

•综述•

Beta多样性分解: 方法、应用与展望

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摘要: Beta多样性是指不同群落间物种组成的差异, 由物种周转(或物种替换)和嵌套(或丰富度差异)这两种过程决定。Beta多样性分解是将这两种过程对总体beta多样性的作用进行拆分, 然后分别探讨这两种过程对群落间物种组成差异的影响。2010年之后, 人们提出了beta多样性分解的方法, 其中占据主导地位的是由Andrés Baselga于2010年提出的BAS法(总体beta多样性分解为物种周转和嵌套组分)和由János Podani和Dénes Schmera于2011年以及José C. Carvalho等于2012年提出的POD法(总体beta多样性分解为物种替换和丰富度差异组分)。这两种分解方法引起了持续的争论, 促进了该领域的快速发展。作者归纳分析了2010年后有关beta多样性分解的文献后发现, 使用BAS法的论文无论在发表量和引用次数上都多于POD法(75% vs. 20%)。Beta多样性分解的研究主要集中在欧洲(45%), 研究类群则以动物(64%)为主。本文在回顾beta多样性分解方法的提出及其发展过程的基础上, 从时空维度(纬度梯度、海拔梯度、生境片段化过程以及季节和年际动态)、多样性的不同方面(物种、功能和谱系多样性)和不同生物类群之间的比较等研究角度出发, 进一步阐述了beta多样性分解方法在探讨生物多样性分布格局以及形成机制中的应用。对于beta多样性分解的研究, 我们认为需要深入探讨的问题有: (1) beta多样性分解方法的比较分析和整合; (2) 结合物种多度信息探讨beta多样性及其组分的分布格局; (3) 对大尺度下beta多样性分解的结果进行普适性验证。

关键词: 岛屿生物地理学; 生物多样性保护; 群落构建; 嵌套; 周转; 功能多样性; 谱系多样性; 生境片段化

Beta-diversity partitioning: methods, applications and perspectives

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Abstract: Beta diversity describes the variation in species composition among communities within a region and it is determined by two antithetic processes: species turnover (or species replacement), and nestedness (or difference in richness). Beta-diversity partitioning aims to separate these two processes when examining species composition among communities, and to reveal their underlying mechanisms. Since 2010, the partitioning methods were proposed following two dominant frameworks: the BAS method proposed by Andrés Baselga in 2010 (partitioning overall beta diversity into turnover and nestedness components) and the POD method proposed by János Podani and Dénes Schmera in 2011 and José C. Carvalho et al. in 2012 (partitioning overall beta diversity into species replacement and richness difference components). With the continuous debate on the nature of the BAS and POD methods, studies on beta-diversity partitioning have developed rapidly worldwide. We reviewed journal articles in the field of beta-diversity partitioning since 2010. Results showed that the number of publications and citations using the BAS method were greater than those using the POD method (75% vs. 20%). In those publications, most of study sites were located in Europe (45%) and research taxa were dominated by animals (64%). Here, we introduce the history and development of beta-diversity partitioning, potential applications in studying biodiversity distributions across spatial-temporal scales (latitudinal/altitudinal gradients, habitat fragmentation, seasonal and annual dynamics), multiple-faceted diversity (taxonomic, functional and phylogenetic diversity), and comparisons among various biological taxa. We point out the following directions in the field of beta-diversity partitioning in the future: (1) the synthesis and comparative analysis of the methods of beta-diversity partitioning; (2) examining patterns of overall beta diversity and its components by incorporating species abundance; and (3) testing the

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generality of results yielded from beta-diversity partitioning across large scales.

Key words: island biogeography; biodiversity conservation; community assembly; nestedness; turnover; functional diversity; phylogenetic diversity; habitat fragmentation

20世纪60年代, 美国生态学家Robert H. Whittaker提出了3种不同尺度的物种多样性: alpha多样性、beta多样性和gamma多样性(Whittaker, 1960)。alpha多样性指特定区域或群落的物种丰富度; gamma多样性表示多个群落的物种丰富度总和; beta多样性则表示不同群落间的物种组成变化, 即“与环境梯度或环境格局相关的群落组成变化的幅度或群落分化的程度”(Rosenzweig, 1995; 陈圣宾等, 2010; Legendre & De Cáceres, 2013)。Whittaker (1960)把beta多样性定义为 γ/α , 即倍性分配法, 其中 γ 为gamma多样性, α 为alpha多样性。此后, 虽然生态学家多次提及beta多样性, 但直到1972年才有专门论述beta多样性概念与度量方法的论文发表(Whittaker, 1972)。之后, Cody (1975)重新定义了Whittaker (1972)提出的beta多样性和gamma多样性, 强调gamma多样性的尺度比beta多样性更大(陈圣宾等, 2010)。

随着beta多样性研究的逐渐深入, 加性分配法($\beta = \gamma - \alpha$)和相似性(或相异性)指数等多种beta多样性测定方法被提出(Tuomisto, 2010a, b; Anderson et al, 2011)。在这些方法中, 相似性或相异性指数最为常用, 并被广泛用来测定群落物种组成在时间或空间维度上的变化。这些指数中Jaccard和Sørensen指数应用最广, 其次为Simpson和Bray-Curtis指数(陈圣宾等, 2010)。此外, beta多样性亦被定义为种-面积曲线的斜率(z) (Rosenzweig, 1995; Ricotta et al, 2002; Qian et al, 2013)、距离衰减效应(distance-decay effect) (Nekola & White, 1999; Soininen et al, 2007; Bellier et al, 2014)、群落总方差(total variance of community data) (Legendre & De Cáceres, 2013)和区域与局域物种丰富度间的差异(Ricklefs, 1987; Qian et al, 2013)等各种形式。Beta多样性测量方法的发展进一步扩展了其在生态学和保护生物学中的应用, 诸如被用来进行生物地理区域划分(Williams, 1996; Baselga et al, 2012; Mouillot et al, 2013), 以及保护区选址和保护区网络设置等(Wiersma & Urban, 2005; McKnight et al, 2007; Socolar et al, 2016)。

广义的beta多样性是指不同地点间物种组成的差异, 然而不同地点间的物种丰富度差异会导致地点间物种组成的变化, 因而在分析beta多样性的空间格局时应避免物种丰富度差异的干扰(Kraft et al, 2011; Qian et al, 2013)。早在20世纪90年代和本世纪初, Harrison等(1992)、Williams (1996)和Lennon等(2001)就开创性地提出群落间物种组成差异起源于两种不同的过程: 物种周转或替换(species turnover, or replacement)和物种丧失或增加(species loss or gain)。其中, 物种周转表示不同群落间的物种替换, 而物种丧失会导致群落间物种丰富度产生差异(Lennon et al, 2001)。当物种丰富度差异沿着某一梯度呈现出有序排列时, 拥有较少物种的群落将是拥有较多物种的群落的子集, 此时就会呈现出嵌套格局(nestedness pattern)(Patterson & Atmar, 1986; Wang et al, 2010; James et al, 2012; Staniczenko et al, 2013)。Beta多样性分解方法就是区分这两种过程对总体beta多样性的作用, 以及探讨这两种过程如何共同影响不同时空维度的物种分布格局(Baselga, 2010; Podani & Schmera, 2011)。目前, 有关beta多样性分解的研究快速发展, 这引起了众多生态学家和生物地理学家的关注(Legendre, 2014)。

2010年, beta多样性分解方法被系统地提出之后, 该研究领域的论文数量快速增加(图1A)。2017年1月6日, 基于16篇有关beta多样性分解方法的核心论文(附录1), 我们在Web of Science数据库中对其引用论文进行系统性地检索, 共获得引用论文551篇, 其中349篇开展了beta多样性分解的分析, 占总检索论文的63%。我们提取这349篇论文的发表年份、期刊名、研究类群、研究区域和被引用次数等关键信息进行归纳分析, 其中使用Baselga方法(Baselga, 2010)(简称BAS法)的论文占75% (共计被引用2,111次), 使用Podani和Schmera方法(Podani & Schmera, 2011)(简称POD法)的占20% (共计被引用434次), 两种方法共同分析的论文占1% (共计被引用27次), 以及使用其他分解方法的论文占3% (共计被引用161次)。研究区域主要集中在欧洲(45%)、南美洲(18%)和北美洲(11%), 其中欧洲地区以法国

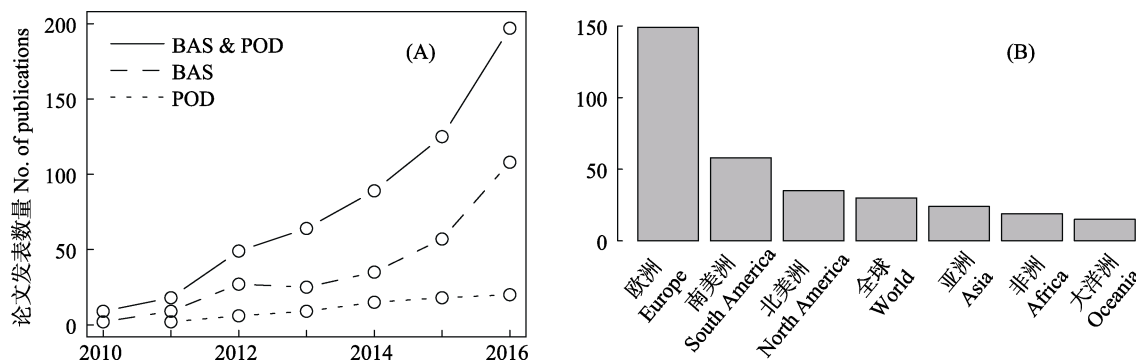


图 1 2010–2016 年间 β 多样性分解研究领域的论文发表状况。(A) 引用 BAS 法和 POD 法的年度论文发表数量, 以及使用 BAS 法或 POD 法分析数据的年度论文发表数量; (B) 地区分布

Fig. 1 Publications for studies in the field of beta-diversity partitioning from 2010 to 2016. (A) Number of annual publications cited BAS and POD methods, and using BAS or POD method to analyze the data; (B) Distribution of research areas

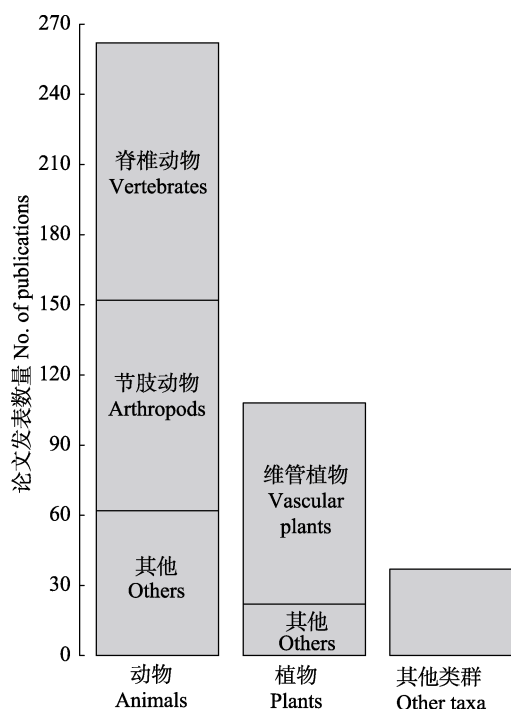


图 2 2010–2016 年间 β 多样性分解论文所涉及的生物门类及相应发表论文数量

Fig. 2 Number of publications for each biological taxon in the field of beta-diversity partitioning from 2010 to 2016

