotte (2013)	Comunidades simuladas	Correlação
Gallardo et al. (2011)	invertebrados	correlação

Apêndice capítulo 1

Table S1: Metrics that make up the groups formed in co-metric analysis with their respective original reference or an example of application and the abbreviation of the metric. The abbreviation correspond to the same used in Figure 2 of main text.

Indices	Refference (proposer of index or an example of utilization)	Abbreviation/Simbol(if exist)
Taxonomic dimension		
Beta diversity indices		
Berger-Parker	Sheldon and Thoms (2006)	D
Dominance indices	Berger and Parker (1970)	
Estability		
Fisher's alpha	Beck et al. (2006)	$Fischer's\ \alpha$
Hilsenhoff Biotic Index	Waite et al. (2004)	HBI
Margalef	Sheldon and Thoms (2006)	D_{mg}
Menhinick	Sheldon and Thoms (2006)	D_{mn}
Rarity indexes	Renio et al (2008)	
Richness		
Shannon	Korallo et al. (2007)	$H^{'}$
Simpson	Martínez et al.	D
Total diversity	Desrochers and Anand (2005)	
Phylogenetic dimension		
Taxonomic entropy	Ricotta and Avena (2003)	
Total complexity	Desrochers and Anand (2005)	
Net Relatedness Index	Webb (2000)	NTI
Nearest Taxon Index	Webb (2000)	NRI
Mean Pairwise Phylogenetic Distance	Webb (2000)	MPD
Mean Nearest Taxon Distance	Webb (2000)	$MNTD$
Taxonomic diversity	Clarke and Warwick (1998)	Δ
Variance in taxonomic distinctness	Korallo et al. (2007)	Λ^{+}
Average taxonomic distinctness	Clarke and Warwick (1998)	Δ^{+}

Phylogenetic distinctness	Clarke and Warwick (2001)	Φ^2
Phylogenetic Diversity	Faith (1992)	PD
Functional dimensions		
Functional Divergence	Villéger et al. (2008)	FDiv
Functional Especialization	Villéger et al. (2010)	FEso
Functional Dispersion	Laliberté and Legendre (2010)	FDis
Functional Richness	Villéger et al. (2008)	FRic
Functional Eveness	Villéger et al (2008)	FEve
Rao's quadratic diversity	Rao (2010)	Q
Community Weighted Mean trait value	Ricotta and Moretti (2011)	CWM
Functional Diversity *	Venail et al. (2010)	
Volum of the morphological space	Moreno and Solis (2006)	
Functional Diversity	Petchey and Gaston (2002)	
Functional Redundancy	Brown et al. (2011)	

Appendix S2 – Bibliographic data

We list here all bibliography used to extract the metrics of diversity used in co-metric analysis.

1 Adler, P.B. and Bradford, J.B. Compensation: an alternative method for analyzing diversity-productivity experiments. *Oikos* 96, 411-420

2 Albert, C. H. *et al*. (2012) On the importance of intraspecific variability for the quantification of functional diversity. *Oikos* 121, 116–126 (2012)

3 Albert, C.H. *et al*. (2012) On the importance of intraspecific variability for the quantification of functional diversity. *Oikos* 121, 116-126

4 Alhamad, M.N. *et al*. (2010) Relationships between herbaceous diversity and biomass in two habitats in arid Mediterranean rangeland. *Journal of Arid Environments* 74, 277-283

5 Al-sabouni, N. *et al*. (2007) Vertical niche separation control of diversity and size disparity in planktonic foraminifera. *Marine Micropaleontology* 63, 75-90

6 Amaral-zettler, L.A. *et al.*(2010) Microbial community structure across the tree of life in the extreme Río Tinto. *The ISME Journal* 5, 42-50

7 Amici, V. *et al.* (2012) Effects of an afforestation process on plant species richness : A retrogressive analysis. *Ecological Complexity* 9, 55–62

8 Anderson, M.J. *et al.* (2005) Consistency and variation in kelp holdfast assemblages : spatial patterns of biodiversity for the major phyla at different taxonomic resolutions. *Journal of Experimental Marine Biology and Ecology* 320, 35-56

9 Anderson, M.J. *et al.* (2011) Navigating the multiple meanings of biodiversity : a roadmap for the practicing ecologist. Ecology Letters 14, 19-28

10 Andersson, E. *et al.* (2007) Measuring social- ecological dynamics behind the generation of ecosystem services. *Ecological Applications* 17, 1267-1278

11 Andreasen, C. and Skovgaard, I. (2009) Crop and soil factors of importance for the distribution of plant species on arable fields in Denmark. *Agriculture, Ecosystem and Environment* 133, 61-67

12 Arita, H.T. and Rodríguez, P. (2002) Geographic range, turnover rate and the scaling of species. *Ecography* 5, 541-550

13 Arscott, D.B. *et al*. Lateral organization of aquatic invertebrates along the corridor of a braided floodplain river Lateral organization of aquatic invertebrates along the corridor of a braided floodplain river. *J. N. Am. Benthol. Soc.* 24, 934-954

14 Arthaud, F. *et al*. (2012) Eutrophication and drought disturbance shape functional diversity and life-history traits of aquatic plants in shallow lakes. *Aquat. Sci.* 74, 471-481

15 Assaf, T.A. *et al*. (2011) The relationship between plant diversity and productivity in natural and in managed. *Applied Ecology and Environmental Research* 9, 157-166

16 Attard, E. *et al*. (2011) Soil environmental conditions rather than denitrifier abundance and diversity drive potential denitrification after changes in land uses. *Global Change Biology* 17, 1975–1989

17 Avolio, M.L. *et al*. (2012) Measuring genetic diversity in ecological studies. *Plant Ecol.* 213, 1105-1115

18 Ayres, E. *et al*. (2007) Unique similarity of faunal communities across aquatic – terrestrial interfaces in a polar desert ecosystem. *Ecosystems* 10, 523-535

19 Badano, E.I. and Cavieres, L.A. (2006) Ecosystem engineering across ecosystems: do engineer species sharing common features have generalized or idiosyncratic effects on species diversity. *Journal of Biogeography* 33, 304-313

20 Badano, E.I. and Marquet, P.A. (2009) Biogenic habitat creation affects biomass–diversity relationships in plant communities. *Perspectives in Plant Ecol, Evol & Systematics* 11, 191-201

21 Bailey, R.C. *et al*. (2007) Integrating stream bioassessment and landscape ecology as a tool for land use planning. *Freshwater Biology* 52, 908–917

22 Bain, M.B. (2011) Target fish communities for restoration of waterways supporting society and nature. *J. Appl. Ichthyol*. 27, 86-93

23 Banville, M.J. and Bateman, H.L. (2012) Urban and wildland herpetofauna communities and riparian microhabitats along the Salt River , Arizona. *Urban Ecosyst.* 15, 473-488

24 Barnes, D.K.A. and Bell, J.J. (2002) Coastal sponge communities of the West Indian Ocean : taxonomic affinities , richness and diversity. *Afr. J. Ecol.* 40, 337-349

25 Beck, J. (2011) Links between the environment , abundance and diversity of andean moths. *Biotropica* 43, 208-217

26 Beck, J. and Schwanghart, W. (2010) Comparing measures of species diversity from incomplete inventories : an update. *Methods in Ecology and Evolution* 1, 38-44

27 Beck, J. *et al*. (2006) Effects of habitat disturbance can be subtle yet significant: biodiversity of hawkmoth-assemblages (Lepidoptera : Sphingidae) in Southeast-Asia. *Biodiversity and Conservation* 15, 465-486

28 Bell, J.J. (2007) Contrasting patterns of species and functional composition of coral reef sponge assemblages. *Marine Ecology Progress Series* 339, 73-81

29 Bell, T. *et al*. (2005) The contribution of species richness and composition to bacterial services. *Nature* 436, 1157-1160

30 Bennie, J. *et al*. (2011) Measuring biodiversity across spatial scales in a raised bog using a novel paired-sample diversity index. *Journal of Ecology* 99, 482-490

31 Besemer, K. *et al*. (2009) Bacterial community composition of stream biofilms in spatially. *Applied and Environmental Microbiology* 75, 7189-7195

32 Bhagwat, S.A. *et al*. (2005) A landscape approach to biodiversity conservation of sacred groves in the western ghats of India. *Conservation Biology* 19, 1853-1862

33 Biles, C.L. *et al*. (2002) Bioturbation , ecosystem functioning and community structure. *Hydrology and Earth System Science* 6, 999-1005

34 Bilton, D.T. *et al.* (2009) Ecology and conservation status of temporary and fluctuating ponds in two areas of southern England. *Aquatic Conservation: Mar. Freshw. Ecosyst*. 146, 134-146

35 Bishop, C.L. *et al.* (2010) Community-level changes in Banksia woodland following plant pathogen invasion in the Southwest Australian Floristic Region. *Journal of Vegetation Science* 21, 888–898

36 Blomqvist, M.M. *et al.* (2003) Declining plant species richness of grassland ditch banks-a problem of colonisation or extinction? *Biological Conservation* 109, 391-406

37 Bowers, R.M. *et al.* (2011) Sources of bacteria in outdoor air across cities in the midwestern United States. *Applied and Environmental Microbiology* 77, 6350-6356

38 Brandmayr, P. *et al.* (2009) In situ extinction of carabid beetles and community changes in a protect suburban forest during the past century: the “Bosco Farneto” near Trieste, Italy. *J. Insect Conserv.* 13, 231-243

39 Brokovich, E. *et al.* (2008) Descending to the twilight-zone: changes in coral reef fish assemblages along a depth gradient down to 65 m. *Marine Ecology Progress Series* 371, 253-262

40 Bronicka, M. *et al.* (2007) Abundance and diversity of fungi in a saline soil in central-west New South Wales, Australia. *SYDOWIA* 59

41 Brooks, S.S. *et al.* (2002) Assessing stream ecosystem rehabilitation: limitations of community sructure. *Restoration Ecology* 10, 156-168

42 Brown, B.L. (2003) Spatial heterogeneity reduces temporal variability in stream insect communities. *Ecology Letters* 6, 316-325

43 Brown, B.L. (2007) Habitat heterogeneity and disturbance influence patterns of community temporal variability in a small temperate stream. Hydrobiologia 586, 93-106

44 Brown, K.A. *et al.* (2011) Assessing natural resource use by forest-reliant communities in madagascar using functional diversity and functional redundancy metrics. PLoS ONE 6. DOI: 10.1371/journal.pone.0024107

45 Brown, M.T. *et al.* (2006) Species diversity in the Florida Everglades , USA :a systems approach to calculating biodiversity. *Aquat. Sci.* 68, 254-277

46 Burns, K.C. (2007) Is tree diversity different in the Southern Hemisphere? Journal of Vegetation Science 18, 307-312

47 Bussell, J.A. *et al.* (2007) Patterns in the invertebrate assemblage associated with Corallina officinalis in tide pools. *Journal of the Marine Biological Association of the United King* 87, 383-388

48 Cadotte, M.W. *et al*. (2008) Evolutionary history and the effect of biodiversity on plant productivity. *PNAS* 105, 17012-17017

49 Cadotte, M.W. *et al.* (2010) Phylogenetic diversity metrics for ecological communities : integrating species richness, abundance and evolutionary history. *Ecology Letters* 13, 96-105

50 Cantonati, M. and Spitale, D. (2009) The role of environmental variables in structuring epiphytic and epilithic diatom assemblages in springs and streams of the Dolomiti Bellunesi National Park (south-eastern Alps). *Fundamental and Applied Limnology* 174, 117-133

51 Caprio, E. *et al.* (2009) Native oak retention as a key factor for the conservation of winter bird diversity in managed deciduous forests in northern Italy. *Landscape Ecol.* 24, 65-76

52 Cardinale, B.J. (2011) Biodiversity improves water quality through niche partitioning. *Nature* 472, 86-89

53 Cardinale, B.J. *et al.* (2009) Does productivity drive diversity or vice versa ? A test of the multivariate productivity – diversity hypothesis in streams. *Ecology* 90, 1227-1241

54 Cardoso, P. (2012) Diversity and community assembly patterns of epigean vs . troglobiont spiders in the Iberian Peninsula. *International Journal of Speleology* 41, 83-94

55 Carpenter, C. (2005) The environmental control of plant species density on a Himalayan elevation gradient. *J. Biogeogr.* 32, 999–1018

56 Caruso, T. *et al*. (2012) Relative role of deterministic and stochastic determinants of soil animal community : a spatially explicit analysis of oribatid mites. *Journal of Animal Ecology* 81, 214-221

57 Carvalheiro, L.G. *et al*. (2010) Pollination services decline with distance from natural habitat even in biodiversity-rich areas. *Journal of Applied Ecology* 47, 810-820

58 Cassey, P. *et al*. (2006) A stochastic model for integrating changes in species richness and community similarity across spatial scales. *Oikos* 115, 207-218

59 Chalcraft, D.R. *et al*. (2008) The relationship between productivity and multiple aspects of biodiversity in six grassland communities. *Biodivers. Conserv*. DOI: 10.1007/s10531-008-9457-6

60 Chandy, S. *et al*. (2006) Additive partitioning of diversity across hierarchical spatial scales in a forested landscape. *Journal of Applied Ecology* 792-801

61 Chiarucci, A. *et al.* (2012) Old and new challenges in using species diversity for assessing biodiversity. *Phil. Trans. R. Soc. B* 366, 2426-2437

62 Clavero, M. (2006) Homogenization dynamics and introduction routes of invasive freshwater fish in the iberian peninsula. *Ecological Applications* 16, 2313-2324

63 Cleary, D.F.R. *et al.* (2005) Associations of bird species richness and community composition with local- and landscape-scale environmental factors in Borneo. *Landscape Ecology* 20, 989-1001

