



第三届现代生态学讲座 中国·北京

The Third International Symposium on Modern Ecology, Beijing, China

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# 第三届现代生态学讲座

## 论文摘要集



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# 论文摘要集

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## 分子生态学的揭示力及其对宏观生物学的冲击

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分子生态学作为多学科交叉的新兴学科近十多年获得了空前的发展, 这包括分子标记理论的日趋成熟、实验方法和技术手段的长足进步, 群体遗传新理论体系的建立和完善, 以及分子数据分析方法的突破, 因而使许多宏观生物学研究领域(生态、种群、分类、进化、行为、保护生物学以及生物地理演化等)发生了革命性的飞跃。可以说, 宏观生物学正由传统的以观察、测量、归纳和推理为主的描述性研究向以通过对生物及其种群遗传构成变化的分析而检验和证明科学假设、发现和揭示机制和规律为主的机制性研究转变, 因而使得对具有普遍意义的科学规律、进化过程和机制的探索成为可能。分子生态学研究在许多方面具有传统学科所无法替代的独特揭示力, 例如它赋予我们超越时空限制的研究能力, 即从大空间尺度上追溯过去、评估现在并推测未来演化趋势的研究能力, 而且还从理论上为这种研究的可行性提供了保证。因此, 分子生态学研究给宏观生物学带来了空前的冲击, 简单概括为: 第一, 分子生态学研究从生命现象最深的层次上揭示生物个体、种群、物种以及更高阶元间的差别和共性, 区别遗传和非遗传、同源和非同源(趋同、趋异等)性征, 因此, 极大地提高了我们的分辨能力; 第二, 分子生态学研究不但能定性地, 而且可定量地描述个体、种群、物种间的差别, 追溯和拟合导致这些变化的气候、生态、地质地理、人类活动等因素及其所影响的时空尺度; 第三, 分子生态学研究极大地延伸了我们所能研究的宏观生物学问题的空间跨度、时间尺度、微观尺度、系统性、复杂性、可比性和精确度, 因此空前地提高了我们对具有普遍意义的科学规律、进化过程和机制的探索能力; 第四, 分子生态学研究多方面地促进了众多学科间的交叉、融合和发展, 一方面使得许多学科之间的界限变得模糊或消失, 另一方面催生了新的交叉学科, 因而前所未有地改变了我们的视野、思维方式和思维习惯; 第五, 众多分子生态学研究案例表明, “遗传”和“进化”是解决很多宏观生物学问题所必须考虑的因素, 尽管这些因素本身并不一定能直接导致有关问题的解决。总而言之, 分子生态学研究近十多年来所累积的成果表明, 我们对许多宏观生物学问题至今为止所作的探索还需要在更宽阔的视野下、进行更深层次上的思考和研究, 分子生态学理论、技术和方法空前地拓展了我们的研究空间、提升了我们解决复杂问题的能力; 在实验技术和方法日臻成熟的今天, 分子生态学解决宏观生物学问题的能力的进一步提高在很大程度上依赖于分子进化理论、数据分析理论和方法的进一步突破。



### 植物群落内光环境的异质性和植物的生理生态响应

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对绿色植物来说光既是能源也是传递信息的媒体。绿色植物通过光合作用把光能储存到植物体内，太阳能由此进入生物圈，所以研究植物如何利用光一直是植物生理生态学的核心。在自然环境里尤其是在植物群落内，光强、光质都在不断变化。这些变化可快可慢，可大可小，或者瞬息万变，或者从容有序四季循环，或如林内的光斑，同一叶片上有明暗之分，或如林窗内与林冠下的光明与阴暗，相映成趣。光环境的这种时空变化或时空分布的异质性决定着植物光合作用和其他生命活动，也是影响生态系统的结构和功能的最重要因素之一，这或许是近十多年植物光环境的异质性以及植物对光利用的动态过程受到注意的主要原因。这个报告将主要讨论植物群落内的光合有效光即波长从 400 到 700nm 的可见光的时空异质性，所提出的基本问题是：光环境异质性具有哪些特性以及植物对光环境异质性如何反应。

探讨光环境的异质性可以从比较不同植物群落光环境的时间变动和空间分布开始。植物群落不同，光的垂直分布差异很大。比如草原或草本群落内的光合有效光主要在群落的中下层被吸收，而在阔叶林尤其是热带阔叶林光的吸收主要在群落的上层。光环境的水平分布的异质性取决于冠层结构、天空云量等，草本群落内光的水平分布在小尺度上的空间异质性比森林群落高，而空间自相关总是晴天低阴天高。阳斑，通常指在植物群落里比背景的散射光高的那一部分光，扮演着植物群落内光环境在时空变动的主要角色，在大多数植物群落内阳斑常常占有一天总光能的 60% 以上。植物群落内光环境的异质性受许多因子的影响如叶片排列、植物株型、冠层构造、风速风向、天空云量以及太阳高度等等。所有这些使得对植物群落内光环境异质性的测定和描述仍然遇到很多困难。

植物有很多机制来对周围光环境的异质性作出种种反应、驯化和适应。对光环境异质性的驯化和适应发生在比较大的时空尺度上。该报告只讨论发生在单叶水平上的与阳斑有关的一些研究。这些研究指出，许多森林的下层植物尤其是热带雨林的植物有相当大的一部分光合碳同化是在阳斑下进行的。植物利用阳斑进行光合作用的基本过程，如光由弱到强时的光诱导反应和由强到弱的照后二氧化碳固定反应的生理过程已比较清楚。报告将讨论不同植物在不同环境条件下这两个主要生理过程的一些特征，并试图通过这些讨论来进一步探讨植物群落内光环境异质性的生态学效应。对后者，我们的研究似乎才刚刚开始。



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### Heterogeneity of light environment and its ecological consequences

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Light is both an energy source and a medium of information for green plants. Sun light provides energy for photosynthesis, through which solar energy enters the biosphere. In natural environments, light is highly variable both in time and space. The spatial and temporal heterogeneity of light environment is thought to be the major determinant for plant photosynthesis, growth, and productivity at scales from leaf to ecosystem. This review focuses on the heterogeneity of photosynthetic light, with wavelengths ranging from 400 to 700 nm and referred to as the photosynthetic photon flux within plant canopies. The primary questions in the review are (1) what is the physical nature of light heterogeneity? and (2) how do plants respond to this heterogeneity?

To address the first question, we compared the patterns of spatial distribution and temporal variation of light among various plant canopies. The vertical gradient of light varies considerably in different plant canopies. In grasslands, most light is absorbed at the middle or lower canopy layers, but a large proportion is often absorbed in the upper layers of broadleaf forests. Horizontal distribution within plant canopies depends not only on canopy structure, but also largely upon sky conditions. Small-scale spatial heterogeneity seems to be a more predominant feature in grass than in forest canopies. Spatial correlation coefficients are always lower under sunny skies than under clouds. Sunflecks, which refer to the light exceeding certain threshold values above the background diffuse light, play the most important role in the spatial and temporal heterogeneity of light environment within plant canopies. In most plant canopies surveyed so far, sunflecks often prevail less than 10% of the daytime, but they contribute more than 50% of total daily light energy. Factors including leaf arrangements, plant architecture, canopy structure, wind velocity (speed) and wind direction, sky conditions and solar elevations can all result in the light variations. However, measurements are still not sufficient for a comprehensive assessment of light heterogeneity in plant canopies, particularly those in forests, which can be critical for modeling photosynthesis and production for different ecosystems.

Plants show a large variety of mechanisms in their responses, acclimation and adaptation to the temporal and spatial variation of light environment. The acclimation and adaptation are often considered as the “response” of plants to the large-scale heterogeneity of light environments. This review will focus mainly how plants respond photosynthetically to sunflecks at the single leaf level. Evidences so far reveal that a significant proportion of carbon gain in canopy leaves, particularly those of tropical forest canopies is contributed by sunflecks. Physiologically, photosynthetic utilization of sunflecks is determined by two



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major processes, the limitation of photosynthetic induction response to an increase of light and the carbon gain during post-illumination CO<sub>2</sub> fixation. However, compared with our understandings of the biochemical and physiological mechanisms of these two processes, much remains unanswered about their ecological consequences. This review will discuss the species differences in induction responses and post-illumination CO<sub>2</sub> fixation, and environmental controls on the two photosynthetic processes, which will provide some important insights into our understanding on the ecological roles of light heterogeneity within plant canopies.





