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植物功能性状对生态系统服务影响研究进展

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摘　要　全面认识和理解生态系统服务的形成机制是维持其持续供给的前提。植物功能性状直接参与多种生态系统过程, 影响生态系统服务供给, 探讨植物功能性状与生态系统服务的关系是揭示生态系统服务形成机制的重要途径。该文采用系统的文献综述方法, 分析了植物功能性状与生态系统服务关系的研究特点, 总结了影响不同生态系统服务的主要植物功能性状, 阐述了可能的影响途径。结果表明: 植物功能性状与生态系统服务关系研究以草地和森林等自然生态系统为主; 大部分研究集中在生态系统供给服务和支持服务, 包括生物量、净初级生产力、土壤肥力等; 根据植物功能性状对不同生态系统服务的影响程度, 植物功能性状可以聚类为土壤保持服务相关性状、水分循环相关性状、多功能相关性状、产品提供服务与养分循环相关性状以及授粉与生物控制服务相关性状; 并阐述了植物功能性状指标影响不同的生态系统服务途径。围绕植物功能性状对生态系统服务的影响, 今后尚需进一步探讨生态系统多功能性、植物功能性状相关性、气候变化和人类活动不确定性、时空尺度差异等因素对二者关系的影响。

关键词　植物功能性状; 生态系统服务; 生态系统服务形成机制; 生态系统功能

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Effects of plant functional traits on ecosystem services: a review

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Abstract

Comprehensively understanding the mechanisms underlying the formation of ecosystem services is a prerequisite for maintaining the sustainable supply of ecosystem services. Plant functional traits directly participate in a variety of ecosystem processes, which in turn affect the supply of ecosystem services. Revealing the relationship between plant functional traits and ecosystem services is an important way to understand the formation mechanism of ecosystem services. Based on a systematic literature review, 86 papers on plant functional properties and ecosystem services were retrieved in the Web of Science database, and data for 466 pairs of plant functional traits and ecosystem services and 83 plant functional traits were collected. The current status of research on the relationship between plant functional traits and ecosystem services was revealed. Moreover, the main plant functional traits that affect different ecosystem services and their mechanisms underlying their impacts were also demonstrated. The results show that the research on the relationship between plant functional traits and ecosystem services mostly focuses on natural ecosystems such as grasslands and forests. Most of these studies focus on ecosystem products providing and supporting services, including biomass, net primary productivity, and soil fertility. Based on the impacts of plant functional traits on different ecosystem services, the plant functional traits can be clustered into five categories: soil-conservation-related traits, water-cycle-related traits, ecosystem-multifunction- related traits, product-providing-related traits, and pollination-biocontrol-related traits. The impacts of climate change, human activities, and variations in spatial and temporal scales on the relationship between plant functional traits and ecosystem services need to be further explored.

Key words　plant functional trait; ecosystem service; ecosystem service formation mechanism; ecosystem function

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生态系统服务是指由生态系统与生态过程所形成并维持的人类赖以生存的自然环境条件与效用(Daily, 1997; 欧阳志云等, 1999)。人类活动以及气候变化导致的生态系统服务退化对人类经济社会可持续发展造成巨大威胁, 全面认识和理解生态系统服务形成机制是保护和提升生态系统服务的前提(欧阳志云和郑华, 2009)。认识生态系统服务与生物多样性的关系是探究其形成机制的重要途径(Cardinale *et al*., 2012; 文志等, 2020)。依据优势度假说和生态位互补性假说, 研究者们已经探讨了多种生物多样性指数(物种多样性、功能多样性以及系统发育多样性)与不同类型生态系统服务(如: 生物量生产、土壤固碳、土壤肥力维持等)的关系(Cardinale *et al*., 2006; Tscharntke *et al*., 2012; Bardgett & van der Putten, 2014; Handa *et al*., 2014)。然而, 生物多样性指数在解释生态系统服务形成机制上仍存在较大的不确定性, 如Staples等(2019)对澳大利亚植树造林项目的研究发现, 生物多样性无法有效预测生态系统的生物量。

