



黄土高原腹地人工林下草本层群落构建机制

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摘要 群落构建机制是生态学研究的核心论题。生态位理论和中性理论是阐明群落构建的两种主要理论, 但这两种理论分别强调的环境过滤和扩散限制对群落构建的影响尚存争议。该研究以黄土高原人工林下草本层群落为研究对象, 将群落物种组成数据与地理空间、气候、地形以及生物因子相结合, 运用随机森林模型(RF)和基于距离矩阵的多元回归方法(MRM), 探究了各个因子的重要性, 并通过邻体主坐标矩阵(PCNM)和基于距离的冗余分析(db-RDA)分别筛选显著的空间结构和环境因子, 最后结合筛选出的PCNM特征值和环境变量进行方差分解。研究结果显示: 1)林下草本层群落组成相似性随地理距离和生境差异的增加而减小。2)地理距离与生境差异共同解释了群落组成相似性变化的47.8%。其中, 空间因子和环境因子的独立解释率分别为14.1%和9.8%, 两者的联合解释率为23.9%。3)地理距离和年降水量是引起研究区内物种组成变化的关键因子, 且地理距离的重要性大于年降水量。在黄土高原腹地, 扩散限制与环境过滤共同主导了人工林下草本层群落的构建过程。

关键词 群落构建; 生态位理论; 中性理论; 环境过滤; 扩散限制; β 多样性; 林下草本层群落

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Community assembly of herbaceous layer of the planted forests in the central Loess Plateau, China

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Abstract

Aims Many competing theories seek to identify the mechanisms behind the community assembly. Niche theory and neutral theory are among the two most competing mechanisms. Exploring factors controlling the patterns of β -diversity is an approach to reveal the underlying mechanisms of community assembly. In this paper, we aim to reveal the β -diversity pattern of understory in planted forests of the central Loess Plateau and to evaluate the relative influences of deterministic (environmental filtering) and stochastic (dispersal limitation) processes on the community assembly.

Methods We sampled in total 107 sites of planted forests spatially spreading over the central Loess Plateau. In each site, three plots (10 m \times 10 m) were randomly designed each at a distance of about 50 m. The floristic composition, community structure, and environmental conditions were investigated in each plot. We calculated the dissimilarity (β_{sim}) of species composition, geographic distance and environmental divergence for each of the 5 671 site pairs. We used random forest (RF) to quantify the influence of the selected factors on species composition, and distance-based multivariate regression method (MRM) to fit the relationship between dissimilarity, geographic distance and environmental divergence. To quantify how and in what extent the environmental filtering and the dispersal limitation influence the species composition among sites, we performed the principle coordinates of neighbor matrices (PCNM) and distance-based RDA (db-RDA) to select the pronounced independent variables. We then partitioned the variance into three parts, namely, 1) independent contributions of geographic distance; 2) independent contributions of environmental divergence; and 3) the joint contribution of both.

Important findings The community similarity declined with increasing geographical distance and environmental divergence. Geographical distance and environmental divergence together explained 47.8% of variance in

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the dissimilarity in species composition. The spatial variables accounted for 14.1%, while the environmental variables accounted for another 9.8% of the variance in dissimilarity of species composition. Annual precipitation and basal area of trees are the two most important environmental factors influencing the pattern of dissimilarity of species composition. These results implied that both environmental filtering and the dispersal limitation play important roles in shaping the community assembly of the herbaceous layers of planted forests in the central Loess Plateau.

Key words community assembly; niche theory; neutral theory; environmental filtering; dispersal limitation; β diversity; understory community

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揭示群落物种空间分布格局和动态变化机制即群落构建机制是群落生态学的基本目标(Smith & Lundholm, 2010; May *et al.*, 2015; Gibson *et al.*, 2017)。生态位理论(确定过程)和中性理论(随机过程)是阐明该机制的两种主要理论(Page & Shanker, 2018), 但这两个理论对群落构建过程的相对重要性目前仍未达成广泛共识(Leibold & McPeck, 2006)。生态位理论认为物种组成差异格局是环境异质性的产物, 共存物种间的生态位分化、资源竞争等确定性因素是主要决定因子(Chase & Myers, 2011)。然而, 中性理论则认为群落中相同营养级所有个体在生态上等价, 差异主要由扩散限制和生态漂变等随机作用主导(Hubbell, 2001)。近年来的研究则倾向于整合两个理论的观点, 认为确定过程和随机过程均在群落构建过程中发挥着重要作用(Gravel *et al.*, 2006; Adler *et al.*, 2007; Chase & Myers, 2011)。

