

中国中亚热带北部灌丛群落植物空间周转及其驱动因素

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摘要 环境因子是驱动物种空间周转的重要因素, 灌丛作为亚热带地区重要的植被类型, 探究其群落的物种空间周转格局及其驱动因素, 能够为区域生物多样性保护提供科学依据。该研究以中国中亚热带北部灌丛群落为研究对象, 采用广义相异性模型, 以Bray-Curtis相异性指数为指标, 分析了气候、土壤、地形、人为干扰等因素对灌丛群落物种周转的驱动效应。结果表明, 气候因子对物种周转影响显著, 且随着海拔、坡度、土壤总氮含量、国内生产总值的增加, 物种周转速率显著增加, 而年平均气温和距道路距离对物种周转无显著影响。在过酸过碱的土壤中, 物种周转速率较低, 在pH = 5时, 物种周转速率达到最大值。气候、土壤、地形、人为干扰等因素可以解释灌丛植物群落物种周转的33.55%。其中, 土壤因素的解釋率为26.54%, 而气候和地形、人为干扰因素分别解释了13.39%和3.17%, 土壤pH的相对贡献率(37.28%)最大。综上所述, 环境因子对中国中亚热带北部灌丛群落的物种空间周转过程有重要作用, 其中土壤因子为驱动物种周转的关键因素。

关键词 环境异质性; 灌丛; 物种周转; 广义相异性模型

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Spatial turnover of shrubland communities and underlying factors in northern mid-subtropical China

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Abstract

Aims Environmental factors are among the key factors governing the community species spatial turnover. As one of the widely distributed vegetation types in subtropical region of China, it is important to understand the species composition differences among shrubland communities, which will provide important information for protecting biodiversity and eco-security shield construction in the northern mid-subtropical region, China. However, little is known about which factors drive the species spatial turnover in subtropical region of China. The objectives of this study were to investigate the shrubland community spatial turnover pattern and to determine the key factors that shape the present distribution of species based on the field-based data in northern mid-subtropical China.

Methods Based on the field-based data in mid-subtropical shrublands, we used the generalized dissimilarity modelling (GDM) by the Bray-Curtis dissimilarity index to explore the driving effects of climate, soil, topography, and human disturbance on species turnover of the shrubland communities in northern mid-subtropical China.

Important findings The results showed that climatic factors had significant effects on plant species turnover of the shrubland communities in northern mid-subtropical China. With the increase of altitude, slope, soil total nitrogen content and gross domestic product (GDP), species turnover rate increased significantly. Mean annual air temperature and the distance to road had no significant effects on species turnover. The species turnover rate decreased when soil pH became too acidic or too alkaline, and the rate reached the maximum value when pH was

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5. Climate, soil, topography, and human disturbance explained 33.55% of the species turnover deviances, of which, soil accounted for 26.54% of the GDM deviances, while climate and topography, human disturbance accounted for 13.39% and 3.17% of the GDM deviances, respectively. Soil pH contributed 37.28% of the deviances to the species turnover of shrubland community. In conclusion, environmental factors (especially soil pH) were the major drivers of the species spatial turnover in northern mid-subtropical shrubland communities.

Key words environmental heterogeneity; shrubland; species turnover; generalized dissimilarity modelling (GDM)

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自然界群落中的生物个体在小范围内以随机、规则或聚集的模式分布, 在较大范围内, 生物个体分布呈现出聚集的特点(Levin, 1992; Molles, 2002)。物种周转是指群落中物种组成沿环境梯度的变化(Buckley & Jetz, 2008), 主要取决于环境过滤主导的生态位过程和扩散限制主导的中性过程(Legendre *et al.*, 2009; McFadden *et al.*, 2019; Muñoz Mazón *et al.*, 2021), 二者共同驱动群落物种多样性的异质和聚集分布格局(Soininen *et al.*, 2007; 陈圣宾等, 2010)。

由于环境因素的限制, 不同物种只能在一定范围内栖息生存(Daniel *et al.*, 2019)。这些环境因素通常包括温度、降水、地形、土壤理化性质和人为干扰因子(Roberts & Wuest, 1999; Chi *et al.*, 2014; Feng *et al.*, 2014)。温度和降水通过影响物种生态幅, 决定植物物种的空间分布(Chaine, 2010; Bykova & Sage, 2012; Porfirio *et al.*, 2014)。海拔直接反映地表起伏、地形等因素, 通过影响太阳辐射及降水在空间上的再分配, 影响物种的空间更替(沈泽昊, 2002)。土壤空间异质性与植物水分、养分获取直接相关, 是驱动物种周转的重要因素(Paoli *et al.*, 2006; Ulrich *et al.*, 2014)。人类活动造成的土地利用变化, 改变了物种原生生境, 抑制物种空间更替, 导致区域内生物同质化(Maestre & Cortina, 2004; 陈圣宾等, 2010)。