基于植物功能性状的途径为揭示生态系统服务形成机制提供了重要视角和方法(Diaz *et al*., 2007; Hillebrand & Matthiessen, 2009)。植物功能性状是指影响植物生存、生长和繁殖的适应性与效应特征, 反映植物对环境的响应以及能够影响生态系统功能可测量的性状(Violle *et al*., 2007; 刘晓娟和马克平, 2015), 它能响应环境因素的变化并直接参与生态系统过程, 影响生态系统的属性和功能, 进而影响生态系统服务(Eviner & Chapin III, 2003; Balvanera *et al*., 2006)。Lamarque等(2014)提出“植物功能性状-生态系统属性或过程/功能-生态系统服务”框架, 揭示了在气候变化和人类干扰背景下, 植物功能性状在生态系统服务相互作用与权衡中的重要作用, 为揭示生态系统服务形成机制提供了重要思路。目前, 国内外围绕“植物功能性状与生态系统服务关系”开展了大量研究, 但其中的机制错综复杂, 一种植物功能性状影响多种生态系统服务, 例如: 植物的比叶面积不仅影响生态系统净初级生产力(Klumpp & Soussana, 2009), 而且与生态系统的水文与温度调节服务息息相关(Everwand *et al*., 2014; Lundholm *et al*., 2015); 同一种生态系统服务又受制于多种植物功能性状的共同作用, 例如: 生态系统土壤保持服务的同时受到植物冠层密度、叶片形状和大小、根长密度等多个植物功能性状的控制(Burylo *et al*., 2012a, 2012b; Serna-Chavez *et al*., 2017)。

为了明晰植物功能性状与生态系统服务的关系, 本文通过系统的文献综述, 旨在探讨以下两个具体问题: (1)基于植物功能性状途径, 当前生态系统服务研究有哪些特点? (2)影响生态系统服务的主要植物功能性状及其影响途径是什么? 本文还展望了今后植物功能性状与生态系统服务关系研究的重点。

1 研究方法

为量化研究植物功能性状对生态系统服务影响的研究进展, 我们进行了系统的文献检索和分析: 首先, 从发文数量、生态系统类型、生态系统服务类型和研究尺度四个方面探讨植物功能性状与生态系统服务关系研究的特点; 其次, 使用文献计量分析方法, 总结影响不同类型生态系统服务的主要植物功能性状; 并阐述植物功能性状影响生态系统服务的可能途径。

1.1 文献检索

为扩大检索结果并提高检索效率, 本研究在Web of Science核心集合数据库中进行了两次文献检索: (1)在2019年11月15日, 以“ecosystem services”和“plant functional trait”为关键词, 进行了主题检索, 时间范围默认为所有年限, 检索出496篇文献; (2)在2020年3月4日, 对标题中含有“ ‘biodiversity’ or ‘functional diversity’ or ‘plant functional trait’ ”和“ ‘ecosystem function(ing)’ or ‘ecosystem service’ or ‘ecosystem property’ or ‘biomass’ or ‘productivity’ or ‘production’ or ‘soil organic carbon’ or ‘carbon storage’ or ‘carbon stock’ or ‘decomposition’ or ‘litter’ or ‘soil fertility’ or ‘biocontrol’ or ‘herbivory’ or ‘herbivore damage’ or ‘pest damage’ or ‘pathogen damage’ or ‘pathogen infection’ or ‘pollination’ or ‘soil retention’ or ‘soil erosion’ or ‘temperature’ or ‘heat’ or ‘water’ or ‘hydrology’ or ‘stability’ or ‘ecosystem multifunctionality’ or ‘cultural’ ”的文献进行检索, 最终累积检索出2 237篇文献。在文献筛选中, 首先我们通过判断标题和摘要是否同时含有“生物多样

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性”“植物功能多样性”或“植物功能性状”以及“生态系统服务”或“生态系统功能”，对2 237篇文献进行筛选，剔除了1 811篇无关文献；然后对剩下的426篇文献的内容进行筛选，最终得到文中论述植物功能性状与生态系统服务关系的文献86篇(图1)。

为了揭示植物功能性状影响生态系统服务的总体特征和一般途径，我们选择研究次数高于整体研究次数3%的生态系统服务，进行进一步分析，例如：地上生物量、净初级生产力、土壤有机碳、水文调节、温度调节、生物控制、土壤保持、土壤肥力以及授粉等。这9种生态系统服务可以归属于供给服务、调节服务和支持服务三类(表1)。