β 多样性格局反映群落间物种组成的变化情况(Anderson *et al.*, 2011; Legendre & de Cáceres, 2013), 揭示 β 多样性格局与空间距离和环境异质性之间的关系可衡量生态位理论和中性理论对群落构建过程的相对重要性(Condit *et al.*, 2002; Kraft *et al.*, 2011)。若 β 多样性格局主要受环境过滤影响, 则环境变量对样地间物种组成变化的解释率将最高(Petermann *et al.*, 2015; Jamoneau *et al.*, 2018)。若中性理论占主导地位, 则扩散限制是 β 多样性格局的主要影响因素, 植物种子的拓殖速率与地理距离之间将呈负相关关系。换言之, 地理距离或者空间属性(如采样粒度、研究范围等)将在群落构建过程中扮演更为重要的角色(Seidler & Plotkin, 2006; Page & Shanker, 2018)。

量化确定性和随机过程对群落构建的相对重要性, 可综合考虑空间因子、环境条件以及物种本身

的功能属性差异等因素(Condit & Hubbell, 2002), 通过变差分解法分解群落间 β 多样性的差异进行分析(Legendre *et al.*, 2009; Burrascano *et al.*, 2011; Myers *et al.*, 2013)。Gibson等(2017)在澳大利亚西南部沙地平原的研究中指出, 模型所选变量(气候、土壤和空间变量)共可解释群落物种组成变化的87%, 变差分解的结果表明空间和气候因子解释了绝大部分变化。除了变差分解, 相似性随距离的衰减斜率也是研究群落构建机制的常用方法(Anderson *et al.*, 2011; Siefert *et al.*, 2013)。Tang等(2013)在中国北方主要草原群落的研究表明, 控制环境“空间自相关”的影响后, 群落物种组成相似性随地理距离和环境差异的增大而减小。

黄土高原地区是我国当前主要造林并大量栽植抚育人工林的区域(Fu *et al.*, 2011)。相比于生物热点区, 在环境条件相对恶劣的黄土高原进行群落构建机制的研究相对较少(王丹等, 2013)。该地区现有的经验案例显示, 确定性和随机性过程对群落构建的作用受不同研究对象和研究尺度的影响。王丹等(2013)以黄土高原子午岭地区的草地植物群落为对象, 研究表明确定性过程和随机过程均在群落构建过程中发挥了作用, 但随机过程扮演了更为重要的角色。而王世雄等(2016)对黄土高原油松(*Pinus tabulaeformis*)林群落异质性进行分析后得出, 生境异质性与群落异质性呈现极显著的线性关系, 即认为生态位理论是该区群落构建的主导机制。但已有研究多为集中在某一生境(如马栏林区)的小尺度研究, 对于区域尺度的关注稍显不足。而确定性过程和随机过程对物种组成变化的相对重要性具有尺度效应(Chase, 2014), 并且不同植被类型对于环境和空间因子的响应不同(Tuomisto *et al.*, 2017)。因此, 有必要在区域尺度上探索黄土高原地区的群落构建过程。

林下草本层是森林生态系统的重要组成部分 (Gilliam, 2007), 在森林生态系统中往往占有最高比例的物种多样性(占据森林物种丰富度的90%以上) (Gilliam *et al.*, 2006), 其不仅能促进森林生态系统养分循环, 稳定林分生产力 (Sabatini *et al.*, 2014; Márialigeti *et al.*, 2016), 还能通过与乔木幼苗之间的资源竞争影响乔木种苗的存活、发育与生长 (George & Bazzaz, 2014)。然而, 相比于乔木层物种多样性, 草本层物种多样性尚未引起广泛关注 (尤业明等, 2016)。鉴于黄土高原的特殊性以及林下草本层的重要性, 本研究拟探究以下两个科学问题: (1)黄土高原地区人工林下草本群落 β 多样性呈怎样的格局? (2)环境过滤和扩散限制对人工林下草本群落构建的相对重要性如何?

