

生态交错带及其研究进展

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摘要 生态交错带研究对探索自然生态规律和保护环境有重要意义。近 30a 来 ,有关生态交错带的论文数平均年增 57% ,显示其得到了愈来愈广泛的关注。回顾了生态交错带概念的产生与发展 ,区分了它与边缘、生态边界层与生态过渡带等概念的异同 ,简述了其 7 个基本属性 ,即高生物多样性、丰富的特有种、大量外来种、频繁的物质流动、敏感的时空动态性、结构的异质性和脆弱性 ;总结提炼了生态交错带的基本原理和假说 ,综述了生态交错带的生物多样性产生机制、对全球变化的响应与反馈、生态设计与管理以及生态交错带模型发展和整合的研究进展。提出今后需要大力发展理论研究、多尺度模型转化和多因子综合分析 ,以完善生态交错带理论并支持生态学机理的探索。

关键词 生态交错带 ,生态边界层 ,生态过渡带 ,生物多样性 ,全球变化 ,模型

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A review of ecotone : concepts , attributes , theories and research advances

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Abstract : Ecotone is a unique landscape that displays special ecology attributes and service functions. Investigation of ecotone is significantly beneficial to both exploring novel ecological laws and conserving the vulnerable environment. An increasing attention to ecotone is evidenced by the average annual publication growth rate of 57% in the last 30 years. This paper presents the concepts of and the differences among ecotones , and its related terms (ecological boundary , transitional area , environmental gradient and edge). Specifically , ecotone is a region between two ecological systems with unique ecological properties , and ecological boundary is a generic term including all kinds of interfaces , while transitional area is a description of the scope between adjacent geographic zones. Edges and environmental gradient are terms not confined to ecological discipline. Furthermore , seven basic features of ecotone are summarized in brief as : high-biodiversity , rich ecotonal species , abundant exotic species , frequent material flows , sensitive temporal-spatial dynamics , structure heterogeneity and fragility. Then , we introduced the published principals and hypotheses about ecotone as well as originally presented Gene Hybrid Zone Hypothesis , Habitat Pressure Hypothesis , and System Successional Hypothesis to elucidate the mechanisms of ecotone. At last , research advances are discussed in four aspects : (1) The patterns of

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biodiversity development in ecotones. More and more researches have been exhibiting that ecotone creates genetic diversity although its species richness is still controversial. (2) Responses and feedback to global changes. Ecotone is very sensitive to global changes (warmer climate, disturbances, and biological invasion, etc.). The changes of landscape in ecotones are presumably due to the alteration of varied material flows. (3) Ecological design and management of ecotones. Many researches are performed on the functions of conduit, filter and barrier of ecotones, particularly in land/water interface. The uptake of nutrients by ecotones functions cleaning river water. (4) The models of ecotones and its integration. The dynamic of plants movement and the relationship of plants and soil in ecotones are simulated by kinds of ecotone models. However, integrated models are still deficient. We conclude that the highlights of future research should be ecotone theories, multi-scale models and multi-variable integrated analysis of ecotone patterns to discover ecological mechanisms of ecotone.

Key Words: ecotone; ecological boundary; transitional area; biodiversity; global change; model

生态交错带 (Ecotone) 是一个基本的景观单位^[1,2], 是生态系统管理的重要基础^[3-5]。20 世纪 70 年代以来, 生态研究重点从典型生态系统转移到生态交错带^[6], 之后有关生态交错带论文数目不断增长, 近 5 a 内平均每年发表 86 篇, 1975 ~ 2005 a 平均年增长 57% (图 1)。其结构和功能特殊性的研究覆盖了多个生态学分支领域。2000 年纽约“生态镶嵌界层的结构和功能”(SFEM) 讨论会综合了当时生态界层研究的最新成果, 明确了生态交错带综合研究的必要性和迫切性^[7], 开创了生态交错带研究的新局面。

1 生态交错带及其类似术语

1.1 生态交错带

生态交错带最早由 Clements 提出, 指由气候决定的植物群丛交迭的应力区, 主要包括 3 个类型: 边缘 (Local edges or margins)、树线 (Treeline) 和群落交错带 (Biome ecotone)^[6,8]。后来文献所阐释的概念多是基于两个群落之间的交错带^[7,9,10]。目前普遍认可的定义是 1987 年法国巴黎 SCOPE 会议上确定的, 即“相邻生态系统之间的交错带, 其特征由相邻生态系统相互作用的空间、时间及强度所决定”^[11]。不过这个定义依然是一个起点^[12], 关于定义的争论仍在进行, 比较有代表性的是由 Lloyd 等^[13]综合很多定义后提出的——生态交错带是植被空间变化比相邻区域更迅速的区域。

生态交错带具有明显的尺度特征, 尺度也应是其定义的一部分^[4]。因此, Gosz^[12]提出 5 个等级的生态交错带类型, 依次为植物交错带 (Plant ecotone)、种群交错带 (Population ecotone)、斑块交错带 (Patch ecotone)、景观交错带 (Landscape ecotone) 和群区交错带 (Biome ecotone)。但是, 并非生态交错带的所有基本属性都有尺度依赖性, 例如 Stowe 等^[15]研究了假山毛榉森林-亚高山灌丛交错带的物种多样性与异质性后, 就没有发现其尺度依赖性。

1.2 类似术语比较

生态交错带、生态边界层 (Ecological boundary)、生态过渡带 (Ecological transitional zone)、边缘 (Edges) 与环境梯度带 (Environmental gradients zone) 等常见的术语在不同的文献中, 含义常有所变化, 生态交错带、生态过渡带以及生态边界层有时更被认为是同义语^[16,17], 不同文献中各个术语含义的不统一, 对生态交错带性质以及理论研究都非常不利, 有必要明确各个术语的含义及其它们之间的差异 (表 1)。