的研究居多(10%) (图1B)。该349篇论文共发表在134份国际学术期刊, 主要为 *PLoS ONE* (8%)、*Global Ecology and Biogeography* (7%)、*Journal of Biogeography* (6%)、*Hydrobiologia* (3%) 和 *Freshwater Biology* (3%) (附录2)。研究对象主要为动物(64%)和植物(27%), 其中脊椎动物的研究以鱼类(9%)和鸟类(6%)为主, 其他生物类群(9%)的研究则主要集中于真菌(5%) (图2)。

相较于国际前沿, 我国的 β 多样性分解研究仍较为落后。在本文所统计的349篇论文中, 我国学者的研究仅占2%, 研究区域主要在黄土高原(王世雄等, 2013, 2016)、山东半岛(Wang et al, 2014)、内蒙古草原(Zhang et al, 2014)、浙江千岛湖(Si et al, 2015, 2016)、青藏高原–横断山脉(Wen et al, 2016)和云南西双版纳(Beng et al, 2016)等地。此外, 另有两篇论文报道了云南高原湖泊中淡水鱼类研究(Su et al, 2015; Xu et al, 2015a)。我国从南到北覆盖了热带至寒温带的一系列生物地理区域, 具有丰富的生境多样性。这些特殊的地理条件造就了我国极高的物种多样性, 开展有关 β 多样性分解的研究将有利于更为深入地了解我国生物多样性的分布格局及其维持机制。

1 β 多样性分解的方法

1.1 BAS法和POD法

为了量化 β 多样性的两种不同过程, Baselga (2010)基于Sørensen指数系统地提出了 β 多样性的分解方法(简称BAS法), 即将两两群落间的总体 β 多样性(β_{sor})分解为物种空间周转组分(β_{sim})和嵌套组分(β_{sne})。此后, Podani和Schmera (2011)、Carvalho等(2012)基于Jaccard指数提出将两两群落间的总体 β 多样性(β_{cc})分解为物种空间替换组分($\beta_{\text{-s}}$)和物种丰富度差异组分(β_{rich}) (简称POD法) (表1)。

1.1.1 BAS法

由于Simpson成对相异性指数(Simpson pairwise

表 1 BAS 法(Baselga, 2010)和 POD 法(Podani & Schmera, 2011)的成对相异性指数及各自分解组分的表达式汇总。 a 为共有物种数, b 和 c 分别是两个群落各自特有的物种数。

Table 1 Pairwise dissimilarities and their components of BAS method (Baselga, 2010) and POD method (Podani & Schmera, 2011). a is the number of shared species between two communities, b and c are the numbers of exclusive species of either.

	BAS 法 BAS method	POD 法 POD method
Sørensen 相异性指数 Sørensen dissimilarity	$\beta_{\text{sor}} = \frac{b+c}{2a+b+c}$	—
周转/替换 Turnover/Replacement	$\beta_{\text{sim}} = \frac{\min(b,c)}{a+\min(b,c)}$	—
嵌套/丰富度差异 Nestedness/Richness difference	$\beta_{\text{sne}} = \frac{ b-c }{2a+b+c} \times \frac{a}{a+\min(b,c)}$	—
Jaccard 相异性指数 Jaccard dissimilarity	$\beta_{\text{jac}} = \frac{b+c}{a+b+c}$	$\beta_{\text{cc}} = \frac{b+c}{a+b+c}$
周转/替换 Turnover/Replacement	$\beta_{\text{jtu}} = \frac{2\min(b,c)}{a+2\min(b,c)}$	$\beta_{-3} = \frac{2\min(b,c)}{a+b+c}$
嵌套/丰富度差异 Nestedness/Richness difference	$\beta_{\text{jne}} = \frac{ b-c }{a+b+c} \times \frac{a}{a+2\min(b,c)}$	$\beta_{\text{rich}} = \frac{ b-c }{a+b+c}$

dissimilarity index) (β_{sim})可以排除物种丰富度的影响(Lennon et al, 2001), 因此当两个群落完全不嵌套时, β_{sor} 将等于 β_{sim} (Baselga, 2010; Leprieur et al, 2012)。对于两个不同的群落, β_{sor} 和 β_{sim} 两者之差(β_{sne})则可以表示beta多样性的嵌套组分(Baselga, 2010)。如表1所示, β_{sne} 指数的前半部分 $[|b-c|/(2a+b+c)]$, 与 β_{gl} 指数 $[2|b-c|/(2a+\max(b,c)+\min(b,c))]$ 相近(Lennon et al, 2001; Koleff et al, 2003a), 均是计算物种丰富度的差异(difference in richness); β_{sne} 指数的后半部分 $[a/(a+\min(b,c))]$ 是Simpson相似性指数($1-\beta_{\text{sim}}$), 因此 β_{sne} 能够计算物种丰富度差异中因嵌套而产生的部分。因此, 所有形式的总体beta多样性(β_{sor})均可以分解成物种周转(β_{sim})和嵌套(β_{sne})两个组分(Baselga, 2010)。

若要计算多个群落间的总体beta多样性及其组分值, 一种可能的算法就是计算所有群落的成对相异性指数的平均值(Cardoso et al, 2014, 2015)。但是成对相异性指数并没有考虑到多个群落之间物种的共存格局(co-occurrence pattern) (Diserud & Ødegaard, 2007), 所以需要使用多点相异性指数(multiple-site dissimilarity)计算总体beta多样性及各自组分(Baselga et al, 2007; Baselga, 2013a)。通过借鉴Sørensen成对相异性指数的分解方法, Baselga (2010)把Sørensen多点相异性指数(β_{SOR} ; 公式1)分解为空间周转组分(β_{SIM} ; 公式2)和嵌套组分(β_{SNE} ; 公式3):

$$\beta_{\text{SOR}} = \frac{\left[\sum_{i<j} \min(b_{ij}, b_{ji})\right] + \left[\sum_{i<j} \max(b_{ij}, b_{ji})\right]}{2\left[\sum_i S_i - S_T\right] + \left[\sum_{i<j} \min(b_{ij}, b_{ji})\right] + \left[\sum_{i<j} \max(b_{ij}, b_{ji})\right]} \quad (1)$$

$$\beta_{\text{SIM}} = \frac{\left[\sum_{i<j} \min(b_{ij}, b_{ji})\right]}{\left[\sum_i S_i - S_T\right] + \left[\sum_{i<j} \min(b_{ij}, b_{ji})\right]} \quad (2)$$

$$\beta_{\text{SOR}} - \beta_{\text{SIM}} = \beta_{\text{SNE}} = \frac{\left[\sum_{i<j} \max(b_{ij}, b_{ji})\right] - \left[\sum_{i<j} \min(b_{ij}, b_{ji})\right]}{2\left[\sum_i S_i - S_T\right] + \left[\sum_{i<j} \min(b_{ij}, b_{ji})\right] + \left[\sum_{i<j} \max(b_{ij}, b_{ji})\right]} \times \frac{\left[\sum_i S_i - S_T\right]}{\left[\sum_i S_i - S_T\right] + \left[\sum_{i<j} \min(b_{ij}, b_{ji})\right]} \quad (3)$$

其中 S_i 为群落*i*内的物种数, S_T 为所有群落内的物种数(gamma多样性), b_{ij} 和 b_{ji} 分别为群落*i*和群落*j*各自所特有的物种数。因此, 多点相异性指数中的 $\sum_{i<j} \min(b_{ij}, b_{ji})$ 和 $\sum_{i<j} \max(b_{ij}, b_{ji})$ 分别等同于成对相异性指数中的 b 和 c 组分, 而 $\sum_i S_i - S_T$ 则等同于成对指数中两者共有的 a 组分。

Baselga (2012)亦对Jaccard成对相异性指数进行了类似的分解。按照Baselga (2012)的加和分解法, 可以把Jaccard成对相异性指数(Jaccard pairwise dissimilarity) (β_{jac})分解为类似的空间周转组分(β_{jtu})和

嵌套组分(β_{jne}) (表1)。同理, Jaccard多点相异性指数(β_{jac})可以被分解为空间周转组分(β_{JTU})和嵌套组分(β_{jne}) (Baselga, 2012)。此处, BAS法所指的嵌套组分并不是真正计算嵌套本身(*nestedness per se*), 而是计算beta多样性中由于嵌套格局而产生的部分(*nestedness-resultant component*), 虽然“嵌套”和“因嵌套而产生”之间有一定的联系, 但它们是两个不同的概念(详见1.1.4小节)。

1.1.2 POD法

在成对相异性指数中, 物种替换表示一个物种被另外一个物种替换, 物种丰富度的差异则表示各个群落中特有物种数差值的绝对值, 这与物种组成是否嵌套无关(Carvalho et al, 2012)。因此, 总体beta多样性(β_{cc})可以分解为物种替换(β_{-3})和物种丰富度的差异(β_{rich}) (Podani & Schmera, 2011; Carvalho et al, 2012) (表1) (简称POD法)。两个群落间物种的组成差异($b + c$)与两群落总物种数($a + b + c$)的比为总体beta多样性(Jaccard相异性指数, β_{cc}) (图3) (Colwell & Coddington, 1994) (该表达式与BAS法的Jaccard成对相异性指数相同)。由于群落间会发生物种替换, 两两群落间替换的物种数 $[2\min(b, c)]$ 在总物种数中所占的比例则为 β_{-3} (Williams, 1996; Cardoso et al, 2009)。物种丰富度差异等于一个群落的物种数($b + a$)和另外一个群落物种数($c + a$)差值的绝对值 $|(b + a) - (c + a)|$, 该值在总物种数中的比例为 β_{rich} (Schmera & Podani, 2011; Carvalho et al,

2012)。因此, POD法的表达式为: $\beta_{\text{cc}} = \beta_{-3} + \beta_{\text{rich}}$, 其中 $\beta_{-3} = 2\min(b, c) / (a + b + c)$, 以及 $\beta_{\text{rich}} = |(b + a) - (c + a)| / (a + b + c) = |b - c| / (a + b + c)$ (表1)。

Legendre (2014)基于POD法, 提出了将Sørensen成对相异性指数分解为物种替换(Repl_s)和物种丰富度差异(RichDiff_s)的分解方法, 其中 $\text{Repl}_s = 2\min(b, c) / (2a + b + c)$; $\text{RichDiff}_s = |b - c| / (2a + b + c)$ 。通过比较可以发现, Repl_s 和 RichDiff_s 与POD法分解得出的Jaccard组分分母发生了变化, 而分子等于 β_{-3} 和 β_{rich} 的分子部分。

1.1.3 BAS法和POD法的分解组分对照

表1罗列了BAS法和POD法中使用的成对相异性指数。其中, β_{jne} 的前半部分 $|b - c| / (a + b + c)$ 等于 β_{rich} 。BAS法和POD法的Jaccard成对相异性指数(β_{jac} 和 β_{cc})具有相同的表达式(表1)。自2010年之后, 基于BAS法和POD法的beta多样性分解研究迅速发展。目前, 两种分解方法可由R语言中的 betapart 包(Baselga & Orme, 2012)和 BAT 包(Cardoso et al, 2015)分别实现。本文的附录3中, 我们简要演示了基于BAS法和POD法的成对和多点相异性指数的计算过程。

1.1.4 BAS法和POD法的争论

2010年, 在西班牙生态学家Andrés Baselga提出BAS法之后, 学者们对该方法的争论也随即出现。例如, Podani和Schmera (2011)、Carvalho等(2012)认为BAS法中提到的嵌套只是物种丰富度差异的一种特殊情况, 因此他们基于Jaccard相异性指数把beta多样性分解为物种替换和物种丰富度差异两部分(即POD法)。此后, Almeida-Neto等(2012)指出, BAS法不能计算物种丧失或增加的程度, 因为BAS法的嵌套组分并不能准确计算严格意义上的嵌套格局, 因此建议应该用诸如NODF (the Nestedness metric based on Overlap and Decreasing Fill)等指数 (Atmar & Patterson, 1993; Almeida-Neto et al, 2008) 计算真正的嵌套格局。同时, 由于BAS法分解组分的分母不同, 因而尺度也并不相同, 从而会导致 β_{sim} 高估物种替换的作用(Carvalho et al, 2013)。除此之外, Almeida-Neto等(2012)认为, 在某些特殊情况下, 即使共有物种数为零, BAS法中的多点相异性指数的嵌套组分仍然能够得到非零结果。