1 材料和方法

1.1 研究区概况

地处黄土高原腹地的研究区(34.47°–39.32° N, 107.57°–111.53° E), 面积约 $1.0 \times 10^5 \text{ km}^2$, 最高海拔约2 000 m, 最低海拔约800 m。该区气候具有典型的温带大陆性季风气候特征, 年平均气温3.6–14.3 °C, 年降水量150–750 mm, 且降水主要发生在6–9月。降水最丰富的东南部地区年降水量为600–750 mm, 而西部和西北部仅150–250 mm, 呈现出

从东南向西北显著降低的水分梯度。研究区由暖温带向温带过渡, 植被带跨越了落叶阔叶林带、森林草原带和草原带等(孙龙等, 2016)。

本区域因黄土的自然属性以及历史上强烈的人类活动导致水土流失严重, 因而自20世纪60–70年代起, 广泛开展了人工栽植或飞机播种结合人工抚育管理的造林工程(Xiao, 2014), 造林栽植的树种依局地生境分异特征主要有: 油松、刺槐(*Robinia pseudoacacia*)、小叶杨(*Populus simonii*)等。其林下原生灌木主要有沙棘(*Hippophae rhamnoides*)、柠条锦鸡儿(*Caragana korshinskii*)、黄刺玫(*Rosa xanthina*)等; 成林后的林下, 草本层主要有臭草(*Melica scabrosa*)、赖草(*Leymus secalinus*)、长芒草(*Stipa bungeana*)、蒿类(*Artemisia* spp.)等。

1.2 样地设置及数据预处理

于2014–2016年7–8月, 采用样地系统取样方法, 在研究区沿水分梯度布设样地107个(图1)。其中79个为刺槐林, 19个为小叶杨林, 9个为山杨林。在每个样地内每隔50 m设置3个10 m × 10 m的样方。记录样方内胸径 $\geq 3 \text{ cm}$ 的乔木种名、胸径、高度及枝下高, 估算乔木层盖度。利用胸径计算每木胸高断面积, 按样方累加后得到胸高断面积和; 通过计算每木树高与枝下高的平均差估算样地的冠层厚度。在样方四角设置1 m × 1 m草本层样方, 记录其内物种

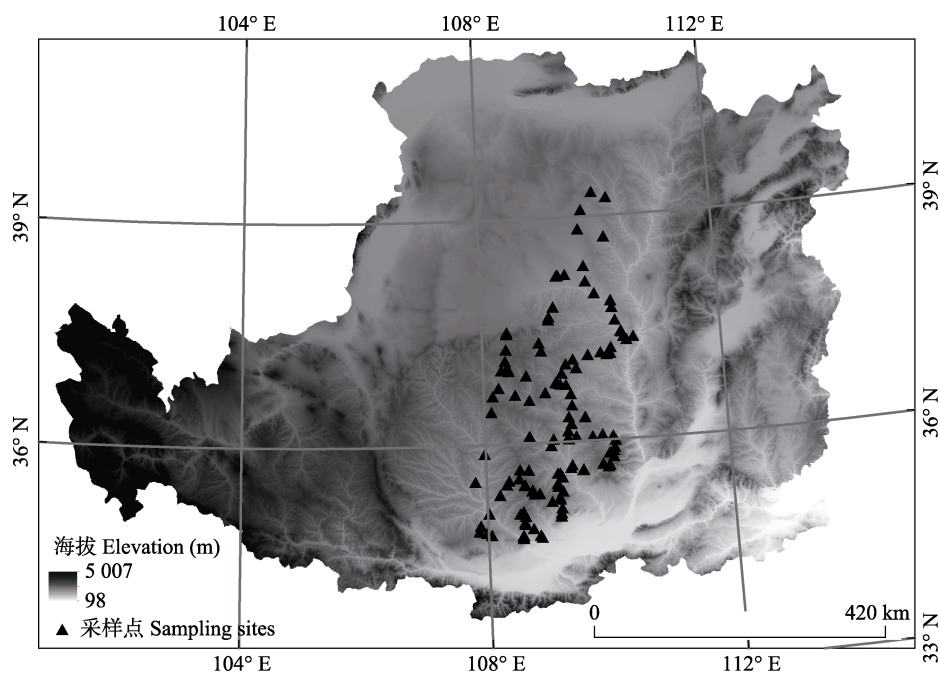


图1 黄土高原研究区概况及调查样地分布。

Fig. 1 Sketch map for the central Loess Plateau, showing the location for 107 sampling sites.

