

ISSN 1000-0933

CN 11-2031/Q

生态学报

Acta Ecologica Sinica



第31卷 第12期 Vol.31 No.12 2011

中国生态学学会

中国科学院生态环境研究中心

科学出版社

主办

出版



中国科学院科学出版基金资助出版

生态学报 (SHENTAI XUEBAO)

第31卷 第12期 2011年6月 (半月刊)

目 次

基于植被遥感的西南喀斯特退耕还林工程效果评价——以贵州省毕节地区为例.....	李昊,蔡运龙,陈睿山,等 (3255)
扩散对破碎化景观上宿主-寄生种群动态的影响	苏敏 (3265)
湿地功能评价的尺度效应——以盐城滨海湿地为例	欧维新,叶丽芳,孙小祥,等 (3270)
模拟氮沉降对杉木幼苗养分平衡的影响.....	樊后保,廖迎春,刘文飞,等 (3277)
中国东部森林样带典型森林水源涵养功能.....	贺淑霞,李叙勇,莫菲,等 (3285)
山西太岳山油松群落对采伐干扰的生态响应.....	郭东罡,上官铁梁,白中科,等 (3296)
长期施用有机无机肥对潮土微生物群落的影响	张焕军,郁红艳,丁维新 (3308)
云南元江干热河谷五种优势植物的内生真菌多样性.....	何彩梅,魏大巧,李海燕,等 (3315)
塔里木河中游洪水漫溢区荒漠河岸林实生苗更新.....	赵振勇,张科,卢磊,等 (3322)
基于8hm ² 样地的天山云杉林蒸腾耗水从单株到林分的转换	张毓涛,梁凤超,常顺利,等 (3330)
古尔班通古特沙漠土壤酶活性和微生物量氮对模拟氮沉降的响应.....	周晓兵,张元明,陶冶,等 (3340)
Pb污染对马蔺生长、体内重金属元素积累以及叶绿体超微结构的影响	原海燕,郭智,黄苏珍 (3350)
春、秋季节树干温度和液流速度对东北3树种树干表面CO ₂ 释放通量的影响	王秀伟,毛子军,孙涛,等 (3358)
云南南部和中部地区公路旁紫茎泽兰土壤种子库分布格局.....	唐樱殷,沈有信 (3368)
利用半球图像法提取植被冠层结构特征参数.....	彭焕华,赵传燕,冯兆东,等 (3376)
黑河上游蝗虫与植被关系的CCA分析	赵成章,周伟,王科明,等 (3384)
额尔古纳河流域秋季浮游植物群落结构特征.....	庞科,姚锦仙,王昊,等 (3391)
九龙江河口浮游植物的时空变动及主要影响因素.....	王雨,林茂,陈兴群,等 (3399)
东苕溪中下游河岸类型对鱼类多样性的影响.....	黄亮亮,李建华,邹丽敏,等 (3415)
基于RS/GIS公路路域水土流失动态变化的研究——以渝昆高速公路为例	陈爱侠,李敏,苏智先,等 (3424)
流域景观结构的城市化影响与生态风险评价.....	胡和兵,刘红玉,郝敬峰,等 (3432)
基于景观格局的锦州湾沿海经济开发区生态风险分析.....	高宾,李小玉,李志刚,等 (3441)
若尔盖高原土地利用变化对生态系统服务价值的影响.....	李晋昌,王文丽,胡光印,等 (3451)
施用鸡粪对土壤与小白菜中Cu和Zn累积的影响	张妍,罗维,崔晓勇,等 (3460)
基于GIS的宁夏灌区农田污染源结构特征解析.....	曹艳春,冯永忠,杨引禄,等 (3468)
底墒和种植方式对夏大豆光合特性及产量的影响.....	刘岩,周勋波,陈雨海,等 (3478)
不同施肥模式调控沿湖农田无机氮流失的原位研究——以南四湖过水区粮田为例	谭德水,江丽华,张骞,等 (3488)
丛枝菌根真菌对低温下黄瓜幼苗光合生理和抗氧化酶活性的影响	刘爱荣,陈双臣,刘燕英,等 (3497)
外源半胱氨酸对铜胁迫下小麦幼苗生长、铜积累量及抗氧化系统的影响	彭向永,宋敏 (3504)
专论与综述	
水平扫描技术及其在生态学中的应用前景	胡自民,李晶晶,李伟,等 (3512)
研究简报	
昆仑山北坡4种优势灌木的气体交换特征.....	朱军涛,李向义,张希明,等 (3522)
不同比例尺DEM数据对森林生态类型划分精度的影响	唐立娜,黄聚聪,代力民 (3531)
苏南丘陵区毛竹林冠截留降雨分布格局	贾永正,胡海波,张家洋 (3537)
外来种湿地松凋落物对土壤微生物群落结构和功能的影响	陈法霖,郑华,阳柏苏,等 (3543)
深圳地铁碳排放量	谢鸿宇,王习祥,杨木壮,等 (3551)