64 Cleary, D.F.R. *et al.* (2009) Butterfly species and traits associated with selectively logged forest in Borneo. *Basic and Applied Ecology* 10, 237-245

65 Clough, Y. *et al.* (2007) Alpha and beta diversity of arthropods and plants in organically and conventionally managed wheat fields. *Journal of Applied Ecology* 44, 804-812

66 Clynick, B.G. *et al.* (2008) Fish assemblages associated with urban structures and natural reefs in Sydney, Australia. Austral Ecology 33, 140-150

67 Cole, H.A. *et al.* (2008) Long-term outcome of precommercial thinning on floristic diversity in north western New Brunswick , Canada. *iForest* 1, 145-156

68 Collier, K.J. and Smith, B.J. (2006) Distinctive invertebrate assemblages in rockface seepages enhance lotic biodiversity in northern New Zealand. *Biodiversity and Conservation* 15, 3591-3616

69 Comas, L.H. *et al.* (2011) Quantifying species trait-functioning relationships for ecosystem management. Applied Vegetation Science 14, 583-595

70 Connoly, J. *et al.* (2011) Phylogenetically diverse grassland are associated with parwise interspecific processes that increase biomass. *Ecology* 97, 1385-1392

71 Cook, W.M. and Faeth, S.H (2006) Irrigation and land use drive ground arthropod community patterns in an urban desert irrigation and land use drive ground arthropod community patterns in an urban desert. *Community and Ecosystem Ecology* 35, 1532-1540

72 Cowlishaw, G. *et al.* (2005) Structure and operation of a bushmeat commodity chain in southwestern Ghana. *Conservation Biology* 19, 139-149

73 Cummings, J. and Reid, N. (2008) Stand-level management of plantations to improve biodiversity values. *Biodivers. Conserv.* 17, 1187-1211

74 Davis, A. *et al*. (2011) Landscape and urban planning do fire and rainfall drive spatial and temporal population shifts in parrots? A case study using urban parrot populations. *Landscape and Urban Planning* 100, 295-301

75 DeClerke, F. *et al*. (2006). Species richness and stand stability in conifer forests of the sierra nevada. Ecology 87, 2787-2799

76 Desgranges, J.L. *et al*. (2006) Modelling wetland bird response to water level. *Environmental Monitoring and Assessment* 113, 329-365

77 Desrochers, R.E. and Anand, M. (2005) Quantifying the components of biocomplexity along ecological perturbation gradients. *Biodiversity and Conservation* 14, 3437-3455

78 Diggins, T.P. and Newman, A.M. (2009) Environmental and spatial influences on benthic community composition in wooded headwater streams in Zoar Valley. *Hydrobiologia* 630, 313-326

79 Djigal, D. *et al.* (2012) Cover crops alter the soil nematode food web in banana agroecosystems. *Soil Biology and Biochemistry* 48, 142-150

80 Dormann, C.F. *et al.* (2007) Effects of landscape structure and land-use intensity on similarity of plant and animal communities. *Global Ecology and Biogeography* 16, 774-787

81 Dover, C.L.V. (2002) Community structure of mussel beds at deep-sea hydrothermal vents. *Mar. Ecol. Prog. Ser*. 230, 137-158

82 Duprè, C. *et al*. (2010). Changes in species richness and composition in european acidic grassland over the past 70 years: the contribution of cumulative atmospheric nitrogen deposition. *Global Change Biology* 16, 344-357

83 Economo, E.P. and Keitt, T.H. (2010) Network isolation and local diversity in neutral metacommunities. Oikos 119,1355-1363

84 Eingenbrod, F. *et al*. (2008) Accessible habitat: an improved measure of the effects of habitat loss and roads on wildlife populations. *Landscape Ecol*. 23, 159-168

85 Eisenhauer, N. *et al.* (2011) Impact of above- and below-ground invertebrates on temporal and spatial stability of grassland of different diversity. *Journal of Ecology* 99, 572-58

86 Ellis, N. *et al*. (2012) Gradient forests: calculating importance gradients on physical predictors. *Ecology* 93, 156-168

87 Engen, S. *et al*. (2011) Disentangling the effects of heterogeneity, stochastic dynamics and sampling in a community of aquatic insects. *Ecological Modelling* 222, 1387-1393

88 Erman, S.B. and Warren, P.S. (2011) The conservation value of residential yards : linking birds and people. *Ecological Applications* 21, 1327-1339

89 Eros, T. (2007) Partitioning the diversity of riverine fish : the roles of habitat types and non-native species. *Freshwater Biology* 1400-1415

90 Fairbanks, D.H.K. *et al*. (2002) Scales and consequences of human land transformation on South African avian diversity and structure. *Animal Conservation* 5, 61-73

91 Faith, D. *et al*. (2009) The cladistic basis for the Phylogenetic Diversity (PD) measure links evolutionary features to environmental gradients and supports broad applications of microbial ecology's "Phylogenetic Beta Diversity". *International Journal of Molecular Science* 10, 4723

92 Ficetola, G.F. *et al.* (2007) Vertebrates respond differently to human disturbance: implications for the use of a focal species approach. *Acta Oecologica* 31, 109-118

93 Finn, D.S. *et al.* (2011) Small but mighty: headwaters are vital to stream network biodiversity at two levels of organization. *J. N. Am. Benthol. Soc.* 30, 963-980

94 Fleishman, E. *et al.* (2003) Effects of floristics, physiognomy and non-native vegetation on riparian bird communities in a Mojave. *Journal of Animal Ecology* 72, 484-490

95 Fleishman, E. *et al.* (2006) Effects of environmental heterogeneity and disturbance on the native and non-native flora of desert springs. *Biological Invasions* 8, 1091-1101

96 Flenner, I. and Sahlén, G. (2008) Dragonfly community re-organisation in boreal forest lakes: rapid species turnover driven by climate change?. *Insect Conservation Diversity* 1, 169-179

97 Flynn, D.F.B. *et al* (2008) Hierarchical reliability in experimental plant assemblages. *Journal of Plant Ecology* 1, 59-65

98 Fontana, S. *et al.* (2011) How to manage the urban green to improve bird diversity and community structure. *Landscape and Urban Planning* 101, 278-285

99 Foster, B.L. *et al.* (2011) Seed availability constrains plant species sorting along a soil fertility gradient. Journal of Ecology 99, 473-481

100 Fox, J.W. (2004) Effects of algal and herbivore diversity on the partitioning of biomass within and among trophic levels. *Ecology* 85, 549-559

101 Fritz, S.A. and Purvis, A. (2010) Phylogenetic diversity does not capture body size variation at risk in the world's mammals. *Proc. R. Soc. B.* DOI: 10.1098/rspb.2010.0030

102 Gagné, S.A. and Fahrig, L. (2010) The trade-off between housing density and sprawl area: minimising impacts to forest breeding birds. *Basic and Applied Ecology* 11, 723-733

103 Gerisch, M. *et al.* (2012) More species, but all do the same: contrasting effects of flood disturbance on ground beetle functional and species diversity. *Oikos* 121, 508-515

104 Gheskiere, T. *et al*. (2005) Nematodes from wave-dominated sandy beaches: diversity, zonation patterns and testing of the isocommunities concept. *Estuarine Costal and Shelf Science* 62, 365-375

105 Gongalsky, K.B. *et al*. (2008) Do boundaries of soil animal and plant communities coincide? A case study of a Mediterranean forest in Russia. *European Journal of Soil Biology* 44, 355-363

106 Gotmark, F. *et al*. (2008) Are small sedentary species affected by habitat fragmentation? Local vs. landscape factors predicting species richness and composition of land molluscs in Swedish conservation forests. *J. Biogeogr*. 35, 1062-1076

107 Green, J.L. and Plotkin, J.B. (2007) A statistical theory for sampling species abundances. *Ecology Letters* 10, 1037-1045

108 Green, J.L. *et al.* (2004) Spatial scaling of microbial eukaryote diversity. *Nature* 285, 282-285

109 Guerrero, A.C. (2010) Passive restoration in biodiversity hotspots : consequences for an atlantic rainforest lizard taxocene. *Biotropica* 42, 379-387

110 Guiasu, R.C. and Guiasu, S. (2010) New measures for comparing species diversity found in two or more habitats. *International Journal of Uncertainty Fuzziness and Knowledge-Based Systems* 18, 691-720

111 Halpern, B.S. and Floeter, S.R. (2008) Functional diversity responses to changing species richness in reef fish communities. *Mar. Ecol. Prog. Ser.* 364, 147-156

112 Harnik, P.G. *et al.* (2010) Genus age, provincial area and the taxonomic structure of marine faunas. *Proc. R. Soc. B* 277, 3427-3435

113 Harte, J. *et al*. (2008) Maximum entropy and the state-variable approach to macroecology. *Ecology* 89, 2700-2711

114 He, J. *et al*. (2002) Interactive effects of diversity, nutrients and elevated CO2 on experimental plant communities. *Oikos* 97, 337-348

115 Helmus, M.R. *et al*. (2007) Phylogenetic measures of biodiversity. *Am. Nat.*169, E68-E83

116 Hendrickx, F. *et al.* (2007) How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. *Journal of Applied Ecology* 44,340-351

117 Hladyz, S. *et al*. (2011) Impacts of an aggressive riparian invader on community structure and ecosystem functioning in stream food webs. *Journal of Applied Ecology* 48, 443-452

118 Hoffmann, B.D. and Parr, C.L. (2008) An invasion revisited: the African big-headed ant (Pheidole megacephala) in northern Australia. *Biological Invasions* 10, 1171-1181

119 Hottola, J. *et al*. (2009) A unified measure of the number, volume and diversity of dead trees and the response of fungal communities. *Journal of Ecology* 97, 1320-1328

120 Howe, H.F. and Lane, D. (2004) Vole-driven succession in experimental wet-prairie restorations. *Ecological Applications* 14, 1295-1305

121 Howeth, J.G. and Leibold M.A. (2010) Species dispersal rates alter diversity and ecosystem stability in pond metacommunities. *Ecology* 91, 2727-2741

122 Hua, E. *et al*. (2009) Environmental factors affecting nematode community structure in the Changjiang Estuary and its adjacent waters. Journal of the Marine Biological Association of the United Kingdon 89, 109-117

123 Hughes, A.R. and Stachowicz, J.J. (2004) Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. *PNAS* 101, 8998-9002

124 Izsák, J. and Pavoine, S. (2011) New concentration measures as kinds of the quadratic entropy. *Ecological Indicators* 11, 540-544

125 Januschke, K. *et al*. (2011) Effects of stream restoration on riparian mesohabitats, vegetation and carabid beetles. *Biodivers. Conserv*. 20, 3147-3164

126 Jeffries, M. (2005) Local-scale turnover of pond insects: intra-pond habitat quality and inter-pond geometry are both important. *Hydrobiologia* 543, 207-220

127 Jentsch, A. *et al*. (2009) Assessing conservation action for substitution of missing dynamics on former military training areas in Central Europe. *Restoration Ecology* 17, 107-116

128 Jeraldo, P. *et al.* (2012) Quantification of the relative roles of niche and neutral processes in structuring gastrointestinal microbiomes. *PNAS.* DOI: 10.1073

129 Johnston, J.M. (2007) Diversity surfaces and species wave fronts in a soil microarthropod assemblage: adding the dimension of time. *Pedobiologia* 50, 527-533

130 Jousset, A. *et al*. (2011) Intraspecific genotypic richness and relatedness predict the invasibility of microbial communities. *The ISME Journal* 5, 1108-1114

131 Judd, K.E. *et al*. (2006) Variation in dissolved organic matter controls bacterial production and community composition. *Ecology* 87, 2068-2079

132 Kalin, M. *et al*. (2006) Response of phytoplankton to ecological engineering remediation of a canadian shield lake affected by acid mine drainage. *Ecological Engineering* 8, 296-310

133 Kelly, C.K. and Bowler, M.G (2009) Temporal niche dynamics, relative abundance and phylogenetic signal of coexisting species. *Theoretical Ecology* 2, 161-169

134 Kennedy, A.D. *et al*. (2003) Relationship between grass species richness and ecosystem stability in Kruger National Park , South Africa. *Afr. J. Ecol.* 41, 131-140

135 Kéry, M. and Royle, J.A. (2008) Hierarchical bayes estimation of species richness and occupancy in spatially replicated surveys. *Journal of Applied Ecology* 45, 589-598

136 Klaus, V.H. *et al*. (2011) Nutrient concentration and fibre contents of plant community biomass reflect species richness patterns along a broad range of land-use intensities among agricultural grassland. *Perspectives in Plant Ecology, Evolution and Systematics* 13, 287-295

137 Klein, J.A. *et al*. (2008) Decline in medicinal and forage species with warming is mediated by plant traits on the Tibetan Plateau. Ecosystems 11, 775-789

138 Koivisto, M. *et al*. (2011) Succession-driven facilitation of macrofaunal communities in sublittoral blue mussel habitats. *Mar. Biol*. 158, 945-954

139 Korallo, N.P. *et al*. (2007) Are there general rules governing parasite diversity? Small mammalian hosts and gamasid mite assemblages. *Diversity Distrib*. 13, 353-360

140 Krasnov, B.R. *et al*. (2005) Spatial variation in species diversity and composition of flea assemblages in small mammalian hosts : geographical distance or faunal similarity?. *J. Biogeogr*. 32, 633-644

141 Kristiansen, T. (2011) Local and regional palm (Arecaceae) species richness patterns and their cross-scale determinants in the western Amazon. *Journal of Ecology* 99, 1001-1015

142 Kühn, I. *et al*. (2004) The flora of German cities is naturally species rich. *Evolutionary Ecology Research* 6, 749–764

143 Kuhn, J. *et al*. (2011) Spatial variability in macroinvertebrate assemblages along and among neighbouring equatorial glacier-fed streams. *Freshwater Biology* 56, 2226-2244