对于提出的上述质疑, Baselga (2012)分别进行了回应: (1) Podani和Schmera (2011)以及Carvalho等(2012)提出的分解方法框架实际上是相同的(因此

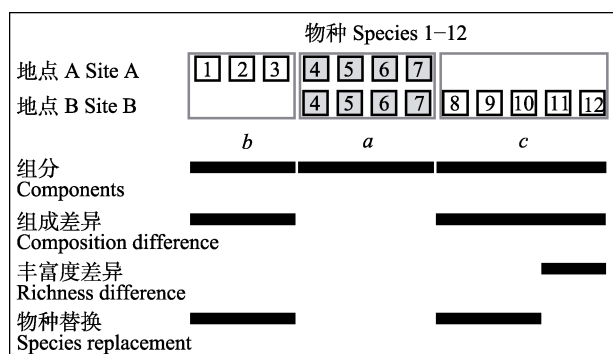


图3 两个研究地点间物种组成示意图。 a 为共有物种数, b 和 c 分别是两个地点各自特有的物种数。两个研究地点间物种的组成差异为 $b + c$, 丰富度差异为 $|b - c|$, 以及物种替换为 $2 \min(b, c)$ 。

Fig. 3 Demonstration of species compositions between two sites. a is the number of shared species, b and c are the species exclusive to each site. The number of compositional differences between two sites is $b + c$. Richness difference is $|b - c|$, and species replacement is given by $2 \min(b, c)$.

本文统一称为POD法); (2) NODF等指数的确可以计算真正的嵌套格局, 但Baselga (2012)中的 β_{sne} 组分并不是为了计算如Almeida-Neto等(2012)所提到的嵌套格局本身, 而是为了计算因嵌套格局而导致的那部分beta多样性, 因此为了避免术语上的重复, Baselga (2012)把之前的嵌套组分(nestedness component)重新命名为“nestedness-resultant component”(本文后续部分依旧采用较为简单的中文翻译, 即嵌套组分); (3)对于Almeida-Neto等(2012)提到的多点相异性指数非零情况, Baselga (2012)承认这是该指数的一个缺点, 不过在实际群落中很少出现共有种为零的特殊情形, 所以在计算过程中, 该指数几乎不会受到该弊端的影响, 何况目前只有BAS法的多点相异性指数可用, 而无其他类似方法可选。此后, Carvalho等(2013)继续指出当达到最大物种丧失时, BAS法计算的嵌套组分会比物种中等程度丧失时低, 从而导致随着物种丧失程度增大, 嵌套组分会形成一个非线性的单峰格局。

然而, POD法也同样饱受质疑。例如, Baselga (2012)认为POD法中表示物种替换的 β_3 指数并不能合理地描述其生态学意义, 因此不予推荐。随后, Leprieur和Oikonomou (2014)通过理论数据模拟和实际数据验证进一步表明: (1) POD法表示物种替换的 β_3 指数在物种丰富度差异变大时, 会低估beta多样性, 并非如其所言该指数对物种丰富度变化不敏感; (2) β_3 指数不符合研究beta多样性的前提条件, 即“互补属性”(complementarity property)(Legendre & De Cáceres, 2013)。因此, Leprieur和Oikonomou (2014)不建议使用POD法所提出的 β_3 指数计算beta多样性, 但Legendre (2014)认为 β_3 指数是 β_{cc} 指数的一个组分, 可以不受“互补属性”的约束。最近, Baselga和Leprieur (2015)继续指出: (1) BAS法的 β_{ju} 指数的变化独立于物种丰富度差异, 而POD法不满足这一条件; (2)参数是否会随着物种替换和丰富度差异而线性变化与模型模拟方式有关, 并且BAS法和POD法解释的概念并不相同; (3) POD法中代表物种丰富度差异的 β_{rich} 指数仅能说明物种丰富度差异的现象, 而BAS法中的 β_{sne} 可以解释因嵌套格局而导致的beta多样性。

自2010年以来, 有关beta多样性分解方法的争论持续发酵。Legendre (2014)对这两种方法进行了归纳总结, 认为: (1)两种方法本质上均为beta多样

性的加和分解; (2)由于两种方法的分解过程, 特别是嵌套或物种丰富度差异指数的不同, 导致其生态学意义也有差异。相较于BAS法, POD法的分解组分易于解释生态学过程; (3) beta多样性分解方法中, 各指数的分子部分用来计算物种替换和丰富度差异(或嵌套), 但由于各指数的分母部分不同, 从而影响了各组分数值上的变化; (4)生态学家需要结合实际情况来选择beta多样性的分解方法, 从而深入探究生态学和生物地理学的问题。尽管Baselga和Leprieur (2015)以及Podani和Schmera (2016)针对性地阐述了各自方法的重要性, 然而正如Legendre (2014)所言, 探讨beta多样性的分解方法只是科学研究的第一步, 更为关键的是利用这些方法分析科学问题, 并且能用恰当的生态学机理对beta多样性和各自组分的格局进行科学地解释。

1.2 Beta多样性分解组分的形成机制

前期的研究表明, 群落物种组成差异(beta多样性)由物种周转及物种的丧失或增加这两种不同的生态过程决定, 所以理解各个生态过程如何决定beta多样性及其组分的分布格局在生物地理学和保护生物学的研究中尤为关键(Williams, 1996; Baselga & Leprieur, 2015; Socolar et al, 2016)。尽管已有大量的研究运用BAS法或者POD法检测物种的空间分布规律, 然而对各组分格局形成机制的阐释却有所差异。物种周转组分用来表示不同地点间的物种替换, 在空间和环境梯度下, 导致物种周转的潜在机制包括环境过滤(environmental filtering)、竞争(competition)和地理隔离(geographical barrier)等(Angeler, 2013; Gutiérrez-Cánovas et al, 2013; Legendre, 2014)。例如, 在环境梯度上通过物种筛选, 不同的物种出现在各自适宜生存的特定的生境中(Gutiérrez-Cánovas et al, 2013); 或者由于山脉的隆起而导致的地理隔离, 使原本连续分布的物种因地理隔离而受到扩散限制, 从而促进异域成种(allopatric speciation)的发生(Leprieur et al, 2011)。群落构建机制研究表明, 优先效应(priority effect)(Fukami, 2015)也可能导致不同群落间具有较高的物种周转速率, 例如当优先到达的物种占据特定的生境后, 可对后续到达的物种进行排斥而导致群落间的物种组成产生替换。

较之于物种周转组分, 物种丰富度差异组分表示在特定环境梯度下因物种的丧失或增加而引起

的群落间物种组成的差异,可能的驱动机制包括生态位的多样性(diversity of niches)以及导致嵌套格局的生态过程等(Legendre, 2014)。其中,嵌套格局典型的解释机理为选择性灭绝(selective extinction)、选择性迁入(selective colonization)和生境嵌套(habitat nestedness)等(Patterson & Atmar, 1986; Ulrich et al, 2009; Wang et al, 2010; Ponisio et al, 2016)。例如,由于物种对环境变化的敏感性不同,受胁物种容易因为选择性灭绝而在环境压力较高的生境中消失,但对环境变化具有较高容忍度的物种则能在不同的生境中存活(Gutiérrez-Cánovas et al, 2013; Si et al, 2016)。另外,历史因素同样可能导致不同区域间具有较大的嵌套组分(Dobrovolski et al, 2012)。比如在冰川消退过程中,由于物种扩散能力的差异而导致高纬度地区的物种是低纬度地区物种的子集(Baselga et al, 2012)。因此,通过对beta多样性分解,我们可以区分不同组分的空间分布格局,进而解释各自组分的形成机制,理解可能的生态学和进化历史过程。但是,在beta多样性分解的研究中,目前提出的机制并不能解释所有的研究案例,因此在分析不同生境中不同类群的分布格局时,需要结合具体的生态和进化背景进行探讨(Baselga, 2010; Legendre, 2014)。

2 Beta多样性分解的应用

随着分解方法的不断发展,beta多样性分解已经广泛应用于生态学、生物地理学和进化生物学领域的研究,进一步结合物种的功能和谱系信息,将更加有助于了解不同时空维度下各种生物类群的分布格局及其驱动机理。本节将主要从时空维度(纬度和海拔梯度、生境片段化过程,以及季节和年际动态)、多样性的不同方面(物种、功能和谱系多样性)和不同生物类群之间的比较研究等方面综合介绍beta多样性分解方法在生物多样性分布格局及保护生物学中的应用。

2.1 时空维度

2.1.1 纬度梯度

物种丰富度的纬度梯度分布格局,即物种丰富度随纬度增加而减少,是生态学以及生物地理学中最基本和最为广泛讨论的科学问题之一(Pianka, 1966; Willig et al, 2003; Hillebrand, 2004)。同时,beta多样性的纬度梯度分布格局也逐渐引起众多生态

学家的关注(Koleff et al, 2003b; Qian & Ricklefs, 2007; Melo et al, 2009; Xu et al, 2015b)。Koleff等(2003b)通过综合研究全球多个类群后发现,仅部分研究证实了低纬度地区具有较高的beta多样性。这可能是由于衡量beta多样性的指数众多且意义并不一致所致(Koleff et al, 2003a)。另外,物种周转和嵌套(物种丧失或增加)两个过程会同时影响beta多样性分布格局(Baselga, 2010; Carvalho et al, 2012)。例如,Baselga等(2012)发现全球两栖类的总体beta多样性(Sørensen相异性指数)并不随纬度变化而变化,但是把总体beta多样性分解之后,则可以清晰地发现低纬度地区具有更高的物种周转,而高纬度地区具有更高的嵌套组分。该研究凸显了大尺度研究中历史气候因子对物种分布的重要性,即随着冰川的消退,两栖类逐渐往两极扩散而导致高纬度地区的物种组成是低纬度地区的子集,而低纬度地区由于受到冰川的影响较小而具有较高的成种效应,从而导致较高的物种周转(Baselga et al, 2012)。最近不少基于纬度梯度的研究都发现历史气候因素是决定beta多样性分布格局的主要因子,并建议在分析纬度梯度时把形成beta多样性的两个组成过程进行独立分析(Hortal et al, 2011; Leprieur et al, 2011; Dobrovolski et al, 2012; Fernandez et al, 2016)。

2.1.2 海拔梯度

物种丰富度沿海拔梯度的分布格局包括随海拔升高而呈现单调递减模式、单峰模式和单调递增模式等(Rahbek, 2005; 吴永杰和雷富民, 2013; Colwell et al, 2016; Wang et al, 2017),这同样强烈地吸引了众多生态学家和生物地理学家的关注(Rahbek, 1995; Colwell & Lees, 2000; Lomolino, 2001; McCain, 2009)。不过相较于alpha或gamma多样性,探讨beta多样性随海拔梯度变化的研究至今还相对比较薄弱(Tang et al, 2012; Mori et al, 2013)。对于较为常见的单峰模式,诸多研究表明这可能仅仅是由于低山物种和高山物种在中度海拔地区交汇而发生了物种周转(Brown, 2001; Herzog et al, 2005; McCain & Beck, 2016)。由于扩散限制、环境过滤等过程均可能决定beta多样性的海拔梯度分布(Qian & Ricklefs, 2007; Jankowski et al, 2009; Andrew et al, 2012; Liu et al, 2015),所以需要组成beta多样性的物种周转和嵌套这两种过程分别进行探讨(Baselga, 2010; Carvalho et al, 2011)。例如, Bishop