期刊基本参数:CN 11-2031/Q * 1981 * m * 16 * 304 * zh * P * ¥ 70.00 * 1510 * 35 * 2011-06



封面图说:自然奇观红海滩·辽宁省盘锦市——在辽河入海口生长着大片的潮间带植物碱蓬草,举目望去,如霞似火,蔚为壮观,人们习惯地称之为红海滩。粗壮的根系加快着海滩土壤的脱盐过程,掉下的茎叶腐质后肥化了土壤,它是大海的生态屏障。

彩图提供:段文科先生 中国鸟网 <http://www.birdnet.cn> E-mail:dwk9911@126.com

扩散对破碎化景观上宿主-寄生种群动态的影响

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摘要: 基于偶对近似模型, 探讨由局部和全局宿主-寄生相互作用共同决定的扩散模式对破坏性景观上疾病入侵与传播的影响。其中, 生境破坏由生境丧失量与生境破碎化程度来描述。模拟结果显示, 宿主和病毒的全局扩散对疾病的入侵与种群密度产生不对称效应; 病毒的全局扩散对系统产生的影响较宿主的全局扩散更为显著。不同扩散模式下, 生境丧失越高或破碎化程度越低, 均将越有害于寄生病毒的入侵; 同时, 生境的破坏程度也显著地影响了入侵阈值对扩散模式的响应机制。研究结果表明, 景观破碎化的空间分布格局以及病毒扩散的限制均可作为物种保护与管理中有效的疾病控制策略。该研究结果在一定意义上丰富和发展了寄生感染理论, 为物种保护提供了生态学理论依据。

关键词: 宿主-寄生; 全局与局部扩散; 生境丧失; 生境破碎; 偶对近似

The effect of dispersal on the population dynamics of a host-parasite system in fragmented landscape

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Abstract: Landscape structure and dispersal strategy are two important factors affecting population dynamics and thus entail profound effects on biological invasions. However, insufficient attention has been paid to the combined effects of landscape structure and dispersal behavior on the epidemic transmission in spatially explicit landscapes. In this paper, pair approximation (a method from statistical physics for deriving ordinary differential equations that approximate the spatial dynamics of populations in a lattice environment) was applied to examine the impact of dispersal strategy, determined by the interplay between local and global host-parasite interactions, to the invasion and spread of epidemics on the fragmented landscape. The intensity of habitat destruction in the model, instead of undergoing a random loss, was quantified by the level of habitat loss and fragmentation. By incorporating the detailed information on dispersal strategy in the spatially structured landscape, we are able to address the following questions: (1) How does the dispersal pattern affect the invasion and transmission of the parasitic disease? (2) How does the impact of dispersal patterns depend on the landscape structure?

By the use of invasion analysis and numerical simulations, the effect of global dispersal in hosts and parasites was found asymmetric in terms of the epidemic invasion and population dynamics. First, the global dispersal of parasites (epidemics) was shown to pose a much stronger impact than the global dispersal of hosts on the invasion threshold of the epidemic disease. Second, the average host density at the equilibrium state enhanced slightly with the increasing proportion of global dispersal in hosts, but declined dramatically with the increasing proportion of global dispersal in parasites. Finally, both the population density of hosts and parasites at equilibrium, measured by the relative occupancy, increased with the increasing proportion of global dispersal, but the impact of global dispersal on the population density of the parasites was more dramatic. Under different dispersal scenarios, high level of habitat loss and low level of habitat fragmentation were shown to be detrimental to the invasion of parasitic disease. The invasion threshold of parasitic disease

基金项目: 国家自然科学基金资助项目(31000192); 中国博士后科学基金资助项目(20100481159); 中央高校基本科研业务费专项资金资助(2010HGJ0200); 合肥工业大学博士学位专项资助(GDBJ2009-037)