## 植物根系的结构功能及其在陆地生态系统物质循环中的地位

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在各个植物器官中，我们对根系的了解最少。根系生存的土壤环境导致采样困难。生活在土壤中的根系不断与周围土壤发生物理、化学和生物作用，很难直接观察它们的生理生态活动，这使得有关根系的知识十分有限。以致于到今天我们仍得面对如根系的结构和功能这类基本的问题。然而，也正是关于根系的知识有限，使根系研究成为一个充满挑战的领域，我们不仅要在数据不足条件下提出富有创新性的理论，还要像最出色的工程师那样设计出研究根系的巧妙方法。

根系作为一个生物结构可从三个角度来研究：结构和功能的关系，形态和生长的规则，以及进化史。在这里我们主要讨论结构和功能的关系，对形态和生长的规则以及进化史只作简单介绍。

根系的结构长期以来一直缺乏一种系统的描述方式，人们只是简单地把根系按直径划分为粗根和细根两部分。这种划分有其合理性：粗根的主要功能是运输水分养分和支撑地上部分，而细根则主要负责养分和水分的吸收。这种划分也有其缺点：不论是粗根还是细根，其所包含的个体根在结构和功能上的差异被忽略了。不过，如果所有细根（或粗根）中的个体根的形态功能指标的频数分布为正态分布，用整个细根水平上的平均值来描述细根的特征也有一定的合理性。

然而，对根系结构尤其是对根系构型的深入研究使基于直径的二分法陷入困境。如果将根系当成河流那样的分形系统来定义，我们发现树木根系是由不同分枝等级的个体根组成的高度有序的集合体。随分枝等级的变化，根系在结构和功能上表现出极大的规律性。此外，不同分枝等级个体根的数量，直径，长度，比根长，表面积，氮含量，呼吸速率等呈现巨大差异，这些差异的存在推翻了过去认为细根在结构功能上基本相似的假设。

个体根在结构和功能上的巨大差异迫使我们重新定义和计算细根周转速率的方法作出修正。细根周转有多种定义，每一种定义和一个特定的测定周转速率方法的相联系。两种目前认为最可靠的方法是微根管法和碳同位素法。在微根管的研究中，细根周转速率被定义为中值寿命的倒数，这种方法测得的细根周转速率约为一年一次。而在碳同位素法中，周转速率被定义为混合细根样品的平均寿命的倒数。这种方法测得的细根周转速率为五到十年一次。由于不同分枝等级根的平均寿命不同，每一分枝等级中的个体根的数量又随分枝等级的降低而以指数方式增加（在这里，最小最短的根被定义为一级根），因此细根是由大量寿命短的低级根和少量寿命长的高级根组成，细根中所有个体根寿命的频数分布严重右偏。这使得微根管法测得的细根中值寿命要比平均寿命小，因而对细根周转速率估计偏高。碳同位素法中所用的混合细根样品中大部分的生物量是由寿命较长，直径较粗的高级根组成，使得这些样品的平均寿命的测值偏高，导致碳同位素法对细根周转速率的估计偏低。新的细根周转的定义和计算方法必须对个体细根在生物量和寿命上的差异给予足够重视，才能使细根周转的测值更接近真实值。

植物根系的构型和生长是否符合分形系统的基本规则也是一个颇有研究价值的问题。解决这一问题需要采集完整根系的形态结构指标。这是一项困难的工作，其成功在很大程度上依赖于根系采





样方法的改进。

根系的进化史的重要性毋庸置疑。但这一问题一直没有得到古植物学家的重视。此外，根系化石之罕见也限制了我们对根的进化史的了解。基于进化生物学和分子生物学证据的一种观点认为：根是植物适应陆地生活的产物，与茎不同源，可能因微生物侵染而形成。随着分子生物学技术在进化生物学中的应用，根系进化之秘相信会逐渐解开。

## Plant root systems: structure, function, and role in nutrient cycling

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Among all plant organs, root is the one we understand the least. This situation is in part due to the “hidden nature” of plant roots. Being buried in the soil thus difficult to sample and observe, the growth of knowledge on roots has been slow. Today, we are still trying to tackle such basic questions as the structure and function of roots. Yet it is these unknowns about roots that make the study of roots a fascinating area of research in which both the ingenuity and stamina of researchers are taxed. Root ecologists are required to formulate the novel theories based on the insufficient data, and to design ingenious techniques to improve the observation of roots.

As with all other biological structures, the study of roots can be conducted from three perspectives, that of linking structure and function, that of rules governing the growth and form, and that of evolutionary history. Here we will focus on the linkage between structure and function, with brief discussions on the rules of root growth and form, and the evolution of roots.

A systematic framework of root structure was absent in the most history of root study. Plant root systems were roughly divided into two parts: fine roots, whose diameter are less than 2mm, and coarse roots, whose diameters are greater than 2mm. This classification has its merits: it recognizes fine roots as the primary structure for resource uptake, and coarse roots the main structure for transport and anchorage. Yet such a classification ignores the differences within the fine (coarse) root guild.

Recent studies of root structure from an architectural point of view have highlighted the flaw of this two-way classification based solely on root diameter. These studies showed that tree fine roots are distinctly different root individuals distributed on highly complex fine root branching networks. These networks of roots, when classified into different branch orders, displayed systematic variations in their morphology and function. When compared to higher orders, more distal lower order (i.e., first order) have thinner diameter with higher specific root length (SRL), higher tissue nitrogen (N) concentrations and higher maintenance respiration rates, lower carbon (C) storage, and shorter lifespan. The marked differences among individual fine roots have overturned the traditional assumption of fine roots being a collection of identical units.



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The complexity and multi-functionality of tree fine roots demand a revision of the definition and calculation method of fine root turnover. Various definitions of fine root turnover exist in the literature, with each associated with a particular method. Among all methods of estimating fine root turnover rate, minirhizotron and C tracer methods have been considered the most promising. Yet the two methods have yielded vastly different turnover rates, with an average turnover rate of 1 yr<sup>-1</sup> reported in minirhizotron studies, and a rate of 0.1-0.3 yr<sup>-1</sup> reported by tracer methods. Because the number of individual roots decreases exponentially with increasing root order, and because the average longevity of each root order differed markedly, longevity distribution of fine roots are inevitably right-skewed, with a large number of short-lived roots on the left of the distribution, and a small number of long-lived roots on the right. In consequence, using the inverse of the median longevity will overestimate root turnover rate in minirhizotron studies, while using the average longevity of a fine root biomass sample (whose biomass is composed of mostly the long-lived root tissue) in tracer methods will underestimate root turnover rate. A more accurate quantification of root turnover requires a clear understanding of both the biomass and longevity of individual fine roots.

With respect to the rules of growth and form of root systems, fractal geometry has been deemed as a powerful model. An empirical test of whether growth and architecture of root systems follows the rules of a self-similar fractal, sampling of complete root systems is needed. This is difficult task, its success hinges upon the improvement of root sampling techniques.

Compared to our understanding of root structure and function, evolutionary history of roots is like a mystery. This is in part due to the lack of preservation of roots in the fossil record. However, based on the evidence of molecular biology, it has been proposed that roots evolved while adapting the land, that roots and shoots are not homologous, and that roots may have emerged due to the infection by root inducing bacteria. The uncovering of the mystery of root evolutionary origin awaits better evidence from both palaeobotanists and the application of molecular techniques in root studies.



### 种群动态、生态位理论和中性宏生态学 (neutral macroecology)

何芳良

(加拿大阿尔伯特大学)

种群动态研究的是种群时空变化及引起和影响这些变化的因子。起源于种群动态理论的生态位理论假设每个物种在群落结构中都有着独特的作用，而这种独特性就是物种共存的条件。尽管生态位理论在连接群落结构与种群动态方面非常重要，但是从种群基本过程去解释群落构建规律一直以来是生态学家所追求的目标。最新发展的生物多样性中性理论 (neutral theory of biodiversity) (Hubbell 2001) 重新激发了人们从种群动态的角度去发展宏生态理论的兴趣。我的目的是：(1) 介绍Hubbell中性理论的概念框架 (conceptual framework)；(2) 回顾中性理论的最新发展；(3) 提出我自己对于中性宏生态学未来发展的带有个人偏见的观点 (biased perspective)。

尽管数学推导越来越复杂，但是中性理论所关心的那些分布区重叠且营养级相近、竞争相同或相似资源的物种所组成的群体，中性理论最初是建立在两个基本的然而却很简单的原则之上。第一个基本假设是群落中各物种在竞争力和重要的种群参数如出生率、死亡率、传播和物种形成等是基本相等的。第二个原则是所谓的“零和游戏” (zero-sum game)。“零和游戏”假设一个群落因被占据而始终处于饱和状态，因此由一个占据者死亡所释放出的空间，必然会被一个新出生的占据者所填补。那么群落生态学的核心主题就应该用这一理论重新解释各种宏生态学模式产生和维持机制，如相对物种丰富度、种数-面积关系、 $\beta$ 多样性和系统发育等。

自从Hubbell的书出版以来，中性理论就成为一个研究的重要主题。近年来许多主要概念和技术已经得到了发展，而这一理论本身的发展也已经远远超出了Hubbell最初那本书的内容。这些发展包括空间结构中性模型 (Chave and Leigh 2002; Chave 2004)、连续时间马尔可夫链模型 (Volkov et al. 2003; McKane et al. 2004; He 2005)、由多变量Evens等位基因分布延伸而来的谱系模型 (Etienne and Olff 2004; Etienne 2005)、抽样理论 (sampling theory) (Vallade and Houchmandzadeh 2003; Alonso and McKane 2004) 和用Simpson指数重新解释Hubble的生物多样性参数 (He and Hu 2005; Nee 2005)。在这里我不是要详细的列举所有的发展，而是集中讨论连续时间马尔可夫链模型并展示如何把种群基本动态过程，如出生、死亡、迁移和物种形成，结合起来解释宏生态的多样性格局。

中性理论为理解群落组成规律提供了许多机会。其中之一就是回答如何调和中性理论与生态位理论这一问题。与生态位范例形成了强烈的对比，当前的中性理论并不要求共存物种间有生态位分化，因而生态位在这里没有发挥作用的空间。如果能够把中性理论和生态位理论的关键要素结合起来解释群落多样性模式，那么这将是一次真正的生态学突破 (Chase 2005)。有待于从理论上突破的挑战性问题还包括：(1) 除了物种丰富度和种数-面积关系外，发展和验证其它重要的宏生态学模式；(2) 估计物种灭绝的时间和速率；(3) 通过真正统一的中性理论把生态多样性与遗传多样性统一起来；(4) 在入侵生物学的背景下理解“零和游戏”对生物多样性保护的意义。



### **Population dynamics, niche theory, and neutral macroecology**

**Fangliang He**

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Population dynamics studies the spatial and temporal changes of populations and the factors that cause and influence those changes. Niche theory, stemming from the theory of population dynamics, assumes that each species plays a unique role in structuring a community and the uniqueness is the condition of species coexistence. Despite the apparent significance of niche theory in linking community structures to population dynamics, the goal to derive the assembly rules of communities from fundamental population processes has been elusive. The newly developed neutral theory of biodiversity (Hubbell 2001) has re-invigorated the interest in developing theoretical understandings of macroecological patterns from the perspective of population dynamics. My objectives are: (1) introduce the conceptual framework of Hubbell's neutral theory, (2) overview its recent development, and (3) provide my biased perspective about the future development of neutral macroecology.