144 Kumar, S. *et al*. (2006) Spatial heterogeneity influences native and nonnative plant species richness. *Ecology* 87, 3186-3199

145 Kuntz, K.L. and Larson, D.W. (2006) Microtopographic control of vascular plant , bryophyte and lichen communities on cliff faces. *Plant Ecology* 185, 239-253

146 Kunza, A.E. and Pennings, S.C. (2008) Patterns of plant diversity in Georgia and Texas salt marshes. *Estuaries and Costs* 31, 673-681

147 La Montaña, E. *et al*. (2006) Response of bird communities to silvicultural thinning of Mediterranean maquis. *Journal of Applied Ecology* 43, 651-659

148 Laggoun-Défarge, F. *et al.* (2008) Cut-over peatland regeneration assessment using organic matter and microbial indicators (bacteria and testate amoebae). *Journal of Applied Ecology* 45, 716-727

149 Lassau, S.A. and Hochuli, D.F. (2008) Testing predictions of beetle community patterns derived empirically using remote sensing. *Diversity Distrib*. 14, 138-147

150 Leis, S.A. *et al*. Effects of short- and long-term disturbance resulting from military maneuvers on vegetation and soils in a mixed prairie area. *Environmental Management* 36, 849-861

151 Leng, X. *et al*. (2010) Spatial variation in ditch bank plant species composition at the regional level : the role of environment and dispersal. *Journal of Vegetation Science* 21, 868-875

152 Lepori, F. (2005) Does restoration of structural heterogeneity in streams enhance fish and macroinvertebrate diversity? *Ecological Applications* 15, 2060-2071

153 Leps, J. *et al*. (2006) Quantifying and interpreting functional diversity of natural communities: practical considerations matter. *Preslia* 78, 481-501

154 Lesak, A.A. *et al.* (2011) Remote sensing of environment modeling forest songbird species richness using LiDAR-derived measures of forest structure. *Remote Sensing of Environment* 115, 2823-2835

155 Levanoni, O. *et al*. (2011) Can we predict butterfly diversity along an elevation gradient from space?. *Ecography* 34, 372-383

156 Lindstrom, E.S. and Ostman, O. (2011) The importance of dispersal for bacterial community composition and functioning. *PLoS ONE* 6. DOI: 10.1371/journal.pone.0025883

157 Lindstrom, E.S. *et al*. (2010) The interplay between bacterial community composition and the environment determining function of inland water bacteria. *Limnol. Oceanogr*. 55, 2052-2060

158 Longhi, M.L. and Beisner, B.E. (2010) Patterns in taxonomic and functional diversity of lake phytoplankton. *Freshwater Biology* 55, 1349-1366

159 Loppi, S. and Frati, L. (2004) Influence of tree substrate on the diversity of epiphytic lichens: comparison between *Tilia platyphyllos* and *Quercus ilex* (central Italy) influence of tree substrate on the diversity of epiphytic lichens. *The Bryologist* 107, 340-344

160 Louette, G. *et al*. (2009) Evaluation of restoration measures in a shallow lake through a comparison of present day zooplankton communities with historical samples. *Restoration Ecology* 17, 629-640

161 Louhi, P. *et al*. (2011) Twenty years of stream restoration in Finland: little response by benthic macroinvertebrate communities. *Ecological Applications* 21, 1950-1961

162 Ludovisi, A. and Taticchi, M.I. (2006) Investigating beta diversity by Kullback – Leibler information measures. *Ecological Modelling* 192, 299-313

163 Luque, J.L. and Poulin, R. (2008) Linking ecology with parasite diversity in neotropical fishes. *Journal of Fish Biology* 72, 189-204

164 MaIard, F. *et al*. (2006) Flood-pulse and riverscape dynamics in a braided glacial river. *Ecology* 87, 704-716

165 Martinez, A.J. *et al*. (2006) Earthworm communities in forest and pastures of the colombian Andes. *Caribbean Jounal of Science* 42, 301-310

166 McClain, C.R. (2004) Connecting species richness, abundance and body size in deep-sea gastropods. *Global Ecol. Biogeogr*. 13, 327-334

167 Mcwethy, D.B. *et al*. (2009) Bird response to disturbance varies with forest productivity in the northwestern United States. *Landscape Ecol*. DOI: 10.1007/s10980-009-9437-6

168 Mendes, R.S. *et al*. (2008) A unified index to measure ecological diversity and species rarity. *Ecography* 31, 450-456

169 Michael, D.R. *et al*. (2008) A forgotten habitat? Granite inselbergs conserve reptile diversity in fragmented agricultural landscapes. *Journal of Applied Ecology* 1742-1752

170 Mikkelson, G.M. *et al*. (2011) Multiple links between species diversity and temporal stability in bird communities across North America. *Evolutionary Ecology Research* 13, 361-372

171 Miller, S.R. *et al*. (2009) Bar- coded pyrosequencing reveals shared bacterial community properties along the temperate gradients of two alkaline hot springs in yellowstone national park. *American Society of Microbiology* 75, 4565-4572

172 Mills, A. and Adl, M.S. (2006) The effects of land use intensification on soil biodiversity in the pasture. *Canadian Journal of Plant Science* 1, 1339-1343

173 Mitchell, M.S. *et al.* (2008) Projected long-term response of southeastern birds to forest management. *Forest Ecology and Management* 256, 1884-1896

174 Moreno, C.E. and Arita, H.T. (2006) Morphological assembly mechanisms in neotropical bat assemblages and ensembles within a landscape. *Oecologia* 149, 133-140

175 Moreno, C.E. *et al*. (2011) Negative impacts of human land use on dung beetle functional diversity. *Plos One* DOI: 10.1371/journal.pone.0017976 1(www.plosone.org)

176 Moretti, M. *et al*. (2006) Biodiversity and resilience of arthropod communities after fire disturbance in temperate forests. *Oecologia* 149, 312-327

177 Morin, P.J. and McGrady-Steed, J. (2004) Biodiversity and ecosystem functioning in aquatic microbial systems: a new analysis of temporal variation and species richness predictability relations. *Oikos* 104, 458-466

178 Morlon, H. *et al*. (2009) Taking species abundance distributions beyond individuals. *Ecology Letters* 12, 488-501

179 Mouillot, D. *et al*. (2005) Functional regularity: a neglected aspect of functional diversity. *Oecologia* 142, 353-359

180 Mu, F.H *et al*. (2002) Large-scale spatial patterns in the community structure of benthic harpacticoid copepods in the Bohai Sea, China. *Raffles Bulletin of Zoology* 50, 17-26

181 Muller, J. and Brandl, R. (2009) Assessing biodiversity by remote sensing in mountai- nous terrain : the potential of LiDAR to predict forest beetle assemblages. *Journal of Applied Ecology* 46, 897-905

182 Muller, S.D. *et al*. (2012) A palaeoecological perspective for the conservation and restoration of wetland plant communities in the central French Alps, with particular emphasis on alder carr vegetation. *Review of Palaeobotany and Palynology* 171, 124-139

183 Myers, J.O. and Harms, K.E. (2009) Local immigration, competition from dominant guilds, and the ecological assembly of high-diversity pine savannas. *Ecology* 90, 2745-2754.

184 Myers, M.C. *et al*. (2012) Butterfly response to floral resources during early establishment at a heterogeneous prairie biomass production site in Iowa, USA. *J. Insect Conserv*. 16, 457-472

185 Nelson, S.M. (2007) Butterflies (Papilionoidea and Hesperioidea) as potential ecological indicators of riparian quality in the semi-arid western United States. *Ecological Indicators* 7, 469-480

186 Ni, J. *et al*. (2007) Scale-dependent relationships between plant diversity and above-ground biomass in temperate grasslands, south-eastern Mongolia. *Journal of Arid Environments* 68, 132-142

187 Nimmo, D.G. *et al*. (2011) The decoupling of abundance and species richness in lizard communities. *Journal of Animal Ecology* 80, 650-656

188 Norberg, J. (2004) Biodiversity and ecosystem functioning: a complex adaptive systems approach. *Limnology and Oceanography* 49, 1269-1277

189 Ortega-Álvarez, R. and MacGregor-Fors, I. (2010) What matters most? relative effect of urban habitat traits and hazards on urban park birds. *Ornitologia Neotropical* 21, 519-533

190 Ostfeld, R.S. and LoGiudice, K. (2003) Community disassembly, biodiversity loss, and the erosion of an ecosystem service. *Ecology* 84, 1421-1427

191 Pacarevic, M. *et al*. (2010) Biodiversity on Brodway – enigmatic diversity of the societies of ants (Formicidae) on the streets of New York City. *PLoS ONE*. DOI: 10.1371/journal.pone.0013222

192 Pachepsky, E. *et al*. (2007) Consequences of intraspecific variation for the structure and function of ecological communities Part 2: linking diversity and function. *Ecological Modelling* 207, 277-285

193 Packham, J.M. *et al*. (2002) Macrofungal diversity and community ecology in mature and regrowth wet eucalypt forest in Tasmania: a multivariate study. *Austral Ecology* 27, 149-161

194 Paillex, A. *et al*. (2009) Large river floodplain restoration: predicting species richness and trait responses to the restoration of hydrological connectivity. *Journal of Applied Ecology* 46, 250-258

195 Parnell, J.J. *et al*. (2011) Phylogenetic distance in Great Salt Lake microbial communities. *Aquatic Microbial Ecology* 64, 267-273

196 Parnell, J.J. et al. Biodiversity in microbial communities: system scale patterns and mechanisms. *Molecular Ecology* 18, 1455-1462

197 Parris, K.M. (2006) Urban amphibian assemblages as metacommunities. *Journal of Animal Ecology* 75, 757-764

198 Partel, M. *et al*. (2007) Contrasting plant productivity–diversity relationships across latitude: the role of evolutionary history. *Ecology* 88, 1091-1097

199 Passy, S.I. and Blanchet, F.G. (2007) Algal communities in human-impacted stream ecosystems suffer beta-diversity decline. *Diversity Distrib*. 13, 670-679

200 Pavoine, S. (2012) Clarifying and developing analyses of biodiversity: towards a generalisation of current approaches. *Methods in Ecology and Evolution* 3, 509-518

201 Pavoine, S. and Bonsall, M.B. (2011) Measuring biodiversity to explain community assembly: a unified approach. *Biological Reviews* 2, 792-812

202 Pearson, C.V. and Dyer, L.A. (2006) Trophic diversity in two grassland ecosystems. *Journal of Insect Science* 6, 1-11

203 Pelicice, F.M. and Agostinho, A.A. (2009) Fish fauna destruction after the introduction of a non-native predator (*Cichla kelberi*) in a neotropical reservoir. *Biol. Invasions* 11, 1789-1801

204 Pelicice, F.M. *et al.* (2008) Simple relationships to predict attributes of fish assemblages in patches of submerged macrophytes. *Neotropical Ichthyology* 6, 543-550

205 Pélissier, R. and Couteron, P. (2007) An operational, additive framework for species diversity partitioning and beta-diversity analysis. *Journal of Ecology* 95, 294-300

206 Pérez-Quintero, J.C. (2011) Distribution patterns of freshwater molluscs along environmental gradients in the southern Guadiana River basin (SW Iberian Peninsula). *Hydrobiologia* 678, 65-76

207 Phillips, L.B. *et al.* (2010) Applying species–energy theory to conservation: a case study for North American birds. *Ecological Applications* 20, 2007-2023

208 Pipan, T. *et al.* (2008) Studies of the fauna of percolation water of huda luknja, a cave in isolated karst in northeast slovenia. *Acta Carsologica* 37, 141-151

209 Piper, J.K. *et al.* (2007) Effects of species richness on resident and target species components in a prairie restoration. *Restoration Ecology* 15, 189-198

210 Pitcher, C.R. *et al.* (2012) Exploring the role of environmental variables in shaping patterns of seabed biodiversity composition in regional-scale ecosystems. *Journal of Applied Ecology* 49, 670-679

211 Polley, H.W. *et al.* Dominant species constrain effects of species diversity on temporal variability in biomass production of tallgrass prairie. *Oikos* 116, 2044-2052

212 Poos, M.S. *et al.* (2009) Functional diversity indices can be driven by methdological choices and species richness. *Ecology* 90, 341-347

213 Potter, K.M. and Woodall, C.W. (2012) Trends over time in tree and seedling phylogenetic diversity indicate regional differences in forest biodiversity change. *Ecological Applications* 22, 517-531

214 Proulx, R. *et al.* (2000) Use of recurrence analysis to measure the dynamical stability of a multi-species community model. *Eur. Phys. J. Special Topics* 164, 117-126

215 Ptacnik, R. *et al.* (2012) Regional species pools control community saturation in lake phytoplankton. *Proc. R. Soc. B* 277, 3755-3764

216 Pueyo, Y. *et al*. (2006) Is the analysis of plant community structure better than common species diversity indices for assessing the effects of livestoch grazing on a Mediterran arid ecosystem?. *Journal of Arid Environments* 64, 698-712

217 Punyasena, S.W. *et al*. (2008) The influence of climate on the spatial patterning of Neotropical plant families. *J. Biogeogr*. 35, 117-130

218 Purdy, B.G. *et al*. (2005) Naturally saline boreal communities as models for reclamation of saline oil sand tailings. *Restoration Ecology* 13, 667-677

219 Randhawa, H.S. and Poulin, R. (2010) Determinants of tapeworm species richness in elasmobranch fishes: untangling environmental and phylogenetic influences. *Ecography* 33, 866-877

220 Rayburn, A.P. and Wiegand, T. (2012) Individual species–area relationships and spatial patterns of species diversity in a Great Basin, semi-arid shrubland. *Ecography* 35, 341-347

221 Reed, S.C *et al*. (2010) Microbial community shifts influence patterns in tropical forest nitrogen fixation. *Oecologia*. DOI: 10.1007/s00442-010-1649-6