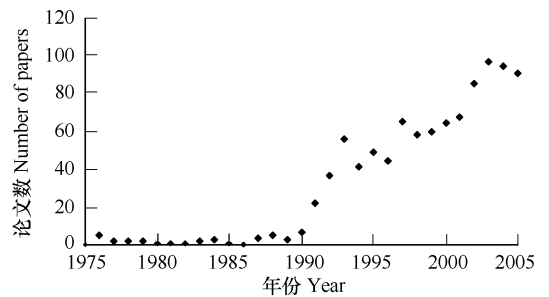


图 1 1975 ~ 2005 年生态交错带论文数量年动态

Fig. 1 Annual number of papers on ecotone from 1975 to 2005

数据来源于 2006-01-04 检索 ISI web of science 数据库; 1975 ~ 2005 年间题目、关键词或摘要出现“Ecotone”的论文数量 Annual number of publications (1975 - 2005) from the ISI Web of Science database that included “ecotone” in their title, abstract, or key words. The search was conducted on 4 January 2006 using the science database only and including all documents types

表 1 生态交错带及其相关术语的定义与描述

Table 1 The definitions and/or descriptions of ecotone and its related terms

名称 Term	命名人 Nomenclator	年代 Year	定义 Definitions/Descriptions
生态交错带 Ecotone	F. E. Clements	1905	气候决定的植物群丛交迭的应力区 Tension zones between climatically determined plant associations where species overlapped
	SCOPE 会议 SCOPE (Scientific Committee On Problems of the Environment meeting)	1987	相邻生态系统之间的过渡带 Transitional areas between adjacent ecological systems
生态边界层 Ecological boundary	Institute of Ecosystem Studies (IES) 研讨会 Workshop of IES	2000	是相邻斑块之间的区域,是复杂和多维的,标显斑块的极限 The zones between two neighboring patches, are complex and multidimensional and mark patch limits 边缘
边缘 Edge	F. E. Clements/A. Leopold	1907/1933	边界线/群落之间狭窄的过渡区 Margins or narrow transitional area between communities
生态过渡带 Ecological transitional area	没有特定的描述人,有时指大尺度气候地理带之间过渡地带 No specific nomenclator, transitional area between geographical zones or climate zones		
环境梯度带 Environmental gradients	没有特定描述人,指环境因子迅速变化的区域 No specific nomenclator, a zone where environmental factors change fast		

早期文献中生态交错带的含义比较狭窄,主要着力于两个相对同质群落之间随着时间变化而出现不同群落类型的敏感区域^[18~20]。SCOPE 会议将生态交错带定义范围扩大,指两个生态系统之间的区域,也内含了尺度特性。因为其定义一直处于讨论之中,即便目前不同文献中所指的生态交错带的具体含义仍不尽相同。尽管如此,生态交错带是一个生态学专有名词,具备特有的生态学特征。

边缘本身没有生态学的特有含义,泛指一个系统的边界区域。Leopold^[21]提出边缘效应,即景观边缘的物种丰富度高于其相邻生境的现象,生态交错带本是相邻生态系统的边缘,常常表现出边缘效应,因此在有关生态交错带的研究中,边缘效应频频出现。但不同学者对其界定不尽相同^[21~22],生态斑块的交错区也常被称作边缘,而有些文献所指的边缘和生态交错带概念一致^[23]。

环境梯度带被用来表达环境因子的梯度特性,表示空间上的某种环境指标的梯度变化。例如,水分梯度,海拔梯度,温度梯度,盐度梯度等,仅指环境本身的梯度特性,易于量化。环境梯度带主要是物理层面的,与生态交错带具有生态特性和规律的本质不同。生态交错带一般都具有环境梯度的特点,但环境梯度带不一定是生态交错带。

生态交错带和生态过渡带在中文文献里常被混用。尽管都可以指两种生态系统之间的区域,但前者具有独特的生态特征和多尺度性,是生态学专有名词,而后者则是泛泛的普通描述,没有特定的生态学特征。有时指大尺度气候带、地理带之间的地带,具备部分生态交错带特征。因此,为了不造成意义表达的混淆并与国际表达相一致,生态交错带不宜包括气候带、地理带之间的过渡带,而用生态过渡带描述这种区域。

生态边界层是一个总称,涵盖了生态交错带、生态过渡带、边缘、梯度带等常见类似生态交错带术语的含义。SFBEM 会议提出,多种类似术语的出现,造成对生态系统边界或者生态系统交接区域规律和特点描述的差异,这对于重点的生态区域的规律认识及其理论的提出都是不利的,因而提出生态边界层一词,试图能从综合的角度来促进生态交接区域的研究发展^[24]。生态边界层适用于各个层次和尺度、物理和生物分界面,Cadenasso^[25]给出了其 6 个基本特征,即:生态边界层与其毗邻斑块具有共性或完全不同,梯度性更明显,宽度取决于梯度性,大小和位置随划分特征的不同而变化,功能依赖于生物流或者物质流、能量流、信息流或者梯度性决定的内在过程,是三维的。Strayer^[26]根据其来源与可维持性、空间结构、功能和时间动态等 4 个方面讨论了其分类体系和相应特征。可见,生态边界层忽视经常使用的类似术语之间的差异,将生态边界以及交界区域全部涵盖,关于其生态特征、范围的差异不严格区分,可以对相关的经验研究结果进行全面的系统分析和综合。

2 生态交错带的基本属性与理论

2.1 基本属性

一般认为生态交错带有 7 个基本属性,即高物种多样性、丰富的特有种、大量的外来种、频繁的物质流动、敏感的时空动态性、结构的异质性和脆弱性。

生态交错带受到关注,源于其表现了比相邻系统更高的物种多样性^[10 27~31]。随着生物多样性丧失的加剧以及环保意识的增强,生态交错带的生物多样性特征愈发受到重视。但是也有文献报道,生态交错带不一定体现较高的物种多样性^[13 32]。

生态交错带存在丰富的特有种^[33~35],这一般被作为交错带的基本特征之一^[36~38]。但并不是每个交错带都会出现特有种^[13 32 39~42]。生态交错带具有较高的外来种比例^[6 42],很多论文报道了外来种入侵生态交错带^[43~46],但是 Walker 等^[41]认为这一结论的证据不是很充足。Lloyd 等^[13]及 Walker^[41]认为较大比例的外来种和特有种依赖于具体的生态条件和物种的生态特性。