Although the mathematical formulations are increasingly sophisticated, the neutral theory that concerns groups of sympatric and trophically similar species competing for the same or similar resources was originally built on two fundamental, yet simple tenets. The first one postulates that species in a community are functionally equivalent in terms of competitiveness and vital demographic rates such as birth, death dispersal and speciation. The second tenet is the so-called zero-sum game that assumes a community is constantly saturated with occupants so that the space freed up from a death must be filled in by a birth. The central themes of community ecology could then be reinterpreted from the theory, resulting in new explanations for the origin and maintenance of a variety of macroecological patterns, including the relative species abundance, the species-area relationship,  $\beta$  diversity, and phylogeny.

Since the publication of Hubbell's book, the neutral theory has become a most intensively studied subject. Several major conceptual and technical developments have now been made and the theory has been advanced much beyond the original version of Hubbell's. These include spatially structured neutral model (Chave and Leigh 2002; Chave 2004), continuous time Markov chain model (Volkov et al. 2003; McKane et al. 2004; He 2005), the genealogical model extended from multivariate Ewens allele distribution (Etienne and Olf 2004; Etienne 2005), sampling theory (Vallade and Houchmandzadeh 2003; Alonso and McKane 2004), and the reinterpretation of the fundamental biodiversity in terms of the Simpson index (He and Hu 2005; Nee 2005). Instead of counting all these developments in detail, I will focus on the continuous time Markov chain model and show how fundamental population dynamic processes such as birth, death, migration and speciation could be incorporated to interpret macroecological



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diversity patterns.

The theoretical framework of the neutral theory provides many opportunities for major theoretical contributions to understanding community assembly rules. One such opportunity lies in the answers to the question of how to reconcile neutral theory and niche theory. The current neutral theory, in sharp contrast with the niche paradigm, does not require niche differentiation for species coexistence and thus leaves no room for niche to play a role. A real ecological breakthrough will be made if key elements of both neutral and niche theories can be combined to account for community diversity patterns (Chase 2005). Challenging problems awaiting theoretical assaults also include: (1) developing and testing other important macroecological patterns besides the species-abundance and species-area relationships, (2) estimating time and rates of species extinction, (3) integrating ecological diversity and genetic diversity by a truly unified neutral theory, and (4) understanding the implications of the zero-sum game to diversity conservation in the context of invasive biology.

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### 植物和生态系统对全球变化响应的地下生物调控机制

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人类行为正在引起地球环境系统的一系列急剧变化, 尤其是大气组分、气温、植物种类与群落结构的变化。对于这些全球性变化, 诸如大气 CO<sub>2</sub> 浓度与气温上升, 氮沉降增加和外来物种入侵等, 陆地生态系统也在发生一些相应的快速响应。但是, 至今大量研究注意力主要集中在陆地生态系统地上部分, 对地下植物根系和土壤生物响应方面的认识还比较欠缺。植物根系是地下生态系统过程的主要驱动力, 它通过资源竞争和生物拮抗效应来改变植物的生存与生长, 进而影响陆地生态系统的植物群落结构和功能。土壤中生活大量的微生物和微小动物, 它们通过调控土壤养分的植物有效性, 以及影响土壤结构和抑制土生病原体的活性, 来实现对陆地生态系统的调节作用。在本文中, 我们首先回顾了地下生物过程对 CO<sub>2</sub> 浓度升高、氮沉降增加、气温变暖和外源物种入侵响应方面的试验结果。然后, 我们综合归纳了植物和生态系统对人为活动所引起的大气组分和植物物种组成变化响应的土壤生物调节机制。最后, 本文还指出了在全球变化对植物-微生物互作影响研究领域的一些知识空白, 并就如何提高全球变化对生态系统结构和功能影响的试验方法提出了一些具体建议。

关键词: 全球变化; 根系; 土壤生物; 营养竞争



## Belowground Controls Over Plant and Ecosystem Responses to Global Change

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The Earth is undergoing rapid environmental changes due to human activities, especially in the composition of its atmosphere composition, surface temperature and the composition and structure of the plant community. Terrestrial ecosystems rapidly respond to various global change components such as elevated atmospheric CO<sub>2</sub> and N inputs, surface warming and invasion of alien species. Attention has so far been largely focused on aboveground plants, and responses of belowground roots and soil biota remain under-appreciated. Plant roots are the primary driver of belowground ecosystems and impact the structure and functioning of plant community through altering the survival and growth of co-existing plants via resource competition and allelopathy. Soil contains an enormous diversity in microorganisms and microfauna that exert their influence on ecosystem functioning through regulating nutrient availability for plants, impacting soil structure and suppressing pathogen activities. Here, we first review the experimental evidence that documents belowground responses to elevated atmospheric CO<sub>2</sub> and N inputs, climatic warming, and invasion of alien species. Then, we synthesize the mechanisms through which soil biota mediate plant and ecosystem feedbacks to human-induced alterations in atmospheric composition and plant species composition. Finally, efforts will be directed to identify gaps in knowledge of effects of global change components on plant-microbial interactions and to suggest the experimental approaches that may improve our understanding of long-term consequences of resulting changes on the structure and functioning of terrestrial ecosystems.

**Keywords:** Global change, roots, soil biota, nutrient competition





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### 景观生态学：人物、概念、问题和挑战

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在过去20年里, 现代景观生态学已成为生态学的一个重要分支, 为自然资源管理和生物保护, 提供急需的理论依据。景观生态学在中国发展迅速; 近年来, 已有大量的研究论文发表。

借此讲座, 我将着重讨论四个题目: 景观生态学中的重要概念和领袖人物, 景观生态学研究中存在的问题, 及景观生态学所面临的重大挑战。首先, 我将讨论景观生态学中的几个重要概念, 包括空间格局与过程的关系, 尺度与尺度转换, 空间异质性及生境破碎化。同时, 我将介绍一些在北美景观生态学研究举足轻重的领袖人物, 包括Forman, Franklin, O' Neill, Pickett, Turner 和 Wiens。为大家深入研究景观生态学, 提供一些线索。然后, 我将指出景观生态学研究(尤其是在中国)一些重要缺陷。它们包括研究论文缺少理论构架与科学论题, 错将景观数量分析作为研究的唯一目的等。这些问题影响景观生态学的发展, 必须避免或加以修正。

最后, 我将讨论当今景观生态学研究中所面临的四个挑战。一是空间格局与生态过程关系的建立; 二是景观生态学缺乏大尺度试验, 从而导致许多假说不能得到有效验证; 三是如何运用已知的景观异质度量度, 来改善景观预测; 四是如何确定景观变化或两个景观的差异是否显著。

景观生态学是生态学的一个新分支。因此, 中国学者没有任何理由总是跟在西方学者后面。中国景观生态学者应该, 也能够在短期内站到景观生态学研究的前沿, 为景观生态学的发展做出显著的贡献。

关键词: 空间格局与过程的关系, 尺度, 空间异质性, 图幅比较



## **Landscape Ecology: People, Concepts, Problems, and Challenges**

**Harbin Li**

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Modern landscape ecology has established its position in ecology in the past 20 years, serving as important principles in natural resource management and biological conservation. Landscape ecology has also shown rapid development in China; a large number of research papers have been published in recent years.

In this lecture, I will focus on four subjects: people, concepts, problems, and challenges. First, I will discuss a few important concepts in landscape ecology, including relationships between spatial pattern and process, scale and scaling, spatial heterogeneity, and habitat fragmentation. In association with these concepts, I will highlight some researchers in North America who have made significant contributions to the development of landscape ecology. Any student of landscape ecology should know these names: Richard Forman, Jerry Franklin, Robert O'Neill, Stewart Pickett, Monica Turner, John Wiens, and more.

Then, I will point out some of the problems in landscape ecological research (especially in China), such as lacking theoretical context and good research questions, and mistreating quantitative analysis as the sole objective. These problems must be avoided or corrected because they impede the advancement of landscape ecology. Finally, I will talk about four major challenges that we face today in landscape ecological research and applications: (1) establishing effectively relationships between landscape pattern and process, (2) conducting experimentation to test hypotheses at the landscape scale, (3) utilizing known spatial heterogeneity to improve prediction of landscape change, and (4) determining significance level in comparing two landscapes.

Landscape ecology is a young branch of ecology. Thus, there is no reason that researchers in China should simply follow the footsteps of western scientists. Chinese landscape ecologists should, and will soon (I hope), stand in the forefront of landscape ecological research, making significant contributions to its development.