等(2015)对南非高山蚂蚁群落的研究发现, 物种组成差异随着海拔升高而增大, 这主要是由物种周转引起的。标准化后的物种周转和嵌套组分随海拔升高两者呈现相反的趋势, 表明群落的构建是由确定性过程(deterministic process)导致的。Foord和Dippenaar-Schoeman (2016)对南非山地蜘蛛群落的研究发现, 虽然总体beta多样性主要都是由物种周转组成, 但物种周转和嵌套组分对东西坡向的群落组成差异的贡献程度不同。标准化后的群落格局与随机群落没有显著性差别, 表明随机过程(stochastic process)对蜘蛛群落的构建具有重要作用。随着beta多样性分解方法的发展, 单独分析组成beta多样性的周转和嵌套过程将有助于更好地理解海拔梯度上的群落构建机制(Bryant et al, 2008; Wang et al, 2012; Marini et al, 2013; Mori et al, 2015)。

2.1.3 生境片段化

由于人类活动的加剧, 生境丧失与片段化对生物多样性的影响成为保护生物学的重要研究内容(Wilcove et al, 1998; Sodhi et al, 2010; Pimm et al, 2014; Wilson et al, 2016)。生境的丧失将导致较小斑块中的动物群落具有更高的灭绝风险, 因此普遍认为较小的斑块由于具有较低的保护优先等级而受到较少的关注(Pimm et al, 1993; Krauss et al, 2010; Halley & Iwasa, 2011; Gibson et al, 2013)。但是, 因生境片段化形成的单个小斑块虽然难以承载一个种群, 而多个邻近的小斑块却因为分散了灭绝风险或通过“景观补偿效应”(landscape complementation)对生物多样性的维持有所贡献(Guadagnin et al, 2005; Fahrig, 2017), 因此小斑块可能依旧拥有潜在的保护价值而不能忽略(Benedick et al, 2006; Kattan et al, 2006; Si et al, 2015)。在空间维度上, beta多样性的物种周转和嵌套组分均能反映不同的保护学策略, 即如果嵌套组分占优势, 那么该研究区域内具有较多物种的地点拥有较高的保护等级; 而如果空间周转组分占主导则意味着所有研究地点对beta多样性的贡献相似, 那么所有地点都需要保护, 没有优先级之分(Baselga, 2010; Gutiérrez-Cánovas et al, 2013)。Si等(2015)对千岛湖片段化生境岛屿上的繁殖鸟类和蜥蜴群落的研究发现, 不管是鸟类还是蜥蜴, 总体beta多样性均是由物种周转过程主导。Wu等(2017)对千岛湖岛屿上的蜘蛛群落研究同样发现周转过程在总体beta多样性中占主导地位。这

表明在开展千岛湖生物多样性保护时, 除了考虑较大岛屿或者生境较为丰富的岛屿之外, 还应该包括其他小型岛屿或生境较为单一的岛屿。因此在片段化生境中开展物种保护以及保护区设计时, 除了考虑不同斑块内的物种丰富度, 还需要分析不同群落间的beta多样性分布格局及其背后的驱动过程, 这将有利于制定科学有效且具有针对性的生物多样性保护策略(Wiersma & Urban, 2005; 斯幸峰, 2014; Socolar et al, 2016)。

2.1.4 季节动态

研究生态系统结构和功能的稳定性对于保护生物多样性尤为重要, 然而由于生物群落所生存的外部环境(生物和非生物)并不是一成不变的, 生物群落的空间组成也将产生动态变化。例如, Bishop等(2015)在研究雨季和旱季蚂蚁群落沿海拔梯度的物种和功能beta多样性变化时, 发现旱季蚂蚁总的beta多样性和周转组分高于雨季, 这极有可能是由旱季食物匮乏而引起的。基于相同的方法, Foord和Dippenaar-Schoeman (2016)也发现蜘蛛群落沿海拔梯度分布存在相似的季节变化。以上两项研究均强调生物可通过改变其生态位宽度或者食物结构来适应环境的季节性变化。而对于有较强扩散能力的鸟类而言, 它们对季节性生境和气候的响应则更为明显。Chen等(2017)通过研究千岛湖鸟类繁殖季和冬季留鸟及候鸟beta多样性组分与片段化栖息地结构的关系后发现, 留鸟群落的空间结构表现出极强的季节差异性。冬季鸟类的beta多样性高于繁殖季, 并且受物种丰富度差异组分的影响更大; 而繁殖季鸟类的空间结构主要是物种替换导致的。这表明鸟类群落的季节性差异不仅仅受食物季节性差异的影响, 也与鸟类在不同季节的行为有关(Chen et al, 未发表数据)。综上所述, 研究生物群落时间维度上的季节周转, 对我们了解群落组成的稳定性以及生物与环境之间的关系都有着重要的意义(Sheldon et al, 2011; Legendre, 2014; Foord & Dippenaar-Schoeman, 2016)。

2.1.5 年际动态

运用beta多样性分解的方法研究群落在时间维度上的变化, 将有助于了解生态系统对局部环境乃至全球气候变化的响应规律, 有利于生态学家更为深入地理解群落的构建机制并制定更加完善的生物多样性保护策略(Sheldon et al, 2011; Boeiro et al,

2013; Si et al, 2014; Urban, 2015)。在时间维度上, 如果周转组分的增加程度大于嵌套组分的降低程度, 则表明所有群落对区域多样性具有更加相似的贡献, 因此所有群落均可能是潜在的保护目标; 如果嵌套组分的增加程度大于周转组分的减小程度, 则表明部分群落对区域多样性的贡献更大, 从而需要优先考虑这些特定的群落。同理, 如果周转和嵌套组分随时间稳定变化(temporal stability), 那么对于维持区域多样性而言, 无需额外实施保护对策; 但是, 如果周转和嵌套组分的大小随时间交错变化, 则难以基于目前的结果提出生物多样性保护建议(Angeler, 2013; 斯幸峰, 2014; Lamy et al, 2015; Si et al, 2015)。Angeler (2013)对瑞典26个湖泊的水生无脊椎动物长达17年的研究发现, 总体beta多样性并未发生显著性变化, 但物种空间周转组分却一直在增加, 而嵌套组分一直在减少。因此, 从生物多样性保护角度来讲, 在时间维度上所有生态系统对局域多样性具有更加相似的贡献而均需要保护。Lewis等(2016)对苏格兰滨海草地34年的研究发现, 相较于周转组分, 气候变化对嵌套组分影响更大。在群落构建机制的研究中, Baselga等(2015)发现法国西南地区农田生境中的鸟类群落在25年间没有明显的时间分布格局, 推测可能是由于较强的随机性过程所导致。Habel等(2016)对德国东南部蝶类和蛾类的近2个世纪的研究发现嵌套组分占据主导地位, 并且随着时间推移群落组成更为相似, 这跟生境特化种的减少和泛化种的增加有关。在对农田生境的研究中, Uchida和Ushimaru (2015)发现抛荒地(abandoned terrace)里的植物和直翅目昆虫在时空维度上均具有较高的周转组分, 而在耕地(intensive terrace)里的植物在时间维度上具有较高的嵌套组分, 表明对耕地减少刈割频度并对抛荒地进行刈割将有助于生物多样性恢复。

2.2 物种、功能和谱系多样性

虽然早在20世纪60年代, beta多样性概念已由美国生态学家Robert H. Whittaker提出(Whittaker, 1960, 1972), 用以表示不同研究地点之间生物群落的组成差异(Tuomisto, 2010a, b; Anderson et al, 2011), 但是传统的物种beta多样性分析难以确定不同群落间物种在功能上的组成差异(Petchey & Gaston, 2002; Stegen & Hurlbert, 2011; Villéger et al, 2012)。因此, 基于功能alpha多样性(functional alpha

diversity) (Tilman, 2001; Petchey & Gaston, 2006; Villéger et al, 2008), 最近有学者提出了功能beta多样性的概念(functional beta diversity), 以期描述不同群落之间功能多样性的组成变化(Swenson et al, 2011a; Si et al, 2016)。除了物种在功能上的差异, 物种间还具有不同的进化历史(Faith, 1992; Webb et al, 2002), 因此在度量不同群落间的物种组成变化时, 需要基于谱系beta多样性来探讨群落的构建机制(Cavender-Bares et al, 2009; Swenson et al, 2011b; Cardoso et al, 2014)。

由于物种beta多样性既不考虑物种的进化历史, 也不考虑物种的功能特征(Fukami et al, 2005; Siefert et al, 2013), 因此物种组成相异的两个群落, 可能会具有非常相似的功能特征, 例如具有相同的营养级、相似的形态特征等等(Villéger et al, 2012; Terborgh, 2015; Loiseau et al, 2017; Si et al, 2017)。另一方面, 当不同群落的物种beta多样性较高时, 并不一定意味着具有较高的功能beta多样性或者谱系beta多样性, 因为不同的物种可能具有相似的功能特征或者进化历史(Webb et al, 2002; McGill et al, 2006; Si et al, 2016; Liu et al, 2017)。例如, Villéger等(2013)对欧洲25个主要河流流域的鱼类分析后发现, 总体beta多样性的差异是由于周转组分导致的, 即物种beta多样性远大于功能beta多样性, 却具有相似的嵌套组分。这表明这些流域的不同鱼类具有相似的功能性状, 从而出现较高的物种周转和较低的功能周转组分。对于物种beta多样性与谱系beta多样性而言, 两者亦反映了各自不同的维持机理(Losos, 1996; Webb, 2000; Graham & Fine, 2008; Swenson et al, 2011b)。例如, Cardoso等(2014)对欧洲的兽类和葡萄牙亚速尔群岛的节肢动物研究发现, 谱系beta多样性的丰富度差异组分变化反映了扩散限制和生境过滤的作用; 而物种替换组分的变化可能与环境的干扰有关。因此, 对于不同的群落, 分别基于物种、功能和谱系beta多样性进行综合分析, 将能更为深入地理解驱动不同群落间组成变化的生态学机理(Devictor et al, 2010; Villéger et al, 2013; Cardoso et al, 2014; Bishop et al, 2015)。