名称、盖度和高度。采用手持GPS仪记录样地的地理信息(经纬度、海拔),使用罗盘测量坡度、坡向。最后,将3个样方各个变量取均值用于后续的样地数据分析。

将0°–360°的方位角按照余弦公式转化为0–1的坡向指数 $TRASP$,以反映生境的干湿状况, $TRASP$ 值越大表示生境越干热(刘秋锋等,2006),计算公式如下:

$$TRASP = \frac{1 - \cos((\pi/180)(aspect - 30))}{2} \quad (1)$$

式中, $TRASP$ 为转换后的坡向指数, $aspect$ 为坡向的角度数值。

气候数据来源于WorldClim数据库(2.0版, <http://www.worldclim.org/>, 分辨率1 km × 1 km)。利用ArcGIS10.2软件,提取黄土高原地区各样地相应经纬度坐标处的年平均气温和年降水量数据。

1.3 数据分析

1.3.1 β 多样性与距离矩阵计算

采用目前衡量 β 多样性常用的相似性或相异性指数度量群落物种组成变化,本研究选取基于有无二元数据的Simpson相异指数(β_{sim})计算配对样地间物种组成的差异(Baselga, 2010),具体公式如下:

$$\beta_{sim} = \min(b, c) / [(\min(b, c) + a)] \quad (2)$$

其中, b 和 c 为两样地的独有种, a 为两样地共有种。 β_{sim} 的范围为0–1,分别代表两配对样地间物种组成的最大相似度和最小相似度。

计算107个样地所有配对样地即5 671对样地间物种组成变化,在等距离投影下基于各样方的经纬度计算得到样地间地理距离矩阵。为了度量群落间生境异质性的变化,本研究选取气候因子(年平均气温、年降水量)、生物因子(胸高断面积和、乔木高、冠层厚度、乔木层盖度、草本层盖度及草本层高度)以及生境因子(海拔、坡度和坡向)等构建环境距离矩阵。为消除变量间因量纲差异引起的环境分异对测量结果造成的潜在影响,将上述环境变量进行标准化(平均值为0,标准差为1),然后将该11个变量分别转换为欧式距离矩阵。样地间物种组成变化作为响应变量矩阵,地理距离矩阵和环境距离矩阵作为解释变量矩阵。

1.3.2 统计分析

运用随机森林模型(RF)评估上述各因子对群落物种组成的相对重要性(以节点纯度的增加表示)。

随机森林模型除了可以在一定程度上忽略解释变量间的空间自相关问题(Marmion *et al.*, 2009),还可以处理群落物种组成与解释变量的非线性关系(Breiman, 2001)。由于群落 β 多样性的样对数据之间不独立,采用置换检验(999次)对基于距离矩阵的多元回归(MRM)(Legendre *et al.*, 1994)系数进行检验。再由基于距离的冗余分析法(db-RDA)(Legendre & Anderson, 1999),用向前选择筛选出显著的环境变量。通过邻体主坐标矩阵(PCNM)(Borcard & Legendre, 2002)筛选显著的空间结构,最后基于筛选出的环境变量和PCNM特征向量进行变差分解,以将物种组成变化分解为以下3个部分:(1)环境独立解释量(Env);(2)空间独立解释量(Geo);(3)环境和空间的联合解释量($Env-Geo$)。

上述分析由R 3.3.3软件完成,样方间距离矩阵计算、 β 多样性计算以及RF分别由“fossil”(Vavrek, 2012)、“ecodist”(Goslee *et al.*, 2007)和“randomForest”(Ehrlinger, 2015)程序包实现,MRM模型、db-RDA分析以及PCNM建模则由“vegan”程序包实现(Dixon, 2003)。

2 结果

2.1 地理距离和环境差异与群落构建的相关性

回归分析结果显示, β 多样性与地理距离与环境差异均呈极显著的正相关关系($p < 0.001$,图2B),表明 β 多样性随地理距离和环境差异的增大而增大,且 β 多样性随地理距离的变化速率略大于其随环境差异性的变化速率(地理距离 $r = 0.518$ > 环境差异 $r = 0.504$,图2B)。这也就意味着地理距离和环境差异越大,样地间物种组成相似性越小。