Keywords: relationship between spatial pattern and process, scale, spatial heterogeneity, map comparison



### 全球变化以及森林生态系统对多重压力的响应

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由于人类活动而导致的大气化学和物理学的变化正在对陆地生态系统产生广泛的影响。除了温室气体引起的气候变化效应外，CO<sub>2</sub>、O<sub>3</sub>浓度的升高和N的沉积作用对生态系统动态和功能也产生直接或间接的影响。相对而言，人们对单一因子变化对植物和土壤产生直接或次要的生理影响了解较多，但对于跨越时空尺度的多重胁迫对生态系统的影响则知之甚少。像FACE研究等这种大尺度、生态系统水平的野外试验，一般仅能在实验中调控一种或二种变化因子，还不能提供足够的信息以预测生态系统对全球变化的响应。

在大西洋中部、覆盖面积约为460,000 km<sup>2</sup>温带森林中，我们运用生态系统模拟方法来研究多个环境因子变化是如何相互影响碳动态的。结果表明，CO<sub>2</sub>浓度的上升导致森林生产力的增加，但这种生长增强大部分被对流层臭氧所减少。通常，高N的沉降和高浓度的CO<sub>2</sub>相互作用可增加森林对碳的吸收。然而，持续的、高水平的N的沉降将使许多地方达到N饱和，而其它资源则受限制。当森林N达到饱和时，木材中的碳收集减少，并且由于N输出的突然增加导致水质下降。在过去的几十年里，气候的跨年变化增加了森林对大气化学变化响应的复杂性。更根本的是，这些多重胁迫一起改变了森林生理学和生态系统的过程。我们用森林清查数据和MODIS数据对模拟结果进行了验证。模拟结果和地面实测吻合较好。本研究也证明了，运用机理模型模拟方法来检验气候-森林相互作用的复杂性和预测森林生态系统对环境变化的响应的必要性。



## Global Change and Responses of Forest Ecosystems to Multiple Stresses

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Changes in atmospheric chemistry and physics due to human activities are causing widespread impacts on terrestrial ecosystems. Besides the effects of climate change induced by greenhouse gasses, elevated CO<sub>2</sub>, O<sub>3</sub> and N deposition also have direct or indirect impacts on ecosystem dynamics and functioning. Relatively, we know well the direct and secondary physiological effects of single-factor changes on plants and soils, but less about effects of multiple interacting stresses on ecosystems across temporal and spatial scales. A few large-scale, ecosystem level field experiments, like FACE studies, generally only manipulate one or two changing factors that can be carried out in experiments and cannot provide sufficient information to predict the responses of ecosystems to global change.

In this study, we used an ecosystem modeling approach to investigate how multiple environmental changes interactively affect carbon dynamics in Mid-Atlantic temperate forests that cover approximately 460,000 of lands. Our results indicate that elevated CO<sub>2</sub> increases forest productivity, but the enhanced growth was largely reduced by troposphere O<sub>3</sub>. Currently, higher N deposition interacts with higher CO<sub>2</sub> to increase forest C sequestration. However, continued deposition of N at high levels will cause many areas to become saturated as other resources become restricted. As forests are saturated with N, carbon accumulation in forest woody product will be reduced, and water quality will be degraded because of an abrupt increase in N export. Changes in inter-annual variability of climate during past decades add complexity to forest responses to changes in atmospheric chemistry. More fundamentally, these multiple stresses together have seemingly altered forest physiology and ecosystem processes. We validated the modeling results with observations from forest inventory and the MODIS satellite. The modeling outputs are well validated/compared by the ground-based measurements. This research demonstrates the needs of using mechanistic modeling approaches to examine the complexity of climate-forest interactions and forecast ecosystem responses to environmental change.



### 21 世纪生态学面临的挑战及其使命

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当代人类活动的强烈干预推动地球系统演化进入了人类纪 (Anthropocene Era) 的新纪元。以 20 世纪后期全球环境快速变化和社会经济全球化为标志, 人类活动已经成为全球生态系统演变的主要驱动力。土地利用直接改变了全球 1/3 以上的陆地覆盖格局, 水资源利用量达到地表径流的一半以上, 人工固氮超过自然过程固氮能力的总和, 全球气候发生了千年未有的持续快速变暖趋势, 对自然资源整体利用超过其再生能力 20% 左右。这些变化在全球尺度上深刻地改变了生态系统格局、结构和过程, 许多生态系统服务功能出现下降或衰退趋势, 威胁生态系统本身和人类社会的持续发展能力。在 21 世纪, 世界人口和经济将持续增长 (尤其是在占人口大多数的发展中国家), 人类活动影响的广度和深度进一步增强, 气候变暖速率可能超过过去一万年任何时期的自然变化速率, 给全球生态系统带来前所未有的压力。

在这一时期, 人类活动对地球系统运行的影响赶上甚至超过了自然变化, 使其以前所未有的速率, 向一个未知的方向和轨道。人类活动导致的地球系统变化威胁其赖以持续生存与发展的环境资源基础, 人类社会面临适应、管理和控制这些变化巨大挑战。人类活动广度和强度的迅速增长推动地球系统演化进入了“人类世”(Anthropocene Era) 的新纪元。

应对人类活动主导的全球尺度生态系统变化是 21 世纪生态学面临的巨大挑战, 但同时也为生态学成为引导社会经济发展的主流学科提供了际遇。21 世纪生态学的使命是在全球环境以前所未有的速度变化的背景下为实现生态与社会经济系统的协调持续发展提供理论支持和技术途径。为完成这一使命, 生态学面临全面的调整和变革。生态学主要研究对象应从自然生态系统转移到人类活动干扰和人工管理的生态系统, 从小尺度生态系统转移到区域生态系统及其对全球环境变化的响应和适应; 研究领域从揭示生态系统自然变化和维持机制转移到人工控制机制, 从生态系统基础理论转移到生态系统管理策略与调控技术; 应用研究从生态恢复和修复到人工生态系统的设计和建造; 研究方法从分门别类的单一学科和单一系统研究转移到应用地球系统科学的多学科综合研究, 从单一尺度试验观测到多尺度试验观测、跨尺度机理分析和大尺度变化预测。

生态学研究领域和方法已经开始出现重大转变, 其主要推动力是 IGBP 和 IHDP 等国际组织联合发起的以全球持续性 (Global sustainability) 为目标的地球系统科学联合研究计划 (Earth System Science Partnership Joint Projects, ESSP) 和联合国发起的千年生态系统评估 (Millennium Ecosystem Assessment, MA)。ESSP 计划打破了对大气、海洋和陆地的分割, 把地球系统作为一个整体进行研究, 以人类活动—环境—生态系统相互作用为中心, 进一步强调人文与物理过程、自然与社会科学方法的紧密结合。MA 以生态系统可持续性及其对人类福利影响为中心, 综合评估全球各种生态系统服务功能的现状和未来变化, 以探索增强生态系统可持续性管理能力为目标。生态学研究方法也发生了根本性变化, 建立了应用各种新技术手段从生物群落到全球生态系统的多尺度试验、



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观测和研究网络。例如，定量遥感应用于观测全球和区域尺度生态系统格局的变化，大型试验装置应用于揭示生态系统对环境变化响应和适应机制，涡度相关测定技术应用于观测生态系统与大气能量和物质交换通量以小时为单元、连续 10 余年的动态变化。以多尺度观测为基础的数据—模型融合（Data-model fusion）是近年来发展起来的生态系统研究新途径，它包括应用多尺度观测数据建立和验证跨尺度机理模拟模型；应用动态观测数据连续驱动和引导机理模拟运行，现实地定量表达和预测大尺度生态系统时空变化。



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# Biodiversity and Ecosystem Functioning: History, Progress, and Prospects

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The relationship between biodiversity and ecosystem functioning (BEF) is one of the most fundamental issues in ecology, which has critically important implications for conservation, natural resource management, and global sustainability. Unfortunately, our current understanding of BEF is neither precise nor complete. Traditionally, BEF studies have been done primarily through "poking" (small experiments) and "peeking" (short-term observations). While long-term observational studies and simulation modeling are critically important, field manipulative experiments are still the only way to genuinely test hypotheses directed to the mechanisms of biodiversity effects. The past decade has evidenced a flurry of experimental studies focusing on the effects of biodiversity on ecosystem properties and processes, which has indeed greatly enriched our knowledge of BEF. While ecologists seem to have come to a broad consensus on certain general issues just recently, a great deal of what we know about BEF is still clouded with uncertainties. In this presentation, I will review the history and major achievements in BEF, and identify key research questions for future research.

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### 生物多样性热点地区及其保护对策的研究进展

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近年来, 物种灭绝的加剧, 遗传多样性的减少, 以及生态系统特别是热带森林的大面积破坏, 引起了国际社会对生物多样性问题的极大关注, 纷纷采取措施予以保护。然而, 由于投入的人力和财力的限制以及政策等方面存在的问题, 生物多样性丧失的态势并没有从根本上得到遏制。从保护的效率上考虑, 保护行动应有明确的目标或重点的对象(地区或类群等)。自然保护国际(Conservation International)一直倡导的热点地区途径受到国际社会的重视。对于生物多样性保护策略的制订包括自然保护区的合理布局等具有重要的参考价值。

Myers (1988)在分析热带雨林受威胁程度的基础上, 提出了热点地区的概念, 并于两年后主要根据维管束植物特征将其扩大到全球, 提出了包括 18 个热点地区的划分方案。经过近 10 年的应用, 在汲取相关的研究成果的基础上, 修订了全球生物多样性热点地区的方案(Myers, 2000)。其修订方案包括 25 个热点地区。热点地区的选择主要根据物种特有程度和受威胁程度。物种主要指维管束植物。此外, 也参考除鱼类以外的脊椎动物。每个热点地区至少包括 1500 种特有维管束植物(占世界植物总数的 0.5%), 且原始植被的丧失率大于 70%。事实上, 选出的 5 个热点地区中, 有 15 个地区含特有维管束植物 2500 种以上, 10 个地区的特有维管束植物 5000 种以上; 25 个热点地区中有 11 个地区的原始植被丧失率大于 90%, 3 个地区的原始植被丧失率大于 95%。25 个热点地区的面积总和为 210 万 km<sup>2</sup>, 仅占陆地总面积的 1.4%, 而其分布着全球 4.4% 的植物物种和 3.5% 的脊椎动物物种(鱼类除外); 其原始植被有 8.8% 已丧失。25 个热点地区中有 15 个分布有热带雨林, 5 个有地中海型植被; 9 个热点地区部分或全部由岛屿组成; 16 个热点地区位于热带, 这 16 个地区主要是发展中国家, 面临的威胁十分严重。由于人类现代农业导致的富养化、工业化和城市化, 伴随着大面积森林的砍伐、生境的破坏、动植物资源的过度利用和外来种的入侵, 即使物种极为丰富的热带雨林的生物多样性也在急剧下降(Sala, 2003)。Brook 等(2003)研究新加坡地区 183 年陆地和淡水生物的物种灭绝与生境破坏之间的关系。在大尺度水平上, 新加坡 183 年来生境丧失了 95%, 有记录的生物类群总的生物多样性至少丧失了 28%。不同的生物类群灭绝速率不同, 蝶类、淡水鱼、鸟类和哺乳动物生物多样性丧失的比率高达 34—43%, 而且与大面积的森林砍伐和生境的改变所导致的生境丧失是密切相关的; 同样维管植物、甲壳类、昆虫等生物多样性丧失的比率约为四分之一, 但是两栖类和蜥蜴类的灭绝速率却只有 5—7%。Brook 等(2003)根据用马来西亚同类地区的生物多样性估计, 新加坡有记录和无记录的生物多样性丧失的比率可能高达 73%, 用生物多样性模型预测新加坡生物多样性丧失的比率是 50.4%, 所灭绝的生物类群大多数是以森林为生境的。导致新加坡生物多样性灭绝的主要原因是起初的大面积森林砍伐以及后来城市化所导致的生境破坏, 新加坡现存的生物多样性前景黯淡: 根据联合国科教文组织的标准, 新加坡 77% 的生物多样性面临灭绝。在东南亚地区各国的热带雨林也面临与新加坡同样