收稿日期: 2010-05-18; **修订日期:** 2010-08-16

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was increased gradually with the increase of habitat loss, but declined monotonously with the increase of the clustering degree of lost patches. Meanwhile, the invasion threshold of parasitic disease reached the peak when all dispersal events were completely local; this indicates that local dispersal was preferred for controlling the invasion and spreading of disease. Results also showed that the mechanistic response of the invasion threshold to the proportion of local dispersal in all dispersal events could be altered under different levels of habitat destruction. When habitat destruction is severe (i. e. high proportion of habitat loss and low correlation between adjacent unsuitable habitat), the influence of global dispersal has been proved to be more important on disease transmission. However, when habitat destruction is subtle, the global dispersal plays only a weak effect on disease transmission. We thus suggest that it is possible to control disease transmission by modifying the spatial structure of the landscape and the dispersal capacity of epidemics. This work highlights the importance of encompassing more realistic spatial patterns of landscape and dispersal in conservation planning and has extended and enriched the research of population and community epidemiology.

Key Words: host-parasite; global and local dispersal; habitat loss; habitat fragmentation; pair approximation

传染性病毒已被证实为影响物种生存与动态的关键因素^[1-4]。自 Anderson 和 May^[5]从理论上论证了寄生对宿主的调节强度以来,有关寄生感染对生态系统影响方面的研究越来越受到重视,并且得到了深入的发展^[6-8]。已有研究表明,空间结构是影响疾病传播的重要因素之一,尤其对于疾病传染是通过感个体与健康个体的直接接触而发生的^[4,9]。然而,不同的宿主-寄生系统将会存在不同程度的局部生殖与感染相互作用。完全的局部和全局相互作用只是现实的生态和传染病系统的两种极端情形。Boots 和 Sasaki^[6], Webb 等^[8]研究结果表明,扩散作用(全局与局部扩散)对疾病动态与病毒进化产生重要的影响。另外,生境的丧失与破碎化直接导致了斑块化生境间物种成功迁移率的下降^[10-11]。因此,有必要探讨基于破碎化景观上的空间扩散模式对宿主-寄生传染病系统动态的影响。经典的生境破坏研究往往假设丧失的斑块在景观中呈现空间随机的分布模式。然而,由于现实的生境往往展现了某种程度的空间相关(或聚集),从而导致该随机性假设与真实生境的非随机结构存在差距。本文,我们将基于具有空间结构的生境破坏景观,采用偶对近似模型来探讨完全局部以及局部与全局作用的混合扩散模式对宿主-寄生系统的影响。

1 偶对近似模型

为了讨论扩散对破碎化景观上宿主-寄生系统动态的影响,设计了一个微生物寄生感染的宿主-寄生(SI)网格模型。破碎化景观包含两种生境类型:可适合生境和不适合生境,其中不适合的生境不能被物种所侵占^[12-14]。不适合生境斑块的比例记作 p_u ,它代表了生境丧失量。聚集度参数 $q_{u/u}$ 代表了丧失斑块的空间自相关性,表示对不适合斑块随机所选择的一个邻体也是不适合生境的概率^[15],其代表了生境破碎化程度。因此,可适合生境斑块的比例是 $p_s = 1 - p_u$,其聚集度可以用如下表达式来描述 $q_{s/s} = 1 - \frac{p_u}{1 - p_u}(1 - q_{u/u})$ 。寄生感染相互作用的网格动态模型设置在上述所给的破碎化景观上,每一个斑块存在 4 种可能的状态:不适合生境(1),可适合空斑块生境(0),易感染个体所占据的斑块(S)或者被已感染个体所占据(I)。

易感染宿主产生的后代以 $r(1-L_s)$ 的概率扩散到邻体的可适合空斑块,而剩余的生殖率 rL_s 全局扩散到可适合空斑块(L_s 代表宿主个体全局生殖的比例, $0 \leq L_s \leq 1$)。寄生感染是通过相邻斑块间已感染个体和易感染个体之间的接触来传播的。假设寄生感染同时可发生在局部和全局尺度上,局部感染和全局感染的概率分别为 $\beta(1-L_I)$ 与 βL_I , $0 \leq L_I \leq 1$ 。另外,假设因寄生感染的影响致使感染个体的死亡率($d+\alpha$)比易感染个体(d)高。而且个体死亡后,适合且被占据斑块可以变成空斑块,并能够在下个世代被宿主个体的后代重新占据。

