

青藏高原北部多年冻土区草地植物多样性

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摘要: 研究了青藏高原北部多年冻土区草地群落植物多样性的特征。研究表明: 草地群落间丰富度指数差异不显著, 均匀度指数和多样性指数差异显著($P < 0.05$)。均匀度指数表现为高山嵩草(*Kobresia pygmaea*)草甸<紫花针茅(*Stipa purpurea*)草原<矮嵩草(*K. humilis*)草甸<青藏苔草(*Carex moorcroftii*)草甸, 多样性指数表现为高山嵩草草甸<矮嵩草草甸<紫花针茅草原<青藏苔草草甸。修路时破坏的矮嵩草草甸在次生恢复过程中, 离公路 100 m 处群落的丰富度指数, 均匀度指数和多样性指数大于原生群落, 而原生群落的多样性又大于 30 m 和 50 m 处群落的多样性。地上草地群落植物多样性伴随地下冻土退化过程表现为, 以 1 m² 样方统计时, 各个演替群落间的丰富度指数差异不显著, 而以 100 m² 样条统计时, 高寒草甸和草原化草甸的丰富度指数显著大于沼泽草甸和稀疏草原($P < 0.05$), 但均匀度和多样性指数在两种统计面积时均表现为先增加后下降的变化趋势。

关键词: 青藏高原多年冻土区; 草地群落; 物种多样性; 冻土退化; 青藏公路

Plant species diversity of grassland plant communities in permafrost regions of the northern Qinghai-Tibet Plateau

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Abstract: The Qinghai-Tibetan Plateau is a key genetic resource region for plant flora and river resources in China, and has the largest and most species-rich alpine grassland ecosystem. Grassland plays a very important role in animal production, biodiversity and water conservation. Changes to grassland communities resulting from degradation of frozen soil and highway construction affect the processes of ecology. To gain insight into the contribution of biodiversity to the stability of this grassland ecosystem, there is an urgent need to study the effect of degradation of frozen soil and highway construction on the plant biodiversity of the grassland communities.

A survey of biodiversity was undertaken during 2001 and 2002 along the Qinghai-Tibetan Highway from Xidatan (94°10.016'E, 35°43.063'N) to the southern Tanggulashan Pass (33°07.120'E, 91°52.670'N), to study the change of species diversity between plant communities, and the effect of degradation of frozen soil and highway construction on plant biodiversity of grassland communities in the permafrost regions of the Qinghai-Tibetan Plateau. Thirty-two spots were selected according to the different grassland communities present (*Kobresia pygmaea* meadow, *Kobresia humilis* meadow, *Carex moorcroftii* meadow and *Stipa purpurea* steppe community) and the successional communities series (marsh meadow, steppe meadow, steppe meadow and steppe) in the process of frozen soil degradation. Two or three sampling zones of 1 m × 100 m were

基金项目: 国家重点基础研究发展规划资助项目(G2000018602); 国家自然科学基金资助项目(30270255); 中国科学院知识创新工程重大资助项目(KZCX1-SW-04)

收稿日期: 2003-02-14; **修订日期:** 2003-10-08

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Foundation item: Chinese "973" Key Basic Research Program (No. G2000018602); National Natural Science Foundation of China (No. 30270255); Knowledge Innovation Project of CAS (No. KZCX1-SW-04)

Received date: 2003-02-14; **Accepted date:** 2003-10-08

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designed at each spot (75 in total). Each sampling zone contained ten $1\text{ m} \times 1\text{ m}$ plots which were arranged every other 10 m. In each plot, all plant species present were counted, and coverage and frequency were recorded. Environmental factors including latitude, longitude, and altitude were measured by GPS and recorded. Biomass was measured by harvesting and drying. The species diversity of the plant communities was calculated using the Shannon-Wiener (diversity) index (H), the Pielou (evenness) index (J), and richness index (species number) (S).