生态交错带的重要特征之一就是控制或调节横穿景观格局的生态流,即物质、能量和有机体的流动^[47 48]。生态交错带可作为生态流的通道(Conduit)、过滤器(Filter)、障碍(Barrier)、源(Source)和库(Pool)^[49]。生态交错带物质流动的特性集中体现在河岸生态交错带和湿地交错带,以及主要生源要素 C、N、P 和 S 在生态交错带的运移、转化和输入输出过程或其特殊性。

生态交错带时空变化表现为植被组成、结构、优势种、生活史或者土壤的营养条件变化等^[50 51],包括区域和面积变化^[52],还可能受气候、人类干扰等影响^[53 54]。Cook^[55]通过长期实验发现,景观结构对群落结构和动态演替有多方面影响,并随时间推移更加明显。因此,生态交错带时空动态变化也主要是其本身特有的景观结构复杂性的结果。

生态交错带的异质性即群落镶嵌性明显。来自相邻生态系统或者群落的物种因为边缘效应,或生境斑块化,形成多种群落并存的景观。但并非每个生态交错带都会有异质性特点,因交错带位置和特点的差异而不同^[41]。

生态交错带的脆弱性指对干扰或环境变化的敏感性以及生态系统的难以恢复性,因此有学者认为交错带即脆弱带^[56]。不过,常学礼等^[17]提出只有表现出退化趋势的交错带才是脆弱带。生态交错带脆弱性集中反映在农牧交错带、绿洲荒漠交错带等人地关系紧张区。

近来又发现了生态交错带的一些新特征。例如,在生态交错带,同一个种对同一个环境因子的响应可以表现出完全不同的几个特征,生态交错带不仅是一个植被分布非连续带,而且是环境因素梯度带,还是一个诸如花粉传播特征、叶长、固氮能力、种子寿命等特征谱的非连续带^[57]。

2.2 基本原理和功能假说

生态交错带理论应能解释其基本特征,揭示其生态学过程。有关生态交错带理论的研究相比实验研究要少得多。在多数理论研究文献中,只是对其概念发展或基本特征作些阐释^[58 59],少部分文献提出了一些基本原理和功能假说。本研究根据对大量的生态交错带文献的综合分析,总结或提出以下的原理和假说。

2.2.1 质量效应原理

交错带物种多样性的现象用空间质量效应(Spatial mass effect)原理来解释,最先是由 Shmida 提出的。指在一个区域不能建群的物种的某些个体在该区域能生存下来。也就是说一个种的某些个体从它自身能够成功建群的区域转移到一个不适其生存的区域^[60]。质量效应原理的存在,使得交错带相邻生态系统的物种能够在交错带共存,表现出比相邻系统更多的物种多样性。

2.2.2 中等差异假说

质量效应并不能完全解释交错带物种多样性特征。因此 Kunin 提出中等差异假说作为质量效应原理的补充。当两个相邻斑块之间的差异处于中等程度时,质量效应最强,而当差异过大或者过小时,质量效应较弱^[61]。很多的交错带表现出物种减少的特点,即相邻系统物种不能跨越系统边界而在交错区域成活,这可能

是两种相邻系统的差异较大,物理流加强,而生物流降低的结果。

2.2.3 繁殖体密度假说

繁殖体密度假说主要从相邻斑块种及种群特性影响质量效应的强度来解释交错区域景观特征受到的影响。一个植物种能够成功入侵相邻斑块的可能性在某种程度上取决于入侵的繁殖体的数量。因此种子生产力大的品种将比弱的品种具有更强的在不适合生存的目的斑块的生存能力。种子扩散能力的种间差异也是一个重要因素,扩散更远的品种更容易跨越环境边界^[61]。所以,相邻斑块种群的不同性质也决定了其交错带的景观特征的不同。

2.2.4 基因杂交区假说

从大量越来越多的遗传方面的实验研究的结果提出,生态交错带是一个基因杂交带,通过基因重组和突变,可能产生新种,即所谓的交错带特有种^[62]。特有种可能适宜这种镶嵌的生境并能被保持下来,交错带形成其特有的生境^[63],这有利于提高交错带的生物多样性。即使交错带没有表现出物种多样性,它也内涵了丰富的基因多样性。

2.2.5 生境压力假说

生态交错带具有不同的环境因素,对相邻系统的物种构成了选择压力,有些物种可以跨越边界而在交错带存活。跨入生态交错带的物种和相邻系统的物种可能形成生殖隔离,随着选择压力和选择方向的不同,可能产生新种。而很多相邻系统的物种也许并不能穿越系统边界在交错带存活^[64],形成交错带物种多样性降低,具有很高的不稳定性和脆弱性。因此交错带特征可能与相邻系统物种类型紧密相关^[13,41]。

2.2.6 热力学第二定律

SFBEM 会议提出生态交错带相邻系统生产力不同,导致能量流动将从高生产力斑块流向低生产力斑块,符合热力学第二定律原理。生态交错带具有高的边缘/面积比率,这种特性导致具有高的边缘周转和通透性,物质能量流动加强^[7]。所以生态交错带具有强的物质流动的特点,时空动态性增强。

2.2.7 系统演替假说

生态交错带构成了一个独立的生态系统,其在时间轴上处于动态连续的演替之中,Kolasa^[4]提出生态交错带的识别以及特征都依赖于时间轴上的点,不同时间点上生态交错带的大小以及性质都会发生变化。SFBEM 会议也提出在不同时间点上观察,生态交错带的植被或者群落特征都会表现不同的特点,因此生态交错带处于不断演替的状态,对生态交错带的具体描述,应该指明其所处的演替阶段的差异。对生态交错带特性以及机制的研究应将其作为一个演替的动态系统。

关于生态交错带的原理和假说非常复杂,目前还没有一个统一的原理可以解释所有的交错带现象,生态交错带的尺度特性,多维性以及特征和功能的多样性使得建立唯一的交错带理论非常困难。但是综合的理论研究仍然显得非常必要。

3 生态交错带重要研究进展

3.1 生态交错带与高生物多样性

空间质量效应^[65]、植被镶嵌化^[6]、人类干扰^[66]、高生产力和较大的环境变化^[67]都可能造成其生物多样性增加。Kies^[23]提出可以从4个方面来解释生物多样性增加的响应,即生态流(包括物质流动、生物流动和能量流动)、资源的可接近性、资源的配置以及种间相互作用。斑块尺度上植被组成的变异可能只是因优势种特征和土壤结构性质的变化而不同,与地理分布范围及相邻群系是否出现不相关^[68]。近来,更多的研究从遗传水平探索生态交错带生物多样性产生的原因。