1.2 文献分析

针对86篇文献进行分类与统计。首先，根据每篇文献的发表时间、生态系统类型以及研究尺度，进行分类，着重记录每篇文献中所研究的生态系统服务类型和采用的植物功能性状指标，最终得到植物功能性状有83个(表2)，最后，统计文中得出单个植物功能性状指标(如比叶面积的群落加权均值(CWMSLA)、比叶面积的功能差异(FDSLA))影响生态系统服务的证据466组。在植物功能性状及其对生态系统服务影响途径分析中，我们计算影响各类生态系统服务的植物功能性状出现频率，并将频率高于

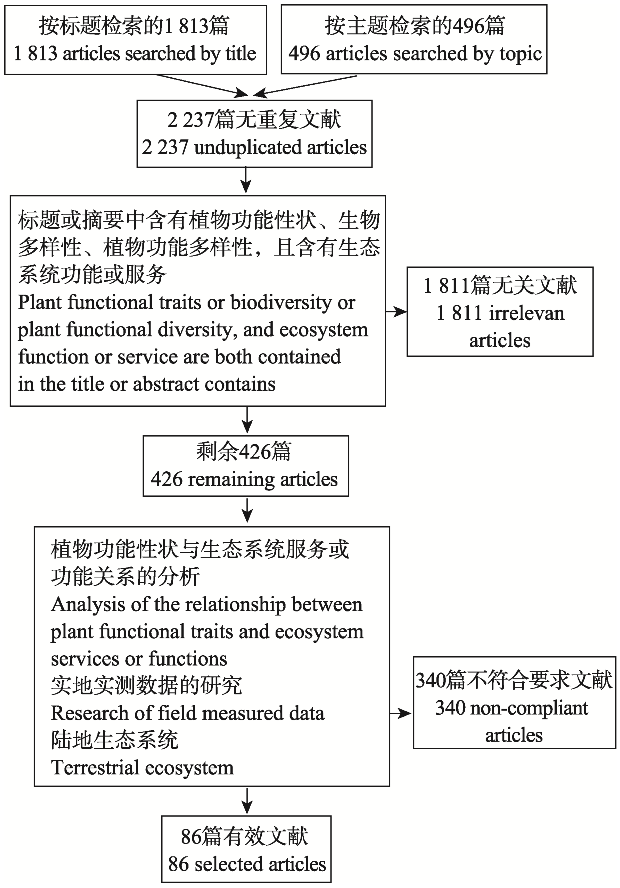

图1 植物功能性状与生态系统服务研究的文献筛选流程。
Fig. 1 Flow diagram of literature filtering for research on plant functional traits and ecosystem services.

表1 生态系统服务分类与内涵
Table 1 Classification and connotation of ecosystem services

生态系统服务类别 Ecosystem service type	生态系统服务 Ecosystem service	定义内涵 Definition and connotation	参考文献 Reference
供给服务 Provisioning service	生物量 Biomass	生态系统内所有物种的总质量(干质量) The mass (dry mass) of all species in the ecosystem	Grigulis *et al*., 2013; Adair *et al*., 2018
	净初级生产力 Net primary production	生态系统在给定的时间内积累的化学能的量，通常由碳生物量表示 The amount of chemical energy, typically expressed as carbon biomass, that ecosystem accumulate in a given length of time	Quétier *et al*., 2007
调节服务 Regulating service	土壤有机碳含量 Soil organic carbon content	生态系统中的土壤有机碳储量 Soil organic carbon sequestration in the ecosystems	Adair *et al*., 2018
	水文调节 Water regulation	生态系统参与水文过程而形成的调洪补枯效应 Ecosystems mitigate flood and increase base flow in dry season through participating hydrological processes	Wen *et al*., 2019
	温度调节 Heat regulation	生态系统通过影响热量交换而调节大气温度 Ecosystems regulate air temperature by affecting heat exchange	Lundholm *et al*., 2015
	土壤保持 Soil retention	生态系统固持土壤、减少土壤侵蚀的效应 Ecosystems retain soils and reduce soil erosion	Burylo *et al*., 2012a
	生物控制 Biocontrol	生态系统控制有害生物(如害虫、有害杂草等)的效应 Ecosystems control pests (e.g., harmful insects and weeds)	Storkey *et al*., 2013; Santala *et al*., 2019
支持服务 Supporting service	土壤肥力 Soil fertility	生态系统通过促进物质分解和矿化从而提高土壤肥力的效应 Soil fertility is increased by promoting organic material decomposition and mineralization	Handa *et al*., 2014
	授粉 Pollination	生态系统通过支持授粉昆虫活动而产生的效应 Ecosystems provide habitats for pollinator to increase productivity	Fornoff *et al*., 2017; Robleño *et al*., 2018