2.3 不同生物类群的比较研究

不同的生物类群具有不同的进化历史和生物学特征, 因此形成不同的beta多样性分布格局。在相同的环境梯度或者地理区域中对比研究不同生物

类群, 可以将不同类群群落间的组成变化与类群特征联系起来(Bryant et al, 2008; Dobrovolski et al, 2012; Calderón-Patrón et al, 2013)。其中, 物种扩散能力是影响物种分布的重要因素(Nekola & White, 1999), 因此具有较强扩散能力的陆栖脊椎动物能够较为容易地越过地理屏障, 从而形成较低的beta多样性(Steinitz et al, 2006; Qian, 2009)和较高的周转组分(Baselga et al, 2012)。例如, 相比于扩散能力相对较弱的兽类、两栖类和爬行类等陆生脊椎动物类群, 鸟类具有较强的扩散能力(飞行能力)而呈现出相对较低的beta多样性(Harrison et al, 1992)。Si等(2015)在千岛湖的研究中同样发现, 相较于鸟类, 蜥蜴由于其较弱的扩散能力, 更容易受到不同岛屿间水域隔离作用的影响而具有较高的总体beta多样性以及相对较高的嵌套组分。在微生物的beta多样性研究中发现, 由于微生物具有较强的扩散作用, 容易形成较低的beta多样性, 但同时由于微生物具有较高的环境选择性, 也可能因此形成较高的beta多样性(Martiny et al, 2006; Wang et al, 2016)。此外, 长期的进化历史过程也会影响物种在大尺度上的分布格局(Qian & Ricklefs, 2007; Jetz et al, 2012)。例如, 冰川效应影响了欧洲生物的地理分布(Svenning et al, 2011)。由于变温动物对低温更为敏感(Buckley & Jetz, 2008), 因此相较于恒温的鸟类和兽类, 两栖类动物更有可能由于冰川效应的影响而快速消失。同时, 由于其较低的扩散能力, 在冰期之后, 两栖类的物种迁入率(拓殖率)也较低(Baselga, 2010)。Dobrovolski等(2012)研究新大陆(New World)的冰川效应后也发现了类似的格局: 鸟类具有最大的空间周转组分, 而两栖类的空间周转组分最低。除了生物类群间扩散能力的差异之外, 不同动物类群间的食性差异、活动节律, 植物类群中的物候差异, 以及它们对气候变化的响应都可能影响物种的分布格局, 从而对组成总体beta多样性的周转和嵌套组分产生影响。随着beta多样性分解研究的迅速发展, 以及全球范围内物种分布数据的积累, 例如通过公民科学(citizen science)的方式收集众多鸟类分布的数据(斯幸峰和丁平, 2011), 将有助于探讨不同生物类群间群落组成的时空变化。

3 Beta多样性分解的展望

2010年, BAS法的提出推动了beta多样性分解

领域的迅速发展, 但是beta多样性分解方法本身也受到了诸多批评(见本文1.1.4小节)。虽然BAS法和POD法在计算过程中有所差异, 但是在实际案例中, 分别使用两种方法分析可能会得到相似的结果。因此, 对于大多数研究而言, 一种可行的做法是同时使用BAS法和POD法对相同数据进行分析, 比较两者所得到的结果(Wu et al, 2017)。如果结果相同且研究内容不探讨分解方法, 可选择BAS法或POD法中的一种进行分析; 如果两种方法得到的结果不同, 则需要对研究对象的可能机制进行进一步分析, 从而选择合适的beta多样性分解方法。目前对beta多样性分解方法的争议, 另外一种可能的解决途径是发展出一套可以融合这两种分解方法并弥补两者缺点的新方法, 或者提出新的分解方法(Legendre & De Cáceres, 2013; Ensing & Pither, 2015; Ricotta & Pavoine, 2015; Shimadzu et al, 2015), 从而结束对两种方法本身的争论。但是截至目前, 还未有新的方法能在beta多样性分解领域达成共识, 因此对于beta多样性分解方法的争论还将继续存在。

相较于物种频度分布数据(presence/absence distributions), 基于物种多度数据(abundance)的研究同样具有重要的生态学意义, 并有利于探讨beta多样性及其组分的时空格局(Legendre, 2014; Li et al, 2016)。由于优势种在群落中占据着核心的生态位, 因此优势种可能更容易受到生境过滤等确定性过程的影响(Umaña et al, 2015), 而稀有种由于其种群较小, 更易受到随机过程的影响(Orrock & Watling, 2010)。目前, 基于多度数据的beta多样性分解方法已经提出(Baselga, 2013b; Podani et al, 2013; Baselga, 2017), 在今后的研究中可以通过整合物种分布和多度的信息来探讨beta多样性及其组分的时空分布格局和形成机制。

目前在有关beta多样性分解的研究中, 与区域尺度相比, 在更大时空维度下对beta多样性分解的结果进行普适性验证的研究相对较少(Leprieux et al, 2011; Dobrovolski et al, 2012)。此外, 应加强在同一区域内对多个生物类群进行综合分析, 并探讨不同生物类群间的总体beta多样性及其组分的贡献程度是否一致。对于岛屿系统中物种beta多样性的周转和嵌套组分, Wu等(2017)整合分析了全球岛屿上陆生动物的群落结构(共18个研究案例), 结果表明94%的研究中周转组分大于嵌套组分, 这说明至少

在岛屿系统中总体beta多样性主要取决于物种的周转过程。此外,从不同时空维度或者多样性的不同方面整合分析周转和嵌套组分在总体beta多样性中所占比例的研究还鲜有报道。在同一地点对多个生物类群进行综合分析,虽然国际上有不少研究平台具有这样的研究条件(Si et al, 2015; Thorn et al, 2016),但至今未有类似的研究报道。

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参考文献

- Almeida-Neto M, Frensel D, Ulrich W (2012) Rethinking the relationship between nestedness and beta diversity: a comment on Baselga (2010). *Global Ecology and Biogeography*, 21, 772–777.
- Almeida-Neto M, Guimarães P, Guimarães PR, Loyola RD, Ulrich W (2008) A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos*, 117, 1227–1239.
- Anderson MJ, Crist TO, Chase JM, Vellend M, Inouye BD, Freestone AL, Sanders NJ, Cornell HV, Comita LS, Davies KF (2011) Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology Letters*, 14, 19–28.
- Andrew ME, Wulder MA, Coops NC, Baillargeon G (2012) Beta-diversity gradients of butterflies along productivity axes. *Global Ecology and Biogeography*, 21, 352–364.
- Angeler DG (2013) Revealing a conservation challenge through partitioned long-term beta diversity: increasing turnover and decreasing nestedness of boreal lake meta-communities. *Diversity and Distributions*, 19, 772–781.
- Atmar W, Patterson BD (1993) The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia*, 96, 373–382.
- Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19, 134–143.
- Baselga A (2012) The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography*, 21, 1223–1232.
- Baselga A (2013a) Multiple site dissimilarity quantifies compositional heterogeneity among several sites, while average pairwise dissimilarity may be misleading. *Ecography*, 36, 124–128.
- Baselga A (2013b) Separating the two components of abundance-based dissimilarity: balanced changes in abundance vs. abundance gradients. *Methods in Ecology and Evolution*, 4, 552–557.
- Baselga A (2017) Partitioning abundance-based multiple-site dissimilarity into components: balanced variation in abundance and abundance gradients. *Methods in Ecology and Evolution*, 8, doi: 10.1111/2041-1210X.12693.
- Baselga A, Bonthoux S, Balent G (2015) Temporal beta diversity of bird assemblages in agricultural landscapes: land cover change vs. stochastic processes. *PLoS ONE*, 10, e0127913.
- Baselga A, Gómez-Rodríguez C, Lobo JM (2012) Historical legacies in world amphibian diversity revealed by the turnover and nestedness components of beta diversity. *PLoS ONE*, 7, e32341.
- Baselga A, Jiménez-Valverde A, Niccolini G (2007) A multiple-site similarity measure independent of richness. *Biology Letters*, 3, 642–645.
- Baselga A, Leprieux F (2015) Comparing methods to separate components of beta diversity. *Methods in Ecology and Evolution*, 6, 1069–1079.
- Baselga A, Orme CDL (2012) betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution*, 3, 808–812.
- Bellier E, Grøtan V, Engen S, Schartau AK, Herfjndal I, Finstad AG (2014) Distance decay of similarity, effects of environmental noise and ecological heterogeneity among species in the spatio-temporal dynamics of a dispersal-limited community. *Ecography*, 37, 172–182.
- Benedick S, Hill JK, Mustaffa N, Chey VK, Maryati M, Searle JB, Schilthuizen M, Hamer KC (2006) Impacts of rain forest fragmentation on butterflies in northern Borneo: species richness, turnover and the value of small fragments. *Journal of Applied Ecology*, 43, 967–977.
- Beng KC, Tomlinson KW, Shen XH, Surget-Groba Y, Hughes AC, Corlett RT, Slik JWF (2016) The utility of DNA metabarcoding for studying the response of arthropod diversity and composition to land-use change in the tropics. *Scientific Reports*, 6, 24965.
- Bishop TR, Robertson MP, Rensburg BJ, Parr CL (2015) Contrasting species and functional beta diversity in montane ant assemblages. *Journal of Biogeography*, 42, 1776–1786.
- Boeiro M, Carvalho JC, Cardoso P, Aguiar CAS, Rego C, de Faria e Silva I, Amorim IR, Pereira F, Azevedo EB, Borges PAV, Serrano ARM (2013) Spatial factors play a major role as determinants of endemic ground beetle beta diversity of Madeira Island Laurisilva. *PLoS ONE*, 8, e64591.
- Brown JH (2001) Mammals on mountainsides: elevational patterns of diversity. *Global Ecology and Biogeography*, 10, 101–109.
- Bryant JA, Lamanna C, Morlon H, Kerkhoff AJ, Enquist BJ,

- Green JL (2008) Microbes on mountainsides: contrasting elevational patterns of bacterial and plant diversity. *Proceedings of the National Academy of Sciences, USA*, 105, 11505–11511.
- Buckley LB, Jetz W (2008) Linking global turnover of species and environments. *Proceedings of the National Academy of Sciences, USA*, 105, 17836–17841.
- Calderón-Patrón JM, Moreno CE, Pineda-López R, Sánchez-Rojas G, Zuria I (2013) Vertebrate dissimilarity due to turnover and richness differences in a highly beta-diverse region: the role of spatial grain size, dispersal ability and distance. *PLoS ONE*, 8, e82905.
- Cardoso P, Borges PAV, Veech JA (2009) Testing the performance of beta diversity measures based on incidence data: the robustness to undersampling. *Diversity and Distributions*, 15, 1081–1090.
- Cardoso P, Rigal F, Carvalho JC (2015) BAT—biodiversity assessment tools, an R package for the measurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. *Methods in Ecology and Evolution*, 6, 232–236.
- Cardoso P, Rigal F, Carvalho JC, Fortelius M, Borges PAV, Podani J, Schmera D (2014) Partitioning taxon, phylogenetic and functional beta diversity into replacement and richness difference components. *Journal of Biogeography*, 41, 749–761.
- Carvalho JC, Cardoso P, Borges PAV, Schmera D, Podani J (2013) Measuring fractions of beta diversity and their relationships to nestedness: a theoretical and empirical comparison of novel approaches. *Oikos*, 122, 825–834.
- Carvalho JC, Cardoso P, Crespo LC, Henriques S, Carvalho R, Gomes P (2011) Determinants of beta diversity of spiders in coastal dunes along a gradient of mediterraneity. *Diversity and Distributions*, 17, 225–234.
- Carvalho JC, Cardoso P, Gomes P (2012) Determining the relative roles of species replacement and species richness differences in generating beta-diversity patterns. *Global Ecology and Biogeography*, 21, 760–771.
- Cavender-Bares J, Kozak KH, Fine PVA, Kembel SW (2009) The merging of community ecology and phylogenetic biology. *Ecology Letters*, 12, 693–715.
- Chen SB, Ouyang ZY, Xu WH, Xiao Y (2010) A review of beta diversity studies. *Biodiversity Science*, 18, 323–335. (in Chinese with English abstract) [陈圣宾, 欧阳志云, 徐卫华, 肖纛 (2010) Beta多样性研究进展. *生物多样性*, 18, 323–335.]
- Cody ML (1975) Towards a theory of continental species diversities: bird distributions over Mediterranean habitat gradients. In: *Ecology and Evolution of Communities* (eds Cody ML, Diamond JM), pp. 214–257. Harvard University Press, Cambridge.
- Colwell RK, Coddington JA (1994) Estimating terrestrial bio-diversity through extrapolation. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 345, 101–118.
- Colwell RK, Gotelli NJ, Ashton LA, Beck J, Brehm G, Fayle TM, Fiedler K, Forister ML, Kessler M, Kitching RL (2016) Midpoint attractors and species richness: modelling the interaction between environmental drivers and geometric constraints. *Ecology Letters*, 19, 1009–1022.
- Colwell RK, Lees DC (2000) The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology & Evolution*, 15, 70–76.
- Devictor V, Moullot 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. *Ecology Letters*, 13, 1030–1040.
- Diserud OH, Ødegaard F (2007) A multiple-site similarity measure. *Biology Letters*, 3, 20–22.
- Dobrovolski R, Melo AS, Cassemiro FAS, Diniz-Filho JAF (2012) Climatic history and dispersal ability explain the relative importance of turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 21, 191–197.
- Ensing DJ, Pither J (2015) A novel multiple-site extension to pairwise partitioned taxonomic beta diversity. *Ecological Complexity*, 21, 62–69.
- Fahrig L (2017) Ecological responses to habitat fragmentation *per se*. *Annual Review of Ecology, Evolution, and Systematics*, 48, doi: 10.1146/annurev-eolsys-110316-022612.
- Faith DP (1992) Conservation evaluation and phylogenetic diversity. *Biological Conservation*, 61, 1–10.
- Fernandez LD, Fournier B, Rivera R, Lara E, Mitchell EAD, Hernandez CE (2016) Water-energy balance, past ecological perturbations and evolutionary constraints shape the latitudinal diversity gradient of soil testate amoebae in south-western South America. *Global Ecology and Biogeography*, 25, 1216–1227.
- Foord SH, Dippenaar-Schoeman AS (2016) The effect of elevation and time on mountain spider diversity: a view of two aspects in the Cederberg mountains of South Africa. *Journal of Biogeography*, 43, 2354–2365.
- Fukami T (2015) Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Annual Review of Ecology, Evolution, and Systematics*, 46, 1–23.
- Fukami T, Bezemer TM, Mortimer SR, Putten WH (2005) Species divergence and trait convergence in experimental plant community assembly. *Ecology Letters*, 8, 1283–1290.
- Gibson L, Lynam AJ, Bradshaw CJA, He F, Bickford DP, Woodruff DS, Bumrungsri S, Laurance WF (2013) Near-complete extinction of native small mammal fauna 25 years after forest fragmentation. *Science*, 341, 1508–1510.