生态交错带栖息地多样化创造了多样的物种形态,随之而产生了可遗传的多样物种。环境梯度变化产生形态变异、交配方式变异,生殖隔离通过生态交错带进化并保持^[64]。不同栖息地选择比地理隔离更能引起适应性形态分化^[63]。依赖栖息地的选择影响一些具有生态意义的特征,形成形态和行为分化^[69],这些分化特征促进了相应的交配,从而建立沿着环境梯度的遗传分化的机制。生态交错带存在杂交区现象^[62],杂交种的

适应性比来自不同区域的纯种的适应能力强^[70]。生态交错带促进了基因杂交,产生了更多的可保持的遗传变异。此外,生态交错带还对基因漂移有重要阻碍作用^[71]。

当然,也有生态交错带具有较低物种多样性的报道^[15, 72, 73],但没有解释其原因。然而低物种多样性并不意味着低的遗传多样性。Thomas 等^[74]对非洲热带森林和草原生态交错带 6 种绿鸭 (*Andropadus virens*) 与热带森林 6 种绿鸭形态和遗传分化进行了比较研究,发现生态交错带通过自然选择获得较多遗传变异,对增加热带森林生物多样性起着重要作用,即使该交错带没有高的物种多样性。

3.2 生态交错带对全球变化的响应与反馈

生态交错带是一个温度敏感地带,气候变暖对其植被变化有显著影响,这一现象在很多森林草原交错带尤为明显,即森林向草地的侵入^[75, 76]。中国长白山落叶松、白桦沼泽生态交错带的沼泽群落可能在 50 ~ 60 a 的时间内演替为地带性森林群落^[77]。这种侵入演替可通过首先侵入森林边缘或种子雨区域或两者并行等多种方式进行^[78, 79]。

除了气候变暖,其它全球变化因子对交错带动态变化也有重要影响,例如干扰。火灾可促进森林向草地侵入^[80],增加火灾频率也可抑制侵入发生^[81]。人类活动增强可改变交错带环境^[82, 83],如放牧加速森林向草原侵入^[79, 80]。美国德州中部海岸带雪鹅放养对狐米草优势群落产生影响,与气候叠加造成海岸带景观斑块化^[84]。人为改变海岸带环境造成南方芦苇 (*Phragmites australis*) 的扩张^[85]。作为全球变化的一个重要现象,生物入侵在交错带的发生可能是因为气候变化改变了种间相互作用和繁殖方式。Elliott 和 Baker 发现入侵种开始建群靠种子繁殖,爆发则主要通过无性繁殖,特别年份进行有性生殖,长期气候变暖导致外来种入侵和大量持续繁殖^[86]。

生态交错带植被与气候的响应关系与物质流动有关,交错带植被组成的不同以及地貌梯度会导致其化学物质循环差异,从而对气候变化有不同的反馈。不同纬度、不同经度以及不同土壤特性,尤其是不同土壤氮含量和 pH 值的交错带,对大气碳量的贡献不同^[87]。气候变暖引起的氮循环速率差异可能是土壤水分状况和植被覆盖度差别的结果^[88]。氮矿化作用是影响交错带与气候变暖响应关系的重要因子,能更有效地阐述二者间的响应关系^[89]。Hood^[90]等发现交错带土壤碳氮比的样带梯度变化可以解释 78% 可溶性有机碳和 70% 的可溶性有机氮的浓度变化。交错带植被对气温变化的响应也影响甲烷通量^[91]。

3.3 生态交错带与生态系统管理

生态交错带具有加强或者集中物质转移及生物流动的特点。Tobias^[92]研究发现河口湿地边缘 1 ~ 1.5 m 湿地集中了所有氮循环过程,那里的有机物质和铵是最丰富的。Hood^[93]等发现在夏末和秋季高山带湖泊海藻和微生物是树线以上有机碳的重要源,这种流动过程不仅影响了亚高山带湖泊系统有机碳的含量,也影响了其化学性质。明确物质流动途径可全流域有效管理相关生态系统。

在景观尺度上,湿地影响许多功能性景观特性^[94]。微生物过程,截留悬浮物质,以及植物吸收都促进了营养在湿地生态交错带的保持。这种营养保持功能在不同的湿地类型有所不同,氮的吸收率变化范围从 14% 到 100%,而磷从 4% 到 80%^[95]。因而,在不同程度上,湿地生态交错带通过截留营养和沉淀物提高了下游水质。生态交错带的截留和过滤功能已经被应用于景观设计和环境治理。

3.4 生态交错带模型与整合研究

生态交错带模型研究自 90 年代以来逐渐成为有吸引力的研究方向,主要模拟交错带植被结构与变动过程,包括植物个体水平^[96, 97]、植被水平^[54]和生态系统水平模拟植被动态规律^[98],预测其对环境变化的响应。

Peters 的 ECOTONE 模型可以反映并预测气候和土壤水分变化下优势种的生活史和木本植物向草地推进的情况^[97]。FORSAT 模型,从火灾频率、气候和土壤肥沃度,解释森林草原带的动态,并能基于未来气候变化预测植被的响应^[99]。

Ries 和 Sisk^[100]建立了不同种的边缘效应概念模型,可以预测边缘效应的具体变化。Malanson^[101]等应用模型得出,土壤资源平均分配不是决定生态交错带植被分布规律的唯一原因。Callaghan^[102]等发现对交错带

植被动态模拟应纳入人为因素。Sanderson^[103]等模拟美国加州海岸带盐沼植被结构分布规律时,发现其分布规律只与距离不同大小的潮水沟的累积距离有关。Peters^[104]以几十年的观测资料建立模型,阐明美国北部草原沙漠交错带两种草本植物的分布变动对气温和降雨的响应。Seastedt^[105]利用概念模型,解释了冻土森林交错带以及高海拔湖泊系统之间能量流动、物质转移过程、大气输入和内生资源如何被加强和削弱的过程。