表2 影响生态系统服务的主要植物功能性状
Table 2 Major plant functional traits influencing ecosystem services

类型 Type	植物功能性状 Plant functional trait	解释 Explanation	参考文献 Reference
植株 Plant	生活型 Life form	植物的年度周期或外貌特征 The annual cycle or appearance characteristics of plants	Storkey *et al*., 2013
	繁殖方式 Reproduction mode	有性或无性繁殖 Sexual or asexual reproduction	Paquette & Messier, 2011
	冠层结构 Canopy architecture	冠层大小和厚度 Canopy size and thickness	Lundholm *et al*., 2014
	生长速率 Relative growth rate	一段时间内生物量增长量 Biomass growth over a period of time	Everwand *et al*., 2014
	最大高度 Max height	成熟植株的最大高度 Maximum height of a mature plant	Zhang *et al*., 2018
	茎生长速率 Stem growth rate	植物高度与生长年龄的比值 Ratio of plant height to growth age	Moonen *et al*., 2019
	茎质量百分比 Stem mass ratio	茎生物量占植株生物量的比例 Ratio of stem biomass to plant biomass	Zhang *et al*., 2018
	叶质量百分比 Leaf mass ratio	叶片生物量占植株生物量比例 Ratio of leaf biomass to plant biomass	Zhang *et al*., 2018
	根质量百分比 Root mass ratio	根生物量占植株生物量的比例 Ratio of root biomass to plant biomass	Zhang *et al*., 2018
	花质量百分比 Flower mass ratio	花生物量占植株生物量的比例 Ratio of flower biomass to plant biomass	Zhang *et al*., 2018
	叶茎质量比 Leaf:stem ratio	叶片和茎的干质量的比 Ratio of the dry mass of the leaf to the stem	Storkey *et al*., 2015
	根茎比 Root:shoot ratio	根与茎的干物质量比 Dry matter ratio of root to stem	Zhang *et al*., 2018
	耐阴性 Shade tolerance	植物忍耐阴蔽的能力, 常用无量纲量表示 The ability of plants to tolerate shade, often expressed as a dimensionless	Paquette & Messier, 2011
	耐旱性 Drought tolerance	植物忍耐干旱的能力, 常用无量纲量表示 The ability of plants to tolerate drought, usually dimensionless	Paquette & Messier, 2011
	耐涝性 Waterlogging tolerance	植物忍耐洪涝的能力, 常用无量纲量表示 The ability of plants to withstand floods, often expressed in dimensionless terms	Paquette & Messier, 2011
种子 Seed	种子质量 Seed mass	单颗种子的质量 The mass of a single seed	Paquette & Messier, 2011
	种子数量 Seed number	单位面积生产的种子数量 Number of seeds produced per unit area	Santala *et al*., 2019
	种子长度 Seed length	单颗种子或多颗种子的平均长度 The average length of a single seed or multiple seeds	Rolo *et al*., 2016
花 Flower	开花时间 Time of flowering	植物开始开花时间 The time plant starting to bloom	Pakeman, 2014
	花期长度 Duration of flowering	开花的持续时间 Duration of flowering	Fornoff *et al*., 2017
	花形状 Flower shape	花冠的形状 Corolla shape	Sole-Senan *et al*., 2017
	花对称性 Flower symmetry	花朵的对称性, 单边/双边 Symmetry of flowers, unilateral/bilateral	Fornoff *et al*., 2017
	授粉模式 Pollination mode	植物的授粉媒介 Pollinator	Zirbel *et al*., 2017
	花大小和密度 Flower size and density	花的直径和单位面积花朵数量 Flower diameter and number of flowers per unit area	Fornoff *et al*., 2017
	花序类型 Inflorescence type	花在花轴上的排列顺序 The order of flowers on the flower axis	Fornoff *et al*., 2017
	紫外线反射率 UV reflectance	植物对紫外线的反射率 Plant reflectance to ultraviolet	Fornoff *et al*., 2017
	花颜色 Flower color	花朵的反射光谱范围 Reflectance spectrum range of flowers	Fornoff *et al*., 2017
	花蜜类型 Nectar type	花蜜的可及性以及糖、氨基酸含量 Availability of nectar, sugar and amino acid content	Fornoff *et al*., 2017
	花的高度 Flower height	花朵的高度 Flower height to ground	Fornoff *et al*., 2017
叶 Leaf	叶片数量 Leaf number	单个枝条上叶片的数量 Number of leaves on a single branch	Li *et al*., 2015
	长叶时间 Time of leafing	植物叶片开始生长时间 Plant leaf start time	Pakeman, 2014
	叶面积 Leaf area	单个叶片或多个叶片平均的单侧投影面积 The average single-sided projected area of a single blade or multiple blades	Cornelissen *et al*., 2003
	叶片厚度 Leaf thickness	叶片的厚度 Blade thickness	La Pierre & Smith, 2015
	叶片韧性 Leaf toughness	穿透叶片最宽部分(避免中脉)所需的力 The force required to penetrate the widest part of the leaf (avoid the midrib)	La Pierre & Smith, 2015
	叶片组织密度 Leaf tissue density	单位面积的叶片鲜质量 Leaf fresh mass per unit area	Wen *et al*., 2019
	叶片形状 Leaf shape	叶片的形状, 常用宽与长的比率表示 The shape of the blade, usually expressed by the ratio of width to length	Burylo *et al*., 2012a
	叶片寿命 Leaf lifespan	叶片从生长到凋落的时间 Time from growth to fall of leaves	Wright *et al*., 2004
	比叶质量 Leaf mass per area	单位面积的叶片干质量 Dry mass of leaf per unit area	Wright *et al*., 2004