- Graham CH, Fine PV (2008) Phylogenetic beta diversity: linking ecological and evolutionary processes across space in time. *Ecology Letters*, 11, 1265–1277.
- Guadagnin DL, Peter ÂS, Perello LFC, Maltchik L (2005) Spatial and temporal patterns of waterbird assemblages in fragmented wetlands of southern Brazil. *Waterbirds*, 28, 261–272.
- Gutiérrez-Cánovas C, Millán A, Velasco J, Vaughan IP, Ormerod SJ (2013) Contrasting effects of natural and anthropogenic stressors on beta diversity in river organisms. *Global Ecology and Biogeography*, 22, 796–805.
- Habel JC, Segerer A, Ulrich W, Torchyk O, Weisser WW, Schmitt T (2016) Butterfly community shifts over 2 centuries. *Conservation Biology*, 30, 754–762.
- Halley JM, Iwasa Y (2011) Neutral theory as a predictor of avifaunal extinctions after habitat loss. *Proceedings of the National Academy of Sciences, USA*, 108, 2316–2321.
- Harrison S, Ross SJ, Lawton JH (1992) Beta diversity on geographic gradients in Britain. *Journal of Animal Ecology*, 61, 151–158.
- Herzog SK, Kessler M, Bach K (2005) The elevational gradient in Andean bird species richness at the local scale: a foothill peak and a high-elevation plateau. *Ecography*, 28, 209–222.
- Hillebrand H (2004) On the generality of the latitudinal diversity gradient. *The American Naturalist*, 163, 192–211.
- Hortal J, Diniz-Filho JAF, Bini LM, Angel Rodriguez M, Baselga A, Nogues-Bravo D, Rangel TF, Hawkins BA, Lobo JM (2011) Ice age climate, evolutionary constraints and diversity patterns of European dung beetles. *Ecology Letters*, 14, 741–748.
- James A, Pitchford JW, Plank MJ (2012) Disentangling nestedness from models of ecological complexity. *Nature*, 487, 227–230.
- Jankowski JE, Ciecka AL, Meyer NY, Rabenold KN (2009) Beta diversity along environmental gradients: implications of habitat specialization in tropical montane landscapes. *Journal of Animal Ecology*, 78, 315–327.
- Jetz W, Thomas G, Joy J, Hartmann K, Mooers A (2012) The global diversity of birds in space and time. *Nature*, 491, 444–448.
- Kattan GH, Franco P, Saavedra-Rodríguez CA, Valderrama C, Rojas V, Osorio D, Martínez J (2006) Spatial components of bird diversity in the Andes of Colombia: implications for designing a regional reserve system. *Conservation Biology*, 20, 1203–1211.
- Koleff P, Gaston KJ, Lennon JJ (2003a) Measuring beta diversity for presence-absence data. *Journal of Animal Ecology*, 72, 367–382.
- Koleff P, Lennon JJ, Gaston KJ (2003b) Are there latitudinal gradients in species turnover? *Global Ecology and Biogeography*, 12, 483–498.
- Kraft NJB, Comita LS, Chase JM, Sanders NJ, Swenson NG, Crist TO, Stegen JC, Vellend M, Boyle B, Anderson MJ (2011) Disentangling the drivers of β diversity along latitudinal and elevational gradients. *Science*, 333, 1755–1758.
- Krauss J, Bommarco R, Guardiola M, Heikkinen RK, Helm A, Kuussaari M, Lindborg R, Öckinger E, Pärtel M, Pino J, Pöyry J, Raatikainen KM, Sang A, Stefanescu C, Teder T, Zobel M, Steffan-Dewenter I (2010) Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecology Letters*, 13, 597–605.
- Lamy T, Legendre P, Chancerelle Y, Siu G, Claudet J (2015) Understanding the spatio-temporal response of coral reef fish communities to natural disturbances: insights from beta-diversity decomposition. *PLoS ONE*, 10, e0138696.
- Legendre P (2014) Interpreting the replacement and richness difference components of beta diversity. *Global Ecology and Biogeography*, 23, 1324–1334.
- Legendre P, De Cáceres M (2013) Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. *Ecology Letters*, 16, 951–963.
- Lennon JJ, Koleff P, Greenwood J, Gaston KJ (2001) The geographical structure of British bird distributions: diversity, spatial turnover and scale. *Journal of Animal Ecology*, 70, 966–979.
- Leprieur F, Albouy C, De Bortoli J, Cowman PF, Bellwood DR, Mouillot D (2012) Quantifying phylogenetic beta diversity: distinguishing between ‘true’ turnover of lineages and phylogenetic diversity gradients. *PLoS ONE*, 7, e42760.
- Leprieur F, Oikonomou A (2014) The need for richness-independent measures of turnover when delineating biogeographical regions. *Journal of Biogeography*, 41, 417–420.
- Leprieur F, Tedesco PA, Huguéy B, Beauchard O, Dürr HH, Brosse S, Oberdorff T (2011) Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes. *Ecology Letters*, 14, 325–334.
- Lewis RJ, Marrs RH, Pakeman RJ, Milligan G, Lennon JJ (2016) Climate drives temporal replacement and nested-resultant richness patterns of Scottish coastal vegetation. *Ecography*, 39, 754–762.
- Li SP, Cadotte MW, Meiners SJ, Pu Z, Fukami T, Jiang L (2016) Convergence and divergence in a long-term old-field succession: the importance of spatial scale and species abundance. *Ecology Letters*, 19, 1101–1109.
- Liu C, Dudley KL, Xu Z-H, Economo EP (2017) Mountain metacommunities: climate and spatial connectivity shape ant diversity in a complex landscape. *Ecography*, 40, doi: 10.1111/ecog.03067.
- Liu YN, Tang ZY, Fang JY (2015) Contribution of environmental filtering and dispersal limitation to species turnover of temperate deciduous broad-leaved forests in China. *Applied Vegetation Science*, 18, 34–42.
- Loiseau N, Legras G, Gaertner JC, Verley P, Chabanet P,

- Mérigot B (2017) Performance of partitioning functional beta-diversity indices: influence of functional representation and partitioning methods. *Global Ecology and Biogeography*, 26, doi: 10.1111/geb.12581.
- Lomolino M (2001) Elevation gradients of species-density: historical and prospective views. *Global Ecology and Biogeography*, 10, 3–13.
- Losos JB (1996) Phylogenetic perspectives on community ecology. *Ecology*, 77, 1344–1354.
- Marini L, Bertolli A, Bona E, Federici G, Martini F, Prosser F, Bommarco R (2013) Beta-diversity patterns elucidate mechanisms of alien plant invasion in mountains. *Global Ecology and Biogeography*, 22, 450–460.
- Martiny JBH, Bohannan BJ, Brown JH, Colwell RK, Fuhrman JA, Green JL, Horner-Devine MC, Kane M, Krumins JA, Kuske CR (2006) Microbial biogeography: putting microorganisms on the map. *Nature Reviews Microbiology*, 4, 102–112.
- McCain CM (2009) Global analysis of bird elevational diversity. *Global Ecology and Biogeography*, 18, 346–360.
- McCain CM, Beck J (2016) Species turnover in vertebrate communities along elevational gradients is idiosyncratic and unrelated to species richness. *Global Ecology and Biogeography*, 25, 299–310.
- McGill BJ, Enquist BJ, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, 21, 178–185.
- McKnight MW, White PS, McDonald RI, Lamoreux JF, Sechrest W, Ridgely RS, Stuart SN (2007) Putting beta-diversity on the map: broad-scale congruence and coincidence in the extremes. *PLoS Biology*, 5, e272.
- Melo AS, Rangel TFL, Diniz-Filho JAF (2009) Environmental drivers of beta-diversity patterns in New-World birds and mammals. *Ecography*, 32, 226–236.
- Mori AS, Shiono T, Haraguchi TF, Ota AT, Koide D, Ohguchi T, Kitagawa R, Maeshiro R, Aung TT, Nakamori T, Hagiwara Y, Matsuoka S, Ikeda A, Hishi T, Hobara S, Mizumachi E, Frisch A, Thor G, Fujii S, Osono T, Gustafsson L (2015) Functional redundancy of multiple forest taxa along an elevational gradient: predicting the consequences of non-random species loss. *Journal of Biogeography*, 42, 1383–1396.
- Mori AS, Shiono T, Koide D, Kitagawa R, Ota AT, Mizumachi E (2013) Community assembly processes shape an altitudinal gradient of forest biodiversity. *Global Ecology and Biogeography*, 22, 878–888.
- Mouillot D, De Bortoli J, Leprieux F, Parravicini V, Kulbicki M, Bellwood DR (2013) The challenge of delineating biogeographical regions: nestedness matters for Indo-Pacific coral reef fishes. *Journal of Biogeography*, 40, 2228–2237.
- Nekola JC, White PS (1999) The distance decay of similarity in biogeography and ecology. *Journal of Biogeography*, 26, 867–878.
- Orrock JL, Watling JI (2010) Local community size mediates ecological drift and competition in metacommunities. *Proceedings of the Royal Society of London B: Biological Sciences*, 277, 2185–2191.
- Patterson BD, Atmar W (1986) Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biological Journal of the Linnean Society*, 28, 65–82.
- Petchey OL, Gaston KJ (2002) Functional diversity (FD), species richness and community composition. *Ecology Letters*, 5, 402–411.
- Petchey OL, Gaston KJ (2006) Functional diversity: back to basics and looking forward. *Ecology Letters*, 9, 741–758.
- Pianka ER (1966) Latitudinal gradients in species diversity: a review of concepts. *The American Naturalist*, 100, 33–46.
- Pimm SL, Diamond J, Reed TM, Russell GJ, Verner J (1993) Times to extinction for small populations of large birds. *Proceedings of the National Academy of Sciences, USA*, 90, 10871–10875.
- Pimm SL, Jenkins CN, Abell R, Brooks TM, Gittleman JL, Joppa LN, Raven PH, Roberts CM, Sexton JO (2014) The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, 344, 987–997.
- Podani J, Ricotta C, Schmera D (2013) A general framework for analyzing beta diversity, nestedness and related community-level phenomena based on abundance data. *Ecological Complexity*, 15, 52–61.
- Podani J, Schmera D (2011) A new conceptual and methodological framework for exploring and explaining pattern in presence-absence data. *Oikos*, 120, 1625–1638.
- Podani J, Schmera D (2016) Once again on the components of pairwise beta diversity. *Ecological Informatics*, 32, 63–68.
- Ponisio LC, M'Gonigle LK, Kremen C (2016) On-farm habitat restoration counters biotic homogenization in intensively managed agriculture. *Global Change Biology*, 22, 704–715.
- Qian H (2009) Beta diversity in relation to dispersal ability for vascular plants in North America. *Global Ecology and Biogeography*, 18, 327–332.
- Qian H, Chen SB, Mao LF, Ouyang ZY (2013) Drivers of β -diversity along latitudinal gradients revisited. *Global Ecology and Biogeography*, 22, 659–670.
- Qian H, Ricklefs RE (2007) A latitudinal gradient in large-scale beta diversity for vascular plants in North America. *Ecology Letters*, 10, 737–744.
- Rahbek C (1995) The elevational gradient of species richness: a uniform pattern? *Ecography*, 18, 200–205.
- Rahbek C (2005) The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters*, 8, 224–239.
- Ricklefs RE (1987) Community diversity: relative roles of local and regional processes. *Science*, 235, 167–171.
- Ricotta C, Carranza ML, Avena G (2002) Computing