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的问题。目前东南亚 46% 的森林遭到破坏, 到 2100 年, 东南亚 74% 的森林将被破坏。根据经验模型, 到下世纪, 该地区 13—42% 的生物多样性将面临灭绝, 将占全球灭绝生物的一半。

海洋生物多样性成为关注的热点。日本东京大学的生物学家在进行海洋线虫调查时发现大量的新种。他们和其他的 100 多位海洋生物学家于 2003 年 10 月在美国华盛顿召开会议, 共同探讨海洋生物多样性研究计划。决定利用网络平台, 发布海洋生物多样性分布图和相关信息。以期告诉人们海洋生物多样性在过去的分布、现在的分布, 以及未来可能在何处发现新的物种或新的分布地点。目前已经发现的海洋生物约为 21 万种, 在网上可以查到的相关信息的只有 2 万 5 千种 (<http://www.iobis.org>)。专家们估计可能有 10 倍于已发现种类海洋生物有待发现。来自 53 个国家的 300 多位专家参加海洋生物多样性的普查工作。在技术上有了很大的改进: 探头与遗传读码器 (Genetic bar code reader) 结合鉴定深海鱼的种类, 且形成了全球性的网络; 用相机计数大西洋微小的甲壳类动物; 利用卫星标记监测金枪鱼和三文鱼的种群动态; 历史学家查阅大量的捕鱼档案以重建过去 500 年间某些海洋鱼类的种群数量。这是一种全新的、国际性的、大尺度的海洋生物多样性调查途径。目前已知海洋鱼类有 15300 种, 专家们估计可能会有 20000 种, 预期在 2010 年时会有 2000 个新种被发现。据分类学家统计, 每年新发表的海洋动植物新种约 1700 个。在现有项目的基础上, 专家们建议重视北冰洋生物多样性的考察, 可能会有大量的新发现。由美国、加拿大和俄罗斯的专家组成的小组拟利用新一代潜艇开展此项工作。另一个可能的趋势是研究类群的个体越来越小, 特别是微小的海洋细菌和浮游生物。目前至少有 500 名鱼类分类学家, 还可以应付当前的工作。线虫等类群分类学家则极度缺乏。即使现有的线虫分类学家的工作效率提高 10 倍, 也需要几千年时间命名大部分线虫。因此, 分类学家队伍建设应该特别重视 (Malakoff, 2003)。Mora 等 (2003) 以印度洋和太平洋的珊瑚礁鱼类为例, 研究了生物多样性的异质性分布。结果显示, 物种的主要起源中心同时影响大尺度的物种多度分布格局和局域群落结构。随着人类海洋捕捞业的发展, 鱼类资源受到很大威胁。为了海洋渔业的可持续发展, 需要开展全球性的长时期的资源前景预测。Pauly 等 (2003) 根据大量的资料对海洋渔业的发展态势的预测显示海洋渔业正向深海发展、对生物多样性造成严重影响、渔获物从上世纪 80 年代后期的每年 8000—8500 万吨以每年 50 万吨的速度下降。渔获物下降的态势由于燃料价格上扬而加剧。

Pimm 和 Lawton (1998) 评述了与此相关的进展, 在肯定热点地区途径积极意义的同时, 援引 van Jaarsveld 等 (1998) 关于南部非洲的研究结果以及 Ando 等 (1998) 关于美国受威胁物种的研究结论, 指出热点地区途径也存在一定的不足。Kitching (2000) 认为 44% 已知的植物多样性和 35% 非鱼类的脊椎动物只被保护在占地球面积 12% 的 25 个单个热点地区, 这是远远不够的。哈佛大学的 Wilson 认为: 人们通常认为生物多样性的保护应由政府负责, 但是要保护地球上 70% 的物种需要投入 280 亿美元, 而且物种多样性丰富的地区大多集中在热带地区贫困地区。因此, Wilson 认为私人投资保护生物多样性也是一种应该采纳的途径 (Laurance 2001)。Smith (2001) 认为: 虽然划分多样性保护的热点地区, 但是随着全球气候的变化, 物种及其依赖的生境可能会转移, 所以现在的生物多样性热点不一定是未来的热点。因此, 保护一个种群在其特有的生境及一段变化的环境上是十分必要的。在保护实践中, 还应借鉴其他相关的研究成果。例如, 世界自然基金会 (WWF) 的生态区为基础的保护途径, 提出全球 200 个重要生态区方案 (Global Ecoregion 200), 具有一定的参考价值 (<http://www.wwf.org>)。物种丰富度和稀有性以及物种分布格局及其形成机制等对于生物多样性保



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护而言也应予以重视。

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### 二十一世纪生物入侵研究与入侵生物学的发展

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自二十世纪七十年代, 世界环境科学领域, 特别是生态学领域, 发生了深刻的转变。众多研究环境危机的学科应运而生, 促进了现代生态学的崛起与发展。也给生态学家带来了前所未有的挑战与机遇。泛义的生物入侵指由非本地或本地受抑制物种取代本地或原有的物种, 改变原有生态系统的结构、功能和效益, 减少物种多样性, 给本地生态系统带来生态和经济上的损失, 但目前的生物入侵研究多指外来引进物种, 入侵生物学是一门与 21 世纪同步的生态学科, 发展迅速。其突出特点是多学科结合, 着眼于入侵生物的预测、防止、根除、管理和利用。入侵生物学与保护生物学、全球变化生态学、恢复生态学等紧密相关, 平行发展。生物入侵的跨区域和全球性促使全球生态学家的密切合作, 采用“比较研究”的手段来研究生物入侵, 即比较入侵生物在原产地与入侵地之间在生活史、生态环境、遗传结构等方面的差异, 追踪入侵生物的扩展路线与途径, 进而弄清入侵机理, 找出有效的控制、管理根除方法。此外, 比较入侵物种与入侵地的同属异种植物的差异也是行之有效的方面。也有研究者提出用同属异种、本地种来治理入侵种。入侵生物学目前主要的研究目标与成果可归纳为: 1) 制定各种政策防止进入; 2) 发展先进的预测模型与手段; 3) 有效地管理使其早期根除或维持在最低水平; 4) 弄清入侵机理; 5) 研究入侵对生态系统的效应。本文着重介绍后三方面, 即有效管理、入侵机理及入侵效应的进展。利用生物控制来根除或管理入侵生物虽有近 100 年历史, 近期在某些地区, 如在南非对某些入侵种的控制已取得较好的效果, 可是, 也有日益增加的对生物控制、引进天敌手段的质疑与争论。主要基于引进天敌对非控制种的危害及扩散到其他地区的危害。因此, 引进天敌一定要慎重, 要仔细筛选, 最好是作为迫不得已的最后一策。使用入侵生物来治理入侵生物, 是生物入侵治理的另一重要发展。一些资深生态学家提出“入侵植物既是生态恢复的障碍, 也是解决问题的变化”“外来植物在生态系统恢复中的余地”等。如用生物工程技术来培育不育品种, 阻止某些可利用的园林、花卉、观赏入侵植物的进一步扩散。利用入侵水生植物降低农业用水的营养元素含量等。在某些被严重干扰的生态系统, 用入侵植物暂时代替被替代种发挥生态功能, 以观其用, 不必一律打击。入侵机理的研究取得较大进展, 各种假说纷纷而起, 并且有较强的针对性, 即为预测和根除入侵生物提供依据。最值得一提的是“天敌释放”和“新式武器”假说, 它们都着眼于原产与入侵生境的地下生物环境, 强调地下微生物、寄生虫、病毒天敌和植物分泌的化学物质等对某些入侵生物的作用。本文给出较详细的介绍。最后, 我们还将提出中国入侵生物学研究的重点与方向的建议。



## Biological Invasions and Invasion Biology in the 21th Century

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Since the 1970s, environmental sciences worldwide, particularly the field of ecology, have changed dramatically. Increased emphasis has been placed on two important features: problem-solving and multidisciplinary integration. Diverse new ecological disciplines emerged rapidly responding to human mediated environmental crises. These new disciplines have contributed to developing modern ecological theory and, in combination with the large scale nature of human disturbance, provide unprecedented challenges and opportunities for ecologists to conduct research at scales rarely attempted before. Invasion Biology is just such a new discipline. Biological invasion, by definition, includes both introduced alien and previously limited native species displacing native species thereby disrupting ecosystem structure, function, and natural services. However, recent bioinvasion literature almost exclusively focuses on the first category, alien species. Invasion biology is an integrative science, closely related to conservation biology, global change ecology, restoration ecology, et al. Frequently, the spatial extent of biological invasions is enormous and intercontinental exchange is common place. Both, the species exchange distance and the spatial extent of invasion motivated the use of a comparative approach to study species exchanges between its native range and invaded habitats. This approach fosters international collaborations and bilateral efforts to stem the increase in exotic invasions. To understand invasive mechanisms and effectively battle against invaders, it is important to compare life history, habitat biology and ecology, genetic structure between native and invaded ranges, as well as, trace the source population and invasion pathways. Moreover, it is also valuable to compare differences between cogenetic species to identify invasion mechanisms and screen potential biocontrol species. The major achievements of recent bioinvasion research include: 1) developing policies to control the importation of alien species, 2) establishing predictive models, including spatial models using GIS, 3) exploring management practices for early invasive eradication or low level maintenance, 4) understanding mechanisms of invasiveness, and 5) identifying the impacts on invaded habitats. In the present paper, we emphasize contributions made toward the last three.