灌丛作为重要的陆地植被类型, 在中国广泛分布, 占中国陆地总面积的9.0% (Su *et al.*, 2020), 在维持生物多样性和缓解气候变化中发挥着不可替代的作用(Piao *et al.*, 2009; Yi *et al.*, 2021; 张蕾等, 2021)。灌丛从起源上可划分为原生灌丛和次生灌丛。其中, 原生灌丛主要为高寒灌丛和旱生灌丛(郭焱培等, 2021), 而次生灌丛主要为人类活动干扰导致的原生植被退化而形成的次生植被类型(尤誉杰等, 2018)。

我国中亚热带北部, 地处亚热带湿润气候区, 长期受人类活动干扰, 地带性常绿阔叶林大面积退化丧失, 形成了大面积的次生灌丛(杨一, 2015)。次生灌丛已成为我国中亚热带北部地区主要的植被类型(Su *et al.*, 2020)。目前, 对亚热带灌丛的研究主要集中在群落特征和物种多样性特征(张亚茹等, 2013; 刘梦等, 2017)、物种多样性影响因素(张慧等, 2017; 王飞等, 2018)等方面, 掌握了亚热带灌丛群落物种基本组成及其空间分布。但是, 灌丛物种组成在空间上的周转格局如何? 是什么因素驱动了物种周转? 到目前为止, 该方面的研究鲜有报道。本研究拟探究环境因子驱动下中亚热带北部灌丛群落物种空间周转格局, 以期为区域生物多样性保护和生态系统管理提供科学依据。

1 材料和方法

1.1 研究区概况

中亚热带北部位于25.96°–31.46° N, 106.14°–121.19° E, 包括安徽、浙江、江西、湖南、湖北、重庆等省市(图1)。属亚热带季风气候, 年平均气温16–21 °C, 最冷月平均气温5–12 °C, 最热月平均气温25–30 °C, 全年无霜期为270–300天, ≥10 °C的年积温4 000–6 500 °C, 年降水量为1 000–2 000 mm。土壤类型以红壤、黄壤为主(中国植被编辑委员会, 1980), 地带性植被为常绿阔叶林。主要灌丛类型有枹栎(*Quercus serrata*)灌丛、茅栗(*Castanea seguinii*)灌丛、杜鹃(*Rhododendron simsii*)灌丛、白栎(*Quercus fabri*)灌丛、盐肤木(*Rhus chinensis*)灌丛、黄荆(*Vitex negundo*)灌丛、檵木(*Loropetalum chinense*)灌丛、马桑(*Coriaria nepalensis*)灌丛等(中国科学院中国植被图编辑委员会, 2007)。

1.2 样地调查

1.2.1 样点布设和样方设置

依据《中国植被》关于灌丛群系种类、分布及

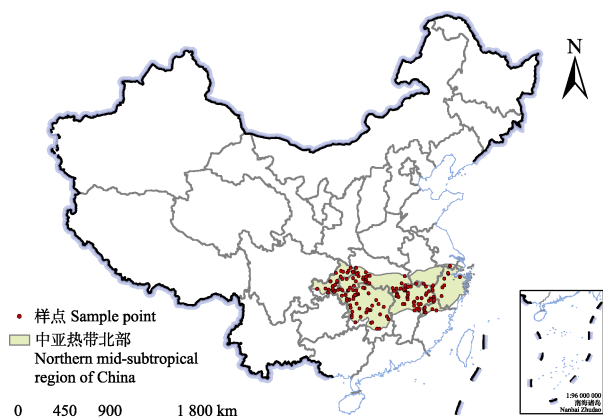


图1 中国中亚热带北部灌丛植物群落样点分布。

Fig. 1 Geographical distribution of samples of shrubland communities in northern mid-subtropical China.

面积的描述(中国植被编辑委员会, 1980), 基于中国植被区划(中国科学院中国植被图编辑委员会, 2007), 在中亚热带北部以县为单位, 布设灌丛群落样地。布设灌丛样地时, 在满足抽样调查数量和面积的基础上, 兼顾类型, 选择灌丛群落物种组成、群落结构和生境相对均匀, 且群落连片分布、斑块面积大于 $100\text{ m} \times 100\text{ m}$ 的区域, 设置3个重复样方。如果灌丛群落不连片分布, 3个样方需分开布置, 每个样方连片群落面积需大于 $25\text{ m} \times 25\text{ m}$, 且3个样方的分布距离不超过 250 m , 并保证样地四周有 10 m 以上的缓冲区。本研究共调查200个样地(图1)。每个样地沿对角线设置3个 $5\text{ m} \times 5\text{ m}$ 的样方。3个样方边缘两两之间最小距离为 5 m , 最大距离不超过 50 m , 每个样方内沿对角线布置3个 $1\text{ m} \times 1\text{ m}$ 小样方, 进行草本层植物群落调查。