基于上述所给的迭代规则,可以构造出下面的偶对近似模型。这里,全局密度 $P_\sigma(t)$ ($\sigma \in \{S, I, 0, 1\}$) 描述了 t 时刻随机选择的一个斑块,其状态是 σ 的概率。双密度 $P_{\sigma\sigma'}$ 代表了随机选择的一对相邻斑块,其状态是

$\sigma\sigma'$ 的概率。局部密度 $Q_{\sigma/\sigma'}$ 是一个条件概率,指的是状态为 σ' 的斑块随机选择其一个相邻斑块状态为 σ 的概率。 $Q_{\sigma/\sigma'\sigma''}$ 代表 $\sigma'\sigma''$ 偶对斑块中随机选择 σ' 斑块的一个邻体是 σ 的条件概率($\sigma', \sigma'' \in \{S, I, 0, 1\}$)。有 $P_{\sigma\sigma'} = P_\sigma Q_{\sigma'/\sigma} = P_{\sigma'\sigma} = P_{\sigma'} Q_{\sigma'/\sigma'}$, $P_\sigma = \sum_{\sigma'} P_{\sigma\sigma'}$, $\sum_{\sigma'} Q_{\sigma'/\sigma} = 1$, $p_u = P_1$, $P_{11} = p_u q_{u/u}$ 以及 $p_s = P_0 + P_S + P_I$ 。根据偶对近似的方法,三联体关联密度可用偶对密度来代替(即 $Q_{\sigma/\sigma'\sigma''} \approx Q_{\sigma/\sigma'}$)^[4,16]。最终,可得到7个独立变量,即 $P_s, P_I, P_{ss}, P_H, P_{0I}, P_{SI}$,而其它所有单密度和双密度变量都可以由这7个变量导出。偶对近似方程如下:

$$\begin{aligned}\frac{dP_s}{dt} &= r(1-L_s)P_S Q_{0/S} + rL_s P_S P_0 - dP_s - \beta(1-L_I)P_S Q_{I/S} - \beta L_I P_S P_I \\ \frac{dP_I}{dt} &= \beta(1-L_I)P_I Q_{S/I} + \beta L_I P_S P_I - (d+\alpha)P_I \\ \frac{dP_{ss}}{dt} &= 2r(1-L_S)\{\theta + (1-\theta)Q_{S/0S}\}P_{S0} - 2dP_{ss} - 2\beta P_{ss}\{(1-L_I)(1-\theta)Q_{I/SS} + L_I P_I\} + 2rL_S P_{S0} P_S \\ \frac{dP_H}{dt} &= 2\beta(1-L_I)\{\theta + (1-\theta)Q_{I/SI} + L_I P_I\}P_{IS} - 2(d+\alpha)P_H \\ \frac{dP_{00}}{dt} &= r\{(1-L_S)(1-\theta)Q_{S/00} + L_S P_S\}P_{00} - r\{(1-L_S)[\theta + (1-\theta)Q_{S/0S} + L_S P_S]P_{S0} - \\ &\quad dP_{S0} + dP_{ss} + (d+\alpha)P_{IS} - \beta\{(1-L_I)(1-\theta)Q_{I/S0} + L_I P_I\}P_{S0} - \\ \frac{dP_{0I}}{dt} &= \beta\{(1-L_I)(1-\theta)Q_{I/S0} + L_I P_I\}P_{S0} + dP_{IS} + (d+\alpha)P_H - (d+\alpha)P_{0I} - \\ &\quad r\{(1-L_S)(1-\theta)Q_{S/0I} + L_S P_S\}P_{0I} \\ \frac{dP_{SI}}{dt} &= rP_{0I}\{(1-L_S)(1-\theta)Q_{S/0I} + L_S P_S\} + \beta P_{ss}\{(1-L_I)(1-\theta)Q_{I/SS} + L_I P_I\} - (2d+\alpha)P_{SI} - \\ &\quad \beta P_{SI}\{(1-L_I)[\theta + (1-\theta)Q_{I/SI}] + L_I P_I\}\end{aligned}$$

式中, r 代表宿主的生殖率, β 是病毒的传播率; L_s, L_I 分别是宿主和病毒的长距离扩散比例; $\theta = 1/z$ (z 是邻体斑块的数目); d 是宿主个体的死亡率; α 是指由病毒感染而引起的额外死亡率。