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表2 (续) **Table 2** (Continued)

类型 Type	植物功能性状 Plant functional trait	解释 Explanation	参考文献 Reference
	比叶面积 Specific leaf area	单位质量的叶面积 Leaf area per unit mass	Cornelissen *et al*., 2003
	叶片氮含量 Leaf nitrogen content	叶片中氮的含量 Nitrogen content in leaves	Wright *et al*., 2004
	叶片磷含量 Leaf phosphorus content	叶片中磷的含量 Phosphorus content in leaves	Lin *et al*., 2016
	叶碳氮比 Leaf carbon:nitrogen ratio	叶片碳氮含量之比 Ratio of leaf carbon content to nitrogen content	Fu *et al*., 2014
	叶碳磷比 Leaf carbon:phosphorus ratio	叶片碳磷含量之比 Ratio of leaf carbon content to phosphorus content	Schuldt *et al*., 2014
	叶氮磷比 Leaf nitrogen:phosphorus ratio	叶片氮磷含量之比 Ratio of leaf nitrogen content to phosphorus content	Finegan *et al*., 2015
	叶其他营养元素含量 Leaf other elements content	叶片除碳、氮、磷外其他元素的含量, 如钾、镁等 The content of other elements besides carbon, nitrogen, and phosphorus in leaves, such as potassium, magnesium, etc.	Kröber *et al*., 2015
	叶木质素含量 Leaf lignin content	叶片中木质素的含量 Lignin content in leaves	Schindler & Gessner, 2009
	叶片酚类含量 Leaf polyphenolic content	叶片中多酚类的含量 The content of polyphenols in leaves	Schuldt *et al*., 2014
	叶片单宁含量 Leaf tannin content	叶片中单宁的含量 Tannin content in leaves	Patoine *et al*., 2017
	叶片碳含量 Leaf carbon content	叶片中碳的含量 The content of carbon in leaves	Zhang *et al*., 2018
	叶片碳同位素比值 Leaf δ^{13}C	叶片碳同位素特征 Leaf carbon isotope signature	Orwin *et al*., 2018
	叶片干物质含量 Leaf dry mass content	叶片干质量与鲜质量的比值 The ratio of leaf dry mass to fresh mass	Fu *et al*., 2014
	叶片总叶绿素含量 Leaf total chlorophyll content	叶片中叶绿素的含量 Chlorophyll content in leaves	Bu *et al*., 2019
	叶脉密度 Leaf vein density	单位面积叶片的叶脉长度 Vein length per unit area of leaf	Hanif *et al*., 2019
	光合同化速率 Photosynthetic assimilation rates	在光饱和条件下测得健康叶片的光合速率 The photosynthetic rate of healthy leaves measured under light saturation conditions	Everwand *et al*., 2014
	气孔导度 Stomatal conductance	健康叶片的气孔对水蒸气的传导率 Transmission rate of water vapor to stomata of healthy leaves	Everwand *et al*., 2014
茎 Stem	木材密度 Wood density	单位体积木材的干物质量 Dry matter mass per unit volume of wood	Burylo *et al*., 2012a
	茎干物质含量 Stem dry matter content	茎干质量占鲜质量的百分比 The percentage of stem dry mass to fresh mass	Fu *et al*., 2014