1.2.2 灌丛群落调查

本研究于2017年6月至2019年11月开展, 按灌木层、草本层分层完成群落样方调查。记录 $5\text{ m} \times 5\text{ m}$ 灌木层样方内每株灌木种名、高度、基围(离地表 3 cm)、冠幅(长短轴)、物候期。同时, 记录 $1\text{ m} \times 1\text{ m}$ 草本层小样方全部草本植物种名、平均高度、盖度。

1.2.3 土壤取样及测试

在 $5\text{ m} \times 5\text{ m}$ 样方对角线, 选择3个土壤采样点, 去除未分解及半分解凋落物层, 采集 $0\text{--}20\text{ cm}$ 土壤样品, 混合装入自封袋或布口袋, 带回实验室进行土壤理化性质分析。采用电位法(LY/T 1239—1999)测定土壤pH, 采用重铬酸钾氧化-外加热法(LY/T 1237—1999)测定土壤有机碳含量, 采用半微量凯氏法(LY/T 1228—2015)测定土壤氮(N)含量, 采用

酸溶法(LY/T 1232—2015)测定土壤磷(P)含量。

1.3 自然环境和人为干扰因子数据

依据灌丛群落样点地理坐标, 从全国 $\geq 0\text{ }^{\circ}\text{C}$ 积温(AAT0)、 $\geq 10\text{ }^{\circ}\text{C}$ 积温(AAT10)、年平均气温(T_a)、年降水量(P_a)和湿润指数(IM)等气候栅格数据集(中国科学院资源环境科学与数据中心, <https://www.resdc.cn/Default.aspx>)提取 $\geq 0\text{ }^{\circ}\text{C}$ 积温、 $\geq 10\text{ }^{\circ}\text{C}$ 积温、年平均气温、年降水量和湿润指数等灌丛群落样点气候数据。该数据基于全国1915个站点气象数据, 利用反向距离加权平均法内插出全国气象空间分布数据集, 分辨率为 $500\text{ m} \times 500\text{ m}$ 。

从中国国内生产总值(GDP)空间分布和人口空间(POP)分布千米网格数据集(中国科学院资源环境科学与数据中心, <https://www.resdc.cn/Default.aspx>)提取每个灌丛群落样点的国内生产总值、人口密度。该数据利用多因子权重分配法, 将以行政区为基本统计单元的数据展布到栅格单元上, 从而实现数据的空间化。基于2018年土地利用数据、道路数据以及2000年居民点空间分布数据, 通过ArcGIS 10.2空间分析欧氏距离模块, 计算灌丛植物群落样方调查点距最近道路或居民点的欧氏距离, 即为样点距道路或居民点的最近距离(Haddad *et al.*, 2015; Zang *et al.*, 2020)。海拔、坡度、坡向等地形数据由样点所在地实测得到。

1.4 数据处理与统计分析

1.4.1 样地环境因子的描述性统计

使用R 4.2.1软件对样地环境因子进行描述性统计, 通过Pearson相关系数评估各个环境因子间的相关关系。

1.4.2 广义相异性模型(GDM)分析

使用Bray-Curtis相异性指数, 计算样点间群落成分的相异性(d_{ij}), 代表物种空间周转差异(Koleff *et al.*, 2003)。

$$d_{ij} = 1 - \frac{2A}{2A + B + C} \quad (1)$$

式中, A表示样点*i*和样点*j*所共有的物种数, B表示样点*i*独有的物种数, C表示样点*j*独有的物种数。

本研究采用GDM, 以样点间的所有物种Bray-Curtis相异性指数作为响应变量, 以样点间样条函数(I-spline)变换的环境因素、地理距离变量差值作为预测变量, 使用指数函数连接响应变量和预测变量, 变换结构后得(Ferrier *et al.*, 2007; Overton

et al., 2009):

$$-\ln(1 - d_{ij}) = b + \sum_{k=1}^P |f_k(x_{ki}) - f_k(x_{kj})| \quad (2)$$

式中, 截距 b 是一个常数, k 为预测变量, P 为预测变量的数量, x_{ki} 和 x_{kj} 分别表示样点 i 、 j 的 k 变量的实际观测值。函数 f_k 通过变换对每个预测变量的拟合方式, 以满足随着地理距离的增加, 群落物种相异性越大的特点(Poulin, 2003)。