2 结果分析

偶对近似的解析结果非常复杂繁琐,因此,本文采用入侵分析方法和数值方法来解析疾病动态^[16]。图1给出了不同扩散模式下,入侵阈值随着生境丧失量和破碎化程度的变化动态。病毒的入侵阈值是以确保病毒成功入侵的最低感染率 β_c 来表示。首先,图1a显示:4种不同扩散模式下,生境丧失 ρ_u 的增加均可导致入侵阈值的逐渐增长。而图1b表示:伴随着丧失生境的空间自相关性(破碎化) $q_{u/u}$ 的增加,入侵阈值在不同扩散模式下均呈现下降趋势。其次,图1说明在完全的局部扩散下($L_s=L_I=0$),疾病入侵阈值最高。这一结果暗示了生境破坏和局部扩散均有利于抑制疾病的入侵和传播。

同时,图1也显示出生境的破坏程度显著地影响了入侵阈值对扩散模式的响应机制(图1)。在生境严重丧失的情形下(高生境丧失量或者低生境聚集度),全局扩散对疾病传播的重要性显得较为明显,而在低破坏程度下全局扩散的作用较弱。特别是在生境破坏程度较轻时,通过比较 $L_s=0, L_I=0$ 与 $L_s=0.5, L_I=0$ 以及 $L_s=0, L_I=0.5$ 与 $L_s=0.5, L_I=0.5$ 两对不同扩散模式下的疾病入侵阈值,可以发现宿主的全局扩散作用基本消失(图1)。另外,通过比较不同扩散模式下的入侵阈值,发现宿主的全局扩散比例 L_s 和疾病的全局扩散比例 L_I 对疾病传播产生的影响并不对称。

为了进一步清晰地表示出扩散对疾病传播产生的不对称性,给出不同全局扩散水平下宿主种群的总体占据比例($P_s^*+P_I^*$)以及疾病相对占据比例($P_I^*/(P_s^*+P_I^*)$)在平衡时刻的等高线图(图2)。从图2中很显然的看出 L_s 对种群密度产生的影响较 L_I 低。随着 L_s 的增加,整个宿主平衡时刻的密度呈现微弱的增加趋势,然而随着 L_I 的增加却表现出急剧下降的动态(图2a)。图2b显示,疾病的相对占据比例随着 L_s, L_I 的增加均呈现增加趋势,但是后者的影响较前者更为显著。以上结果揭示出宿主的全局扩散能力和疾病的扩散能力产生

了极为不对称的结果,并且前者对疾病动态的影响明显弱于后者。

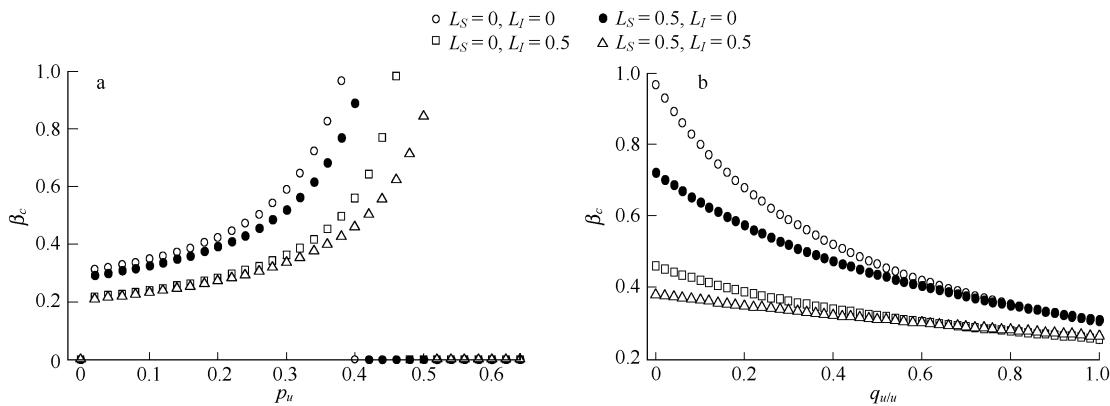


图1 不同扩散模式下,入侵阈值(β_c)随生境丧失(p_u , a)和生境破碎化($q_{u/u}$, b)的变化趋势

Fig. 1 Invasion thresholds (β_c) are as a function of the habitat loss (p_u , a) and habitat fragmentation ($q_{u/u}$, b) under different dispersal patterns, respectively