	分支数量 Number of branches	从主茎分叉的开花分支或从次级枝干上的分支数 Flowering branches branching from the main stem or secondary branches	Adamidis *et al*., 2019
	茎投影面积 Projected stem area	茎在水流动方向上接触面积 Stem contact area in the direction of water flow	Kervroedan *et al*., 2018
	茎比质量 Specific stem density	茎的干质量与茎体积之比 The ratio of stem dry mass to stem volume	Kervroedan *et al*., 2018
	茎直径 Maximum stem diameter	基茎(根部上方2–6 cm)的直径 Diameter of the base stem (2–6 cm above the root)	Fu *et al*., 2014
	茎导度 Stem conductance	单位木质部面积和单位压力梯度下的水流量 Water flow per unit xylem area and unit pressure gradient	Kröber *et al*., 2015
	茎氮含量 Stem nitrogen ratio	单位干质量茎的氮含量 Nitrogen content per dry mass of stem	Belshe *et al*., 2018
	木材抗腐性 Wood decay resistance	木材腐烂的速度 Rate of wood decay	Zhang *et al*., 2018
根 Root	根长/生物量 Root length/biomass	根的总长度或生物量 Total root length or biomass	Pommier *et al*., 2018
	根的分布形态 Root distribution	根系在土壤中分布的形态 The distribution of roots in the soil	Matheny *et al*., 2017
	根深 Rooting depth	主根在土壤中分布的深度 Depth of taproot distribution in the soil	Fu *et al*., 2014
	根长密度 Root length density	单位体积土壤中的总根长 Total root length per unit volume of soil	Burylo *et al*., 2012b
	比根长 Specific root length	单位干质量的根长度 Root length per dry mass	Cornelissen *et al*., 2003
	根干物质含量 Root dry mass content	根干质量与鲜质量的比值 Root dry mass and fresh mass ratio	Pommier *et al*., 2018
	根氮含量 Root nitrogen content	根中氮元素的含量 Nitrogen content in roots	Zhang *et al*., 2018
	根磷含量 Root phosphorus content	根中磷元素的含量 Phosphorus content in roots	Hanif *et al*., 2019
	氮吸收 Nitrogen uptake	单位时间内氮吸收量 Nitrogen absorption per unit time	Abalos *et al*., 2014
	根系外表面积 External area of root surface	根系的外表面积 External surface area of root system	Burylo *et al*., 2012b
	根系体积 Volume of roots	根系的体积 Root volume	Zhu *et al*., 2015
	根系直径 Root diameter	吸收根的平均直径 Average diameter of absorbing roots	Burylo *et al*., 2012b
	根组织密度 Root tissue density	单位体积根的生物量 Root biomass per unit volume	Burylo *et al*., 2012b
	根碳含量 Root carbon content	单位干质量根的碳含量 Carbon content per dry mass root	Zhang *et al*., 2018
	根碳氮比 Root carbon:nitrogen ratio	根中碳氮含量之比 Ratio of carbon to nitrogen content in roots	Zhang *et al*., 2018

表2 (续)　**Table 2** (Continued)