将基于群落调查的物种数据与年平均气温、年降水量、地形、土壤等环境数据, 以及国内生产总值、人口分布情况、距道路距离(d_{Road})、距居民点距离(d_{Respt})等干扰数据, 代入GDM, 计算各因子对物种空间相异性的影响效应。采用偏回归方法, 绘制偏响应图, 区分以上因素对物种更替的单独或共同影响, 偏响应图中的曲线形状变化可指示不同梯度下预测变量对 β 多样性的影响, 斜率越大, 表明预测变量在此梯度上每单位变化差异越大, 物种更替速率越快(Mokany et al., 2022)。GDM在运行过程中会自动剔除对物种周转没有显著影响的预测变量(Ashcroft et al., 2010), 此时将不再有偏响应图输出(戴美霞等, 2017)。使用基于矩阵置换的gdm::varImp方法(Mokany et al., 2022), 检测预测变量的相对重要性, 预测变量的重要性被量化为置换变量与未置换之间解释的偏差变化百分比, 以上分析均在R 4.2.1软件中完成。

2 结果

2.1 地形差异与灌丛植物群落物种空间更替

地形差异对中亚热带北部灌丛植物群落物种相异性有显著影响。海拔表现出强变异(变异系数(CV) = 128.16)(表1), 海拔0–500 m范围内, 灌丛群落物种相似性高。海拔>500 m时, 灌丛群落间物种相异性随着海拔增大而显著增加(图2A)。随着坡度的增加, 群落间的物种相异性逐渐降低(图2B)。当坡度>40°时, 物种周转速率增快。相较于坡向(0.15%), 坡度(6.54%)对物种周转的影响更大。

2.2 气候分异与灌丛植物群落物种空间更替

≥ 0 °C积温、湿润指数分异对灌丛植物群落物种相异性影响显著(图2D、2F)。当 ≥ 10 °C积温>5 300 °C以及年降水量>1 460 mm时, ≥ 10 °C积温和年降水量对灌丛群落物种更替产生显著影响(图2E、2G)。 ≥ 10 °C积温达到6 000 °C左右时, 物种周转速率最大。

2.3 土壤理化性质分异与灌丛植物群落物种空间更替

土壤有机碳含量、土壤总氮含量及土壤pH分异均对灌丛植物群落物种相异性呈现出显著影响效应。其中, 随着土壤有机碳含量增加, 群落间物种差异性逐渐减小(图2H)。当土壤总氮含量<1 mg·g⁻¹时, 物种周转速率减缓, 群落物种相似性高, 超过此阈值后, 物种周转速率开始加快(图2I)。以土壤pH为7

表1 中国中亚热带北部灌丛样地环境因子的描述性统计

Table 1 Descriptive statistics of environmental factors in the plots of shrubland communities in northern mid-subtropical China

环境因子 Environmental variable	简写 Abbreviation	平均值±标准误 Mean ± SE	最小值 Minimum	最大值 Maximum	变异系数 CV (%)
≥ 0 °C积温 Accumulated temperature (≥ 0 °C) (°C)	AAT0	5 725.40 ± 54.49	2 045.40	6 715.90	13.46
≥ 10 °C积温 Accumulated temperature (≥ 10 °C) (°C)	AAT10	5 100.49 ± 55.66	1 216.10	5 947.00	15.43
年平均气温 Mean annual air temperature (°C)	T _a	15.65 ± 0.16	3.80	18.40	14.38
年降水量 Mean annual precipitation (mm)	P _a	1 467.53 ± 15.78	1 047.50	1 892.90	15.21
湿润指数 Moisture index	IM	67.28 ± 1.89	14.85	174.01	39.70
海拔 Altitude (m)	Alt	258.98 ± 1.95	7.00	2 818.00	128.16
坡度 Slope (°)	Slope	27.32 ± 1.03	0.00	80.00	53.18
坡向 Aspect (°)	Aspect	159.91 ± 7.51	0.00	351.00	66.42
土壤有机碳含量 Soil organic carbon content (mg·g ⁻¹)	SOC	13.99 ± 1.41	0.00	118.55	142.46
土壤总氮含量 Soil total nitrogen content (mg·g ⁻¹)	TN	1.35 ± 0.10	0.09	9.07	100.74
土壤总磷含量 Soil total phosphorus content (mg·g ⁻¹)	TP	0.59 ± 0.03	0.09	3.34	74.57
土壤pH Soil pH	pH	5.84 ± 0.11	3.87	9.34	27.05
国内生产总值(10 ⁴ 元·km ⁻²) Gross domestic product (10 ⁴ yuan·km ⁻²)	GDP	1 130.89 ± 135.31	60.00	21 627.00	169.21
人口空间分布(人·km ⁻²) Population spatial distribution (person·km ⁻²)	POP	261.14 ± 15.34	22.30	2 048.36	83.09
到居民点的距离 Distance to resident (m)	d_{Respt}	630.39 ± 58.72	0.00	3 727.12	131.74
到道路的距离 Distance to road (m)	d_{Road}	153.86 ± 45.20	0.00	2 797.37	415.54