This study showed that the richness species index (S) was not significantly different among the communities, and about ten 10 plant species were present in the survey plots for each plant community, whereas evenness index (J) and diversity index (H) were significantly different ($P < 0.05$) between the *Kobresia pygmaea* meadow community, the *Kobresia humilis* meadow community, the *Carex moorcroftii* meadow community, and the *Stipa purpurea* steppe community. Evenness index measurements decreased gradually: *Kobresia pygmaea* meadow > *Stipa purpurea* steppe > *K. humilis* meadow > *Carex moorcroftii* meadow. Diversity index decreased gradually from *Kobresia pygmaea* meadow community to *Kobresia humilis* meadow community to *Carex moorcroftii* meadow community to *Stipa Purpurea* steppe community.

Compared natural communities with restored communities, this study detected that changes of richness index and evenness index were consistent with diversity index in the restoration process of *Kobresia humilis* meadow after the severe destruction caused by the construction of the Qinghai-Tibetan Highway in 1976. Diversity, richness, and evenness indices of communities in sampling zones 100m from the Highway were larger than those of the natural communities. Species diversity of the natural communities was greater than that of the communities 50 and 30 m from the Highway. The results of this study indicated that the restoration capacity of vegetation was weak in the permafrost regions of the Qinghai-Tibet Plateau after the severe destruction caused by the highway construction.

This study also indicated that the richness index of succession plant community series kept steady within the 1 m^2 plots, but was significantly different within the 100 m^2 sampling zones in the degraded frozen soil. The changeable trend of the diversity index was in accord with the evenness index but not consistent with the richness index. Species diversity and evenness indices increased from marsh meadow to steppe meadow, and decreased from steppe meadow to steppe grassland in the degraded frozen soil with the size of 1 m^2 plots and 100 m^2 sampling zone.

Key words: permafrost regions of the Qinghai-Tibet Plateau; grassland community; species diversity; degradation of frozen soil; Qinghai-Tibetan Highway

文章编号:1000-0933(2004)01-0149-07 中图分类号:Q143,Q948,S812.3,S718.54 文献标识码:A

生物多样性是当前群落生态学中十分重要的研究内容之一^[1],但受空间尺度和生态系统复杂性的影响,目前生物多样性的研究多限于遗传多样性、物种多样性、生境多样性和景观多样性^[2],且以物种多样性的研究较多^[3]。物种多样性反映了种间生态位的差异,目前对草地群落物种多样性的研究主要集中于其随环境梯度和群落演替的变化^[4~6],以及人为干扰对它的影响^[7~8]。青藏高原是全球海拔最高的一个独特地域单元^[9],拥有世界上面积最大,海拔最高,生命种群比较丰富且保护较好的高寒自然生态系统^[10],不仅是我国重要的高山植物基因库,而且是我国生态安全的重要屏障^[11]。各种草地生态系统是当地牧民赖以生存的物质基础,也是生命支持系统的重要组分和环境可持续发展的基本要素,对发展畜牧业、保护生物多样性和维持生态平衡,特别是涵养水源具有重大的作用和价值^[11~16]。据 Tilman 等人和白永飞等人的研究^[17,18],草地的生物多样性是维持区域草地生态系统稳定和生产的基础。人类工程(青藏公路和青藏铁路)和冻土退化给青藏高原高海拔地区相对脆弱的草地生态系统带来了相当大的影响^[9,11,19],经常导致草地生态系统结构和功能的改变,从而影响整个区域的生态过程^[18,20],不仅对本区而且对其毗邻地区的生物,以及生物与环境相互作用组成的生态系统产生深刻影响^[15,21]。国内对青藏高原草地植物多样性的研究多限于东部和东北边缘的森林群落^[21,22],对北部多年冻土区植被的研究集中于植物特性的研究^[12,15,16],而对北部多年冻土区草地群落植物多样性的研究尚未见到报道。因此,研究北部多年冻土区草地植物的多样性特征,以及人类工程和冻土退化对草地群落多样性的影响,对深入研究该区草地生态系统长期忍受极端环境的稳定性具有重要的意义。

1 研究地区与方法

1.1 研究区概况

多年冻土区位于青藏高原腹地,海拔 4 000~5 010 m 之间,地势南高北低,由西向东倾斜。属高原亚寒带半干旱气候,如五道梁($35^{\circ}13'N, 93^{\circ}05'E$)和清水河($33^{\circ}48'N, 97^{\circ}08'E$)的年降水量分别为 262 mm 和 500 mm,年平均气温分别为 -5.6°C 和 -4.9°C , $\geq 0^{\circ}\text{C}$ 的积温为 450°C 和 579°C ^[12]。由于喜马拉雅山阻挡印度洋来的西南季风进入高原,使该区气候寒冷,年仅冬、夏