- β -diversity from species-area curves. *Basic and Applied Ecology*, 3, 15–18.
- Ricotta C, Pavoine S (2015) A multiple-site dissimilarity measure for species presence/absence data and its relationship with nestedness and turnover. *Ecological Indicators*, 54, 203–206.
- Rosenzweig ML (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.
- Schmera D, Podani J (2011) Comments on separating components of beta diversity. *Community Ecology*, 12, 153–160.
- Sheldon KS, Yang S, Tewksbury JJ (2011) Climate change and community disassembly: impacts of warming on tropical and temperate montane community structure. *Ecology Letters*, 14, 1191–1200.
- Shimadzu H, Dornelas M, Magurran AE (2015) Measuring temporal turnover in ecological communities. *Methods in Ecology and Evolution*, 6, 1384–1394.
- Si XF (2014) Species Turnover and Beta Diversity of Breeding Bird Communities in Fragmented Habitats. PhD Dissertation, Zhejiang University, Hangzhou. (in Chinese with English abstract) [斯幸峰 (2014) 片段化生境中繁殖鸟类群落的物种周转和 β 多样性. 博士学位论文, 浙江大学, 杭州.]
- Si XF, Baselga A, Ding P (2015) Revealing beta-diversity patterns of breeding bird and lizard communities on inundated land-bridge islands by separating the turnover and nestedness components. *PLoS ONE*, 10, e0127692.
- Si XF, Baselga A, Leprieur F, Song X, Ding P (2016) Selective extinction drives taxonomic and functional alpha and beta diversities in island bird assemblages. *Journal of Animal Ecology*, 85, 409–418.
- Si XF, Cadotte MW, Zeng D, Baselga A, Zhao YH, Li JQ, Wu YR, Wang SY, Ding P (2017) Functional and phylogenetic structure of island bird communities. *Journal of Animal Ecology*, 86, 532–542.
- Si XF, Ding P (2011) History, status of monitoring land birds in Europe and American and countermeasures of China. *Biodiversity Science*, 19, 303–310. (in Chinese with English abstract) [斯幸峰, 丁平 (2011) 欧美陆地鸟类监测的历史、现状与我国的对策. *生物多样性*, 19, 303–310.]
- Si XF, Pimm SL, Russell GJ, Ding P (2014) Turnover of breeding bird communities on islands in an inundated lake. *Journal of Biogeography*, 41, 2283–2292.
- Siefert A, Ravenscroft C, Weiser MD, Swenson NG (2013) Functional beta-diversity patterns reveal deterministic community assembly processes in eastern North American trees. *Global Ecology and Biogeography*, 22, 682–691.
- Socolar JB, Gilroy JJ, Kunin WE, Edwards DP (2016) How should beta-diversity inform biodiversity conservation? *Trends in Ecology & Evolution*, 31, 67–80.
- Sodhi NS, Wilcove DS, Lee TM, Sekercioglu CH, Subaraj R, Bernard H, Yong DL, Lim SLH, Prawiradilaga DM, Brook BW (2010) Deforestation and avian extinction on tropical landbridge islands. *Conservation Biology*, 24, 1290–1298.
- Soininen J, McDonald R, Hillebrand H (2007) The distance decay of similarity in ecological communities. *Ecography*, 30, 3–12.
- Staniczenko PP, Kopp JC, Allesina S (2013) The ghost of nestedness in ecological networks. *Nature Communications*, 4, 1391.
- Stegen JC, Hurlbert AH (2011) Inferring ecological processes from taxonomic, phylogenetic and functional trait beta-diversity. *PLoS ONE*, 6, e20906.
- Steinitz O, Heller J, Tsoar A, Rotem D, Kadmon R (2006) Environment, dispersal and patterns of species similarity. *Journal of Biogeography*, 33, 1044–1054.
- Su G, Xu J, Akasaka M, Molinos JG, Shin-ichiro SM (2015) Human impacts on functional and taxonomic homogenization of plateau fish assemblages in Yunnan, China. *Global Ecology and Conservation*, 4, 470–478.
- Svenning J-C, Fløjgaard C, Baselga A (2011) Climate, history and neutrality as drivers of mammal beta diversity in Europe: insights from multiscale deconstruction. *Journal of Animal Ecology*, 80, 393–402.
- Swenson NG, Anglada-Cordero P, Barone JA (2011a) Deterministic tropical tree community turnover: evidence from patterns of functional beta diversity along an elevational gradient. *Proceedings of the Royal Society B: Biological Sciences*, 278, 877–884.
- Swenson NG, Stegen JC, Davies SJ, Erickson DL, Forero-Montaña J, Hurlbert AH, Kress WJ, Thompson J, Uriarte M, Wright SJ, Zimmerman JK (2011b) Temporal turnover in the composition of tropical tree communities: functional determinism and phylogenetic stochasticity. *Ecology*, 93, 490–499.
- Tang ZY, Fang JY, Chi XL, Feng JM, Liu YN, Shen Z-H, Wang XP, Wang Z-H, Wu XP, Zheng CY (2012) Patterns of plant beta-diversity along elevational and latitudinal gradients in mountain forests of China. *Ecography*, 35, 1083–1091.
- Terborgh JW (2015) Toward a trophic theory of species diversity. *Proceedings of the National Academy of Sciences, USA*, 112, 11415–11422.
- Thorn S, Bässler C, Bernhardt-Römermann M, Cadotte M, Heibl C, Schäfer H, Seibold S, Müller J (2016) Changes in the dominant assembly mechanism drive species loss caused by declining resources. *Ecology Letters*, 19, 163–170.
- Tilman D (2001) Functional diversity. In: *Encyclopedia of Biodiversity* (ed. Levin SA), pp. 109–120. Academic Press, San Diego.
- Tuomisto H (2010a) A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography*, 33, 2–22.
- Tuomisto H (2010b) A diversity of beta diversities: straighten-

- ing up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. *Ecography*, 33, 23–45.
- Uchida K, Ushimaru A (2015) Land abandonment and intensification diminish spatial and temporal β -diversity of grassland plants and herbivorous insects within paddy terraces. *Journal of Applied Ecology*, 52, 1033–1043.
- Ulrich W, Almeida-Neto M, Gotelli NJ (2009) A consumer's guide to nestedness analysis. *Oikos*, 118, 3–17.
- Umaña MN, Zhang C, Cao M, Lin L, Swenson NG (2015) Commonness, rarity, and intraspecific variation in traits and performance in tropical tree seedlings. *Ecology Letters*, 18, 1329–1337.
- Urban MC (2015) Accelerating extinction risk from climate change. *Science*, 348, 571–573.
- Villéger S, Grenouillet G, Brosse S (2013) Decomposing functional β -diversity reveals that low functional β -diversity is driven by low functional turnover in European fish assemblages. *Global Ecology and Biogeography*, 22, 671–681.
- Villéger S, Mason NW, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89, 2290–2301.
- Villéger S, Miranda JR, Hernandez DF, Mouillot D (2012) Low functional β -diversity despite high taxonomic β -diversity among tropical estuarine fish communities. *PLoS ONE*, 7, e40679.
- Wang GM, Zuo JC, Li XR, Liu YH, Yu JB, Shao HB, Li YZ (2014) Low plant diversity and floristic homogenization in fast-urbanizing towns in Shandong Peninsular, China: effects of urban greening at regional scale for ecological engineering. *Ecological Engineering*, 64, 179–185.
- Wang J, Meier S, Soininen J, Casamayor EO, Pan F, Tang X, Yang X, Zhang Y, Wu Q, Zhou J, Shen J (2017) Regional and global elevational patterns of microbial species richness and evenness. *Ecography*, 40, 393–402.
- Wang J, Pan F, Soininen J, Heino J, Shen J (2016) Nutrient enrichment modifies temperature-biodiversity relationships in large-scale field experiments. *Nature Communications*, 7, 13960.
- Wang J, Soininen J, Zhang Y, Wang B, Yang X, Shen J (2012) Patterns of elevational beta diversity in micro- and macro-organisms. *Global Ecology and Biogeography*, 21, 743–750.
- Wang SX, Wang XA, Guo H (2013) Change patterns of beta-diversity in the succession process of plant communities on Loess Plateau of Northwest China. *Chinese Journal of Ecology*, 32, 1135–1140. (in Chinese with English abstract) [王世雄, 王孝安, 郭华 (2013) 黄土高原植物群落演替过程中的 β 多样性变化. *生态学杂志*, 32, 1135–1140.]
- Wang SX, Zhao L, Li N, Guo H, Wang XA, Duan RY (2016) Community heterogeneity of undergrowth vegetation in *Pinus tabulaeformis* forest on the Loess Plateau of Northwest China. *Chinese Journal of Ecology*, 35, 1197–1203. (in Chinese with English abstract) [王世雄, 赵亮, 李娜, 郭华, 王孝安, 段仁燕 (2016) 黄土高原油松林下群落异质性分析. *生态学杂志*, 35, 1197–1203.]
- Wang YP, Bao YX, Yu MJ, Xu GF, Ding P (2010) Nestedness for different reasons: the distributions of birds, lizards and small mammals on islands of an inundated lake. *Diversity and Distributions*, 16, 862–873.
- Webb CO (2000) Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *The American Naturalist*, 156, 145–155.
- Webb CO, Ackerly DD, McPeck MA, Donoghue MJ (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, 33, 475–505.
- Wen ZX, Yang QS, Quan Q, Xia L, Ge DY, Lü X (2016) Multiscale partitioning of small mammal β -diversity provides novel insights into the Quaternary faunal history of Qinghai-Tibetan Plateau and Hengduan Mountains. *Journal of Biogeography*, 43, 1412–1424.
- Whittaker RH (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, 30, 279–338.
- Whittaker RH (1972) Evolution and measurement of species diversity. *Taxon*, 21, 213–251.
- Wiersma YF, Urban DL (2005) Beta diversity and nature reserve system design in the Yukon, Canada. *Conservation Biology*, 19, 1262–1272.
- Wilcove DS, Rothstein D, Jason D, Phillips A, Losos E (1998) Quantifying threats to imperiled species in the United States. *BioScience*, 48, 607–615.
- Williams PH (1996) Mapping variations in the strength and breadth of biogeographic transition zones using species turnover. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 263, 579–588.
- Willig MR, Kaufman DM, Stevens RD (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics*, 34, 273–309.
- Wilson MC, Chen XY, Corlett RT, Didham RK, Ding P, Holt RD, Holyoak M, Hu G, Hughes AC, Jiang L, Laurance WF, Liu JJ, Pimm SL, Robinson SK, Russo SE, Si XF, Wilcove DS, Wu JG, Yu MJ (2016) Habitat fragmentation and biodiversity conservation: key findings and future challenges. *Landscape Ecology*, 31, 219–227.
- Wu LB, Si XF, Didham RK, Ge DP, Ding P (2017) Dispersal modality determines the relative partitioning of beta diversity in spider assemblages on subtropical land-bridge islands. *Journal of Biogeography*, 44, doi: 10.1111/jbi.13007.
- Wu YJ, Lei FM (2013) Species richness patterns and mechanisms along the elevational gradients. *Chinese Journal of Zoology*, 48, 797–807. (in Chinese with English abstract) [吴永杰, 雷富民 (2013) 物种丰富度垂直分布格局及影响机制. *动物学杂志*, 48, 797–807.]
- Xu J, Su GH, Xiong Y, Akasaka M, Molinos JG, Shin-ichiro