交错带特征的阐释及其生态学过程的描述和模拟都存在尺度转换问题,大尺度交错带规律的模拟研究比较缺乏,而小尺度研究只能说明局部的生态现象。美国国家科学基金长期生态研究网络(LTER)对单个研究区域不同领域的研究数据进行了统一性和一致性整合,积累了支配长期生态系统动态的缓慢生态学过程的海量数据,这对模型的建立和不同尺度的转换都是重要的工作^[106]。目前用统计模型来研究交错带过程,仅见Bowersox和Brown^[107]的报道,值得继续探索。

4 当前研究的不足与未来研究展望

生态交错带各种生态机制并存,因子间关系复杂。几十年来积累了海量的定点观察资料和试验研究结果,但依然难以揭示其生态学过程,甚至一些基本特点的描述也存在分歧。同时大量文献主要集中在对生态交错带基本属性的探索,更多的只是将其作为一个特殊区域用来研究全球变化、生物入侵等热点问题,没有把研究结果与生态交错带的功能和机理联系起来,不利于生态交错带综合性研究,阻碍了其理论研究发展。

今后有关生态交错带的研究,应该把实验结果与生态交错带本身的特性联系起来综合分析,重点应放在不同类型、不同尺度生态交错带特性的比较和联系上,探索生态交错带共性规律和尺度依赖性特点,解释交错带内在机制,丰富生态交错带基础理论。

目前有关生态交错带与全球变化各个因子的关系研究很多,但都局限于某一因子的变化,缺乏各个因子的综合研究。今后需要不同领域研究者加强合作,研究气候、植被、物质流动以及与地理位置和尺度之间的关系,这样有利于揭示更深层的生态规律。因此,模型将是今后研究的主要方向,设计多尺度多因子的试验,收集大量文献,利用建模的方法综合探索各个因子之间的规律是发展的关键。

References :

- [1] Hansen A J, Castri F D, Naiman R J. Ecotones : what and why ? In : A new look at ecotones : Emerging international projects on landscape boundaries. Biol. Int. ,1988 ,17 (Special Issue) 9 -46.
- [2] Wilson J B , Agnew A D Q. Positive-feedback switches in plant communities. Adv. Ecol. Res. ,1992 ,23 :263 -336.
- [3] Neilson R P. Climatic constraints and issues of scale controlling regional biomes. In : Holland M M. , Risser P G. & Naiman R J. eds. Ecotones : the role of landscape boundaries in the management and restoration of changing environments. London ,UK. Chapman & Hall ,1991. 31 -51.
- [4] Kupfer J A , Cairns D M. The suitability of montane ecotones as indicators of global climatic change. Prog. Phys. Geogr ,1996 ,20 (3) :253 -272.
- [5] Allen C D and Breshears D D. Drought-induced shift of a forest-woodland ecotone : rapid landscape response to climate variation. Proc. Natl. Acad. Sci. U. S. A ,1998 ,95 :14839 -14842.
- [6] Risser P G. The status of the science examining ecotones. Bioscience ,1995 ,45 (5) :318 -325.
- [7] Laurance W F , Didham R K , Power M E. Ecological boundaries : a search for synthesis. Trends Ecol. Evol. ,2001 ,16 (2) 70 -71.
- [8] Clements F E. Research methods in ecology. Lincoln Nebraska USA. University of Nebraska Publishing Company ,1905. 334.
- [9] Tansley A G and Chipp T F. Aims and methods in the study of vegetation. London : British Empire Vegetation Committee ,1926.
- [10] Odum E P. Basic Ecology. Philadelphia : Saunders college Publishing ,1983.
- [11] Holland M M. SCOPE/MAB technical consultations on landscape boundaries : report on A SCOPE/MAB workshop on ecotones. Biol. Int. ,1988 ,17 (Special Issue) #7 -106.
- [12] Gosz J R. Ecotone Hierarchies. Ecol. Appl. ,1993 ,3 (3) :369 -376.
- [13] Lloyd K M , McQueen A A M , Lee B J , et al. Evidence on ecotone concepts from switch , environmental and anthropogenic ecotones. J. Veg. Sci ,2000 ,11 (6) :903 -910.
- [14] Kolasa J , Zalewski M. Notes on ecotone attributes and functions. Hydrobiologia ,1995 ,303 (1-3) 1 -7.
- [15] Stowe C J , Kissling W D. Ohlemuller R , et al. Are ecotone properties scale-dependent ? A test from a Nothofagus treeline in southern New

Zealand. *Community Ecology*, 2003, 4 (1) 35—42.