222 Reino, J. *et al*. (2008) Weak relationships between landscape characteristics and multiple facets of stream macroinvertebrate biodiversity in a boreal drainage basin. *Landscape Ecology* 23, 417-426

223 Resetarits, W.J. and Chalcraft, D.R. (2007) Functional diversity within a morfologically conservative genus of predator: implications for functional equivalence and redundancy in ecological communities. *Functional Ecology* 21, 793-804

224 Ribeiro, D.B. *et al*. (2010) Temporal diversity patterns and phenology in fruit-feeding butterflies in the Atlantic Forest. *Biotropica* 42, 410-416

225 Richardson, J.M.L. and Richards, M.H. (2008) A randomisation program to compare species-richness values. *Insect Conservation and Diversity* 1, 135-141

226 Ricotta, C. and Bacaro, G. (2010) On plot-to-plot dissimilarity measure based on species functional traits. *Community Ecology* 11, 113-119

227 Ricotta, C. and Burrascano, S. (2008) Beta diversity for functional ecology. *Preslia* 80, 61-71

228 Ricotta, C. and Moretti, M. (2011) CWM and Rao's quadratic diversity: a unified framework for functional ecology. *Oecologia* 167, 181-188

229 Rodríguez, J. (2006) Structural continuity and multiple alternative stable states in middle Pleistocene European mammalian communities. *Palaeogeography, Palaeoclimatology, Palaeoecology* 239, 355-373

230 Roscher, C. *et al.* (2012) Using plant functional traits to explain diversity–productivity relationships. *PLoS ONE*. DOI: 10.1371/journal.pone.0036760

231 Rossetti, G. *et al.* (2004) Limnological characteristics and recent ostracods (Crustacea, Ostracoda) of freshwater wetlands in the Parco Oglio Sud (Northern Italy). *Int. J. Lim.* 40, 329-341

232 Rowhani, P. *et al.* (2008) Variability in energy influences avian distribution patterns across the USA. *Ecosystems* 11, 854-867

233 Roy, P.S. *et al.* (2005) Validation of geospatial model for biodiversity characterization at landscape level—a study in Andaman & Nicobar islands, India. *Ecological Modelling* 185, 349-369

234 Ruedas, L.A. *et al.* (2004) Community ecology of small mammal populations in Panamá following an outbreak of Hantavirus pulmonary syndrome. Journal of Vector Ecology 29, 177-191

235 Sadler, J.P. *et al*. (2006) Investigating environmental variation and landscape characteristics of an urban–rural gradient using woodland carabid assemblages. *J. Biogeogr*. 33, 1126-1138

236 Safi, K. *et al.* (2012) Understanding global patterns of mammalian functional and phylogenetic diversity. *Phil. Trans. R. Soc. B* 366, 2536-2544

237 Sáfián, S. *et al*. (2011) Butterfly community recovery in degraded rainforest habitats in the Upper Guinean forest zone (Kakum forest, Ghana). *J. Insect Conserv*. 15, 351-359

238 Sall, S.D. *et al*. (2006) Does cropping modify the decomposition function and the diversity of the soil microbial community of tropical fallow soil? *Applied Soil Ecology* 31, 211-219

239 Salles, J.F. *et al*. (2009) Community niche predicts the functioning of denitrifying bacterial assemblages. *Ecology* 90, 3324-3332

240 Savage, J. *et al*. (2011) Effects of habitat size, vegetation cover, and surrounding land use on diptera diversity in temperate nearctic bogs. *Wetlands* 31,125-134

241 Scalercio, S. *et al*. (2007) Multi-scale analysis of butterfly diversity in a Mediterranean mountain landscape: mapping and evaluation of community vulnerability. *Biodivers. Conserv*. 16, 3463-3479

242 Schaffers, A.P. *et al*. (2008) Arthropod assemblages are best predicted by plant composition. *Ecology* 89, 782-794

243 Schmera, D. *et al*. (2009) Measuring the contribution of community members to functional diversity. *Oikos* 118, 961-971

244 Schmitz, H.J. *et al*. (2010) Assemblages of drosophilids (Diptera, Drosophilidae) in mangrove forests: community ecology and species diversity. *Iheringia* 100, 133-140

245 Schoeman, D.S. *et al*. (2008) Measuring species richness on sandy beach transects: extrapolative estimators and their implications for sampling effort. *Marine Ecology* 29, 134-149

246 Schröder, B. *et al*. (2008) A landscape model for quantifying the trade off between conservation needs and economic constraints in the management of a semi natural grassland community. *Biological Conservation* 141, 719-732

247 Schweiger, O. *et al*. (2008) A comparative test of phylogenetic diversity indices. *Oecologia* 157, 485-495

248 Seabloom, E.W. (2007) Compensation and the stability of restored grassland communities. *Ecological Applications* 17, 1876-1885

249 Sekercioglu, C.H. (2002) Effects of forestry practices on vegetation structure and bird community of Kibale National Park, Uganda. *Biological Conservation* 107, 229-240

250 Serrano-Grijalva, L. *et al*. (2011) Effects of shrimp-farm effluents on the food web structure in subtropical coastal lagoons. *Journal of Experimental Marine Biology and Ecology* 402, 65-74

251 Sheldon, F. and Thoms, M.C. (2006) Relationships between flow variability and macroinvertebrate assemblage composition: data from four australian dryland rivers. *River Res. Applic*. 238, 219-238

252 Sherwin, W.B. *et al*. (2006) Measurement of biological information with applications from genes to landscapes. Molecular Ecology 15, 2857-2869

253 Shipley, B. *et al*. (2012) Quantifying the importance of local niche-based and stochastic processes to tropical tree community assembly. *Ecology* 93, 760-769

254 Shukla, R.P. (2009) Patterns of plant species diversity across Terai landscape in north- eastern Uttar Pradesh, India. *Tropical Ecology* 50, 111-123

255 Soininen, J. *et al*. (2012) The relationship between species richness and evenness: a meta-analysis of studies across aquatic ecosystems. *Community Ecology* 169, 803-809

256 Sonnier, G. *et al*. (2010) Plant traits, species pools and the prediction of relative abundance in plant communities: a maximum entropy approach. *Journal of Vegetation Science* 21, 318-331

257 Specht, J. *et al*. (2008) Diversity and beyond: plant functional identity determines herbivore performance. *Journal of Animal Ecology* 77, 1047-1055

258 Springe, G. *et al*. (2006) Biological quality metrics: their variability and appropriate scale for assessing streams. *Hydrobiologia* 566, 153-172

259 Stachová, T. and Lep, J. *et al*. (2010) Species pool size and realized species richness affect productivity differently: a modeling study. *Acta Oecologica* 36, 578-586

260 Stachowicz, J.J. *et al*. (2002) Biodiversity, invasion resistance, and marine ecosystem function: reconciling pattern and process. *Ecology* 83, 2575-2590

261 Steiner, C.F. *et al.* (2005) The influence of consumer diversity and indirect facilitation on trophic level biomass and stability. *Oikos* 110, 556-566

262 Stendera, S.E.S. and Johnson, R.K. (2005) Additive partitioning of aquatic invertebrate species diversity across multiple spatial scales. *Freshwater Biology* 50, 1360-1375

263 Stevens, R.D. *et al*. (2003) Patterns of functional diversity across an extensive environmental gradient: vertebrate consumers, hidden treatments and latitudinal trends. *Ecology Letters* 6, 1099-1108

264 Stohlgren, T.J. *et al*. (2006) Scale and plant invasions : a theory of biotic acceptance. *Preslia* 78, 405-426

265 Strayer, D.L. *et al.* (2012) Biodiversity in Hudson river shore zones: influence of shoreline type and physical structure. *Aquat. Sci*. 74, 597-610

266 Summerville, K.S. *et al*. (2005) Restoring lepidopteran communities to oak savannas: contrasting influences of habitat quantity and quality. *Restoration Ecology* 13, 120-128

267 Svensson, J.R. *et al*. (2007) Maximum species richness at intermediate frequencies of disturbance: consistency among levels of productivity. *Ecology* 88, 830-838

268 Svensson, J.R. *et al.* (2012) Disturbance−diversity models: what do they really predict and how are they tested? *Proc. R. Soc. B* 279, 2163-2170

269 Tan, J. *et al*. (2012) Species phylogenetic relatedness, priority effects, and ecosystem functioning. Ecology 93, 1164-1172

270 Tattersfield, P. *et al*. (2006) Elevational variation in diversity and composition of land-snail faunas in a Tanzanian forest. *Afr. J. Ecol*. 44, 47-60

271 Tavernini, S. *et al*. (2009) Trophic state and seasonal dynamics of phytoplankton communities in two sand-pit lakes at different successional stages. *J. Limnol*. 68, 217-228

272 Taylor, A.F.S. (2002) Fungal diversity in ectomycorrhizal communities: sampling effort and species detection. *Plant and Soil* 244, 19-28

273 Taylor, R.S. *et al.* (2012) Landscape-scale effects of fire on bird assemblages: does pyrodiversity beget biodiversity? *Diversity Distrib*. 18, 519-529

274 Thomaz, S.M. *et al*. (2003) Species richness and beta diversity of aquatic macrophytes in a large subtropical reservoir (Itaipu Reservoir , Brazil): the influence of limnology and morphometry. *Hydrobiologia* 505, 119-128

275 Thomaz, S.M. *et al*. (2008) Influence of aquatic macrophyte habitat complexity on invertebrate abundance and richness in tropical lagoons. *Freshwater Biology* 53, 358-367

276 Tilman, D. *et al.* (2012) Biodiversity impacts ecosystem productivity as much as resourses, disturbance, or herbivory. *PNAS* 26, 10394-10397

277 Tognetti, P.M. *et al.* (2010) Exotic vs native plant dominance over 20 years of old-field succession on set-aside farmland in Argentina. *Biological Conservation* 143, 2494-2503

278 Toni, D.C. *et al.* (2007) Study of the Drosophilidae (Diptera) communities on Atlantic Forest islands of Santa Catarina State, Brazil. *Neotropical Enthomology* 36, 356-375

279 Townsend, C.R. *et al.* (2003) The influence of scale and geography on relationships between stream community composition and landscape variables: description and prediction. *Freshwater Biology* 48, 768-785

280 Unterseher, M. and Tal, O. (2006) Influence of small scale conditions on the diversity of wood decay fungi in a temperate, mixed deciduous forest canopy. *Mycological Research* II0, 169-178

281 Urban-Malinga *et al.* (2008) Gradients in biodiversity and macroalgal wrack decomposition rate across a macrotidal, ultradissipative sandy beach. *Mar. Biol.* 155, 79-90

282 Uys, C. *et al.* (2009) Turnover in flightless invertebrate species composition over different spatial scales in afrotemperate forest in the Drakensberg, South Africa. *Afr. J. Ecol.* 47, 341-351

283 Valdivia, N. and Molis, M. (2009) Observational evidence of a negative biodiversity–stability relationship in intertidal epibenthic communities. *Aquat. Biol.* 4, 263-271

284 Van Dover, C,L, and Doerries, M.B. (2005). Community structure in mussel beds at Logatchev hydrothermal vents and a comparison of macrofaunal species richness on slow and fast spreading mid-ocean ridges. *Marine Ecology* 26, 110-120

285 Vanpeteghem, D. *et al*. (2008) Dynamics of neutral biodiversity. *Mathematical Bioscience* 212, 88-98

286 Vellend, M. (2005) Species diversity and genetic diversity: parallel processes and correlated patterns. The American Naturalist 166, 199-215

287 Venail, P.A. *et al.*(2010) Dispersal scales up the biodiversity−productivity relationship in an experimental source-sink metacommunity. *Proc. R. Soc. B* 277, 2339-2345

288 Vermonden, K. *et al*. (2012) The influence of environmental factors and dredging on chironomid larval diversity in urban drainage system in polders strongly influenced by seepage from large rivers. *J. N. Am. Benthol. Soc*. 30, 1074-1092

289 Villéger, S. *et al*. (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89, 2290-2301

290 Villéger, S. *et al*. (2010) Contrasting changes in taxonomic vs . functional diversity of tropical fish communities after habitat degradation. *Ecological Applications* 20, 1512-1522

291 Waite, I. *et al*. (2004) The effects of macroinvertebrate taxonomic resolution in large landscape bioassessments: an example from the. *Freshwater Biology* 49, 474-489

292 Waldbusser, G.G. *et al*. (2004) The effects of infaunal biodiversity on biogeochemistry of coastal marine sediments. *Limnol. Oceanogr*.49, 1482-1492

293 Walker, S.C and Cyr, H. (2007) Testing the standard neutral model of biodiversity in lake communities. *Oikos* 116, 143-155

294 Wang, Z. *et al.* (2010) Assessment of the restoration of a degraded semi-humid evergreen broadleaf forest ecosystem by combined single-indicator and comprehensive model method. *Ecological Engineering* 36, 757-767

295 Werner, F. A. and Gradstein, S.R. (2008) Seedling stablishment of vascular epiphytes on isolated and enclosed forest trees in a Andrean landscape, Ecuador. *Biodivers. Conserv.* 17, 3195-3207

296 Wertz, S. *et al.* (2007) Declining of soil microbial biodiversity does not influence the resistance and resiliance of key soil microbial functional groups following a model disturbance. *Environ. Microbiol.* 9, 2211-2219

297 Wickings, K.G. and Ruberson, J. (2011) Impact of the red imported fire ant (Hymenoptera: Formicidae) on epigeic arthropods of cotton agroecosystems Impact of the. *Ann. Entomol. Soc. Am.* 104, 171-179

298 Wiegand, T. *et al.* (2007) How individual species structure diversity in tropical forests. *PNAS* 104, 19029-19033 (2007).