类型 Type	植物功能性状 Plant functional trait	解释 Explanation	参考文献 Reference
	极细根百分率 Very fine root fraction	<0.1 mm的根长占总根比例 Ratio of root length <0.1 mm to total root	Garcia *et al*., 2019
	根质量密度 Root mass density	单位体积土壤中的根总生物量 Total root biomass per unit volume of soil	Burylo *et al*., 2012b
	根抗张力强度 Root tensile strength	细根(<0.1 mm)断裂所需的最大力与其截面面积的比值 Ratio of the maximum force required to break fine roots (<0.1 mm) to its cross-sectional area	Burylo *et al*., 2012b
	菌根定植 Mycorrhizal colonization	菌根定植根长占总根长的百分比 Mycorrhiza colonized root length as a percentage of total root length	Elumeeva *et al*., 2018

20%的植物功能性状作为影响该生态系统服务的主要植物功能性状; 最后, 以9种生态系统服务为基础, 对影响每种生态系统服务的主要植物功能性状进行聚类分析, 以探讨植物功能性状影响生态系统服务的主要途径。

2　研究结果

2.1　植物功能性状与生态系统服务关系研究特点

围绕发表的论文数量、涉及的生态系统类型、研究的生态系统服务类型以及涉及的空间尺度, 植物功能性状与生态系统服务关系的研究呈现如下特点:

(1)植物功能性状与生态系统服务关系是新兴的研究领域。在2011年及以前, 植物功能性状与生态系统服务关系研究的文章数量虽然也在逐年上升, 但增长速度较慢, 并且整体数量仍然较少; 在2011年以后, 与该主题相关的研究成果迅速增加。这与研究者们对植物功能多样性与生态系统服务关系的重视, 以及植物功能性状与生态系统服务关系研究里程碑式文章的发表有关(Díaz *et al*., 2007; de Bello *et al*., 2010)(图2A)。

(2)植物功能性状与生态系统服务的研究以自然生态系统为主。植物功能性状与生态系统服务的研究主要集中在自然生态系统上, 包括草地生态系统和森林生态系统, 而关于农业和城市生态系统的研究较少, 这可能是因为生态系统服务的形成机制在自然生态系统中更为复杂(图2B)。

(3)大部分研究集中在与生态系统养分循环和物质生产相关的服务上, 生态系统调节服务关注相对较少。生物量、土壤有机碳含量、土壤肥力以及生态系统净初级生产力4种生态系统服务与植物功能性状关系的研究数量占研究总数的75%, 而生态系统温度调节、生物控制、土壤保持、授粉等生态系统服务的研究数量约占研究总数的25% (图2C)。

(4)植物功能性状与生态系统服务关系的探讨主要集中在生态系统尺度上, 景观尺度和区域尺度上的研究相对较少。样地尺度的研究数量占研究总数的60%以上, 并且9种生态系统服务在该尺度上均有研究。而在其他尺度上, 研究者们关注的重点有所不同: 在景观尺度上, 主要关注种间互作相关的生态系统服务, 如授粉和生物控制服务(Zirbel *et al*., 2017; Bartual *et al*., 2019); 在区域尺度上, 更关注植物功能性状对生态系统生物量和初级生产力的影响; 在控制实验中, 研究人员主要通过梯度实验探讨了植物功能性状与生态系统服务的关系(Schindler & Gessner, 2009; Patoine *et al*., 2017)(图2D)。

(5)植物功能性状对生态系统服务的影响错综复杂, 同一性状可以影响多种生态系统服务, 而同一种生态系统服务又受多个植物功能性状的影响, 但同一植物功能性状对不同生态系统服务的影响程度不同, 例如: 植物花的功能性状(例如花高、花蜜类型、花色)主要影响作物授粉服务和生物控制服务, 而对其他服务的影响极小(图3)。根据植物功能性状对不同生态系统服务的影响程度进行聚类, 植物功能性状可以分为5类: 土壤保持服务相关性状、水分循环相关性状、多功能相关性状、产品提供服务与养分循环相关性状以及授粉与生物控制服务相关性状(图3)。

2.2　植物功能性状对供给服务的影响

供给服务指人类从生态系统中获得生存和发展所必需的各类产品(如木材生产、纤维和燃料等), 陆地生态系统中可使用生物量和净初级生产力作为供给服务的主要指标(Millennium Ecosystem Assessment Board, 2005; de Bello *et al*., 2010)。植物功能性状通过影响生态系统的光合作用过程以及营养分配过程, 进而影响生态系统净初级生产力及生物量。植物的比叶面积、叶干物质含量、叶片氮含量等经济学性状对生态系统光合速率具有重要影响, 而植物最大高度、木材密度以及种子质量等决定了植物生长繁