- [16] Wang Q S, Feng Z W, Luo J C. Ecotones and ecological flows. *Chin. J. Ecology*, 1997, 16 (6) 52—58.
- [17] Chang X L, Zhao A F, Li S G. Spatial-temporal scale and hierarchy of vulnerable ecotone. *J Desert Res*, 1999, 19 (2) :115—119.
- [18] Maarel Van der. Ecotones and ecoclines are different. *J Veg. Sci*, 1990, 1 (1) :135—138.
- [19] Jenik J. Ecotone and ecocline-2 questionable concepts in ecology. *Ekologia CSFR*, 1992, 11 243—250.
- [20] Backeus I. Ecotone versus ecocline-vegetation zonation and dynamics around a small reservoir in Tanzania. *J. Biogeogr*, 1993, 20 209—218.
- [21] Leopold A. Game management. New York : Charles Scribners, 1933.
- [22] Clements F E. Plant physiology and ecology. New York : Henry Holt, 1907.
- [23] Ries L, Fletcher R J Jr, et al. Ecological responses to habitat edges : mechanisms, models, and variability explained. *Annu. Rev. Ecol. Evol. Syst.*, 2004, 35 #91—522.
- [24] Cadenasso M L, Pickett S T A, Weathers K C, et al. An interdisciplinary and synthetic approach to ecological boundaries. *Bioscience*, 2003, 53 (8) 717—722.
- [25] Cadenasso M L, Pickett S T A, Weathers K C, et al. A framework for a theory of ecological boundaries. *Bioscience* 2003, 53 (8) 50—758.
- [26] Strayer D L, Mary E P, William F F, et al. A classification of ecological boundaries. *Bioscience*, 2003, 53 (8) 723—729.
- [27] Zólyomi B. Coenotone, ecotone and their role in preserving relic species. *Acta Bot. Hung.*, 1987, 33 (11) 3—18.
- [28] Petts G E. The role of ecotones in aquatic landscape management. In : Naiman R J and Décamps H eds. *The ecology and Management of Aquatic-terrestrial Ecotones*. Paris : UNESCO Parthenon Pub. Group, 1990. 103—104.
- [29] Weckstrom J, Korhola A. Patterns in the distribution, composition and diversity of diatom assemblages in relation to ecoclimatic factors in Arctic Lapland. *J. Biogr.*, 2001, 28 (1) 31—45.
- [30] Williams S E, Marsh H, Winter J. Spatial scale, species diversity, and habitat structure : Small mammals in Australian tropical rain forest. *Ecology*, 2002, 83 (5) :1317—1329.
- [31] Wurzburger N, Hartshorn A S, Hendrick R L. Ectomycorrhizal fungal community structure across a bog-forest ecotone in southeastern Alaska. *Mycorrhiza*, 2004, 14 (6) 383—389.
- [32] Baker J, French K, Whelan R J. The edge effect and ecotonal species : Bird communities across a natural edge in southeastern Australia. *Ecology*, 2002, 83 (11) 3048—3059.
- [33] Beecher W J. Nesting birds and the vegetative substrate. Chicago, Illinois, USA. Chicago Ornithological Society, 1942.
- [34] Johnston V R. Breeding birds of the forest edge in Illinois. *Condor*, 1947, 49 #45—53.
- [35] Johnston D W, Odum E P. Breeding bird populations in relation to plant succession on the Piedmont of Georgia. *Ecology*, 1956, 37 (1) 50—62.
- [36] Imaz A, Hernandez M A, Arino A H, et al. Diversity of soil nematodes across a Mediterranean ecotone. *Appl. Soil Ecol.*, 2002, 20 (3) :191—198.
- [37] Chan K. Bird community patterns in fragmented vegetation zones around streambeds of the Northern Tablelands, New South Wales. *Australian Bird Watcher*, 1995, 16 :11—20.
- [38] Griggs J. American Bird Conservancy's field guide to all the birds of North America. New York : HarperCollins, 1997.
- [39] Menke S B. Lizard community structure across a grassland-creosote bush ecotone in the Chihuahuan Desert Canadian. *J. Zoology-Revue*, 2003, 81 (11) :1829—1838.
- [40] Nielsen E E, Hansen M M, Ruzzante D E, et al. Evidence of a hybrid-zone in Atlantic cod (*Gadus morhua*) in the Baltic and the Danish Belt Sea revealed by individual admixture analysis. *Mol. Ecol.*, 2003, 12 (6) :1497—1508.
- [41] Walker S, Wilson J B, Steel J B, et al. Properties of ecotones : Evidence from five ecotones objectively determined from a coastal vegetation gradient. *J. Veg. Sci.*, 2003, 14 (4) 579—590.
- [42] Amsterdam N L, Brothers T S, and Spingarn A. Forest fragmentation and alien plant invasion of Central Indiana old-growth forests. *Conserv. Biol.*, 1992, 6 (1) 91—100.
- [43] Ewel J J. Invasibility : lessons from South Florida. In : Mooney H A, Drake J A eds. *Ecology of biological invasions of North America and Hawaii*. New York : Springer-Verlag, 1986. 214—230.
- [44] Elias P. Vertical structure, biomass allocation and size inequality in an ecotonal community of an invasive annual (*Impatiens parviflora* DC) on a clearing in SW Slovakia. *Ekologia (CSFR)*, 1992, 11 299—313.
- [45] Puyravaud J P, Pascal J P, Dufour C. Ecotone structure as an indicator of changing forest-savanna boundaries (Linganamakki Region, southern India). *J. Biogeogr*, 1994, 21 (6) 581—593.
- [46] Duggin J A, Gentle C B. Experimental evidence on the importance of disturbance intensity for invasion of *Lantana camara* L. in dry rainforest-open

forest ecotones in north-eastern NSW , Australia. *Forest Ecol. Manag.* ,1998 ,109 :279 —292.