2.2 地理距离和环境因子对群落构建的解释量

RF和MRM模型的结果显示,除乔木冠层高度和草本层盖度外,其余变量均对物种组成有显著影响(图2A1、2A2)。对样地间物种组成变化解释率最高的变量是地理距离,其次为气候因子中的年降水量、年平均气温以及生物因子中的胸高断面积和。坡度、坡向以及乔木层密度的影响相对较小。

2.3 地理距离和环境差异对群落构建的相对重要性

根据变差分解结果,全部环境因子和空间因子共同解释了物种组成变化的47.8%(表1),空间距离和环境差异的独立解释率分别为14.1%和9.8%,两者联合解释率为23.9%。地理距离的独立解释率略

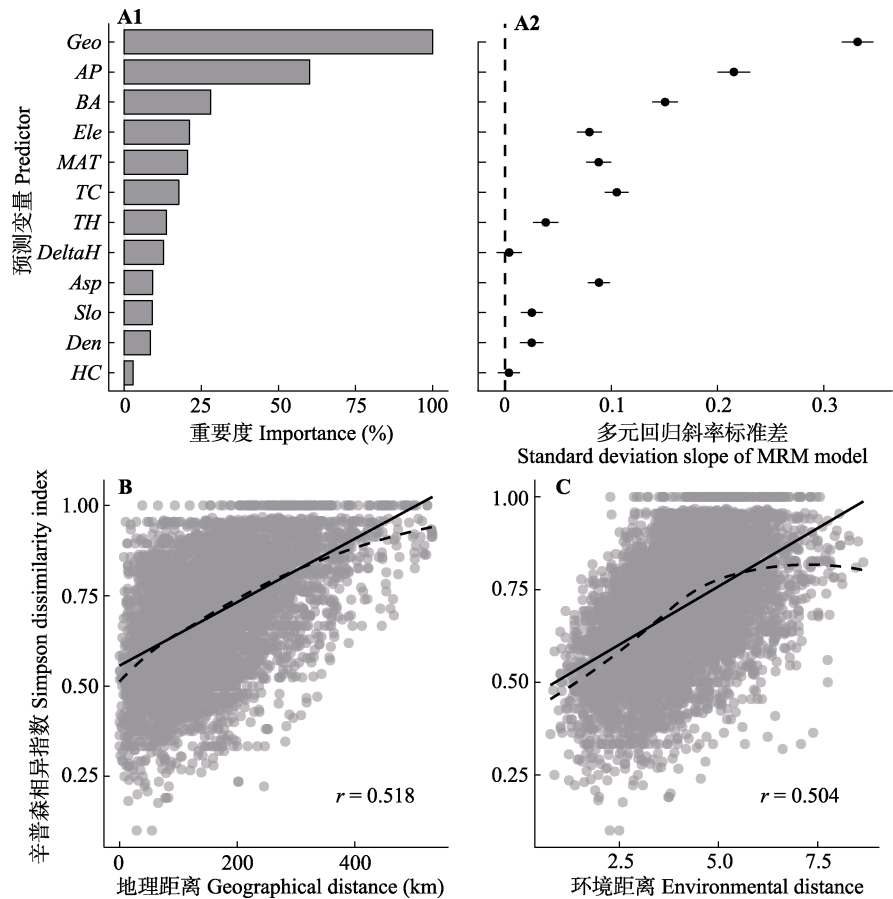


图2 随机森林模型(RF)和基于距离矩阵的多元回归方法(MRM)结果。A1, A2, 分别为生态因子的重要性大小及显著性检验的结果。B, β 多样性与地理距离的关系。C, β 多样性与环境距离的关系。AP, 年降水量; Asp, 坡向; BA, 胸高断面积和; Den, 立木密度; DeltaH, 冠层厚度; Ele, 海拔; Geo, 地理距离; HC, 草本层盖度; MAT, 年均气温; Slo, 坡度; TC, 乔木层盖度; TH, 乔木高。虚线为Lowess拟合线, 实线为线性拟合回归线。

Fig. 2 Results of random forest (RF) model and multiple regression method (MRM) based on distance matrices. The importance of the ecological factors and the test results of significance are shown in A1 and A2, respectively; B and C respectively shows the relationship between dissimilarity of species composition with increasing geographical and environmental distance. AP, annual precipitation; Asp, aspect; BA, basal area; Den, density; DeltaH, delta height; Ele, elevation; Geo, geographical distance; HC, herbaceous coverage; MAT, mean annual temperature; Slo, slope; TC, tree coverage; TH, tree height. Dashed line represents Lowess line, solid for linear fitted regression line.