两季,冬季严寒漫长(达7~8个月),夏季凉爽短促,牧草生长期为3~4月^[13]。植被主要有以紫花针茅草原(*Stipa purpurea*)为优势植物的高寒草原和以嵩草(*Kobresia* spp.)和苔草(*Carex* spp.)为主的高寒草甸。

1.2 研究方法

1.2.1 样地设置与调查 从西大滩(94°10.016'E, 35°43.063'N; 海拔4300 m)到唐古拉山南坡(33°07.120'E, 91°52.670'N; 海拔5000 m),在青藏公路两侧不同的草地群落设置典型样条,样条的走向与所在样点的公路走向垂直。在每个样点,设置2~3条长100 m,宽1 m的样条。在样条上,每隔10 m设置一个1 m×1 m的样方,并记录每条样条的海拔和经纬度。植被调查以小样方为单位,记录每个样方内的建群种,物种数,以及每个物种的覆盖度和德氏多度(计算重要值时分别以1,2,3,4,5赋值),同时,收获地上生物量,带回实验室烘干称重。共调查32个样点,75条样条,750个样方。野外调查分别于2001年8月和2002年7月进行。

1.2.2 物种多样性的测度 选用Shannon-Wiener指数(*H*)、Pielou指数(*J*)和丰富度指数(*S*)讨论群落的物种多样性特征^[4~9,22,23]。

丰富度指数*S*指出现在样条内的物种总数,多样性指数*H*的计算公式为:

$$H = - \sum P_i \ln P_i$$

式中,*P_i*为种*i*的相对重要值,*P_i*=*N_i*/*N*;*N_i*为种*i*的绝对重要值,*N*为种*i*所在样方的各个种的重要值之和,*S*为种*i*所在样条中的物种数目。

均匀度指数*J*的计算公式为:

$$J = - \sum P_i \ln P_i / \ln S$$

采用Simpson优势度指数*D*测定群落内不同物种所起的作用和所占的地位^[24],其计算公式为:

$$D = \sum P_i^2$$

2 结果与讨论

2.1 草地群落间的物种多样性

青藏高原北部多年冻土区高寒草甸主要群落有矮嵩草草甸,青藏苔草草甸,高山嵩草草甸,而高寒草原主要为紫花针茅草原。统计表明,样方中出现的物种种类一般在10种左右,样条内出现的植物种类约为13~24种(表1),群落间植物丰富度指数差异不显著,而均匀度指数差异显著(*P*<0.05),并从高山嵩草草甸,经紫花针茅草原,矮嵩草草甸,到青藏苔草草甸呈下降趋势(表2)。丰富度指群落内种的绝对密度,而均匀度指群落内种的相对密度^[23,25]。种群在群落内的分布和出现的频率不同,说明它们在群落内的作用不同。多样性指数是物种数与均匀度结合起来的一个单一统计量^[26]。对4种主要草地群落的植物丰富度指数、均匀度指数、优势度和多样性的相关性分析结果表明,多样性指数与丰富度指数的相关系数是0.8583,与均匀度指数的相关系数是0.9063,而多样性指数与优势度指数呈负相关,相关系数为-0.8148。而在新疆阿勒泰和东北草原,物种多样性指数与物种丰富度的相关系数均大于其与物种均匀度指数的相关性系数^[8,27],产生这种分异的原因主要是在青藏高原多年冻土

表1 青藏高原多年冻土区不同草地群落的特征

Table 1 Community features of grassland communities in permafrost regions of the Qinghai-Tibet Plateau