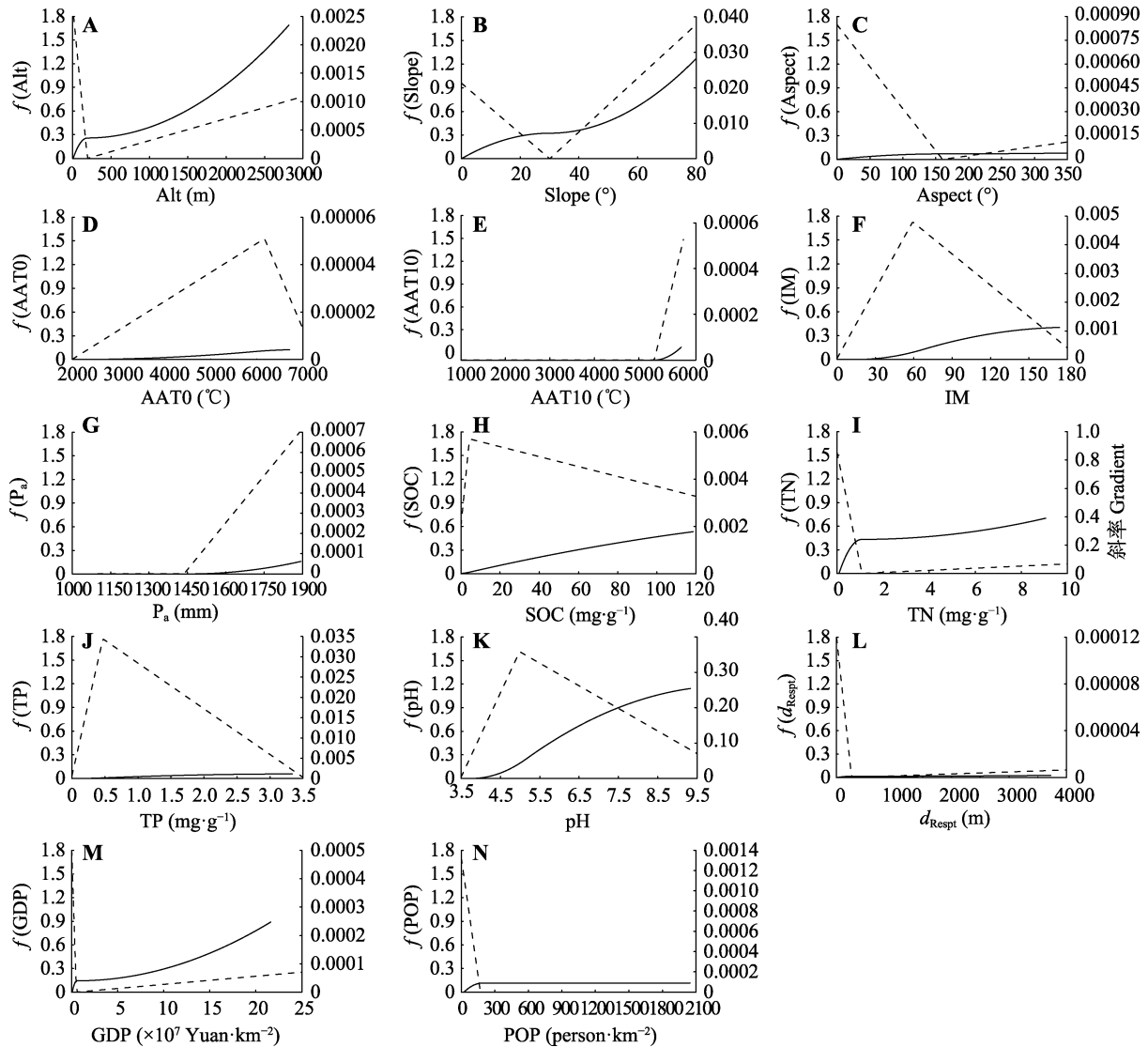


图2 中国中亚热带北部灌丛地形变量(A-C)、气候分异(D-G)、土壤理化性质(H-K)、人为干扰(L-N)与植物群落 β 多样性的关系。AAT0, ≥ 0 °C积温; AAT10, ≥ 10 °C积温; Alt, 海拔; Aspect, 坡向; d_{Respt} , 距居民点的距离; GDP, 国内生产总值; IM, 湿润指数; P_a , 年降水量; POP, 人口空间分布; Slope, 坡度; SOC, 土壤有机碳含量; TN, 土壤总氮含量; TP, 土壤总磷含量。实线为偏响应曲线, 虚线为偏响应曲线的变化斜率, y轴 f (变量)指示I-spline转换函数, 单位为群落相异性连接单位 $-\ln(1 - d_{ij})$, 其中 d_{ij} 指站点*i*和*j*之间的相异性。