$$r=0.5, d=0.1, \alpha=0.05, \theta=1/z=0.25; (a) q_{u/u}=0.3, (b) p_u=0.3$$

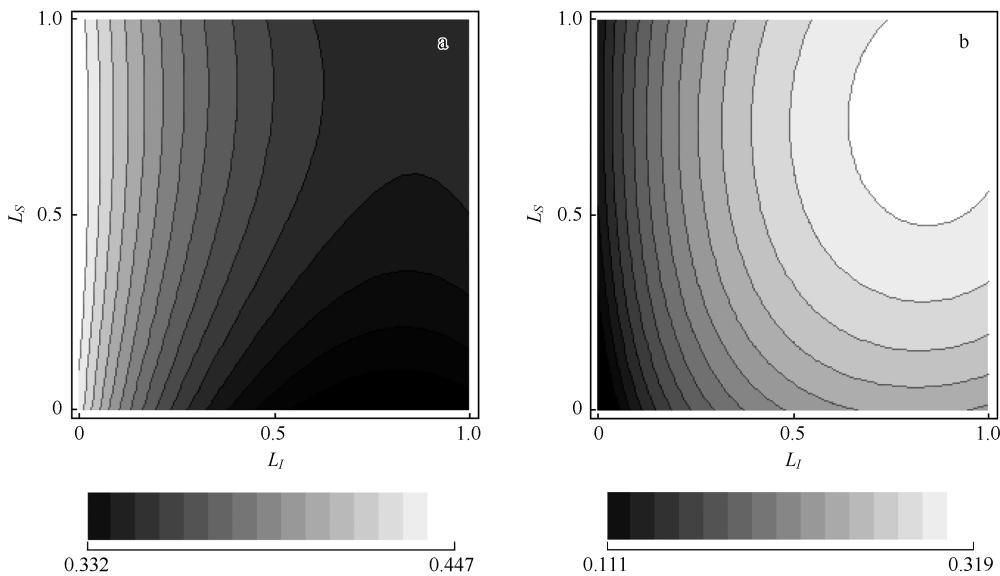


图2 平衡时刻宿主占据比例($P_S^* + P_I^*$, a)与疾病的相对占据($P_I^*/(P_S^* + P_I^*)$, b)随着全局扩散能力(L_S, L_I)的动态变化

Fig. 2 Influence of global dispersal rate (L_S, L_I) on the entire host density ($P_S^* + P_I^*$, a) and disease ($P_I^*/(P_S^* + P_I^*)$, b) at equilibrium

$$r=0.5, d=0.1, \alpha=0.05, \theta=1/z=0.25, p_u=0.3, q_{u/u}=0.5$$

3 讨论

本文中,构造了一个空间破碎化景观上的宿主-寄生传染病模型,并在此基础上率先引入全局扩散比例(L_S, L_I)共同决定下的扩散模式。本文的一个主要结论是宿主和病毒的全局扩散对疾病的入侵与种群密度产生不对称效应。病毒的全局扩散能力对系统产生的影响较宿主的全局扩散更为显著。产生这一区别的主要原因是:宿主与疾病之间存在相互对立的过程(感染作用),宿主种群必须平衡全局扩散带来的个体增长(正效应)和感染几率的增加(负效应)正负两种效应;然而,感染疾病个体的全局扩散为病毒创造了更多接触易感宿主的机会,从而有利于感染发生。

其次,生境的破坏程度影响了入侵阈值对扩散模式的响应机制。高生境破坏同时也限制了扩散成功的概率,从而减弱了全局扩散的影响。进一步揭示了生境破碎的空间结构显著的影响了传染病系统动态。当生境

破碎化程度增加时,适合斑块的空间聚集度也同时增加,所以更多的斑块被具有相同类型的斑块所包围^[4,17],从而生境破碎化有利于病毒的入侵和传播。

以上结果说明,限制已感染疾病个体的扩散与生境的破碎化是阻止疾病在生态系统中迅速传播的有效策略。本文提供了一种抑制疾病传播的方法,即生态控制法,主要是采用人为的方式来仿造生境破坏,同时限制疾病的扩散,从而有效地打断病原体的生长繁育链,干扰和破坏他们赖以生存的必需环境条件,这一方法为控制疾病在生态系统中的传播提供了新思路。然而,自然群落中宿主并不是单一生存的,寄生病毒的成功入侵及其引起的宿主-寄生动态很可能依赖于宿主群落里其它物种成员,例如,捕食者^[18]。探讨扩散对破碎化景观上受疾病干扰的生态群落的影响有待深入研究。

