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功能多样性——生物多样性与生态系统功能关系研究的新视角*

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摘要:生物多样性与生态系统功能的关系是近年来生态学研究的重点.功能多样性是目前反应生态系统功能最好的预测因子,因为它决定了物种多样性与生态系统功能关系的强度和形式.在查阅大量文献的基础上,介绍了功能多样性的概念和研究方法,并比较了不同功能多样性指数的使用特点.同时,论述了功能多样性与传统生物多样性重要指数——物种丰富度之间的关系以及影响因子,功能多样性与生态系统功能的关系以及影响因子,功能多样性研究在实践中的应用,并对功能多样性的研究趋势进行了展望.

关键词:生物多样性;生态系统功能;功能特征;功能多样性
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生物多样性与生态系统功能的关系是当前生态学研究的焦点和难点,在变动的景观中,两者间的关系十分复杂[1-2].首先,干扰影响生物多样性与生态系统功能的关系[3],如不同管理强度的草原以及不同土地利用方式下生物多样性与生态系统功能之间的关系表现出较大的变异[4-5].其次,研究的尺度影响生物多样性与生态系统功能的关系,例如,在不同空间尺度上,这种关系中作为生态系统功能的驱动者存在变化[6],稀有种也可能是某个生态系统功能的主要驱动者[7-8];但在时间尺度上这种关系有时候比较稳定[9-10].另外,生物多样性与生态系统功能的关系,就算在相同的尺度下,也与研究选择的具体环境条件和测定的具体的生态系统功能指标有关[11-12].

生物多样性与生态系统功能的关系虽然复杂[13],科研工作者们依然找出了隐藏在这种关系中的共性规律,即生态系统中不同的生物体对系统提供的服务(或功能)以及在生态系统过程中所作的贡献才是关注的重点和热点[14-17].试验、综述以及大尺度的数据分析结果均显示,功能多样性(functional diversity)是目前反应生态系统功能最好的预测因子[18],已逐渐成为生物多样性研究中除了物种多样性和遗传多样性以外的另一个重要方面.因为功能多样性强调的是功能,与生态系统的功能更加紧密,决定了物种多样性与生态系统功能关系的强度和具体的作用形式,其中功能冗余水平是最重要的测定指标,遗憾的是这方面的研究还很欠缺[19].因此,多样性的重新定义也从物种数转向群落内或生态系统内功能特征的变动,原因在于分类上的物种丰富度只能较弱地影响生态系统功能,在相对较大的尺度上更是如此[20-21].

1 功能多样性概念及研究方法

Tilman[22]定义功能多样性为影响生态系统功能的群落中所有物种及有机物的功能特征值及其变动范围,强调的是特征值的差异性.因此,功能多样性的研究是在测定有机体的功能特征的基础上完成的[16].功能特征是有机体的本质特性,是在漫长的进化过程中形成的,指可影响个体在具体栖境中的表现和适合度的任何定性或定量的特征,如物理的(如植物的叶面积,蚂蚁的头宽),行为上的

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(如蜜蜂独居还是群居,觅食搜索范围),物候上的或节律上的(如植物结实时间,昆虫成虫期时间长度)等等[23-24].有机体的功能特征决定该生物在哪种栖境下生存,与其他物种发生相互作用时具体的方式和强度,甚至是对生态系统功能贡献的大小[23-25].功能特征的测定比物种数的统计要困难得多,然而,由于它充分考虑各个物种在生态系统中的功能作用,克服了物种多样性指数以有无和多寡来同等对待每个物种的不足.因此,相对于物种多样性指数,功能多样性指数与生态系统功能之间具有更强的相关性,测定较小数量的特征值比鉴定整个群落中的每个物种更有效[23-24,26].

当我们获得几种功能特征的数据时,无论采用哪种模型方法,都能在一定程度上说明每个特征对于系统总产量的相对贡献[27],目前被广泛认可的有:Petchey 等[28]提出的功能多样性指数(functional diversity,FD),Villéger 等[29]提出的功能丰富度指数(functional richness index,FRic)、功能均匀度指数(functional evenness index,FEve)和功能分异(趋异)指数(functional divergence index,FDiv)等 3 个功能多样性指数.其中 FRic 是指有机体在群落中所占据的功能空间的大小,体现的是生态空间利用程度的指数,该指数越大,生态空间利用程度越高;FEve 是指在群落内有机体的功能特征在生态空间上分布的均匀程度,多度量化生态功能空间如何被填充的指标,该指数越大,说明对有效资源利用越全面,效率越高;FDiv 表示群落内有机体特征值的差异性,体现了群落内有机体的生态位分化和资源竞争程度,该指数越高,说明群落内有机体生态位互补程度越强,竞争较弱[29].此外,功能特征多样性指数(functional attribute diversity,FAD)、功能分散指数(functional dispersion,FDis)、Rao 指数、CWM 指数(community weighted mean)等也被用于功能多样性测定[30-32].由于功能多样性指数与传统的物种多样性指数有着密切的关系,因此部分研究依然关注这种传统的多样性指数与功能多样性指数的关系,以及这两种不同的多样性指数与生态系统功能的关系[27],包括这些多样性指数如何响应环境压力和干扰的影响[15].