Fig. 2 Relationship between the gradient of topographic variables (A-C), climate variables (D-G), soil physical and chemical properties (H-K), human disturbance (L-N) and β diversity of shrubland communities in northern mid-subtropical China. AAT0, accumulated temperature (≥ 0 °C); AAT10, accumulated temperature (≥ 10 °C); Alt, altitude; d_{Respt} , distance to resident; GDP, gross domestic product; IM, moisture index; P_a , mean annual precipitation; POP, population spatial distribution; SOC, soil organic carbon content; TN, soil total nitrogen content; TP, soil total phosphorus content. Solid line is the partial response curve, and the dashed line is the change slope of the partial response curve. The function f (variable) in y axis indicated the I-spline-transformed function, and its unit was linking unit of community dissimilarity $-\ln(1 - d_{ij})$, d_{ij} represents the dissimilarity between sites i and j .

(土壤呈中性)作为基准, 随着土壤酸碱性增强, 群落间物种相异性逐渐降低, 当 $pH = 5$ 时, 物种周转速率最大(图2K)。土壤总磷含量变化对灌丛植物物种更替影响相对较小(图2J)。

2.4 干扰因素与灌丛植物群落物种空间更替

GDP对灌丛植物群落物种相异性有显著影响, 随着GDP增加, 物种更替速率加快(图2M)。灌丛植

物群落间物种相异性随人口密度和距居民点距离变异的增大而降低。当 $d_{Respt} > 750$ m和 $POP > 200$ 人 $\cdot km^{-2}$ 时, d_{Respt} 和POP的变化不再对灌丛植物群落 β 多样性变化有显著影响(图2L、2N)。而 d_{Road} 对灌丛植物群落物种相异性无显著影响。总体上, 人类活动对物种周转影响不大, 只能单独解释3.17%, 干扰因子相对贡献由大到小依次为GDP (0.35%) >

POP (0.10%) > d_{Respt} (0.03%) > d_{Road} (0)(图3)。

2.5 环境因素和人为干扰因素对物种空间周转的解释

在16个预测变量中,共检出14个环境变量对灌丛植物群落物种空间更替变异有显著影响,其相对贡献排序如图3所示。其中,土壤pH对中亚热带北部灌丛物种空间周转的相对贡献度(37.28%)最高,而年平均气温、距离道路距离对灌丛植物群落物种空间更替变异无显著影响。GDM拟合解释了中亚热带北部灌丛植物群落物种空间更替变异的33.55%。人为干扰、气候与地形、土壤3类因素,对灌丛植物群落物种空间更替变异的解释度分别为3.17%、13.39%、26.54%(图4)。其中,土壤分异解释了灌丛植物群落物种空间更替变异的将近3成。

3 讨论

土壤作为植物主要的养分来源,为植物的生长和发育提供营养物质和水分,影响着植被群落结构与多样性特征(Xing & He, 2019; 罗巧玉等, 2021)。土壤pH通过调节土壤养分元素有效释放和转化以及根系微生物的活动,影响物种分布(Shen *et al.*, 2013; Zhang *et al.*, 2020)。Zhang等(2020)在研究中发现,土壤pH对西南草原藤本植物群落 β 多样性和功能多样性具有较大的影响。本研究发现,土壤pH显著影响物种的空间更替,当pH = 5 (弱酸性)时,群落间物种更替速率达到最大值。这可能是由于亚热带地区土壤pH多以酸性为主(占区域取样点的65%),

植被更适宜在此种土壤中生存,相较于过酸过碱的严苛土壤环境中趋于相似、单一的植被组成,物种更替速率相应加快。

土壤有机碳是微生物活动的碳源和植物可利用养分的主要来源(伍旖旎等, 2022)。本研究发现,土壤有机碳含量与土壤总氮含量显著相关($r = 0.88$, 附录)。而氮、磷是植物生长发育过程中所需的重要营养元素,土壤营养元素含量变化改变植物可利用的生态位空间,从而影响灌丛植物群落间物种相异性(Stein *et al.*, 2014)。Wang等(2015)研究发现,土壤氮含量异质性是中国东北科尔沁草原植物多样性变化的主要影响因素。Zhang等(2022)研究发现,土壤总氮含量独立解释了植物 β 多样性的16%。本研究发现土壤总氮含量显著影响灌丛物种周转,与Zhang等(2022)研究结果一致。Jones等(2016)发现土壤总磷含量对澳大利亚西南部原生植被物种周转解释度最大,但当土壤磷含量大于 $0.05 \text{ mg} \cdot \text{g}^{-1}$ 时,其对物种更替影响则不显著。本研究发现的土壤总磷含量对物种相异性几乎没有影响的结果与之相一致。本研究发现中亚热带北部土壤总磷含量平均为 $(0.59 \pm 0.03) \text{ mg} \cdot \text{g}^{-1}$ (表1),远高于 $0.05 \text{ mg} \cdot \text{g}^{-1}$,土壤总磷含量对灌丛物种更替影响相对较小。