草地群落 Grassland communities	建群种 Dominant species	主要伴生种 Associate species	样方内种数/ 样带内种数* Coverage
矮嵩草草甸 <i>Kobresia humilis</i> meadow	矮嵩草 <i>K. humilis</i>	线叶嵩草 <i>K. capillifolia</i> , 异针茅 <i>S. aliena</i> , 珠芽蓼 <i>Polygonum viviparum</i> , 高山蓼 <i>Draba alpina</i> , 矮火绒草 <i>Leontopodium nanum</i> , 雪白藜 <i>Potentilla nivea</i> 等。	8~12/15~19 60~90
高山嵩草草甸 <i>K. pygmaea</i> meadow	高山嵩草 <i>K. pygmaea</i>	垂穗披碱草 <i>Elymus nutans</i> , 二裂萎陵菜 <i>P. bifurca</i> , 珠芽蓼, 紫羊茅 <i>Festuca rubra</i> , 垫状点地梅 <i>Androsace tapete</i> , 沙生风毛菊 <i>Sanguisorba arenaria</i> , 多枝黄芪 <i>Astragalus polycladus</i> , 小花棘豆 <i>Oxytropis glabra</i> , 草地早熟禾 <i>Poa pratensis</i> , 矮火绒草, 异叶青兰 <i>Dracocephalum faberi</i> 等。	10~14/18~24 65~90
紫花针茅草原 <i>Stipa purpurea</i> steppe	紫花针茅 <i>S. purpurea</i>	青海苔草 <i>C. ivanoviae</i> , 二裂萎陵菜, 甘青兔耳草 <i>Saxifraga tangutica</i> , 小花棘豆, 矮火绒草, 冰草 <i>Agropyron cristatum</i> , 异叶青兰, 紫羊茅, 倒挂水柏枝 <i>Myricaria prostrata</i> 等。	9~13/18~22 50~70
青藏苔草草甸 <i>Carex moorcroftii</i> meadow	青藏苔草 <i>C. moorcroftii</i>	紫花针茅, 粗壮嵩草 <i>K. robusta</i> , 矮火绒草, 拉萨风毛菊 <i>Saussurea kingii</i> , 小叶棘豆, 多枝黄芪等。	7~10/13~16 55~90

* Species number in plots/species number in sampling zones

区,适宜该区生长的物种比东北草原带和阿勒泰地区要少得多,样方间物种丰富度指数差异不显著,因而导致多样性指数与均匀度指数密切相关。研究结果表明,4种草地群落植物多样性指数从高山嵩草草甸,经矮嵩草草甸和紫花针茅草原,到青藏苔草草甸依次降低。

表2 青藏高原多年冻土区草地群落的植物物种丰富度、均匀度、优势度、多样性指数

Table 2 Richness index, evenness index, domination index and diversity index of steppe plant communities in permafrost regions of the Qinghai-Tibet Plateau

群落类型 Community types	样方数 Plots	S	J	D	H
矮嵩草草甸 ^①	78	10±2.14	0.4819±0.0031b	0.1140±0.0021c	1.4895±0.0032b
高山嵩草草甸 ^②	90	12±1.98	0.5283±0.0011a	0.2219±0.0017b	1.5541±0.0274a
紫花针茅草原 ^③	85	11±2.67	0.5013±0.0014a	0.3152±0.0058b	1.4760±0.0054b
青藏苔草草甸 ^④	82	9±3.21	0.4533±0.0117b	0.4502±0.0116a	1.1963±0.0589c

① *Kobresia humilis* meadow; ② *K. pygmaea* meadow; ③ *Stipa purpurea* steppe; ④ *Carex moorcroftii* meadow

2.2 青藏公路修建迹地上草地群落植物多样性的变化

水淹和放牧对草地群落植物物种多样性影响的研究报道较多^[8,28],而交通干线对草地植物群落多样性影响的研究较少。修建公路势必造成公路沿线两侧草地的退化^[19]。以高寒矮嵩草草甸为例,分析人类工程(筑路时间为1976)对草地群落植物多样性的影响。以距离公路200 m处的群落代表原始群落,30,50,100 m分别代表影响强度,距离越远,影响越小。由于放牧方式为游牧,因此,它对草地群落的影响相对是均匀的。