- [47] Forman R T T. The ethics of isolation the spread of disturbance and landscape ecology. In : Turner M G , ed. *Landscape heterogeneity and disturbance*. New York : Springer Verlag ,1987. 213 —229.
- [48] Castri F D. A new look at ecotones emerging international projects on landscape boundaries , *Biol. Int.* ,1988 ,17 (Special Issue) :1 —17.
- [49] Forman R T T , Moore P N. Theoretical foundations for understanding boundaries in landscape mosaics. In Hansen A. J. and Castri F D eds. *Landscape boundaries : consequences for biotic diversity and ecological flows*. New York : Springer Verlag ,1992. 236 —258.
- [50] Gosz J R , Sharpe P J H. Broad-scale concepts for interactions of climate , topography , and biota at biome transitions. *Landscape Ecol.* ,1989 3 (3/4) :229 —243.
- [51] Kieft T L , White C S , Loftin S R , et al. Temporal dynamics in soil carbon and nitrogen resources at a grassland-shrubland ecotone. *Ecology* , 1998 ,79 (2) :671 —683.
- [52] Ross A L , Foster B L , Loving G S. Contrasting effects of plant neighbours on invading *Ulmus rubra* seedlings in a successional grassland. *Ecoscience* ,2003 ,10 (4) :525 —531.
- [53] Noble I R. A model of the responses of ecotones to climate change. *Ecol. Appl.* ,1993 ,3 (3) :396 —403.
- [54] Bachelet D , Lenihan J M , Daly C , et al. Interactions between fire , grazing and climate change at Wind Cave National Park , SD. *Ecol. Model.* , 2000 ,134 (2) :229 —244.
- [55] Cook W M , Yao J Foster B L , et al. Secondary succession in an experimentally fragmented landscape : Community patterns across space and time. *Ecology* ,2005 ,86 (5) :1267 —1279.
- [56] Niu W Y. The discriminatory index with regard to the weakness , overlapness , and breadth of Ecotone. *Acta Ecologica Sinica* ,1989 ,9 (2) :97 —105.
- [57] Lamb E G and Mallik A U. Plant species traits across a riparian-zone/forest ecotone. *J. Veg. Sci.* ,2003 ,14 (6) :853 —858.
- [58] Gao H W. Advancement of theoretical research in ecotone. *Chin. J. Ecology* ,1994 ,13 (1) :32 —38.
- [59] Traut B H. The high salt marsh : A model for ecotone theory. *Ecological Society of America Annual Meeting* ,2001 ,86 :352.
- [60] Shmida A , Wilson M. Biological determinants of species diversity. *J. Biogeogr.* ,1985 ,12 (1) :1 —20.
- [61] Kunin W E. Biodiversity at the edge : A test of the importance of spatial “mass effects” in the Rothamsted Park Grass experiments. *Proc. Natl. Acad. Sci. USA* ,1998 95 :207 —212.
- [62] Gee J M. Gene flow across a climatic barrier between hybridizing avian species , California and Gambel’s quail (*Callipepla californica* and *C. gambelii*). *Evolution* ,2004 ,58 (5) :1108 —1121.
- [63] Smith T B , Calsbeek R , Wayne R K , et al. Testing alternative mechanisms of evolutionary divergence in an African rain forest passerine bird. *J. Evolution. Biol.* ,2005 ,18 (2) :257 —268.
- [64] Patten M A , Rotenberry J T , Zuk M. Habitat Selection , acoustic adaptation , and the evolution of reproductive isolation. *Evolution* ,2004 ,58 (10) :2144 —2155.
- [65] Shmida A , Ellner S. Coexistence of plant species with similar niches. *Vegetatio* ,1984 ,58 (1) :29 —55.
- [66] Okubo S , Kamiyama A , Kitagawa Y , et al. Management and micro-scale landform determine the ground flora of secondary woodlands and their verges in the Tama Hills of Tokyo , Japan. *Biodivers. Conserv.* ,2005 ,14 (9) :2137 —2157.
- [67] Dabrowska-prot E , Luczak J , Wojcik Z. Ecological analysis of two invertebrate groups in the wet alder wood and meadow ecotone. *Ekol. Polska* , 1973 ,21 :753 —809.
- [68] Kroel-Dulay G , Odor P , Peters D P C , et al. Distribution of plant species at a biome transition zone in New Mexico. *J. Veg. Sci.* ,2004 ,15 (4) :531 —538.
- [69] Slabbekoorn H , Smith T B. Habitat-dependent song divergence in the little greenbul : An analysis of environmental selection pressures on acoustic signals. *Evolution* ,2002 ,56 (9) :1849 —1858.
- [70] Cruz R , Garcia C. Using environmental effects on fecundity to compare the adaptive characteristics of the morphs in a hybrid zone of *Littorina saxatilis*. *Evol. Ecol.* ,2003 ,17 (2) :157 —173.
- [71] Wise J , Harasewych M G , Dillon R T. Population divergence in the sinistral whelks of North America , with special reference to the east Florida ecotone. *Mar. Biol.* ,2004 ,145 (6) :1167 —1179.
- [72] Kotze D J , Samways M J. No general edge effects for invertebrates at Afromontane forest/grassland ecotones. *Biodivers. Conserv.* ,2001 ,10 (3) :443 —466.
- [73] Heliola J , Koivula M , Niemela J. Distribution of carabid beetles (Coleoptera , Carabidae) across a boreal forest-clearcut ecotone. *Conserv. Biol.* , 2001 ,15 (2) :370 —377.