海拔作为独特的地形因子,能反映水热条件差异和微生境的共同作用,对群落 β 多样性及物种更替具有显著影响(杨阳等, 2016; 赵鸣飞等, 2017)。Oishi (2021)在探究植物多样性与海拔变化的关系时发现,亚高山交错带的灌木、草本和苔藓植物的 β

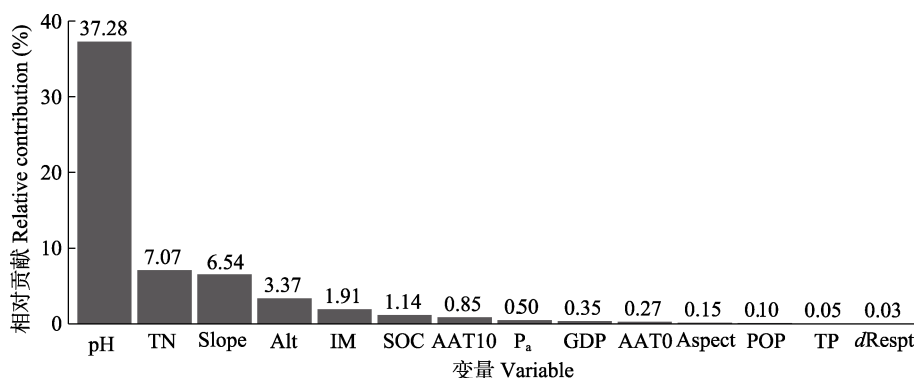


图3 预测变量对中国中亚热带北部灌丛群落间 β 多样性的相对贡献。AAT0, ≥ 0 °C积温; AAT10, ≥ 10 °C积温; Alt, 海拔; Aspect, 坡向; d_{Respt} , 距居民点的距离; GDP, 国内生产总值; IM, 湿润指数; P_a, 年降水量; POP, 人口空间分布; Slope, 坡度; SOC, 土壤有机碳含量; TN, 土壤总氮含量; TP, 土壤总磷含量。

Fig. 3 Relative contribution of predictive variables to inter-community β diversity of shrubland communities in northern mid-subtropical China. AAT0, accumulated temperature (≥ 0 °C); AAT10, accumulated temperature (≥ 10 °C); Alt, altitude; GDP, gross domestic product; IM, moisture index; P_a, mean annual precipitation; POP, population spatial distribution; d_{Respt} , distance to resident; SOC, soil organic carbon content; TN, soil total nitrogen content; TP, soil total phosphorus content.

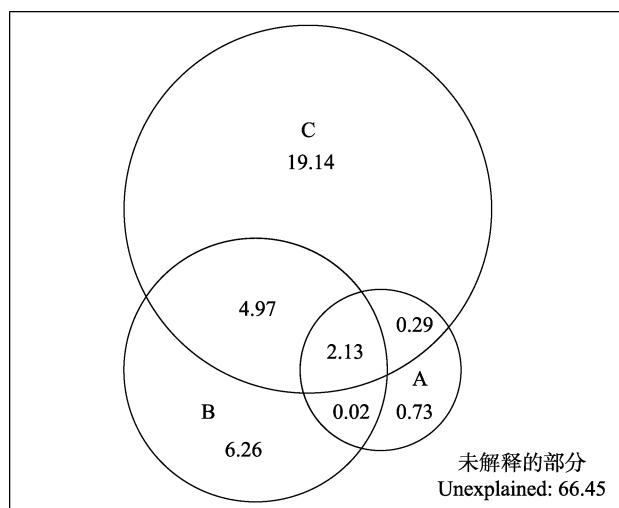


图4 人为干扰(A)、气候与地形分异(B)及土壤异质性(C)对中亚热带北部灌丛群落之间物种更替的解释度(%)。

Fig. 4 Partitional effects (%) of human disturbance (A), climate and topography difference (B) and soil difference (C) on species turnover of shrubland communities in northern mid-subtropical China.