据18条样条的资料统计分析,公路两侧矮嵩草草甸在天然次生恢复的过程中,丰富度指数、均匀度指数和多样性指数的变化趋势基本一致(图1),3个指数在距离公路30 m和50 m处的差异不大,100 m处群落的3个指数不仅远大于30 m和50 m处的群落,而且又大于200 m处的原始群落。高寒矮嵩草草甸的主要伴生种为异针茅(*Stipa aliena*)和羊茅(*Festuca ovina*)等,群落覆盖度较大,致密,并且这些禾本科牧草在资源谱上利用能力较强^[29],在原生群落中,其它草种生存或入侵相对困难,形成相对稳定的顶级群落,而受到轻微干扰后,群落的覆盖度会受到影响和不同程度的破损,原来的顶级平衡状态被打破,优势种群对光和水等资源的垄断利用格局被破坏,这给其它物种的入侵提供了有利条件,也给原来群落内已存在,但资源利用能力较弱的物种生长提供了便利,随着上述两种状况的发生,其物种多样性高于原始群落。这说明修建公路对100 m处的群落干扰轻微,而对30 m和50 m处的群落破坏严重,并且较为接近,原来的植被被全部破坏,所有物种的生境变化很大,物种的恢复从裸地开始,但由于海拔高,温度低,生长季短,物种入侵或土壤中种子发芽生长难度大,恢复相对困难。尽管在人为干扰强度上,多样性变化与放牧对植被群落多样性的影响基本类似,均随梯度增加,多样性降低^[8],它们的区别在于放牧的影响是面上的,而修建交通干线的影响呈条状,仅对公路沿线造成影响,但交通干线两侧累积的面积也不容忽视。因此,修建交通干线时应充分注意其对植被的影响。

2.3 冻土退化过程中草地群落植物物种多样性的变化

据王根绪等人研究了冻土退化过程中高寒沼泽草甸的原生演替模式^[14],即随着多年冻土退化,冻土上限下降,土壤表层水分减少,致使高寒沼泽草甸向高寒草甸演替,一些水生或湿生植物消失,代之以中生或旱中生植物;冻土继续退化,土壤继续干燥,旱生植物成分侵入,植被景观类型向高寒草原化草甸演替;若土壤持续暖干化,冻土消失,植被将发生显著退化,中生草甸植被大量消失,耐旱植被得以发展,在极度干旱生境条件下,植被演替为稀疏草原,甚至沙化。运用空间序列代替时间序列的方法,分析冻土退化过程中高寒沼泽草甸植物多样性的变化情况。

在冻土退化过程中,以样方为统计单位,群落间的丰富度指数差异不大,变化在1~2种之间(图2a),而以样条为统计单位时,群落间的丰富度指数差异变化较大,高寒草甸和草原化草甸的丰富度显著大于沼泽草甸和稀疏草原($P<0.05$)。但样方和样条统计结果均表明,群落间物种均匀度和多样性指数的变化均表现为先增加后降低的趋势(图2b)。高寒沼泽草甸多分布于地势低洼、排水不畅、土壤潮湿、通气不佳的低阶地,主要由耐寒湿