299 Wilkie, K.T.R. *et al.* (2010) Species diversity and distribution patterns of the ants of Amazonian Ecuador. *PLoS ONE*. DOI: 10.1371/journal.pone.0013146

300 Wilkinson, A. *et al.* (2012) Species richness and nitrogen supply regulate the productivity and respiration of ectomycorrhizal fungi in pure culture. *Fungal Ecology* 5, 211-222

301 Williams, N.M. (2011) Restoration of nontarget species: bee communities and pollination function in riparian forests. *Restoration Ecology* 19, 450-459

302 Wisley, B.J. *et al.* (2005) Relationships among indices suggest that richness is an incomplete surrogate for grassland biodiversity. *Ecology* 86, 1178-1184

303 Wittebolle, L. *et al.* (2009) Initial community evenness favours functionality under selective stress. *Nature*. DOI: doi:10.1038/nature07840

304 Woodcock, B.A. *et al.* (2009) Responses of invertebrate trophic level, feeding guild and body size to the management of improved grassland field margins. *Journal of Applied Ecology* 46, 920-929

305 Xu, H. *et al*. (2011) Application of an indicator based on taxonomic relatedness of ciliated protozoan assemblages for marine environmental assessment. *Eviron. Sci. Pollut. Res*. 1213-1221

306 Xu, H. *et al*. (2011) Spatial variation in taxonomic distinctness of ciliated protozoan communites at genus level resolution and relationships to marine water quality in Jiazhou Bay, northern China. Hydrobiologia 665, 67-78

307 Yan, S. *et al.* (2012) A soil fauna index for assessing soil quality. *Soil Biology and Biochemistry* 47, 158-165

308 Yates, M. and Andrew, N.R. (2011) Comparison of ant community composition across different land-use types : assessing morphological traits with more common methods. *Australian Journal of Entomology* 118-124

309 Yin, Z.Y. *et al.* (2005) Species abundance in a forest community in South China: a case of poisson lognormal distribution. *Journal of Integrative Plant Biology* 47, 801-810

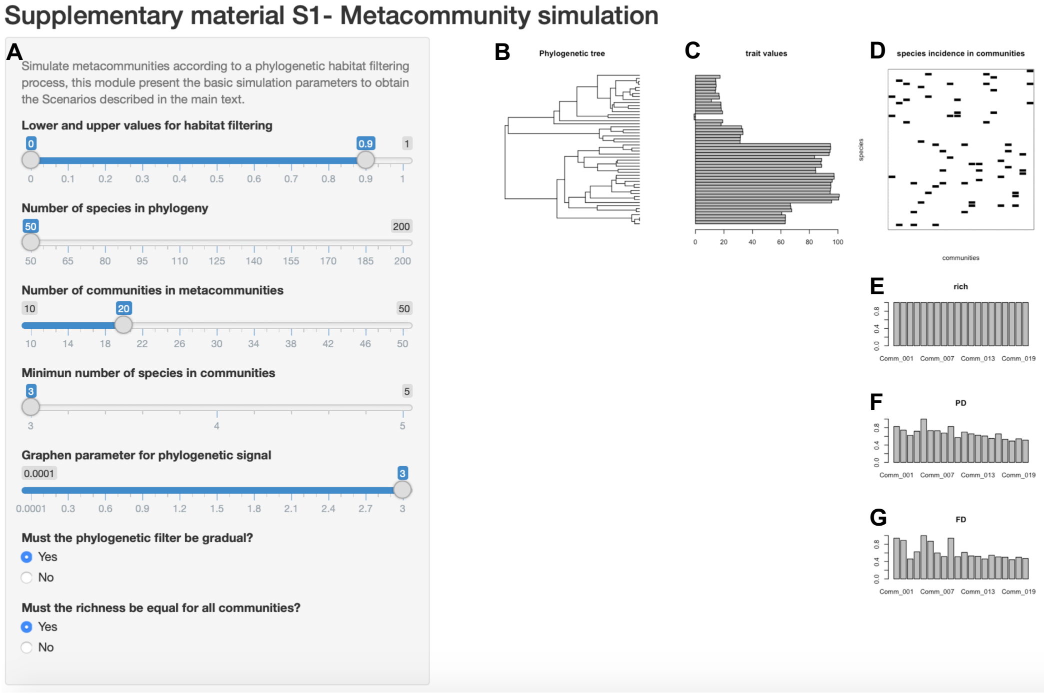
Apêndice capítulo 2

Appendix S1 – Simulation procedure.

We elaborated an interactive simulation module with shiny package for RStudio, in order to the reader explore the basic patterns in simulation procedure used in our work. The module contains a user interface (A in Figure S1) that present the parameters used to simulate a phylogenetic trees (B), species traits (C), communities (D) and calculate three diversity metrics (richness, phylogenetic diversity [Faith, 1999] and functional diversity

[Petchey and Gaston, 2000]. Panels E, F and G respectively). Each modification that is made in any parameters of the user interface triggers the simulation procedure with the generation of a new phylogeny, species traits, community composition and calculation of diversity metrics, following the same methods for simulating communities described in the section *Simulation methodology* in the main text of this work.

The default module initiate showing a pattern in which the community present a phylogeny with 50 species (set with slidebar *Number of species in phylogeny*). The species present high phylogenetical signal in traits (set with slidebar *Grafen parameter for phylogenetic signal*, lower values of Grafen parameter reduce the phylogenetic signal whereas higher values increases phylogenetic signal). The metacommunity was assembled by a process of phylogenetic habitat filter (*sensu* Duarte, 2002) in which, in one extreme only the 10% more phylogenetic related species can occur (set with upper value of slidebar *Lower and upper values for habitat filtering*) and in the other point of the phylogenetic gradient any specie can occur (no phylogenetic restriction, set with lower value of slidebar *Lower and upper values for habitat filtering*), creating a gradient in phylogenetic and functional diversity (bar plots F and G). The richness can be set to be equal in all communities or a gradient in the bottom widget (*Must the richness be equal for all communities?*). Finally, the phylogenetic filter applied can be set to be gradual (default) or not (set with *Must the phylogenetic filter be gradual?*).



Supplementary material S1- Metacommunity simulation

A

Simulate metacommunities according to a phylogenetic habitat filtering process, this module present the basic simulation parameters to obtain the Scenarios described in the main text.

Lower and upper values for habitat filtering: 0 – 0.9

Number of species in phylogeny: 50

Number of communities in metacommunities: 20

Minimun number of species in communities: 3

Graphen parameter for phylogenetic signal: 3

Must the phylogenetic filter be gradual?

● Yes

○ No

Must the richness be equal for all communities?

● Yes

○ No

Figure S1: Layout of interactive simulation module to simulate metacommunities. This comprises the basic parameters used to simulate the scenarios used in the work. A – slide bars and buttons containing parameters that can be modified to obtain the metacommunities; B – phylogeny used to simulate the traits, metacommunities and calculate PD metric; C – bar plot representing trait values for each species in phylogeny; D – representation of species incidence in communities that compose the metacommunity, columns represent communities and lines represent species, the filled space represents the presence of a specie in a community; E, F and G – bar plots representing the values for, respectively, richness (rich), phylogenetic diversity (PD) and functional diversity (FD) for each community.

Each time that some widget control is modified the simulation processes starts again with a new phylogeny, reflecting the same procedure used to perform the simulations used in the section *Simulation methodology* of the main text. The combinations of widget controls will not result in all Scenarios showed in the main text, but comprises the basic controls to obtain the Scenarios used. The application can be accessed at https://gabrielnakamura.shinyapps.io/Supp_matShiny/.

References

Duarte, L. D. S. 2011. Phylogenetic habitat filtering influences forest nucleation in grasslands. - Oikos 120: 208–215.

Petchey, O.L. and Gaston, K.J. 2002. Functional diversity (FD), species richness and community composition. – Ecol. Lett. 5: 402-411.

Faith, D. P. 1992. Conservation evaluation and phylogenetic diversity. - Biol. Conserv. 61: 1–10.

Appendix S2 – R functions for IV

Markdown file containing the arguments and the outputs of IV_function. For the latest version of this function see https://github.com/GabrielNakamura/IV_function.

IV_function

Function to compute Importance Values (adapted from [Willig et al. 2005](http://www.esajournals.org/doi/abs/10.1890/04-0394)).

arguments

inputs:

matrix.M= a matrix with communities in rows and values of metrics in columns;

IV.bootstrap= logical argument, if TRUE the function will compute bootstrap values of IV for matrix.M, if FALSE the function will compute only observed values;

n.sample= number of bootstrap samples to be carried out with matrix.M;

scale= logical argument, if TRUE the matrix.M will be standardized to zero mean and unit variance, if FALSE no standardization is performed;

method= If scale= TRUE, method correspond to the type of standardization imposed to matrix.M before calculation of IVs. The arguments to be used are the same to be passed to the argument method in function decostand() in vegan. Default argument is "max", where the metrics are standardized by their respective maximum value observed between communities.

stopRule= logical, if TRUE the Importance Values of dimensions will be calculated using only significant axes according to Kaiser-Guttman criterion. Default values is TRUE.

output:

list with length two containing observed and bootstrap IVs of components of diversity present in matrix.M. If the option bootstrap= FALSE, the function will return a matrix with one row and column number equal to the number of columns in matrix M.