从目前的研究来看,许多研究在测定和分析功能多样性时都有一定局限性,到底采用哪些指数依赖于数据本身的特点以及比较的测量单位.例如,定性功能特征的测定宜选择 FDis;而比较系统发生的多样性时,则宜采用 Petchey 等提出的 FD 指数[33].如何科学合理的评价功能多样性,需要发展功能多样性指数.另外,发展新的分析方法研究功能特征与环境变量的关系也十分必要,例如基于 R 语言发展的四角分析(fourth corner analysis)就为分析物种的功能特征与数量诸多的环境特征之间的关系提供了新的手段[34].

2　功能多样性与物种丰富度的关系

功能多样性研究中,功能丰富度是焦点之一,尤其是它与物种丰富度之间的关系.某些植物、大型底栖无脊椎动物、鸟类、昆虫等生物类群的物种丰富度和功能丰富度之间具有正相关的关系[35-38],例如,在不同树龄梯度的林分中,功能丰富度和功能多样性随蚂蚁物种丰富度与多样性的增加而增加[39].但是,功能多样性也可能独立于物种多样性振荡,例如功能独特的物种在某个环境建立领地,将导致功能冗余的物种丧失[40].而对于大多数自然系统,功能丰富度和物种丰富度之间的精确关系仍未弄清楚[24].

物种丰富度与功能多样性的关系受多种因素影响.例如,物种丰富度与功能多样性之间的关系受系统中可获得的营养成分影响[41],功能多样的群落在营养增加的时候易于产生群落组成变动及增加多度,因为这样的群落更容易拥有具备开拓新增资源功能特征的物种[42].在营养成分吸收和利用策略方面,群落功能多样性高,则土壤营养成分不良也能供养高的物种多样性[41].物种丰富度与功能多样性之间的关系还受到扰动的影响[43].Mayfield 等[43]对造林地和重度干扰的毁林地的研究发现,在造林地中一些特征的功能丰富度的增加要比物种增加得更为迅速,但同时另一些特征则呈现相反的趋势.Biswas 等[44]发现,在中等干扰程度的温带高地和河岸生态系统,物种多样性、功能丰富度和功能多样性都最大化;然而在适度干扰到强度干扰的一系列河岸生态系统的样地中,物种多样性和物种丰富度持续增加,而功能丰富度下降.Mayfield 等[40]提出,在群落响应土地利用变化中,物种多样性与功能多样性的响应不一致,因此导致二者的关系出现广泛的变动;干扰改变了物种多样性和功能丰富度之间的联系,观察到的关系取决于考虑的特征.

因此,物种丰富度与功能多样性的关系十分复

杂,表现为有相关性或无相关性,相关性又表现为正相关或负相关,两者间的关系取决于环境条件和受干扰强度[45];并且还与选择的多样性指数、分析方法等有关系,例如 Poos 等[46]发现,功能冗余、测定的特征值、环境过滤器、计算方法及物种丰富度都能影响功能多样性指数.

3 功能多样性与生态系统功能的关系

生态系统功能包括生态系统过程、生态系统特性和生态系统稳定性[47].目前关于功能多样性对生态系统功能的影响的假说主要包括多样性假说和质量比假说,这两种假说并不互相矛盾,只是从不同侧面说明了功能多样性与生态系统功能的关系[45].相比其他的生态系统,在农业生态系统内,功能多样性与生态系统之间的关系研究较少[37].已开展的研究均显示无论是植物还是动物、昆虫、微生物等的功能特征与生态系统功能密切相关[48-51],并且功能多样性指数在季节间的变动能反映出生态系统功能的波动[52].但并不是采用的功能特征的指数越多,越能反映出对生态系统功能的影响;有时候单一功能特征与生态系统功能之间的关系超过多个特征组合的功能多样性[53].功能多样性作用于生态系统功能的效果与非生物因子、干扰和管理活动等有关.