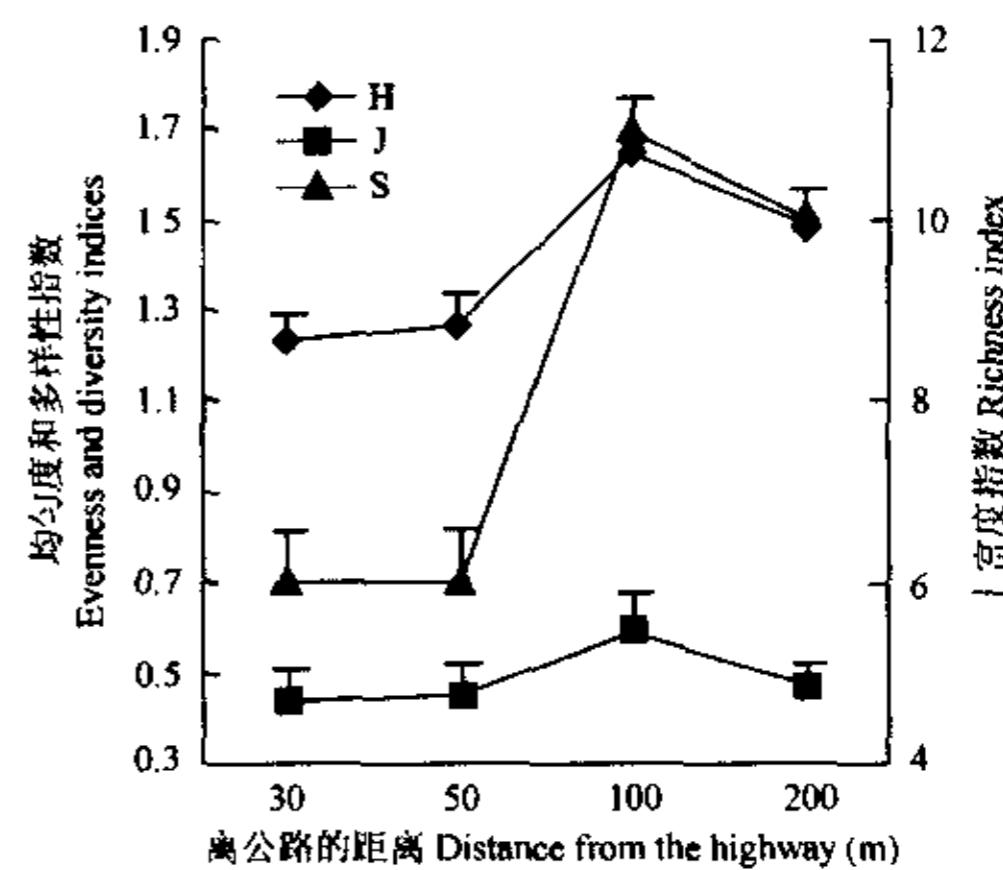
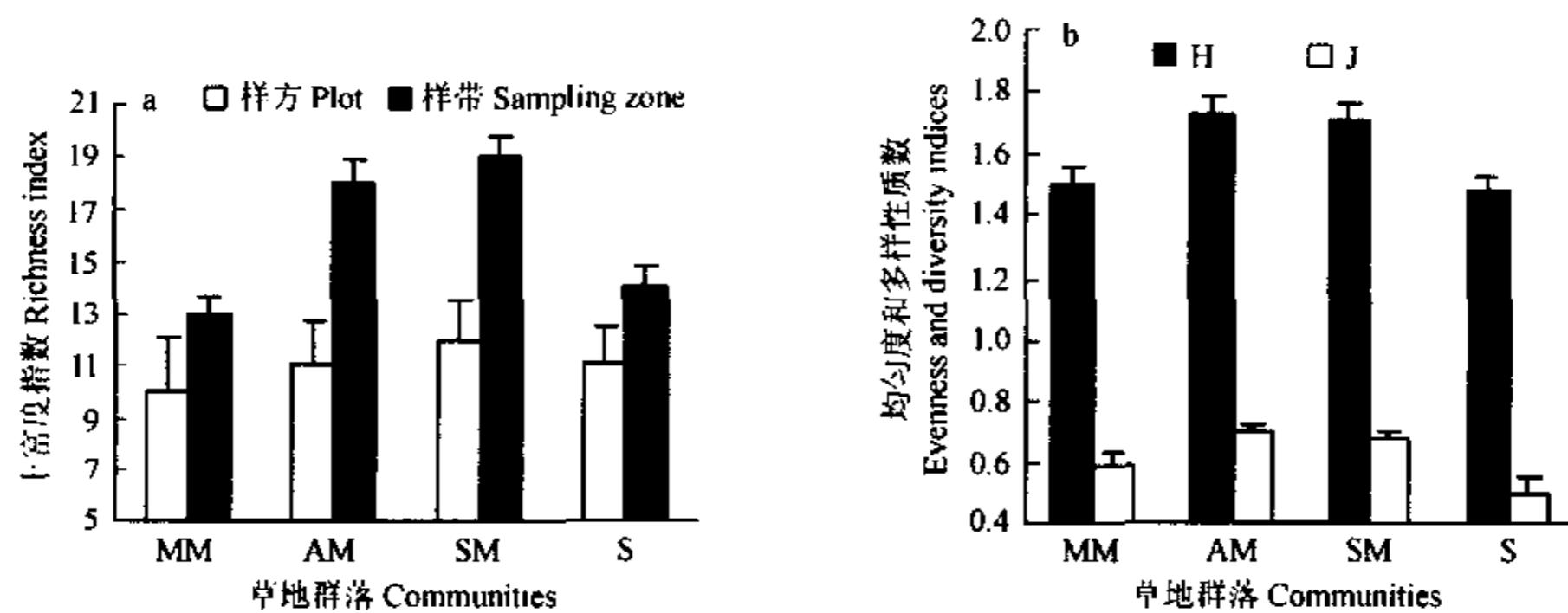