####copy and paste from here#####

```
ImportanceVal<- function(matrix.M, IV.bootstrap= FALSE,
 n.sample= 999, scale= TRUE, method= "standardize",
 stopRule= TRUE){
    library(vegan)
    if(is.matrix(matrix.M) == FALSE){
        matrix.M<- as.matrix(matrix.M)
        if(ncol(matrix.M)<3){
            stop("\n matrix M must be at least 3 components
 of diversity\n")
        }
        if(nrow(matrix.M)<3){
            stop("\n Matrix M must be at least 3
 communities\n")
        }
    }
    matrix.M.stand<-decostand(x = matrix.M, method =
 method, MARGIN = 2)[1:nrow(matrix.M),]
    if(scale == TRUE){
        metric.sqrt.corr<- (prcomp(x = matrix.M.stand,
 scale.= FALSE)$rotation ^ 2)
```

```
        prop.var<- summary(prcomp(x = matrix.M.stand,
scale.= FALSE))$importance[2,]
        names.matrix.IV<- list("IV.resu",
colnames(matrix.M))
        IVs.result<- matrix(nrow= 1, ncol= ncol(matrix.M),
dimnames= names.matrix.IV)
        for(i in 1:nrow(metric.sqrt.corr)){
            IVs.result[,i]<- metric.sqrt.corr[i,] %*%
as.matrix(prop.var)
        }
        if(stopRule==TRUE){
            sig.eigen<-which(prcomp(matrix.M.stand, scale.
= FALSE)$sdev^2>mean(prcomp(matrix.M.stand, scale. =
FALSE)$sdev^2))
            metric.sqrt.corr.sig<- (prcomp(x =
matrix.M.stand, scale.= FALSE)$rotation ^ 2)[,sig.eigen]
            prop.var.sig<- as.matrix(summary(prcomp(x =
matrix.M.stand, scale.=
FALSE))$importance[2,])[sig.eigen,]
            names.matrix.IV<- list("IV.resu",
colnames(matrix.M))
            IVs.result.sig<- matrix(nrow= 1, ncol=
ncol(matrix.M), dimnames= names.matrix.IV)
            for(i in
1:nrow(as.matrix(metric.sqrt.corr.sig))){
                IVs.result.sig[,i]<-
as.matrix(metric.sqrt.corr.sig)[i,] %*%
as.matrix(prop.var.sig)
            }
        }
        if(IV.bootstrap == FALSE){
            if(stopRule==TRUE){
                return(IVs.result.sig)} else {
                    return(IVs.result)
                }
        }
        if(IV.bootstrap == TRUE) {
            matrix.M.boot<- vector("list", n.sample)
            for(i in 1:n.sample) {
                matrix.M.boot[[i]]<-
matrix.M.stand[sample(1:nrow(matrix.M.stand), replace=
TRUE),]
            }
            names.IV.result.boot<- list(c(1:n.sample),
colnames(matrix.M))
            IV.result.boot<- matrix(nrow= n.sample, ncol=
ncol(matrix.M), dimnames= names.IV.result.boot)
            metric.sqrt.corr.boot<- vector("list",
n.sample)
            prop.var.boot<- vector("list", n.sample)
            for(i in 1:length(matrix.M.boot)){
```

```
                metric.sqrt.corr.boot[[i]]<- (prcomp(x =
matrix.M.boot[[i]], scale.= FALSE)$rotation ^ 2)
                prop.var.boot[[i]]<- summary(prcomp(x =
matrix.M.boot[[i]], scale.= FALSE))$importance[2,]
            }
            IVs.result.boot<- matrix(nrow = n.sample, ncol=
ncol(matrix.M), byrow = TRUE)
            for(i in 1:length(metric.sqrt.corr.boot)){
                metric.sqrt.corr.boot[[i]]
                for(j in 1:ncol(matrix.M)){
                    IV.result.boot[i,j]<-
metric.sqrt.corr.boot[[i]][j,] %*%
as.matrix(prop.var.boot[[i]])
                }
            }
            IV.bootstrap.result<- setNames(list(IVs.result,
IV.result.boot), c("IV.obs", "IV.boot"))
            if(stopRule==TRUE){
                IV.result.boot.sig<- matrix(nrow= n.sample,
ncol= ncol(matrix.M.stand), dimnames=
names.IV.result.boot)
                metric.sqrt.corr.boot.sig<- vector("list",
n.sample)
                prop.var.boot.sig<- vector("list",
n.sample)
                for(i in 1:length(matrix.M.boot)){
                    sig.eigen<-which(prcomp(matrix.M.stand,
scale. = FALSE)$sdev^2>mean(prcomp(matrix.M.stand, scale.
= FALSE)$sdev^2))
                    metric.sqrt.corr.boot.sig[[i]]<-
as.matrix((prcomp(x = matrix.M.boot[[i]], scale.=
FALSE)$rotation ^ 2)[,sig.eigen])
                    prop.var.boot.sig[[i]]<-
as.matrix(summary(prcomp(x = matrix.M.boot[[i]], scale.=
FALSE))$importance[2,])[sig.eigen,]
                }
                IVs.result.boot.sig<- matrix(nrow =
n.sample, ncol= ncol(matrix.M.stand), byrow = TRUE)
                for(i in
1:length(metric.sqrt.corr.boot.sig)){
                    metric.sqrt.corr.boot.sig[[i]]
                    for(j in 1:ncol(matrix.M)){
                        IV.result.boot.sig[i,j]<-
metric.sqrt.corr.boot.sig[[i]][j,] %*%
as.matrix(prop.var.boot.sig[[i]])
                    }
                }
                IV.bootstrap.result.sig<-
setNames(list(IVs.result.sig, IV.result.boot.sig),
c("IV.obs_stopRule", "IV.boot_stopRule"))
                return(IV.bootstrap.result.sig)
```

```
            }
            return(IV.bootstrap.result)
        }
    }
    if(scale == FALSE){
        metric.sqrt.corr<- (prcomp(x = matrix.M, scale.=
FALSE)$rotation ^ 2)
        prop.var<- summary(prcomp(x = matrix.M, scale.=
FALSE))$importance[2,]
        names.matrix.IV<- list("IV.resu",
colnames(matrix.M))
        IVs.result<- matrix(nrow= 1, ncol= ncol(matrix.M),
dimnames= names.matrix.IV)
        for(i in 1:nrow(metric.sqrt.corr)){
            IVs.result[,i]<- metric.sqrt.corr[i,] %*%
as.matrix(prop.var)
        }
        if(stopRule==TRUE){
            sig.eigen<-which(prcomp(matrix.M, scale. =
FALSE)$sdev^2>mean(prcomp(matrix.M, scale. =
FALSE)$sdev^2))
            metric.sqrt.corr.sig<- (prcomp(x = matrix.M,
scale.= FALSE)$rotation ^ 2)[,sig.eigen]
            prop.var.sig<- as.matrix(summary(prcomp(x =
matrix.M, scale.= FALSE))$importance[2,])[sig.eigen,]
            names.matrix.IV<- list("IV.resu",
colnames(matrix.M))
            IVs.result.sig<- matrix(nrow= 1, ncol=
ncol(matrix.M), dimnames= names.matrix.IV)
            for(i in
1:nrow(as.matrix(metric.sqrt.corr.sig))){
                IVs.result.sig[,i]<-
as.matrix(metric.sqrt.corr.sig)[i,] %*%
as.matrix(prop.var.sig)
            }
        }
        if(IV.bootstrap == FALSE){
            if(stopRule==TRUE){
                return(IVs.result.sig)} else {
                    return(IVs.result)
                }
        }
        if(IV.bootstrap == TRUE) {
            matrix.M.boot<- vector("list", n.sample)
            for(i in 1:n.sample) {
                matrix.M.boot[[i]]<-
matrix.M[sample(1:nrow(matrix.M.stand), replace= TRUE),]
            }
            names.IV.result.boot<- list(c(1:n.sample),
colnames(matrix.M))
```

```
            IV.result.boot<- matrix(nrow= n.sample, ncol=
ncol(matrix.M), dimnames= names.IV.result.boot)
            metric.sqrt.corr.boot<- vector("list",
n.sample)
            prop.var.boot<- vector("list", n.sample)
            for(i in 1:length(matrix.M.boot)){
                metric.sqrt.corr.boot[[i]]<- (prcomp(x =
matrix.M.boot[[i]], scale.= FALSE)$rotation ^ 2)
                prop.var.boot[[i]]<-
as.matrix(summary(prcomp(x = matrix.M.boot[[i]], scale.=
FALSE))$importance[2,])
            }
            IVs.result.boot<- matrix(nrow = n.sample, ncol=
ncol(matrix.M), byrow = TRUE)
            for(i in 1:length(metric.sqrt.corr.boot)){
                metric.sqrt.corr.boot[[i]]
                for(j in 1:ncol(matrix.M)){
                    IV.result.boot[i,j]<-
metric.sqrt.corr.boot[[i]][j,] %*%
as.matrix(prop.var.boot[[i]])
                }
            }
            IV.bootstrap.result<- setNames(list(IVs.result,
IV.result.boot), c("IV.obs", "IV.boot"))
            if(stopRule==TRUE){
                IV.result.boot.sig<- matrix(nrow= n.sample,
ncol= ncol(matrix.M), dimnames= names.IV.result.boot)
                metric.sqrt.corr.boot.sig<- vector("list",
n.sample)
                prop.var.boot.sig<- vector("list",
n.sample)
                for(i in 1:length(matrix.M.boot)){
                    sig.eigen<-which(prcomp(matrix.M,
scale. = FALSE)$sdev^2>mean(prcomp(matrix.M, scale. =
FALSE)$sdev^2))
                    metric.sqrt.corr.boot.sig[[i]]<-
as.matrix((prcomp(x = matrix.M.boot[[i]], scale.=
FALSE)$rotation ^ 2)[,sig.eigen])
                    prop.var.boot.sig[[i]]<-
as.matrix(summary(prcomp(x = matrix.M.boot[[i]], scale.=
FALSE))$importance[2,])[sig.eigen,]
                }
                IVs.result.boot.sig<- matrix(nrow =
n.sample, ncol= ncol(matrix.M), byrow = TRUE)
                for(i in
1:length(metric.sqrt.corr.boot.sig)){
                    metric.sqrt.corr.boot.sig[[i]]
                    for(j in 1:ncol(matrix.M)){
                        IV.result.boot.sig[i,j]<-
metric.sqrt.corr.boot.sig[[i]][j,] %*%
as.matrix(prop.var.boot.sig[[i]])
```

```
                    }
                }
                IV.bootstrap.result.sig<-
setNames(list(IVs.result.sig, IV.result.boot.sig),
c("IV.obs_stopRule", "IV.boot_stopRule"))
                return(IV.bootstrap.result.sig)
            }
            return(IV.bootstrap.result)
        }
    }
}
```

Appendix S3 – Dimensionality function

Markdown file containing the arguments used in dimensionality_function and its outputs. For the latest version of this function see https://github.com/GabrielNakamura/dimensionality_function.

dimensionality_function

Function to calculate the dimensionality of biodiversity based on evenness of eingenvalues obtained from a PCA, performed on a matrix M (communities described by metrics of biodiversity).

The function are performed accondingly to logic propposed by [Stevens and Tello 2014](http://onlinelibrary.wiley.com/doi/10.1111/geb.12192/abstract) to measure the dimensionality of biodiversity.

arguments

inputs:

matrix.M= a matrix with communities in rows and values of metrics in columns;

scale= logical argument, if TRUE the matrix.M will be standardized acordingly to the argument contained in methods, if FALSE no standardization is performed;

method= If scale= TRUE, method correspond to the type of standardization imposed to matrix.M. The arguments to be used are the same to be passed to the argument method in function decostand() in vegan. Default argument is "standardize", where the metrics are standardized by zero mean and unit variance.

evenness= index of evenness to be applied in eingenvalues derived from PCA on matrix M. May be one of the following arguments: "Camargo" to calculate evenness based on Camargo's index; "Pielou" to calculate evenness based in Pielou's evenness or "both", to calculate both index

output:

numeric, with a value representing the degree of evenness based in one of the two index options or a list with length two containing the results of evenness based on the two option of indexes. The greater the index, greater the dimensionality of the set of communities described by matrix M.

####copy and paste from here###

```
dimensionality<- function(matrix.M, scale= TRUE, method=
 "standardize", evenness= "Camargo"){
    library(vegan)
    library(picante)
    #Camargo's index
    camargo.eveness <- function(n_spec, include_zeros = T){
```

```
        if(is.vector(n_spec)==FALSE){
            stop("\n n_spec must be a vector of abundance
of species \n")
        }
        if (include_zeros){
            n <- n_spec
        }  else{
            n <- n_spec[n_spec > 0]
        }
        S <- length(n)
        camar<-matrix(nrow=length(n), ncol=length(n))
        for (i in 1:S)
        {
            for (j in 1:S)
            {
                p_i <- n[i]/sum(n)
                p_j <- n[j]/sum(n)
                camar[i,j] <- ((abs(p_i - p_j))/S)
            }
        }
        sum.camar<- abs(sum(as.dist(camar, diag= FALSE,
upper= FALSE)))
        return(1-sum.camar)
    }
    #Pielou index
    pielou.evenness<- function(x) {
        library(vegan)
        H<- diversity(x)
        nspec<- length(x)
        J<- H/log(nspec)
        return(J)
    }
    if(is.matrix(matrix.M) == FALSE){
        matrix.M<- as.matrix(matrix.M)
        if(ncol(matrix.M)<3){
            stop("\n matrix M must be at least 3 components
of diversity\n")
        }
        if(nrow(matrix.M)<3){
            stop("\n Matrix M must be at least 3
communities\n")
        }
    }
    matrix.M.stand<-decostand(x = matrix.M, method =
method, MARGIN = 2)[1:nrow(matrix.M),]
    if(scale==TRUE){
        eingen.obs.stand<- (summary(prcomp(x =
matrix.M.stand, scale. = FALSE))$sdev)^2
        eveness.obs.camargo<- camargo.eveness(n_spec=
as.vector(eingen.obs.stand))
```

```
        eveness.obs.pielou<- pielou.evenness(x =
eingen.obs.stand)
        both_evenness<- list(Camargo= eveness.obs.camargo,
Pielou= eveness.obs.pielou)
        if(evenness=="Camargo"){
            return(eveness.obs.camargo)
        }
        if(evenness=="Pielou") {
            return(eveness.obs.pielou)
        }
        if(evenness=="both"){
            return(both_evenness)
        }
    }
    if(scale==FALSE){
        eingen.obs<- (summary(prcomp(x = matrix.M, scale. =
FALSE))$sdev)^2
        eveness.obs.camargo<- camargo.eveness(n_spec=
as.vector(eingen.obs))
        eveness.obs.pielou<- pielou.evenness(x =
eingen.obs)
        both_evenness<- list(Camargo= eveness.obs.camargo,
Pielou= eveness.obs.pielou)
        if(evenness=="Camargo"){
            return(eveness.obs.camargo)
        }
        if(evenness=="Pielou") {
            return(eveness.obs.pielou)
        }
        if(evenness=="both"){
            return(both_evenness)
        }
    }
}
```

Apêndice capítulo 3

Supplementary Material

Appendix S1

Obtaining BD through the raw data approach

We summarize here how BD_{Phy} and BD_{Fun} can be obtained using the raw data approach. The major advantage of calculating BD metrics this way is that it allows BD to be decomposed into a component that represents species contribution to beta diversity (SCBD). We start with a matrix that describes phylogenetic or functional composition of communities (matrix **P** or **X,** respectively) obtained using a fuzzy weighting procedure and use it to compute the square deviation of the proportion of incidence of each species in a community (y_{ij}) with its respective mean incidence in the community ($\bar{y}j$) as described in Equation S1. Each value obtained from Equation S1 composes matrix **S** of square deviations.

$$s_{ij} = \left(y_{ij} - \bar{y}_j\right)^2 \text{ Equation S1.}$$

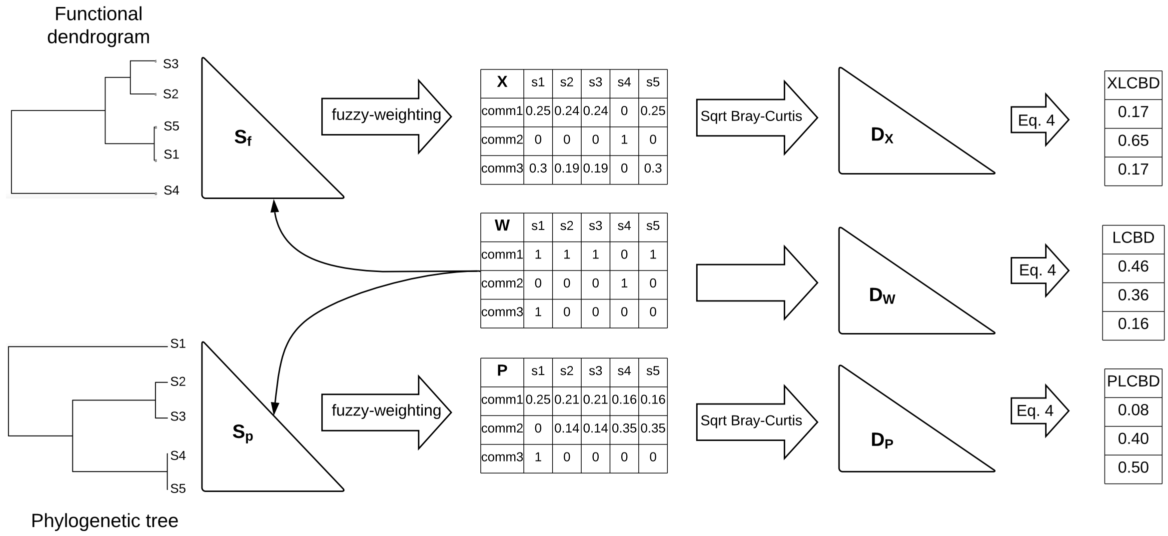
Using Equation S2 we can obtain the BD measure, where *n* corresponds to the total number of sites in the metacommunity and *p* the total number of species.

$$BD_{Phy} \text{ or } BD_{Fun} = \frac{\sum_{i=1}^{n}\sum_{j=1}^{p} s_{ij}}{n-1} \text{ Equation S2}$$

Since BD_{Phy} and BD_{Fun} comprise the total variation in, respectively, matrix **P** and **X**, we can partition it into different components that represent the variation accounted for by the rows of matrix **S** and the variation accounted for by the columns. By summing the rows of matrix **S** we obtain a measure of local contribution for beta diversity (PLCBD for phylogenetic contribution and XLCBD for functional contribution) and by summing the elements in each column of matrix **S** we obtain a measure of species contribution for beta diversity (PSCBD for phylogenetic and XSCBD for functional).