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ACTA ECOLOGICA SINICA Vol. 31 ,No. 12 June ,2011 (Semimonthly)

CONTENTS

Effect assessment of the project of grain for green in the karst region in Southwestern China: a case study of Bijie Prefecture	LI Hao, CAI Yunlong, CHEN Ruishan, et al (3255)
The effect of dispersal on the population dynamics of a host-parasite system in fragmented landscape	SU Min (3265)
The effect of spatial scales on wetland functions evaluation: a case study for coastal wetlands in Yancheng, Jiangsu Province	OU Weixin, YE Lifang, SUN Xiaoxiang, et al (3270)
Effects of simulated nitrogen deposition on nutrient balance of Chinese fir (<i>Cunninghamia lanceolata</i>) seedlings	FAN Houbao, LIAO Yingchun, LIU Wenfei, et al (3277)
The water conservation study of typical forest ecosystems in the forest transect of eastern China	HE Shuxia, LI Xuyong, MO Fei, et al (3285)
The ecological responses of <i>Pinus tabulaeformis</i> forests in Taiyue Mountains of Shanxi to artificial Harvesting	GUO Donggang, SHANGGUAN Tieliang, BAI Zhongke, et al (3296)
The influence of the long-term application of organic manure and mineral fertilizer on microbial community in calcareous fluvo-aquic soil	ZHANG Huanjun, YU Hongyan, DING Weixin (3308)
Endophytic fungal diversity of five dominant plant species in the dry-hot valley of Yuanjiang, Yunnan Province, China	HE Caimei, WEI Daqiao, LI Haiyan, et al (3315)
Seedling recruitment in desert riparian forest following river flooding in the middle reaches of the Tarim River	ZHAO Zhenyong, ZHANG Ke, LU Lei, et al (3322)
Scaling up for transpiration of <i>Pinaceae schrenkiana</i> stands based on 8hm permanent plots in Tianshan Mountains	ZHANG Yutao, LIANG Fengchao, CHANG Shunli, et al (3330)
Responses of soil enzyme activities and microbial biomass N to simulated N deposition in Gurbantunggut Desert	ZHOU Xiaobing, ZHANG Yuanning, TAO Ye, et al (3340)
Effects of Pb on growth, heavy metals accumulation and chloroplast ultrastructure of <i>Iris lactea</i> var. <i>Chinensis</i>	YUAN Haiyan, GUO Zhi, HUANG Suzhen (3350)
Effects of temperature and sap flow velocity on CO ₂ efflux from stems of three tree species in spring and autumn in Northeast China	WANG Xiuwei, MAO Zijun, SUN Tao, et al (3358)
The soil seed bank of <i>Eupatorium adenophorum</i> along roadsides in the south and middle area of Yunnan, China	TANG Yingyin, SHEN Youxin (3368)
Extracting the canopy structure parameters using hemispherical photography method	PENG Huanhua, ZHAO Chuanyan, FENG Zhaodong, et al (3376)
The CCA analysis between grasshopper and plant community in upper reaches of Heihe River	ZHAO Chengzhang, ZHOU Wei, WANG Keming, et al (3384)
Community structure characteristics of phytoplankton in argun River Drainage Area in autumn	PANG Ke, YAO Jinxian, WANG Hao, et al (3391)
Spatial and temporal variation of phytoplankton and impacting factors in Jiulongjiang Estuary of Xiamen, China	WANG Yu, LIN Mao, CHEN Xingqun, et al (3399)
Effect of bank type on fish biodiversity in the middle-lower reaches of East Tiaoxi River, China	HUANG Liangliang, LI Jianhua, ZOU Limin, et al (3415)
Study on dynamic changes of soil and water loss along highway based on RS/GIS: an example of Yujing expressway	CHEN Aixia, LI Min, SU Zhixian, et al (3424)
The urbanization effects on watershed landscape structure and their ecological risk assessment	HU Hebing, LIU Hongyu, HAO Jingfeng, et al (3432)
Assessment of ecological risk of coastal economic developing zone in Jinzhou Bay based on landscape pattern	GAO Bin, LI Xiaoyu, LI Zhigang, et al (3441)
Impacts of land use and cover changes on ecosystem service value in Zoige Plateau	LI Jinchang, WANG Wenli, HU Guangyin, et al (3451)
Effect of chicken manure application on Cu and Zn accumulation in soil and <i>Brassica sinensis</i> L.	ZHANG Yan, LUO Wei, CUI Xiaoyong, et al (3460)
GIS analysis of structural characteristics of pollution sources in irrigable farmland in Ningxia China	CAO Yanchun, FENG Yongzhong, YANG Yinlu, et al (3468)
Effects of pre-sowing soil moisture and planting patterns on photosynthetic characteristics and yield of summer soybean	LIU Yan, ZHOU Xunbo, CHEN Yuhai, et al (3478)
<i>In situ</i> study on influences of different fertilization patterns on inorganic nitrogen losses through leaching and runoff: a case of field in Nansi Lake Basin	TAN Deshui, JIANG Lihua, ZHANG Qian, et al (3488)
Effects of AM fungi on leaf photosynthetic physiological parameters and antioxidant enzyme activities under low temperature	LIU Airong, CHEN Shuangchen, LIU Yanying, et al (3497)
Effects of exogenous cysteine on growth, copper accumulation and antioxidative systems in wheat seedlings under Cu stress	PENG Xiangyong, SONG Min (3504)
Review and Monograph	
The horizon scanning technology and its application prospect in Ecology	HU Zimin, LI Jingjing, LI Wei, et al (3512)
Scientific Note	
The gas exchange characteristics of four shrubs on the northern slope of Kunlun Mountain	ZHU Juntao, LI Xiangyi, ZHANG Ximing, et al (3522)
Effect of DEM data at different scales on the accuracy of forest Ecological Classification system	TANG Lina, HUANG Juecong, DAI Limin (3531)
Canopy interception of rainfall by Bamboo plantations growing in the Hill Areas of Southern Jiangsu Province	JIA Yongzheng, HU Haibo, ZHANG Jiayang (3537)
Effects of exotic species slash pine (<i>Pinus elliottii</i>) litter on the structure and function of the soil microbial community	CHEN Falin, ZHENG Hua, YANG Bosu, et al (3543)
The carbon emission analysis of Shenzhen Metro	XIE Hongyu, WANG Xixiang, YANG Muzhuang, et al (3551)