表1 黄土高原腹地人工林下草本群落物种组成变差分解结果(%)

Table 1 Results of variation partitioning of understory species composition of the planted forests in the central Loess Plateau (%)

分解部分 Partitioned parts	分解结果 Value of each part
纯环境因子解释部分 Pure interpretation of environmental variables	9.8
纯空间因子解释部分 Pure interpretation of geographic variables	14.1
联合解释部分 Joint interpretation	23.9
未解释部分 Unexplained part	52.2

大于环境差异的独立解释率, 两者的独立解释率则均小于联合解释率, 模型残差为52.2%。

3 讨论

3.1 β 多样性与扩散距离的关系

地理距离对林下草本层物种组成变化的独立解释率为14.1%, 这为中性理论在研究区的应用提供了依据。随着地理距离的增加, 群落 β 多样性表现为

明显的上升趋势(图2B), 表明扩散限制确实是黄土高原地区林下草本群落构建过程中的限制因子之一。Neil Gibson等(2017)对澳大利亚西南部沙地平原的物种周转进行研究后也提出物种周转与地理距离相关, 即认为扩散限制是影响物种周转的重要驱动因子。一方面, 黄土高原沟壑纵横的地貌在一定程度上阻碍了植物种子的传播(Saura & Pascual-Hortal, 2007; Urban *et al.*, 2009), 但是扩散能力强的

种子能够扩散到更远的生境中,这进一步体现扩散限制对群落物种组成的影响。地理距离对研究区林下草本群落 β 多样性空间格局形成的重要性也可能是因为扩散能力的差异性在一定程度上可以缓解种间竞争(Mouquet & Loreau, 2003),从而改变群落的物种组成。另一方面,由于黄土高原环境恶劣,生态脆弱,水热条件较差,因而演替时间较短的人工林下较难形成良好的枯枝落叶层,一些植物种子的传播者无法在此生境中存活,进而影响到依靠动物传播的草本植物的扩散速率(Qian, 2009)。

3.2 β 多样性与环境因子的关系

纯环境变量的独立解释率为9.8%,通过RF和MRM分析,进一步发现环境因子中年降水量与胸高断面积和对物种组成变化的影响最大。首先,研究选取的人工林下草本群落位于半湿润-半干旱区的黄土高原,对于该区的草本物种而言,水分是其一大胁迫因子,因此该区物种多样性通常与降水显著相关(Wright *et al.*, 1993)。其次,研究区各样地间年降水量差异较大。而由降水梯度驱动形成的物种组成变化格局也已被证实,Toledo等(2011)在新热带区(Neotropics)的研究以及Réjou-Méchain等(2008)在非洲热带森林的研究均表明群落物种组成受降水梯度的影响。但不同于先前的研究,气候因子中的年平均气温在本区域中发挥的作用相对较小,研究对象不同可能是造成这一差异的主要原因。上述研究多关注于木本植物,而本研究则主要着眼于林下草本植物。上层植被可以发挥缓冲作用,如吸收一定的太阳辐射和削弱风对林下草本层的影响(Liu *et al.*, 2015),从而减少温度变化对林下物种组成的作用。第三,胸高断面积变量在一定程度上能够反映林分的冠层结构特征(尤业明等, 2016),而冠层结构能够影响林分内土壤水分、光照环境以及温湿度等微生境条件的变化(van Oijen *et al.*, 2005),这进一步影响了林下草本物种组成。Ihaddaden等(2013)在阿尔及利亚北部干旱区以及余敏等(2013)在山西小蛇沟的研究也表明冠层结构对林下草本群落物种组成具有重要影响。