Interpreting phylogenetic and functional local components of BD_{Fun} and BD_{Phy}

In order to clarify how components PLCBD and XLCBD can be interpreted as measures of phylogenetic and functional uniqueness, we illustrate in Figure S1 a hypothetical example with a metacommunity. The metacommunity is described by the presence of five species (matrix **W**) with their respective phylogenetic relationships (phylogenetic tree) and a functional dendrogram describing trait similarities among species. Three species occur only in community 1 (sp 2, sp 3 and sp 5 in matrix **W**), consequently, community 1 has the highest value for LCBD, since this is the most unique in terms of species composition. On the other hand, community 3 hosts only species 1, and is the most distinct in terms of evolutionary history. For this reason, despite the lower contribution to the taxonomic component of beta diversity (low LCBD), community 3 has the highest PLCBD (0.50). Finally, community 2 is the most unique in terms of functional composition since it hosts species 4, and is the most distinct regarding its attributes (illustrated in the functional dendrogram).



X	s1	s2	s3	s4	s5
comm1	0.25	0.24	0.24	0	0.25
comm2	0	0	0	1	0
comm3	0.3	0.19	0.19	0	0.3

XLCBD
0.17
0.65
0.17

W	s1	s2	s3	s4	s5
comm1	1	1	1	0	1
comm2	0	0	0	1	0
comm3	1	0	0	0	0

LCBD
0.46
0.36
0.16

P	s1	s2	s3	s4	s5
comm1	0.25	0.21	0.21	0.16	0.16
comm2	0	0.14	0.14	0.35	0.35
comm3	1	0	0	0	0

PLCBD
0.08
0.40
0.50

Figure S1: Schematic representation of a simple example containing one metacommunity composed of three communities and five species, with their occurrence and phylogenetic and functional relatedness described by, respectively, matrix **W**, a phylogenetic tree and a functional dendrogram. Matrices **X** and **P** are the results of a fuzzy weighting procedure applied to matrix **W**, and now describe functional and phylogenetic composition, respectively. Distance matrices $\mathbf{D_x}$, $\mathbf{D_w}$ and $\mathbf{D_p}$ are calculated according to an appropriate dissimilarity index and describe dissimilarity among communities according to functional, taxonomic and phylogenetic dimensions. A measure of the contribution of each local component to total β-diversity related to functional (XLCBD), taxonomic (LCBD) and phylogenetic (PLCBD) dimensions of diversity can be obtained using Equation 4.

Appendix 2

Simulation procedure.

To simulate the four scenarios used to test the performance of BD_{Phy}, BD_{Fun} and their respective component metrics PLCBD and XLCBD, we use an adaptation of the simulation procedure proposed by Peres-Neto et al.(2012), which in turn is an adaptation of a procedure detailed by Minchin (1986) to simulate community composition in n-dimensional environmental gradients. The simulation procedure can be viewed as a three-step process that comprises the following steps: (1) simulation of a phylogenetic tree that describes the evolutionary relationships among species that will compose the species pool; (2) simulation of the traits of these species; and (3) the assembly of a metacommunity based on the traits and a simulated environmental gradient used to allocate species among local communities. Each community in the metacommunity represents a point in the environmental gradient. Below we detail each of these three steps used to simulate metacommunities.

1 – Simulation of the phylogenetic tree.

To simulate the phylogenetic tree we used the function *sim.bdtree* of the *geiger* package (Harmon et al., 2008), which simulates the relatedness of species by a homogeneous birth-death process across all lineages. We set the speciation rate to 0.1 and the extinction rate to zero. This phylogeny was then used to simulate traits for the species.

2 – Simulation of species traits.

We simulated traits using the function *rTraitCont*. We manipulated the phylogenetic signal of traits by modifying the branch lengths of the phylogenetic tree using Grafen's ρ parameter and the function *compute.brlen.* Both *rTraitCont* and *compute.brlen* are of the *ape* package (Paradis et al., 2004). Low values for parameter ρ lengthen shallow branches of the tree, simulating ancient diversification of species, and thus generate low phylogenetic signal in traits. On the other hand, values of ρ that are near 1 lengthen deeper branches, simulating trait variation equivalent to that expected by a Brownian motion model, thus generating high phylogenetic signal in traits. We used $\rho = 0.0001$ to simulate traits with low phylogenetic signal and ρ = 1 to generate traits with high phylogenetic signal. Trait values were scaled to vary between -1 and 101 prior to subsequent analyses.

This trait simulation procedure was previously tested by Duarte et al. (2016), who demonstrated that modifications of ρ generated phylogenetic signal as expected; i.e., low values of ρ generating low phylogenetic signal and values of ρ = 1 generating phylogenetic signal near 1, as quantified by the K statistic (Blomberg, Garland Jr, & Ives, 2003).

3- Metacommunity assembly

From the simulated phylogenetic tree and traits (referred as **F**), we simulated metacommunities using a function that relates the values of attributes in vector **F** with values of an environmental gradient **E** present in each community (with each value in these vectors represented as f_i and e_k, respectivelly). The values of the environmental gradient were simulated from a uniform distribution ranging from 0 to 100. Species abundances in communities were simulated as unimodal response curves where the abundance w_{ik} of the i^{th} species in the k^{th} community (Peres-Neto et al. 2012) is defined as follows:

$$w_{ik} = h_i \exp\left[\frac{-\left(e_k - f_i\right)^2}{2\sigma_i^2}\right] \qquad \text{Equation 1}$$

Vector **h** in equation 1 contains random uniformly-distributed values ranging from 0 to 30 and represents the maximum abundance of each species at its optimum. Based on Equation 1 we simulated metacommunities containing 50 communities.

In summary, the simulation procedure described in Equation 1 can be interpreted as a sampling procedure of each species across an environmental gradient such that each species has distinct probabilities of being sampled at different locations along this gradient (Figure S1). These differences guarantee that the simulated metacommunity would possess variation in the species composition of its communities.

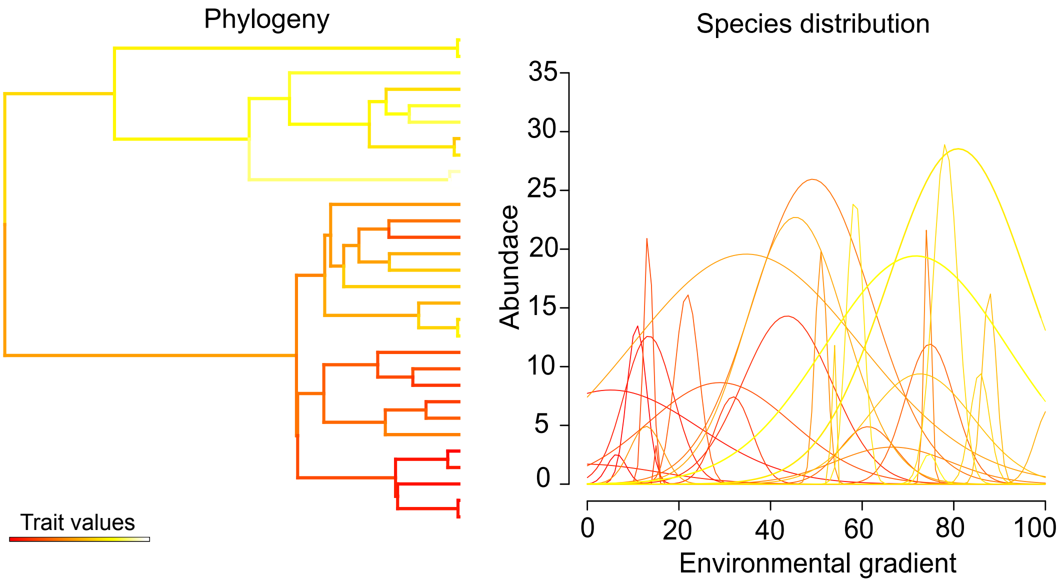


Figure S2: Schematic representation of a phylogenetic tree with species traits represented by colors and a graphic of unimodal response curves for each species present in the phylogeny. Similar species regarding their traits and phylogenetic relationships have a greater probability of being sampled in communities possessing similar values along the environmental gradient. This example illustrates the unimodal response curves for one metacommunity created according to scenario W1,P1,X1.

The four scenarios used to test the metrics proposed in this work were produced by combining the presence or absence of phylogenetic signal in traits with the traits used to calculate the metrics in the following manner: For the situation in which phylogenetic relationships and attributes of species mediate variation in community composition across the metacommunity, species that present similar traits and are phylogenetically similar have greater probability of being sampled at similar points along the environmental gradient. This situation corresponds to the scenario W1,P1,X1, which is illustrated in Figure S2 as an example of the format of unimodal species response curves. For the situation in which variation in community composition is mediated only by the attributes of species, the traits used in assembling the metacommunity do not possess phylogenetic signal, which corresponds to scenario W1,P0,X1. If only phylogenetic relationships mediate variation in community composition, then the traits used to calculate BD_{Fun} are not the same as those that mediate metacommunity assembly (scenario W1,P1,X0). If neither attributes nor phylogenetic relationships of species mediate variation in community composition, the traits used to calculate BD_{Fun} are not the same as those that are responsible for metacommunity assembly, and those that were used to simulate the metacommunity do not possess phylogenetic signal (W1,P0,X0).

The theoretical expectation regarding PLCBD and XLCBD are illustrated in Figure 3. Metacommunities structured by traits with phylogenetic signal will present higher values of PLCBD and XLCBD for communities near the extremes of environmental conditions than communities with environmental values near the mean for the entire metacommunity (high observed F values than that generated by the null models). On the other hand, metacommunities in which the assembly process is not dependent on the phylogenetic relationships of species nor by the traits they possess, will present similar values of PLCBD and XLCBD across all the entire environmental gradient (observed F values similar to that generated by null models).

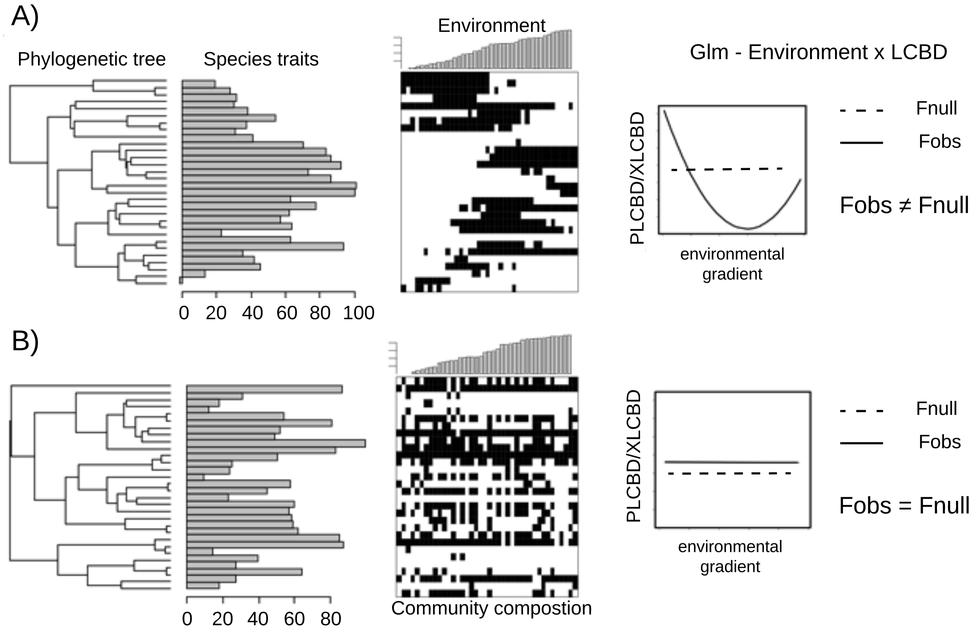


Figure S3: Schematic representation of simulation procedure used to test the performance of PLCBD and XLCBD. Scenario A represents a metacommunity simulated to test the power of PLCBD and XLCBD, in which communities in the extreme of the environmental gradient will present higher values of PLCBD and XLCBD than communities in the middle of the gradient. As a consequence, the F values derived from a model relating PLCBD/XLCBD with environment (F_{obs}) to simulate the communities must be higher than the F values generated from a null model that related null PLCBD/XLCBD. In B we present a metacommunity simulated to test the type I error rate of PLCBD/XLCBD. In this situation F_{obs} must not be different from a null distribution of F values derived from a null model (using as critical value α=0.05).

Appendix S3

Table S1 Provides the results for the raw data approach for calculating BD_{Phy}, BD_{Fun} and their respective components PLCBD and XLCBD.

Table S1: Statistical performance, type I error (alpha 0.05) and power of BD_{Phy}, BD_{Fun} and their components PLCBD and XLCBD calculated by the raw data approach.

Scenario	BD_{Phy}	BD_{Fun}	PLCBD					XLCBD				
	Rejection rate	**Rejection rate**	**Mean R2**	**TI site**	**TI taxa**	**Pw site**	**Pw taxa**	**Mean R2**	**TI site**	**TI taxa**	**Pw site**	**Pw taxa**
W1,P0,X0	0.04	0.05	0.44±0.18	0.94	0.04	-	-	0.25±0.15	0.82	0.03	-	-
W1,P1,X0	0.98	0.05	0.78±0.16	-	-	0.98	0.80	0.22±0.17	0.67	0.05	-	-
W1,P0,X1	0.05	1	0.45±0.17	0.95	0.03	-	-	0.90±0.04	-	-	1	1
W1,P1,X1	0.96	1	0.53±0.14	-	-	0.98	0.66	0.60±0.10	-	-	1	0.96

Scenario = different scenarios used to simulate metacommunities; TI site = type I error for site shuffle procedure; TI taxa = type I error for taxa shuffle procedure; Pw site = statistical power for site shuffle procedure; Pw taxa = statistical power for taxa shuffle procedure.