Classical biocontrol approach, via screening, introducing and releasing host-specific natural enemies from native regions to manage invaders, has a long history over 100 years. Significant progress has been





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reported recently in some countries (e.g. South Africa) and for some species (alligator weed; *Alternanthera philoxeroides*). However, there are increasing considerable concerns and debates about biological control. Impacts on non-target organisms and the potential for the biocontrol organism to itself become invasive are two of major concerns. Therefore, it has been suggested that organisms used for biological control of alien invasive plants must be regarded as guilty until proven innocent and classical biocontrol should only be used as a last resort. Moreover, various experts have suggested: “exotic plant species as problems and solutions in ecological restoration”, and “a place for alien species in ecosystem restoration”. Diverse hypotheses have been proposed to understand mechanisms of species invasiveness and to predict what species may become invasive, including global competition, like invader, biotic resistance, introduction pressure, et al.. Here, we would like to pay special attention to classic enemy release, yet focusing on soil biota and a recent rising hypothesis: novel weapons about allelopathic biochemical compounds. Finally, we propose future research needs to battle biological invasions in China.



## 植物入侵性和克隆性

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### 1、植物入侵性

外来种 (Alien species) 是指由于人类有意或无意的活动被带到了其自然演化区域以外的物种。入侵种 (invasive species) 是指其引种已经或将会损害经济、环境或人类健康的外来种。少数外来种是入侵种。外来种入侵是自然生态系统面临的最重要的全球性问题之一, 它不仅是威胁生物多样性的主要原因, 而且也威胁着全球的生态环境和经济发展。

什么样的环境容易被入侵和什么样的物种容易入侵, 即群落的可入侵性 (invasibility) 和物种的入侵性 (invasiveness), 是生物入侵生态学的两个核心问题。植物的入侵性是它扩展超过它的引种区域, 在新区域生境中定居的能力。生物一旦入侵往往难以被彻底清除、或者清除的代价很大。因此, 在引进外来植物前, 分析其入侵特性, 从而预先识别入侵植物, 以求避免或者减少引进入侵植物是至关重要的。但到目前为止, 关于植物入侵的机制和预测还存在争议。争议的范围从是否能可靠地预测什么物种将会入侵, 一直到什么物种特性 (例如, 生活史、分类单元或地理起源) 会有助于物种的入侵。用来解释植物入侵的理论主要有天敌释放假说、生物抵抗假说、引入后进化假说、入侵植物通过化感作用促进入侵假说等等, 并都处在争议之中。

### 2、植物克隆性

从广义上讲, 克隆植物 (Clonal plant) 是指自然环境条件下具有克隆性 (Clonality) 或无性繁殖 (Asexual reproduction) 习性的植物。克隆性主要包括克隆生长 (Clonal growth) 和无融合生殖 (Apomixis), 其特征是后代的产生不经过减少分裂、后代的遗传结构相同。从狭义上讲, 克隆植物是指具有克隆生长的植物。克隆生长是指在自然条件下, 产生基因型一致、并具有独立于母株生存潜力的后代 (分株) 的过程。克隆性或无性繁殖是植物界广泛存在的生物学现象。根据植物克隆器官 (Clonal organ) 类型的不同, 将克隆植物分成根茎型、匍匐茎型、分蘖型、块茎型等。

克隆生长赋予克隆植物许多特性。首先, 相对于非克隆植物, 克隆植物的遗传学单位与生理学和形态学单位分离。克隆植物的遗传学单位为基株 (Genet), 生理学和形态学单位为分株 (Ramet)。构成克隆植物的基本单位, 分株, 在一定的时间内通过间隔子等相连, 但彼此又都可以相对独立的执行植物生长、繁殖的功能, 当连接物断开后, 成为独立个体。克隆植物区别与非克隆植物的特性包括: 基株灭绝风险分摊、克隆可塑性、克隆整合性、克隆内分工合作、基株移动性与分株放置选择性、有性生殖 / 克隆生长权衡、克隆器官的贮藏功能等等。克隆植物的这些特性在调节群落组织、结构和功能中发挥着独特的作用, 有利于利用环境异质性。





### 3、植物入侵性和克隆性

高入侵性的植物都具有很强的适应性，能够取代本地植物。植物的许多性状，尤其是具有明显适应性意义的性状都不同程度地对其入侵性有所贡献。克隆生长及其派生的性状使克隆植物对异质环境具有独特的适应能力，而异质性是环境的基本属性。克隆植物几乎都具有有性繁殖和无性繁殖（克隆生长和 / 或无融合生殖）两种繁殖方式，而且对两种繁殖方式的投资具有可塑性，能随环境需要而不同。无融合生殖不但具有类似于克隆生长的优势，而且具有种子传播的优势，因此推测无融合生殖可能在某些外来植物种的入侵扩散中具有贡献。无融合生殖现象分布最多的科是禾本科（146 种）和菊科 121 种）。这两个科也是中国主要入侵性植物外来种中最多的两个科，这两者之间的联系尚不清楚。

分析中国 126 个主要入侵性植物，来理解植物的克隆性在其入侵中的作用。根据其入侵性将这些物种分为 3 组，依组 I、组 II、组 III 入侵性顺序降低。在研究的 126 种入侵植物中克隆植物接近半数（44%），而且在 32 种属于组 I 的恶性入侵植物中克隆植物的比例高达 66%。Spearman 相关分析表明植物入侵性与克隆性之间存在正相关关系。这些结果显示：植物克隆性对其入侵性可能具有重要贡献。

喜旱莲子草 (*Alternanthera philoxeroides* (Mart.) Griseb.) 是世界上危害最大的杂草之一，已经成为中国的恶性入侵植物，广泛分布在从湿地到农田的多种生境中。喜旱莲子草的遗传多样性很低，主要依靠克隆生长增加个体数。它不但能以茎节不定根的方式进行克隆生长，而且也能以贮藏根不定芽的方式实现克隆生长。因此喜旱莲子草是一种典型的入侵性克隆植物。我们用实验生态学方法研究喜旱莲子草的克隆性与入侵性的关系，讨论其成为恶性入侵植物的原因。所获得的生理、形态和生长性状的研究结果都支持形成结论：喜旱莲子草的克隆整合性能帮助它忍耐和利用局域养分胁迫和 / 或人为干扰的生境，其克隆性对入侵性有重要贡献。

## Invasiveness and clonality of plants

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Alien species is the one that occurs outside of its historically known natural range, as a result of intentional or accidental dispersal by human activities. Some of alien species, whose introduction does or is likely to cause economic or environmental harm or harm to human health, are invasive. Biological invasions have attracted extensive attention by ecologists because of their significant ecological impacts and economic costs worldwide. Biological invasions are one of the global problems of the natural ecosystems. What habitats will be easily invaded and what species will become invasive, that is, invisibility and invasiveness, are the two key questions of invasion ecology. Invasiveness is the capacity of a plant to spread beyond the site of introduction and become established in new sites. In order to decrease or avoid introduction of invasive plant species, it is paramount to analyze alien plants before introduction



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so that the invasive plant species can be identified beforehand. Unfortunately, to date there is no consensus on invasion mechanisms and predictive models. Controversies range from whether we can reliably predict which species may become invasive to which species characteristics (e.g., life history, taxonomic groups, or geographic origin) contribute to the invasion processes.

Clonal plants are regarded as being especially adaptive in heterogeneous environments and contribute greatly in most ecosystems. Their adaptive advantages are mainly due to their clonality and the derived clonal plasticity and clonal integration. Compared to non-clonals, clonal invaders appear to suffer a disadvantage in the dispersal phase of invasion because ramets are usually not able to be dispersed at long distance. However, most clonal plants possess both asexual (clonal) propagation and sexual reproduction and allocation to both may be plastic in response to environments. A considerable number of invasive plant species have the capability of vigorous clonal propagation and their invasiveness may be related to clonality. For instance, between-ramet clonal integration may improve the ability of clonal plants to tolerate stress and thereby improve the invasion success of individual ramets. It was reported that novel hybrid invasive genotypes may be produced by rare sexual reproduction, fixed by clonal growth, and presents a previously unknown threat to native vegetation.

126 invasive plant species in China was analyzed to understand contribution of clonality to invasion success. These species were categorized into three groups based on their invasiveness. Among the 126 invasive species, 44% are clonal and clonal plants even accounted for 66% of the 32 most invasive alien plant species. The positive correlation between invasiveness and clonality was statistically significant. These findings suggest that clonality had contribution to invasiveness. Alligator weed (*Alternanthera philoxeroides* (Mart.) Griseb), one of the most invasive clonals, was investigated using experimental ecology. The results suggest that the clonal integration help the species endure nutrient-poor microhabitats and effectively exploit patchily distributed nutrients and that in this species clonality greatly contribute to invasiveness.