图1 高寒矮嵩草草甸恢复过程中的物种多样性变化特征

Fig. 1 Change of species diversity in the restoration process of alpine meadow communities

生和湿中生多年地面芽和地下芽植物组成,群落结构简单,层次分化不明显,以禾本科(*Gramineae*),莎草科(*Cyperaceae*)和毛茛科(*Ranunculaceae*)植物为主,主要优势植物是藏嵩草(*K. tibetica*),伴生种常见的有华扁穗草(*Blysmus sinocompressus*),圆穗蓼(*Polygonum macrophyllum*),斑唇马先蒿(*Pedicularis longiflora*),花葶驴蹄草(*Caltha scaposa*),黑褐苔草(*C. atrofusca*)等,由于建群种的绝对优势地位,其它伴生种所占的比例较小,均匀度较低。随着多年冻土的退化,土壤表层含水量下降,这为一些中生植物的入侵提供了条件,中生植物种类的入侵和发展,使群落结构发生了变化,主要优势植物有高山嵩草、矮嵩草、线叶嵩草等,伴生植物有黑褐苔草,草地早熟禾,针茅,矮火绒草,甘肃棘豆(*O. kansuensis*),马先蒿,多裂萎陵菜(*P. multifida*),龙胆(*Gentiana* sp)等,群落已演替成为高山典型草甸,各个种群在群落内的分布相对均匀,因此虽然样方内的丰富度指数变化不大,而多样性指数增加。随着冻土的继续退化,地下水位进一步下降,土壤逐渐变得干燥,水生或湿生的种类消失,群落的建群种从嵩草(高山嵩草,矮嵩草,线叶嵩草,北方嵩草(*K. bellardii*)等)演变成变高山嵩草,异针茅,紫花针茅,伴生种也出现了沙生风毛菊(*S. arenaria*),垫状驼绒藜(*Ceratoides compacta*),青海虎耳草(*Saxifraga qinghaiensis*)等较为旱生的植物,草原植物的出现,草甸植物的比例下降,使群落类型已演变为草原化草甸,虽然物种种类发生变化,湿生种类消失,干旱种类产生,但其在群落内的分布仍然相对均匀,因而其多样性指数与高山草甸相比,变化不大。随着冻土消失,中生草甸植被的消失,耐旱植物得以充分发展,逐渐发展成为稀疏草原,这时耐旱植物又重新占据了绝对优势,促使多样性下降。



MM:沼泽草甸 Marsh meadow; AM:高寒草甸 Alpine meadow; SM:草原化草甸 Steppe meadow; S:稀疏草原 Steppe.

图 2 冻土退化过程中地上群落丰富度指数(a)和群落均匀度及多样性指数(b)的变化

Fig. 2 Richness index and Evenness (a) and diversity indices (b) in the degraded process of frozen soil

3 结 论

青藏高原多年冻土区内草地群落间物种丰富度指数差异不大,均匀度指数从高山嵩草草甸,经紫花针茅草原,矮嵩草草甸,到青藏苔草草甸,呈下降趋势。多样性指数的表现为从高山嵩草草甸,经矮嵩草草甸和紫花针茅草原,到青藏苔草草甸依次降低。

矮嵩草草甸在次生恢复的过程中,丰富度指数,均匀度指数和多样性指数的变化趋势基本一致,修建公路对50 m处的群落干扰严重,而对100 m处的群落干扰较轻。

在冻土退化过程中,以1 m²样方面积统计时,群落间的丰富度指数变化在1~2种之间,而以100 m²样条统计时,高寒草甸和草原化草甸的丰富度显著大于沼泽草甸和稀疏草原,但均匀度和多样性指数在两种统计面积时均表现为先增加后下降的变化趋势。

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