Appendix S4

Phylogenetic hypothesis and species traits

We constructed a phylogenetic tree describing the evolutionary relationship among fish species of Ivinhema River Basin using as a backbone phylogeny the hypothesis proposed by Betancur-R *et al.* (2013). We used other works with specific groups (Santos, 2007; Oliveira *et al.* 2011; Nakatani *et al.* 2011; Armbruster, 2004; Sullivan et al. 2013; Lavoué *et al.* 2012; Hertwig, 2007) to complement and improve the resolution of some families present in the backbone phylogeny. Species present in the sampled sites, but absent in the phylogeny. were replaced by the phylogenetically most closely related species available in the Betacur-R et al. (2013) phylogeny. Species with poorly established phylogenetic relationships, and for which we could not find any study to help elucidate their position, were included at family level, which generated some polytomies in the tree. The phylogeny was data by applying the BLADJ (Branch Length Adjustment) algorithm in Phylocom software (Webb et al. 2008), which estimates the length of non-dated nodes evenly through dated nodes. Dated nodes were those provided by Betancur-R et al. (2013). The phylogeny used to obtain cophenetic distance among species, dated in million years, is presented in Figure S4

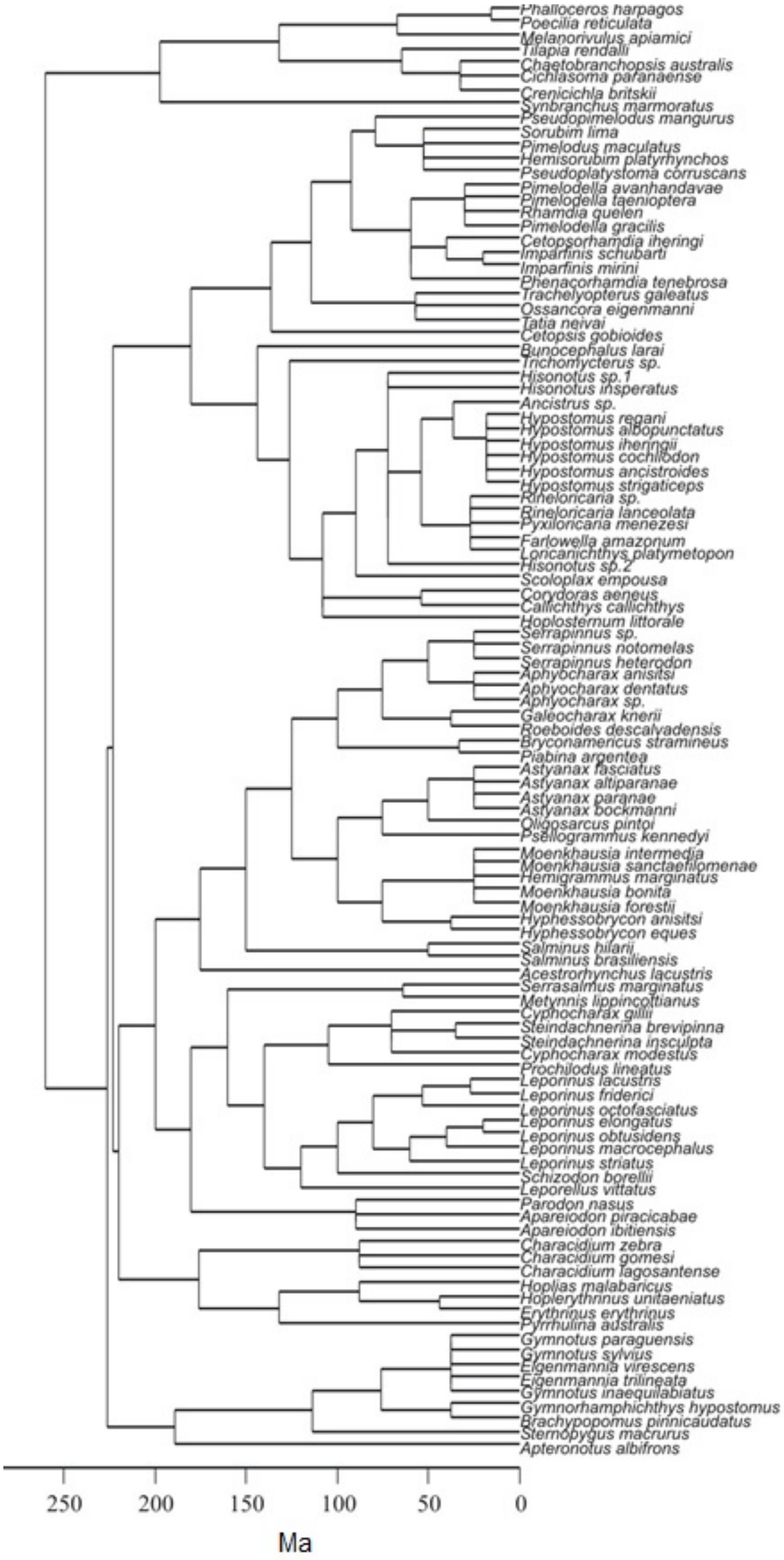


Figure S4: Phylogenetic hypothesis used to obtain cophenetic distance among stream fish species from Ivinhema River Basin, dated in million years.

We adopted a broad definition of functional traits as being those attributes of species that directly or indirectly influenc species performance (*e.g.* growth, reproduction, mortality). In summary, we selected a set of functional traits that are related to feeding, habitat occupation and life history (Gatz Jr. 1979; Winemiller, 1991; Oliveira, 2005). Some linear measures and areas of morphological structures were taken on the left side of three to five adult individuals in order to avoid trait differences do to ontogenetic variation in traits. Others measures (trophic level and maximum length) we obtained from Fishbase (Froese and Pauly, 2013), an online database for fishes. All measures used in this work along with their characteristics and definitions are summarized in Table S2.

Table S2: Functional attributes used to obtain functional distance for fish communities of Ivinhema River Basin

Functional attribute/ Ecomorphological index	Definition	Functional category	Type (continuous or categorical)
Maximum length (ML)	Maximum length known for the specie or the length of the longest specimen sampled. Measured as the distance between the anterior part of the head and the end of the caudal fin.	Habitat use, life history characteristics and diet.	continuous
Relative eye area (REA)	Ratio between the horizontal distance between margin of eyes and squared maximum length. High values are associated with species with greater visual capacity and that inhabit upper areas in the water column (Gatz Jr., 1979).	Diet, habitat use.	continuous
Vertical position of eye (VPE)	Ratio between the vertical distance to the center of pupil and height of head. This measure is associated with foraging position of species in the water column. High values indicate benthonic fishes, low values indicate nektonic fishes. (Gatz Jr., 1979).	Habitat use	continuous
Relative height (RH)	Ratio between maximum vertical distance and maximum length. Inversely related with water velocity and related to ascendant and descendant movements (Gatz Jr., 1979; Winemiller, 1991).	Locomotion, habitat use.	continuous

Aspect-ratio caudal fin (ACF)	Ratio between the squared maximum vertical distance of caudal fin and area of caudal fin. High values indicate greater swimming capacity (Gatz Jr., 1979; Breda, Oliveira & Goulart, 2005).	Locomotion.	continuous
Relative caudal peduncle length (CPL)	Ratio between distance from posterior proximal margin of anal fin and maximum length. Longer peduncles indicate species adapted to rifles (Oliveira, 2005).	Locomotion.	continuous
Relative mouth width (MW)	Ratio between horizontal distance measured inside of fully open mouth at widest point and maximum length. Greater values indicate species with preferences for larger prey (Gatz Jr., 1979).	Diet.	continuous
Trophic level (TL)	Species position in the food web, estimated as 1 plus the mean of trophic level of food items in the diet, weighted by the contribution of different food items.	Diet.	categorical

Taxonomic, functional and phylogenetic contribution of species

Calculation with the raw data approach allows BD to be decomposed into one additional source of variation — species contribution to beta diversity (SCBD). We calculated the original SCBD for species of Ivinhema River Basin, as well as the phylogenetic and functional SCBD (namely PSCBD and XSCBD, respectively). Figure S3 illustrates the rank of species contribution relative to these three components of biodiversity. Each dot represents a species, species names in each graphic represent the three most important species to total BD.

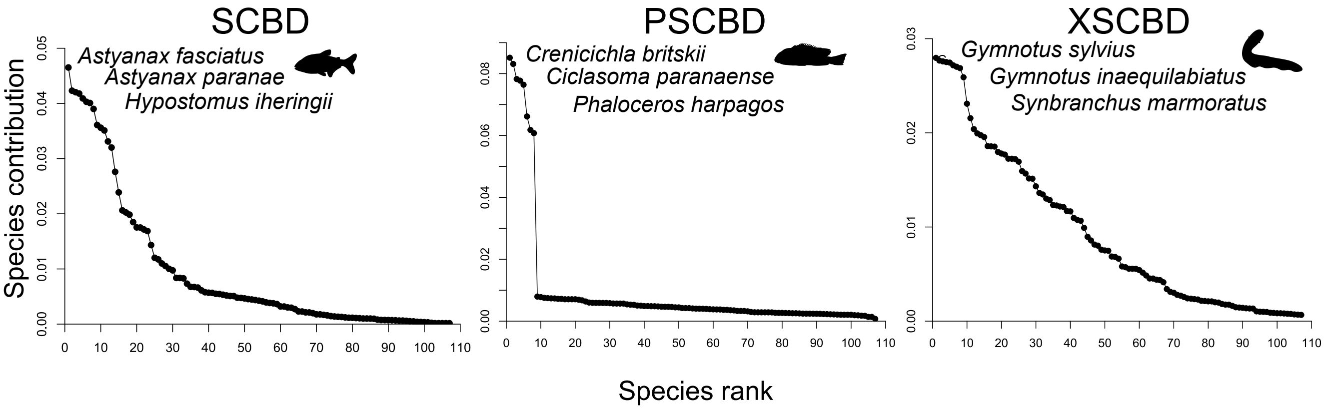


Figure S4: Species rank based on their contribution to BD, BD_{Phy} and BS_{Fun}. Each dot represents a species and the names in each graphic represent the three most important species. The silhouette is a representative of each group of most important species.

Appendix S5

We provide an R function that extends the calculation of BD to include phylogenetic and functional dimensions of diversity using raw data and distance-based approaches, this function and all the updates can be found at https://github.com/GabrielNakamura/BetaDiv_extension. The function calculates the original metric proposed by Legendre and Cáceres (2015), called here WLCBD, and the two new metrics proposed in the present study, PLCBD and XLCBD for phylogenetic and functional dimensions, respectively. We also provide in the function two null models to test the significance of the contribution of each community to the three components of diversity. The first null model, called site shuffle, tests the null hypothesis that the local contribution is a result of random community structure. The second null model, called taxa shuffle, tests the null hypothesis that the local contribution of communities for the functional and phylogenetic dimensions is the result of random phylogenetic or functional structure.

Rejection of the first null hypothesis ($p<0.05$) generated by site-shuffle, indicates that the contribution of a site to beta diversity is a result of a non-random mechanism that structures the observed community composition (species co-occurring in sites). Rejection of the second null hypothesis ($p<0.05$) generated by taxa shuffle, indicates that the local contribution to functional and phylogenetic diversity is the result of functional or phylogenetic similarities observed between species.

References

Blomberg, S. P., Garland Jr, T., & Ives, A. R. (2003). TESTING FOR PHYLOGENETIC SIGNAL IN COMPARATIVE DATA : BEHAVIORAL TRAITS ARE MORE LABILE Published By : The Society for the Study of Evolution TESTING FOR PHYLOGENETIC SIGNAL IN COMPARATIVE DATA : BEHAVIORAL TRAITS ARE MORE LABILE. *Evolution; International Journal of Organic Evolution*, *57*(4), 717–745. doi:10.1111/j.0014-3820.2003.tb00285.x

Duarte, L. D. S., Debastiani, V. J., Freitas, A. V. L., & Pillar, V. D. (2016). Dissecting phylogenetic fuzzy weighting: theory and application in metacommunity phylogenetics. *Methods in Ecology and Evolution*, *7*(8), 937–946. doi:10.1111/2041-210X.12547

Harmon, L. J., Weir, J. T., Brock, C. D., Glor, R. E., & Challenger, W. (2008). GEIGER: Investigating evolutionary radiations. *Bioinformatics*, *24*(1), 129–131. doi:10.1093/bioinformatics/btm538

Legendre, P., Borcard, D., & Peres-Neto, P. (2005). Analyzing Beta Diversity: Partitioning the spatial variation of community composition data. *Ecological Monographs*, *75*(4), 435–450.

Legendre, P., & De Cáceres, M. (2013). Beta diversity as the variance of community data: Dissimilarity coefficients and partitioning. *Ecology Letters*, *16*, 951–963. doi:10.1111/ele.12141

Minchin, P (1987). Simulation of multidimensional community patterns: towards a comprehensive model. *Vegetatio*, 71, 45-156.

Paradis, E., Claude, J., & Strimmer, K. (2004). APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, *20*(2), 289–290. doi:10.1093/bioinformatics/btg412

Peres-Neto, P.-R., Leibold, M., & Dray, S. (2012). Assessing the effects of spatial contingency and environmental filtering on metacommunity phylogenetics. *Ecology*, *93*(8), 14–30. doi:10.1890/11-0494.1