## 恢复生态学进展—北美视角

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由于人类干扰的影响,许多生态系统发生退化或严重受损,导致生物多样性的降低及生态系统服务功能的缺失。近几十年社会对生态环境的退化与恢复的关注及对生态系统服务需求的不断增加刺激了恢复生态学的快速发展。本文试对恢复生态学,尤其是陆地和湿地恢复生态学,在北美的进展作一简要的综述。

生态恢复包括从对遭轻度干扰的生态系统的调节与管理到对遭严重破坏的生态系统的重建之连续统中的任何对受损生态系统的修复。一系列的术语常被用来描述多种类型的生态恢复,但它们经常意义不统一且多无必要。有效的恢复生态学的研究应集中于发展事关生态恢复关键过程的理论与方法:如鉴别导致生态系统退化的生态过程;确定阻碍自然恢复的主要障碍;设定可实现的恢复目标及评估标准;发展反转或减轻生态系统退化的方法及实际措施。

国际恢复生态学会所采用的恢复生态学的定义在过去的 20 年里改变了数次,这在一定程度上反映了本学科理论概念的迅速演化过程。在确定现实性的恢复目标方面,恢复生态学理论的主要变化包括从静态的,单稳定态的,基于生态系统结构的,着眼于单个生态系统的观点演化到动态的,多稳态的,以生态过程为中心的,着重于生态系统的景观背景与功能的观点。同时生态恢复的评估也从基于单一变量的确定值演化到基于多个变量的自然变异域。

恢复生态学的理论框架吸收了许多当今生态学理论的主要进展,如状态转变模型(state-and-transition model),植被连续变化的观念,组装原则(assembly rule),复合种群动态,及尺度概念。恢复生态学的研究与实践同时也催生了新的理论进展及指导原则,如正反馈在生态恢复中的关键角色,启动和引导自恢复过程(autogenic processes),和自设计与设计者设计理论(self design and designer design)。这些生态学原则被用来帮助设计如何修复关键生态学过程,如生态系统与景观的水文过程,养分循环与格局,干扰过程与格局,物种组成与相互作用的动态等等。

因为环境变化多具长期性和不可逆性,如城市化和全球气候变化,开展前瞻性的研究对恢复生态学的发展及生态恢复努力的成功都将是至关重要。对延人为干扰梯度上不同参考系统的长期研究将有助于我们更好的理解和预测生态系统对未来环境变化的响应。将大尺度实验研究融入实际生态恢复项目的设计实现与监测过程中,以此检验与创立生态恢复理论,可为促进恢复生态科学与实践的发展的一个重要途径。空间模拟建模是研究景观和生态系统对未来环境变化及生态恢复措施响应的必要工具。除此之外,生态恢复的实践也迫切需要对生态恢复规划及适应性管理的研究,如建立基于生态过程的设计原则和规划过程来指导如何恢复生态系统及景观功能。



### Progress in Restoration Ecology – A North American Perspective

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Many ecosystems have been degraded or severely damaged by human disturbances, reducing biodiversity and impairing the ecological services provided by these systems. These issues of environmental degradation and increasing societal demand for ecological services in the recent decades have fueled the development and rapid growth of the discipline of restoration ecology. This paper attempts to provide a review of the progress in restoration ecology with a limited scope on mostly North America and on terrestrial and wetland restoration ecology.

There is a continuum of ecological restoration from rebuilding ecosystems that are severely damaged to the limited management of relatively unmodified ecosystems and there are many terms associated with different types of ecological restoration that are often confusing and unnecessary. The efforts are better spent by focusing on the development of conceptual framework and approaches that will help to identify processes leading to degradation or decline and obstacles to natural recovery, determine realistic goals and success criteria of ecological restoration, and develop methods and practical processes to reverse or ameliorate the degradation or decline.

The definition for ecological restoration adopted by the Society for Ecological Restoration International has changed several times in the last two decades, which reflects the evolution of the conceptual framework of the discipline. Some of the key developments of conceptual framework for determine the goals and evaluation criteria of ecological restoration involve the change from static, single-state, structure-based approaches focused on individual ecosystems to dynamic, multiple-state, and process-oriented approaches that focus on landscape context and multi-dimensional evaluation criteria based on the range of natural variations.

Some of the contemporary theoretical development in ecology, such as state-and-transition theory, the view that continuous change in vegetation is the norm, assembly rules, metapopulation dynamics, and the critical concept of scale have become central elements of the conceptual framework of restoration ecology. The research and practice of restoration ecology have also spawned new conceptual development or guiding principles, such as the critical role of positive feedback processes, the approach of initiating and directing autogenic processes, and self-design vs. designer design theories. These ecological principles are used in understanding the challenges of and developing strategies for repairing key ecological processes, such as hydrologic process, nutrient cycling and distribution, disturbance regime, and species



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diversity, interactions and dynamics.

Given the long-term and often irreversible changes in the environment such as urbanization and climate change, anticipatory research is critical to development of restoration ecology and the success of ecological restoration practice. It is especially important to further our understanding of ecosystem response to changing environment at multiple scales through long-term research of reference systems along the gradient of human disturbances. Incorporation of large-scale experiments into restoration projects and their monitoring can be an important approach and allow testing restoration theories and developing new ones, which is essential to the development of the science and practice of restoration ecology. Spatial simulation modeling is an essential tool for exploring future landscape and ecosystem responses to changing environment and restoration interventions. Research on restoration planning and adaptive management, such as development of designing guidelines and planning processes for restoring functional ecosystems and landscapes using process-oriented approaches, is also urgently needed to enhance the practice of ecological restoration.



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### 中国黄土高原的水土流失及生态修复

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黄土高原以其深厚的黄土和严重的水土流失成为世界上一个特殊区域。黄土高原的生态恢复格局、途径和方式在全球独具特色。本文分析了黄土高原水土流失特征,介绍了该区流域综合治理与生态修复长期定位研究成就及未来发展的前景。黄土高原地区总面积 62 万平方公里,水土流失面积达 45%。平均年侵蚀模数 3720 吨/平方公里·年。在过去 20 年来,科学家根据黄土高原小流域治理理论与实践,提出了该区以生态安全、粮食安全及经济可持续发展为目标的生态恢复战略,在黄土高原不同类型区建立了 11 个生态恢复研究、示范小流域及不同尺度长期监测研究定位基地。通过从 1938 年到 2004 年典型小流域人口、土地利用格局、生产力、植被及土壤侵蚀动态分析发现,60 年来,黄土高原流域生态系统经历了破坏、持续破坏及逐步恢复 3 个阶段。造成该区生态系统退化的驱动因素是流域土地利用格局。通过 20 年植被自然恢复演替定位监测表明,尽管由于人类活动的影响黄土高原大部分地区原始植被受到严重破坏,但该区生态系统的退化没有从破坏植被演替的基础,可以依靠自然修复恢复当地植物群落。因此,植被恢复策略是以自然恢复为主,人工建设为辅助措施,选择适合当地生境的树、草种,建立复合植被。通过生物措施、保护耕作措施、工程措施及经济发展措施,黄土高原退化的生态系统 20 年可以得到基本恢复、进入良性循环。最近的研究与实践表明,建立中尺度生态经济恢复模式,是推动黄土高原退耕还林还草、生态建设和经济可持续发展的有效途径。研究提出了水土流失区生态系统恢复、流域健康的目标及评价指标体系。黄土生态经济系统健康内涵是:管理者能够实施合理的经营策略,生态经济系统在侵蚀干旱胁迫下系统能够保持生态安全、生产能力及可持续发展的状态。比较目前黄土高原主要生态经济恢复模式发现,农-果模式表现良好的系统协调能力,农-牧模式健康状况较差,反映出目前该区完全禁牧,实施舍饲养殖的方式尚不能使生态系统迅速改善。通过系统分析不同土地利用方式下土壤基本理化及生物质量特征及其相关性入手,拟定了黄土丘陵区侵蚀环境下土壤质量评价指标体系,揭示了生态恢复重建过程中土壤质量演变规律并建立了土壤质量演变的回归模型。由于黄土高原自然环境的复杂性和水土流失的严重性,对国家大规模退耕还林还草,以植被恢复为核心的生态建设的重要生态过程的环境效应是今后科学家需要高度关注的问题。本文讨论了黄土高原生态修复对生态水文过程、植被演替、生物多样性的影响等环境效应及今后需要深入研究的科学问题。





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# Soil erosion and ecological rehabilitation on the Loess Plateau of China

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The Loess Plateau is well known for its deep loess deposits and serious soil erosion. The Plateau has the special character in rehabilitation patterns and approaches in the worlds. This paper analysis the characteristic of soil erosion on the Plateau and introduced the integrated watershed management and long-term research on the ecosystem rehabilitation as well as its prospective. The Loess Plateau has the area of 0.62 million km<sup>2</sup> with the erosion area of 45% and average erosion rate of 3720 t.km<sup>-2</sup>.a<sup>-1</sup>. In the last 30 years. Based on the theory and practice, the scientist presented management strategy on ecological security, grain food security and economical sustainable development. The 11 of integrated management and long term monitor watersheds were established since 1985. A long term environment change on population, land use pattern, productivity, vegetation and soil erosion from 1938 to 2004 in Zhifanggou watershed of Ansai research station of CERN indicated that the watershed experienced three periods of damage, continue damage and gradually restoration in last 60 years. The driving force of ecosystem succession is land use pattern by human induced impact, however, the monitoring on vegetation succession showed that the such damage has not destroyed the possibility and ability vegetation natural restoration though those original vegetations experienced serious disturbers. It's possible to restore the vegetation through the natural succession incorporated some artificial trees and grasses. The research showed that a degraded watershed could be restored in 20 years by re-vegetation, conservation tillage and engineering practices. The resent research and practice showed that the middle scale model of ecological and economy rehabilitation was an effective approach to promote the land use converting and eco-environment sustainable. The integrated health assessment indicators and its criteria in the watershed ecosystem was presented. Under the erosion situation, the ecosystem health is that the land manager could imply the rational practice and the system has the capability to keep the ecological security, productivity sustainable under the erosion and drought impact. The comparison of different rehabilitation model showed that the agro-fruit model had the higher health index while agro-animal husbandry model had the low health index. The soil quality indicators was also presented in rehabilitation processes. As the serious degradation situation the impact of restoration practice on watershed environment of hydrological process, vegetation succession, productivity, biodiversity were discussed and the further research was suggested in the paper.