- SM, Zhang M (2015a) Complimentary analysis of meta-community nestedness and diversity partitioning highlights the need for a holistic conservation strategy for highland lake fish assemblages. *Global Ecology and Conservation*, 3, 288–296.
- Xu WB, Chen GK, Liu CR, Ma KP (2015b) Latitudinal differences in species abundance distributions, rather than spatial aggregation, explain beta-diversity along latitudinal gradients. *Global Ecology and Biogeography*, 24, 1170–1180.
- Zhang Q, Hou X, Li FY, Niu J, Zhou Y, Ding Y, Zhao L, Li X, Ma W, Kang S (2014) Alpha, beta and gamma diversity differ in response to precipitation in the Inner Mongolia grassland. *PLoS ONE*, 9, e93518.
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附录 Supplementary Material

附录1 有关beta多样性分解方法的核心论文

Appendix 1 Key references related to the methods of beta-diversity partitioning
<http://www.biodiversity-science.net/fileup/PDF/2017024-1.pdf>

附录2 2010至2016年间有关beta多样性分解论文在不同期刊上的发表总数量(仅列发表数量 ≥ 4的期刊)

Appendix 2 Number of total publications for each journal published studies of beta-diversity partitioning (list journals with ≥ 4 publications only) from 2010 to 2016
<http://www.biodiversity-science.net/fileup/PDF/2017024-2.pdf>

附录3 Beta多样性分解的R代码演示

Appendix 3 Demonstration of the R code for beta-diversity partitioning
<http://www.biodiversity-science.net/fileup/PDF/2017024-3.pdf>

斯幸峰, 赵郁豪, 陈传武, 任鹏, 曾嶙, 吴玲兵, 丁平. Beta多样性分解: 方法、应用与展望. 生物多样性, 2017, 25 (5): 464–480.
<http://www.biodiversity-science.net/CN/10.17520/biods.2017024>

附录 1 有关 beta 多样性分解方法的核心论文

Appendix 1 Key references related to the methods of beta-diversity partitioning

- Almeida-Neto M, Frensel D, Ulrich W (2012) Rethinking the relationship between nestedness and beta diversity: a comment on Baselga (2010). *Global Ecology and Biogeography*, 21, 772–777.
- Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19, 134–143.
- Baselga A (2012) The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography*, 21, 1223–1232.
- Baselga A (2013) Separating the two components of abundance-based dissimilarity: balanced changes in abundance vs. abundance gradients. *Methods in Ecology and Evolution*, 4, 552–557.
- Baselga A, Leprieur F (2015) Comparing methods to separate components of beta diversity. *Methods in Ecology and Evolution*, 6, 1069–1079.
- Baselga A, Orme CDL (2012) betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution*, 3, 808–812.
- Cardoso P, Rigal F, Carvalho JC (2015) BAT—biodiversity assessment tools, an R package for the measurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. *Methods in Ecology and Evolution*, 6, 232–236.
- Cardoso P, Rigal F, Carvalho JC, Fortelius M, Borges PAV, Podani J, Schmera D (2014) Partitioning taxon, phylogenetic and functional beta diversity into replacement and richness difference components. *Journal of Biogeography*, 41, 749–761.
- Carvalho JC, Cardoso P, Borges PAV, Schmera D, Podani J (2013) Measuring fractions of beta diversity and their relationships to nestedness: a theoretical and empirical comparison of novel approaches. *Oikos*, 122, 825–834.
- Carvalho JC, Cardoso P, Gomes P (2012) Determining the relative roles of species replacement and species richness differences in generating beta-diversity patterns. *Global Ecology and Biogeography*, 21, 760–771.
- Legendre P (2014) Interpreting the replacement and richness difference components of beta diversity. *Global Ecology and Biogeography*, 23, 1324–1334.
- Leprieur F, Albouy C, De Bortoli J, Cowman PF, Bellwood DR, Mouillot D (2012) Quantifying phylogenetic beta diversity: distinguishing between ‘true’ turnover of lineages and phylogenetic diversity gradients. *PLoS ONE*, 7, e42760.
- Leprieur F, Oikonomou A (2014) The need for richness-independent measures of turnover when delineating biogeographical regions. *Journal of Biogeography*, 41, 417–420.
- Podani J, Ricotta C, Schmera D (2013) A general framework for analyzing beta diversity, nestedness and related community-level phenomena based on abundance data. *Ecological Complexity*, 15, 52–61.
- Podani J, Schmera D (2011) A new conceptual and methodological framework for exploring and explaining pattern in presence-absence data. *Oikos*, 120, 1625–1638.
- Schmera D, Podani J (2011) Comments on separating components of beta diversity. *Community Ecology*, 12, 153–160.

斯幸峰, 赵郁豪, 陈传武, 任鹏, 曾頔, 吴玲兵, 丁平. Beta多样性分解: 方法、应用与展望. 生物多样性, 2017, 25 (5): 464–480.
<http://www.biodiversity-science.net/CN/10.17520/biods.2017024>

附录 2 2010 至 2016 年间有关 beta 多样性分解论文在不同期刊上的发表总数量(仅列发表数量 ≥ 4 的期刊)

Appendix 2 Number of total publications for each journal published studies of beta-diversity partitioning (list journals with ≥ 4 publications only) from 2010 to 2016

期刊名 Journal name	发表论文数 Number of publications	发表论文百分比 (%) Percentage of publications (%)
<i>PLoS ONE</i>	28	8.02
<i>Global Ecology and Biogeography</i>	26	7.45
<i>Journal of Biogeography</i>	21	6.02
<i>Hydrobiologia</i>	12	3.44
<i>Freshwater Biology</i>	10	2.87
<i>Biological Conservation</i>	8	2.29
<i>Forest Ecology and Management</i>	8	2.29
<i>Insect Conservation and Diversity</i>	8	2.29
<i>Methods in Ecology and Evolution</i>	8	2.29
<i>Ecology Letters</i>	7	2.01
<i>Ecography</i>	6	1.72
<i>Ecology and Evolution</i>	6	1.72
<i>Journal of Animal Ecology</i>	6	1.72
<i>Oikos</i>	6	1.72
<i>Scientific Reports</i>	6	1.72
<i>Biodiversity and Conservation</i>	5	1.43
<i>Ecological Indicators</i>	5	1.43
<i>Global Change Biology</i>	5	1.43
<i>Journal of Vegetation Science</i>	5	1.43
<i>Agriculture Ecosystems & Environment</i>	4	1.15
<i>Community Ecology</i>	4	1.15
<i>Diversity and Distributions</i>	4	1.15
<i>Ecological Research</i>	4	1.15
<i>Ecosphere</i>	4	1.15
<i>Fungal Ecology</i>	4	1.15
<i>Proceedings of the Royal Society B: Biological Sciences</i>	4	1.15

斯幸峰, 赵郁豪, 陈传武, 任鹏, 曾嶂, 吴玲兵, 丁平. Beta多样性分解: 方法、应用与展望. 生物多样性, 2017, 25 (5): 464-480.
<http://www.biodiversity-science.net/CN/10.17520/biods.2017024>

附录3 Beta多样性分解的R代码演示

Appendix 3 Demonstration of the R code for beta-diversity partitioning

#本节以千岛湖繁殖鸟类的物种多样性数据(Si et al, 2016)为例, 简要演示 BAS 法和#POD 法成对相异性指数和总体 beta 多样性指数及组分的计算过程。

```
library(betapart) #BAS 法
```

```
library(BAT) #POD 法
```

```
#导入文本格式数据‘comm’。‘comm’一行代表一个群落, 一列代表一个物种。
```

```
comm <- t(read.table("http://sixf.org/files/code/2015/JAnimEcolTableS3Comm.txt"))
```

```
#由于 BAT 中 beta 函数与 R 中基础函数 beta 重名, 因而重命名
```

```
beta.pod.pair <- BAT::beta
```

```
#由于 BAT 中 beta.multi 函数与 betapart 中 beta.multi 函数重名, 因而重命名
```

```
beta.pod.multi <- BAT::beta.multi
```

```
## 成对相异性指数及组分
```

```
BAS.sor.pair <- beta.pair(x=comm,index.family="sorensen") #BAS 法分解 Sørensen
```

```
BAS.jac.pair <- beta.pair(x=comm,index.family="jaccard") #BAS 法分解 Jaccard
```

```
POD.sor.pair <- beta.pod.pair (x=comm, func="soerenzen") #POD 法分解 Sørensen
```

```
POD.jac.pair <- beta.pod.pair (x=comm, func="jaccard") #POD 法分解 Jaccard
```

```
BAS.sor.pair$beta.sor #BAS 法成对相异指数 Sørensen
```

```
BAS.sor.pair$beta.sim #BAS 法空间周转组分  $\beta_{sim}$ 
```

```
BAS.sor.pair$beta.sne #BAS 法嵌套组分  $\beta_{sne}$ 
```

```
#按照同样的方法可计算 BAS.jac.pair$beta.jac, BAS.jac.pair$beta.jtu, BAS.jac.pair$beta.jne
```

```
POD.sor.pair$Btotal #POD 法成对相异指数 Sørensen
```

```
POD.sor.pair$Brepl #POD 法物种替换组分  $\beta_3$ 
```

```
POD.sor.pair$Brich #POD 法丰富度差异组分  $\beta_{rich}$ 
```

```
#按照同样的方法可计算 POD.jac.pair$Btotal, POD.jac.pair$Btotal, POD.jac.pair$Brich。#总体  
beta 多样性及其组分
```

```
BAS.sor.pair <- beta.multi(x=comm,index.family="sorensen") #BAS 法分解 Sørensen
```

```
BAS.jac.pair <- beta.nulti(x=comm,index.family="jaccard") #BAS 法分解 Jaccard
```

```
POD.sor.pair <- beta.pod.multi(x=comm, func="soerenzen") #POD 法分解 Sørensen
```

```
POD.jac.pair <- beta.pod.multi (x=comm, func="jaccard") #POD 法分解 Jaccard
```