- [74] Thomas B S , Robert K W , Derek J G , *et al.* A Role for Ecotones in Generating Rainforest Biodiversity. *Science* , 1997 , 276 (5320) : 1855 – 1857.
- [75] Janssens I A , Freibauer A , Ciais P. Europe's Terrestrial Biosphere Absorbs 7 to 12% of European Anthropogenic CO₂ Emissions. *Science* , 2003 , 300 (5625) : 1538 – 1542.
- [76] <http://ag.arizona.edu/research/archer/research/biblio1.html>
- [77] Mou C C. Succession of *Larix olgensis* and *Betula platyphlla* marsh ecotone communities in Changbai Mountain. *Chin. J. Appl. Ecol.* , 2003 , 14 (11) : 1813 – 1819.
- [78] Doveciak M , Frelich L E , Reich P B. Pathways in old-field succession to white pine : Seed rain , shade , and climate effects. *Ecol. Monogr.* , 2005 , 75 (3) : 363 – 378.
- [79] Norman S P , Taylor A H. Pine forest expansion along a forest-meadow ecotone in northeastern California , USA. *Forest. Ecol. Manag.* , 2005 , 215 (1-3) : 51 – 68.
- [80] Koechy M , Wilson S D. Variation in nitrogen deposition and available soil nitrogen in a forest-grassland ecotone in Canada. *Landscape Ecol.* , 2005 , 20 (2) : 191 – 202.
- [81] Hoffmann W A , Lucatelli VMPC , Silva F J , *et al.* Impact of the invasive alien grass *Melinis minutiflora* at the savanna-forest ecotone in the Brazilian Cerrado. *Divers. Distr.* , 2004 , 10 (2) : 99 – 103.
- [82] Chen P , Gao J H , Zhu D K , *et al.* Analysis of the landscape spatial pattern and influence caused by development and construction activities in coastal ecotone : A case study of Boao District , Hainan Island. *J. Nat. Resour.* , 2002 , 17 (4) : 509 – 514.
- [83] Sun W , Hou Y , Zhang B. An approach to the fluctuation relation among land productivity , population pressure and weakness in ecotone. *Acta Ecologica Sinica* , 2000 , 20 (3) : 369 – 373.
- [84] Miller D L , Smeins F E , Webb J W , *et al.* Mid-Texas , USA coastal marsh vegetation pattern and dynamics as influenced by environmental stress and snow goose herbivory. *Wetlands* , 2005 , 25 (3) : 648 – 658.
- [85] Minchinton T E , Bertness M D. Disturbance-mediated competition and the spread of *Phragmites australis* in a coastal marsh. *Ecol. Appl.* , 2003 , 13 (5) : 1400 – 1416.
- [86] Elliott G P , Baker W L. Quaking aspen (*Populus tremuloides* Michx.) at treeline : a century of change in the San Juan Mountains , Colorado , USA. *J. Biogeogr.* , 2004 , 31 (5) : 733 – 745.
- [87] Sjoogersten S , Turner B L , Mahieu N , *et al.* Soil organic matter biochemistry and potential susceptibility to climatic change across the forest-tundra ecotone in the Fennoscandian mountains. *Global. Change. Biol.* , 2003 , 9 (5) : 759 – 772.
- [88] Shaw M R , Harte J. Response of nitrogen cycling to simulated climate change : differential responses along a subalpine ecotone. *Global Change Biol.* , 2001 , 7 (2) : 193 – 210.
- [89] Sjoogersten S , Wookey P A. The role of soil organic matter quality and physical environment for nitrogen mineralization at the forest-tundra ecotone in Fennoscandia. *Arctic Antarctic Alp. Res.* , 2005 , 37 (1) : 118 – 126.
- [90] Hood E W , Williams M W , Caine N. Landscape controls on organic and inorganic nitrogen leaching across an alpine/subalpine ecotone , Green Lakes Valley , Colorado Front Range. *Ecosystems* , 2003 , 6 (1) : 31 – 45.
- [91] Sjoogersten S , Wookey P A. Spatio-temporal variability and environmental controls of methane fluxes at the forest-tundra ecotone in the Fennoscandian mountains. *Global Change Biol.* , 2002 , 8 (9) : 885 – 894.
- [92] Tobias C R , Anderson I C , Canuel E A , *et al.* Nitrogen cycling through a fringing marsh-aquifer ecotone. *Mar. Ecol. Progr. Ser.* , 2001 , 210 : 25 – 39.
- [93] Hood E , McKnight D M , Williams M W. Sources and chemical character of dissolved organic carbon across an alpine/subalpine ecotone , Green Lakes Valley , Colorado Front Range , United States. *Wat. Resour. Res.* , 2003 , 39 (7) : 1188.
- [94] Johnston C A. Material fluxes across wetland ecotones in northern landscapes. *Ecol. Appl.* , 1993 , 3 (3) : 424 – 440.
- [95] Johnston C A. Sediment and nutrient retention by fresh water wetlands : effects on surface water quality. *Crit. Rev. Environ. Control.* , 1991 , 21 : 491 – 565.
- [96] Menaut J C , Gignoux J , Prado C , *et al.* Tree community dynamics in a humid savanna of the Côte-d'Ivoire : modelling the effects of fire and competition with grass and neighbours. *J. Biogeogr.* , 1990 , 17 : 471 – 481.
- [97] Peters DPC. Plant species dominance at a grassland-shrubland ecotone : an individual-based gap dynamics model of herbaceous and woody species. *Ecol. Model.* , 2002 , 152 (1) : 5 – 32.
- [98] Loehle C , Li B L , Sundell R C. Forest spread and phase transitions at forest-prairie ecotones in Kansas , U. S. A. *Landscape Ecol.* , 1996 , 11 (4) : 225 – 235.

- [99] Favier C, Chave J, Fabing A, *et al.* Modelling forest-savanna mosaic dynamics in man-influenced environments : effects of fire, climate and soil heterogeneity. *Ecol. Model.*, 2004, 171 (1-2) : 85 – 102.
- [100] Ries L, Sisk T D. A predictive model of edge effects. *Ecology*, 2004, 85 (11) : 2917 – 2926.
- [101] Malanson G P, Xiao N C and Alftine K J. A simulation test of the resource-averaging hypothesis of ecotone formation. *J. Veg. Sci.*, 2001, 12 (6) : 743 – 748.
- [102] Callaghan T V, Crawford R M M, Eronen M, *et al.* The dynamics of the tundra-taiga boundary : an overview and suggested coordinated and integrated approach to research. *Ambio*, 2002, Special report (12) : 3 – 5.
- [103] Sanderson E W, Foin T C and Ustin S L. A simple empirical model of salt marsh plant spatial distributions with respect to a tidal channel network. *Ecol. Model.*, 2001, 139 (2-3) : 293 – 307.
- [104] Peters D P C. Climatic variation and simulated patterns in seedling establishment of two dominant grasses at a semi-arid-arid grassland ecotone. *J. Veg. Sci.*, 2000, 11 (4) : 493 – 504.
- [105] Seastedt T R, Bowman W D, Caine T N, *et al.* The landscape continuum : A model for high-elevation ecosystems. *Bioscience*, 2004, 54 (2) : 111 – 121.
- [106] Rastetter E B, Aber J D, Peters D P C, *et al.* Using mechanistic models to scale ecological processes across space and time. *Bioscience*, 2003, 53 (1) : 68 – 76.
- [107] Bowersox M A, Brown D G. Measuring the abruptness of patchy ecotones — A simulation-based comparison of landscape pattern statistics. *Plant Ecol.*, 2001, 156 (1) : 89 – 103.

参考文献 :

- [16] 王庆锁, 冯宗炜, 罗菊春. 生态交错带与生态流. *生态学杂志*, 1997, 16 (6) : 52 ~ 58.
- [17] 常学礼, 赵爱芬, 李胜功. 生态脆弱带的尺度与等级特征. *中国沙漠*, 1999, 19 (2) : 115 ~ 119.
- [56] 牛文元. 生态环境脆弱带 ECOTONE 的基础判定. *生态学报*, 1989, 9 (2) : 97 ~ 105.
- [58] 高洪文. 生态交错带 (Ecotone) 理论研究进展. *生态学杂志*, 1994, 13 (1) : 32 ~ 38.
- [77] 牟长城. 长白山落叶松和白桦-沼泽生态交错带群落演替规律研究. *应用生态学报*, 2003, 14 (11) : 1813 ~ 1819.
- [82] 陈鹏, 高建华, 朱大奎, 等. 海岸带生态交错带景观空间格局及其受开发建设的影响分析——以海南万泉河口博鳌地区为例. *自然资源学报*, 2002, 17 (4) : 509 ~ 514.
- [83] 孙武, 侯玉, 张勃. 生态脆弱带波动性、人口压力、脆弱度之间的关系. *生态学报*, 2000, 20 (3) : 369 ~ 373.