从本质上说,在生态系统内,有机体的功能多样性体现是通过巨大的异质性资源利用来实现的,即资源利用差异越大,功能多样性越高,生态系统的功能也随之增加[24].简单地说,假如群落内每个有机体具有不同且相互补充的功能特征,那么这些有机体将分布在互不交叉重叠的空间生态位上.因此,可以预见随着物种数量的增加,整个生态位将被逐渐被占满,生态系统的这个方面的功能逐渐增加[54].Díaz 等[19]也发现关于功能多样性对生态系统功能的影响的一个较好的解释就是:由于栖境的异质化,功能特征值变异增大,增加了栖境中资源的利用效率,导致功能多样性指数高,生态系统功能增强.除了在物种的层面上,在更低分类层面上的功能多样性也影响生态系统的功能,包括种内层面,甚至基因层面[55].

4 功能多样性在实践中的应用

功能多样性影响生态系统的功能受多个机制同时作用[56],因此弄清楚每个机制的相对重要性有利于我们充分认识功能多样性在生态系统功能中的作用,从而更好地指导生产实践.无论是哪种类型的生态系统,生态恢复的目的就是建立稳定的、具功能的生态系统[57].在管理或恢复的生态系统中,随着时间的延续,高的功能多样性导致高的稳定性,因为多个功能特征有利于系统抵御非生物因子的变动[30].

我国山地面积广阔,其中西南地区尤为显著,山地面积占土地总面积的比例高达 92.6%[58],是生态环境较为脆弱的地区,也是生态地位十分重要的区域[58].近些年来由于生态恢复的加强和人工林广泛种植,导致土地利用强度高度分离,山地土地利用模式呈现典型的镶嵌结构[59-61].而农业景观的变换能极大降低功能多样性,旨在恢复物种丰富度的管理策略可能无法充分保护功能多样性,因为物种丰富度和功能多样性对经营管理活动反应极为不同[62].因此,基于不同物种对生态系统的功能变化幅度非常大,我们应把保护的重点放在功能多样性而不仅仅是物种丰富度上.

5 功能多样性研究趋势

生物多样性与生态系统功能关系的研究是当今国际重大科学前沿领域之一.人类生产活动通常引起物种多样性降低[44].生物多样性是生产力的驱动者[63],生物多样性降低,生物量减少,在自养生物、消费者和分解者上都找到证据[64-67].这种逻辑性有其合理的一面,即某个有机体是否出现以及出现的频次,肯定影响其在生态系统功能中的作用有无和大小.然而,有机体在生态系统中体现其功能是通过其提供的功能或服务实现的,即该有机体具备某种特征,占据了某个生态位.因此更应该关注某个生态位上的特异性的功能特征值是否存在.资源是生物多样性与生态系统功能关系的纽带,因此在消费者-资源间的能量流动与生态系统过程之间的联系十分紧密,生物多样性丧失在营养级间的影响更为强烈[68].今后的研究中,更应该在多个营养级间的食物网背景下分析多样性变化导致的生态系统功能的变化[69].甚至有研究者提议还应关注营养级间的非摄食关系[70],比如捕食者存在能降低猎物的多度,但是当多个捕食者存在时,猎物的降低程度要小许多[71].

事实上,人类正在开展的生态系统修复、生态系统保护和生态系统管理的目标很明确,除了保护

生物多样性本身外,更重要的是就是希望保护生态系统所提供的服务和功能,其中人类赖以生存的功能如储存碳[72-74]和生产食物[75]必须优先保护.相对于传统的多样性指数,功能多样性指数能较好地预测生态系统的功能[76].功能多样性的研究是当前生物多样性与生态系统功能关系研究发展的趋势[18].其中基于功能特征是一个重要的途径来描述食物网的功能结构[77].因此,功能多样性是研究生物多样性与生态系统功能关系的新视角,但同时我们也面临许多新的问题,主要有三个方面:第一需要不断发掘新的功能特征,充分反映生物在生态系统中的功能;第二,需要发展新的功能多样性指数,来科学合理的评价生物的功能多样性;第三,需要发展新的分析方法,研究功能特征与环境变量的关系.

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Functional diversity: a new view point in the relationship between biodiversity and ecosystem functioning research

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Abstract: Relationship between biodiversity and ecosystem functioning is the present focus of ecological research, functional diversity is the best predictor of ecosystem functioning to determine the intensity and form in the relationship between biodiversity and ecosystem functioning. In this article, based on the review of the great deal of scientific literatures, the definition of functional diversity and its study methods were introduced, and the application of each functional diversity index was also compared. The relationship between functional diversity and the important index of traditional biodiversity: species richness and its factors, the relationship between functional diversity and ecosystem functioning and its factors were argued. Meanwhile, the application of functional diversity in ecosystem management practice, and the research trend of functional diversity were discussed.

Key words: biodiversity; ecosystem functioning; functional trait; functional diversity