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编辑部主任 孔红梅

执行编辑 刘天星 段 靖

生态学报
(SHENGTAI XUEBAO)
(半月刊 1981 年 3 月创刊)
第 31 卷 第 12 期 (2011 年 6 月)

ACTA ECOLOGICA SINICA
(Semimonthly, Started in 1981)
Vol. 31 No. 12 2011

编 辑	《生态学报》编辑部 地址: 北京海淀区双清路 18 号 邮政编码: 100085 电话: (010) 62941099 www. ecologica. cn shengtaixuebao@ rcees. ac. cn	Edited by Editorial board of ACTA ECOLOGICA SINICA Add: 18, Shuangqing Street, Haidian, Beijing 100085, China Tel: (010) 62941099 www. ecologica. cn Shengtaixuebao@ rcees. ac. cn
主 编	冯宗炜	Editor-in-chief FENG Zong-Wei
主 管	中国科学技术协会	Supervised by China Association for Science and Technology
主 办	中国生态学学会 中国科学院生态环境研究中心 地址: 北京海淀区双清路 18 号 邮政编码: 100085	Sponsored by Ecological Society of China Research Center for Eco-environmental Sciences, CAS Add: 18, Shuangqing Street, Haidian, Beijing 100085, China
出 版	科学出版社 地址: 北京东黄城根北街 16 号 邮政编码: 100717	Published by Science Press Add: 16 Donghuangchenggen North Street, Beijing 100717, China
印 刷	北京北林印刷厂	Printed by Beijing Bei Lin Printing House, Beijing 100083, China
发 行	科学出版社 地址: 东黄城根北街 16 号 邮政编码: 100717 电话: (010) 64034563 E-mail: journal@ cspg. net	Distributed by Science Press Add: 16 Donghuangchenggen North Street, Beijing 100717, China Tel: (010) 64034563 E-mail: journal@ cspg. net
订 购	全国各地邮局	Domestic All Local Post Offices in China
国外发行	中国国际图书贸易总公司 地址: 北京 399 信箱 邮政编码: 100044	Foreign China International Book Trading Corporation Add: P. O. Box 399 Beijing 100044, China
广告经营 许 可 证	京海工商广字第 8013 号	



ISSN 1000-0933
CN 11-2031/Q

国内外公开发行

国内邮发代号 82-7

国外发行代号 M670

定价 70.00 元