多样性随海拔升高而增加。Sanchez-Gonzalez和Lopez-Mata (2005)在探究墨西哥内华达山脉北部环境变量与物种多样性关系时发现,物种 β 多样性沿海拔升高呈稳定增长趋势,中间海拔相邻站点间 β 多样性较低,而高海拔站点间 β 多样性较高(物种替换率接近100%)。本研究发现,随海拔升高,物种空间更替速率加快。200 m以下的低海拔地区,能够维持较高的物种更替速率,可能因为人为经济生产活动增加了生境的异质性。在200–500 m的中海拔地区,物种更替速率几乎为0,群落结构较为稳定。随海拔的增加,常绿灌丛向落叶灌丛加速更替,群落间物种相异性增加。不同坡向的光照强度与光照时间存在差异,会改变太阳辐射强度的空间分布(余丹琦等, 2022),坡度则影响土壤养分淋溶,坡度、坡向等地形因素共同影响物种多样性的格局(李添甜, 2018)。Wang等(2021)研究发现,坡度、坡向等地形因素对灌丛 β 多样性均具有较大的影响,本研究结果与之相一致。此外,本研究还发现当坡度 $>40^\circ$ 时,物种周转速率随坡度增加逐渐增快,这可能是因为坡度大的地形条件更容易受到干扰,比如土壤侵蚀或大风,通过改变资源的可利用性,导致物种周转速率加快(Chapman & McEwan, 2013)。

气候因素是决定群落间物种多样性空间格局的重要因素(dos Santos *et al.*, 2015; Hamid *et al.*,

2019)。Liu等(2015)研究发现,随着气温升高,中国温带落叶阔叶林物种 β 多样性增加。Zhang等(2014)发现草原物种 β 多样性随降水量增加而显著增加。本研究发现 $\geq 0^\circ\text{C}$ 积温、 $\geq 10^\circ\text{C}$ 积温、年降水量、湿润指数等气候因素均与灌丛群落物种相异性呈显著的相关关系,但气候因素差异对物种周转的解释度没有占主导地位,可能是因为亚热带地区并没有明显的生境限制,如湿润指数平均值为67.28,表明中亚热带北部地区为潮湿区,水热条件较为充足(李家湘等, 2017)。本研究同时发现,气候与地形因子和土壤因子交互作用,共同解释了中亚热带北部灌丛物种相异性的32.82%。这可能是因为水热要素影响土壤微生物活性,改变土壤养分状态,进而影响物种更替(Qian *et al.*, 2017)。

亚热带地区高强度的农业生产活动及经济建设,使森林遭到频繁的砍伐,土地利用类型和土地覆盖度发生了显著改变,物种生境退化或破碎化,物种丰富度下降甚至灭绝,物种相异性降低(中国植被编辑委员会, 1980; 陈圣宾等, 2010; 段语凤等, 2020)。王应刚等(2016)在探究晋中盆地人口聚集地与植物多样性关系时发现,植物 β 多样性沿着村庄-乡镇-县市梯度降低。城镇化建设会对植被群落造成人为干扰,改变原生植被生境(郭正刚等, 2004)。本研究发现,随着GDP的增加,物种周转速率加快,表明人为干扰加剧了资源的异质性,物种生境受土地利用类型的改变退化或丧失,物种适生范围缩小而面临被淘汰的风险,物种更替加快。

GDM模型的解释度范围为20%–50% (Mokany *et al.*, 2022)。姜小蕾等(2020)使用GDM模型对崂山次生林群落 β 多样性格局及其驱动因素的研究发现,11个环境变量共同解释了灌木植物 β 多样性的28.38%。本研究通过GDM模型发现,14个环境变量解释了灌丛植物群落物种周转的33.55%。季节性气候影响物候,进而决定物种的空间分布(Bykova *et al.*, 2012)。Davidar等(2007)发现,季节性气候是山地雨林树木 β 多样性的关键驱动因素。此外,生物因素,如群落内物种种间关系,也是驱动物种周转的主要因素。余丹琦等(2022)发现,灌木高度和地径大小显著影响灌木层 β 多样性。增加最暖季平均气温和降水季节性等表征季节性气候的非生物因素和生物因素等环境变量,预计可提高对灌丛群落物种周转的解释率,这也是今后研究需关注的重点。

中亚热带作为重要的植被恢复区, 探究其灌丛群落物种空间周转的驱动因素, 能为该地区生物多样性保护和恢复提供依据。本研究发现环境因子在中亚热带北部灌丛植物空间周转过程中具有重要作用, 其中土壤pH等因子是决定中亚热带北部灌丛植物群落周转的主要因素。

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附录 中国中亚热带北部灌丛群落不同环境因子之间的相关性

Supplement Correlation between different environmental factors of shrubland communities in northern mid-subtropical China

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