**Key words:** soil erosion, ecosystem rehabilitation, Loess Plateau





## 生态系统服务功能研究现状及发展趋势

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人类在开发和利用自然生态系统过程中，只片面强调其市场价值或直接使用价值，忽略了自然生态系统所具有的其他生态效用或生态价值。自然生态系统对人类社会的效用被低估了，近年来，生态系统服务功能及其价值评估的研究逐渐成为生态学研究的一个热点。

目前国外有关生态系统服务功能及其价值评估的研究已经广泛开展。从 20 世纪 70 年代开始至 20 世纪 90 年代中期，主要是对生态系统服务功能的概念、内涵和生态服务类型以及分类进行研究。同期，也在积极探讨有关生态资产和生态系统服务功能的价值评价理论和方法，为今后生态系统价值评估的开展和区域、全球生态系统服务评估框架的建立提供了重要的理论基础。

1997 年是生态系统服务功能及其经济价值评价研究发展的一个转折点。Daily、Costanza 和 Pimentel 等相继发表了对生态系统服务功能或经济价值的评价研究结果，掀起了生态系统服务功能研究的高潮。Daily 等主要从生态学基础探讨生态系统服务功能及其价值的特性，生态系统服务功能与生物多样性之间的联系。Costanza 等则更多从经济学的角度研究生态系统服务功能的经济价值，并探讨生态系统服务功能评价的方法与技术。Pimentel 等也估算了生态系统服务功能的价值，并与 Costanza 等的研究结果进行了对比。同时另外几位学者，如 Turner 和 Naeem 等也在从事生态系统服务功能的研究。Turner 注重生态系统服务功能经济价值评估的技术与方法的研究，而 Naeem 则更关注生态系统服务功能变化的机制，特别是生物多样性与生态系统服务功能变化之间的相互作用。同时几乎所有的科学家都认为生态系统服务功能价值评价的最终目的是为决策者提供政策制定的依据，促进生态系统服务功能的可持续发挥。而千年生态系统评估 (MA) 的开展，则更加全面地探讨了生态系统服务功能概念、与人类福利之间关系、变化的驱动因子、评价的尺度问题、评价技术与方法、评价过程中的分析方法以及评价结果与最终的政策制定，并在全世界范围内广泛开展了案例研究，MA 是一次以面向决策者为目标的全世界生态系统服务功能评价研究。

国外生态系统服务功能研究主要集中在以下几个方面：(1) 生态系统服务功能概念、内涵及其分类体系的研究；(2) 生态系统服务功能变化机制及其与生物多样性相互作用关系的研究；(3) 生态系统服务功能价值评估技术研究，包括经济价值评估方法、能量为基础的价值评估方法、效益转换方法等；(4) 不同方法和不同情境下，全球、地区、区域、单个生态系统或单项服务功能经济价值评价研究；(5) 生态系统服务功能经济价值评估结果的可靠性、评价方法的局限性、评价过程中尺度问题等研究。

目前国外对生态系统服务功能的研究从理论、变化机制、评估技术与方法、案例研究等方面做了较为全面的探索，极大的促进了生态系统服务功能及其价值评估研究的发展。同时，生态系统服务功能研究进一步发展的趋势有：

1. 生态系统服务功能的变化机制及其驱动力，以及与生物多样性之间的相互作用还需要有进



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一步的研究;

2. 虽然理论上提出了很多生态系统服务功能价值评估技术与方法,但是大部分方法的实用性还需要加强;
3. 生态系统服务功能特征尺度的选择,以及评价过程中的尺度问题,如从大到小和从小到大的评价结果的尺度推移、多尺度生态系统服务功能评价的应用;
4. 生态系统服务功能评估过程中效益转换方法的应用;
5. 生态系统服务功能经济价值评估结果如何从单个服务、个人价值评价结果集合为一个综合的结果;
6. 评价过程中不可能获得一个完全准确和可靠的生态系统服务功能经济价值,需要多情景分析或时间序列的动态变化分析;
7. 评价结果如何转换为决策者可用于决策过程的有用信息。

国内生态系统服务功能研究是从20世纪90年代中期逐渐发展起来的。最初研究更多的集中在对国外生态系统服务功能概念、内涵、评估方法研究成果的介绍以及对生态系统服务功能理论的探讨。1997年Costanza等有关全球生态系统服务功能经济价值的研究引起了国内众多学者的注意。我国众多专家和学者开始对全球、区域、城市以及单一生态系统(主要集中在森林生态系统)或者单个物种生态系统服务功能及其价值评估理论与方法进行积极探讨,国内有关生态系统服务功能的研究随之有了较大发展。

在今后研究工作中,发展的趋势主要有:

1. 开展全面、系统的生态系统服务功能(自然状态下和人为干扰状态下)实验研究,为研究生态系统服务功能形成机理和变化提供数据基础;
2. 在生态系统实验结果的基础上对生态系统服务功能产生、变化及人为导致改变的机理进行研究;
3. 对特定生态系统类型(特别是农田、草地、湿地和水域)或者单项生态系统服务功能(如养分循环、生物多样性维持等)及其经济价值评估进行研究;
4. 对生态系统服务功能价值评估的哲学基础、估价方法、估价的生态学背景等进行研究,建立全面生态系统评估框架(森林、草地、湿地、农田、水域等生态系统),为生态系统管理提供全面科学的依据;
5. 在研究过程中引入数学模型、地理信息系统技术,为区域乃至全球生态系统服务功能及其价值评估研究提供方法和技术保障。



## Current Situation and Development Trend in Ecosystem Services

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Over the decades, great emphasis has been put into market value and direct utilization value of natural ecosystem in its development and utilization over the decades, while ignoring other eco-functions and values of the system. Therefore, functions of natural ecosystems to human society have been underestimated. Realization of this problem and related negative effects has made the research on ecosystem services and values an increasingly hot topic in the field of ecology.

Study on ecosystem service and assessment of the value has been conducted in many countries. From the 1970s to the middle 1990s, the focus was mainly on the concept, contents, classification, as well as exploration of theory and method of eco-asset and ecosystem service, and the progress in those fields have provided very important theoretical basis for further research of ecosystem services and assessment, and establishment of framework for the assessment of regional and global ecosystem service.

The year of 1997 is an important turning point for the development of ecosystem service and assessment following the publications from Daily, Costanza and Pimentel. Daily's contribution is focused on the salient features of ecosystem service and values, and relations between ecosystem service and biodiversity based on ecological theory. Costanza and others, however, emphasizes on economic theory for identification of economic values of ecosystem service and value, and exploration of method and technique for the assessment. Pimentel and others estimate values of ecosystem service in comparison with the findings of Costanza. In addition, some other researchers such as Turner and Naeem are also involved in the field of ecosystem services. Turner put efforts on methods and techniques in assessment of economic values, while Naeem on change mechanisms of ecosystem service, particularly on interaction between biodiversity and ecosystem functions. Despite variation on research focuses, it is agreed that the ultimate destination of assessment of ecosystem service is provision of scientific basis for decision making. Great progress on ecosystem service and value research has been made since the development of Minimum Assessment (MA). MA is a research on global ecosystem service with an aim of provision of decision support. It focuses on concept of ecosystem services, relations between ecosystem service and human welfare, driving forces of the ecosystem changes, scales and methods and techniques for the assessment, and application of assessment results for decision making.

Research on ecosystem service in foreign countries covers the following aspects: (1) concept, contents and classification of ecosystem service, (2) relations between change mechanism of ecosystem function and biodiversity, (3) methods and techniques in assessment of ecosystem values including economic assessment, energy based assessment, efficiency transformation method, etc, (4) economic values of an



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individual ecosystem or a ecosystem function at global, regional and district levels based on different methods and scenarios, and (5) reliability of economic assessment, limitation of the assessment methods and scales for the assessment. Those researches have made significant contributions to the theory, change mechanism, methods and techniques, and case studies of ecosystem service and assessment.

Development trend in ecosystem services could be summarized as follows: (1) Change mechanism and driving forces of ecosystem services, and its relations with biodiversity; (2) Applicability of methods and techniques having been used for assessment of ecosystem service; (3) Scales for ecosystem service and assessment. For instance, assessment from large to small scales or reverse, and application of multi-scale assessment; (4) Application of efficiency transformation method in the assessment; (5) Integration of assessment results covering single services and individual services into a composite one; (6) Consideration of scenario analysis and time series analysis into assessment; (7) Transformation of assessment into decision making process.

Concept of ecosystem service has been introduced in China in the middle 1990s. And the first researches focus on concept, contents, assessment methods, and theoretical background of the ecosystem services following essential progress made by Costanza and others in 1997. Specifically, efforts are put into global, regional and city ecosystems and singly ecosystem (e.g., forest ecosystem), ecosystem functions and values of an individual species, and theory and method in ecosystem assessment. Further research fields could be: (1) A complete and systematic experimental research on ecosystem function under natural and human disturbance to provide scientific data basis for ecosystem formulation and changes; (2) Mechanisms in ecosystem formulation, change dynamics and driving forces; (3) Ecosystem services and economic values of specific eco-types such as farmland, grassland, wetland and water body, or individual ecosystem services such as nutrition cycling, maintenance of biodiversity; (4) Philosophy basis, assessment method and ecological foundations for ecosystem service assessment, and establishment of assessment framework for forest, grassland, wetland, farmland, and water body ecosystems; (5) Introduction of mathematic modes, GIS techniques for provision of technical support for ecosystem service and value assessment.