3.3 环境过滤和地理距离对群落构建的相对重要性

β 多样性随地理距离的衰减为中性过程在群落物种组成过程中发挥的作用提供了证据,而其与环境距离的衰减关系也说明环境因素如年降水量、乔木胸高断面积、年平均气温等也会影响群落的物种

组成。并且,地理距离与环境因子的联合解释率大于二者的独立解释率,这表明生态位过程(确定性过程)和中性过程(随机过程)共同作用于黄土高原区林下草本层群落构建过程,这与较多的前人研究结果(卢品等, 2013; 谭珊珊等, 2013)相一致。

本研究结果显示,相比于纯环境因子,群落间物种组成相似性变化更多地被空间因子所解释(表1),这可能是因为随机过程和确定过程的相对作用大小具有尺度效应(Chase, 2014; Tan *et al.*, 2017)。研究尺度越大,环境异质性越高,环境因子对群落物种组成的过滤作用越明显(Viana *et al.*, 2016)。反之,则随机过程的作用更为重要。如Jones等(2016)对澳大利亚西南部植物区系、Tang等(2013)对中国三大主要草原群落物种周转格局的大尺度研究结果均表明环境过滤发挥了更为重要的作用。而Chust等(2006)对巴拿马热带森林乔木 β 多样性格局以及王丹等(2013)对子午岭草地群落的小尺度研究则表明地理距离在群落构建过程中占主导地位。与上述小尺度研究相比,虽然本研究区域南北跨度约达509 km,东西距离约为200 km,但可能由于黄土高原区相对均质的气候和土壤等环境条件使得研究区仍然没有包含足够的环境差异。因而即使研究区资源相对贫乏,水热条件较为严苛,样地间的相似生境依然减弱了环境过滤对物种周转的作用(Chase, 2014)。与Bohlman等(2018)在亚马孙地区的研究得出的结论相似。

从生活型的角度看,与乔木相比,林下草本植物受气候,尤其是受冬季低温的限制较小(Donoghue, 2008)。这可能是因为,草本植物尤其是一年生草本植物,生活史周期较短,这有利于其躲避极端气候或干旱的胁迫。而当气候条件适宜时,草本植物也许可以从地下种库中迅速重建其种群(Grime, 1977)。因而,水热条件对林下草本的限制作用相对较小。另一方面,草本植物倾向于产生质量较小,利于风媒传播的种子(赵鸣飞等, 2017),这些策略均有助于草本植物扩散到适宜其生存的生境中。理论上,草本植物受扩散能力限制的可能性较小。但可能由于黄土高原地区沟壑纵横,破碎化程度较高,特殊的生境条件限制了该区林下草本植物的扩散距离。除此之外,某些环境因子(如年降水量、年平均气温)的空间变化特征也可能会增加空间因子的解释率

(Page & Shanker, 2018)。

草本植物对气候等环境条件相对较低的依赖性以及较强的扩散能力可能也解释了模型中环境因子和空间因子对林下草本群落 β 多样性的解释率较低的原因。除此之外,模型的较大残差(52.2%,表1)还可能是受此次研究中尚未测量因子的影响。例如,人为干扰以及土地利用方式等因子(Page & Shanker, 2018);再如,土壤类型、土壤元素、土壤湿度等因子也可能影响草本植物的定殖(Jones *et al.*, 2008)。但也有研究认为,黄土高原的土壤类型较为单一,土壤类型作为环境过滤的影响较小(王丹等, 2013)。

4 结论

研究通过揭示黄土高原人工林下草本层植物群落 β 多样性格局与空间距离和环境异质性之间的关系,为生态位理论和中性理论在群落构建过程中的相对重要性提供了依据。研究表明,以扩散限制为代表的中性过程和以环境过滤为代表的生态位过程对群落构建均起着重要作用。RF和MRM分析的结果则进一步表明环境过滤主要通过年降水量与胸高断面积和发挥作用。我们的模型解释了50%左右的物种组成变化,未解释的部分可能是 β 多样性还受我们在此次研究中尚未考虑的人为干扰以及其他尚未测量的环境和空间变量等因素的影响。另外,不可忽略的是环境因子具有空间自相关性,因此可能未被测量的生境因子增大了地理距离对本研究的解释率,这一问题将在以后的研究中作进一步的研究证明。

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