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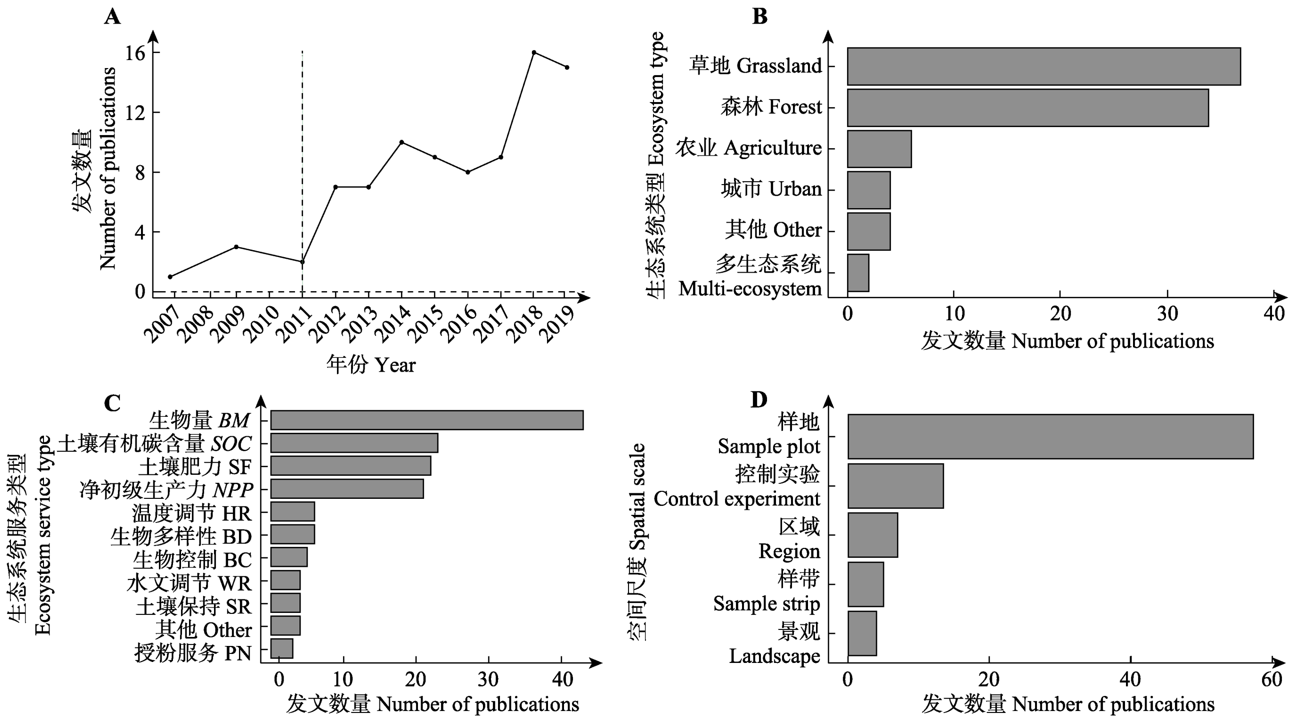

图2　植物功能性状与生态系统服务关系研究的特点。

Fig. 2　Characteristics of the current research on the relationship between plant functional traits and ecosystem services. BC, biocontrol; BD, biodiversity; *BM,* biomass; HR, heat regulation; *NPP,* net primary production; PN, pollination; SF, soil fertility; *SOC*, soil organic carbon content; SR, soil retention; WR, water regulation.

殖的养分分配策略, 是影响生态系统生物量蓄积的重要因素(Westoby, 1998; Golodets *et al*., 2009)。

从生物量来看, 影响供给服务的主要植物功能性状有植物最大高度、比叶面积、叶片氮含量、木材密度、叶片面积以及叶干物质含量等(图3)。来自成熟森林生态系统的证据表明, 植物最大高度是影响生物量最强的植物功能性状指标(Adair *et al*., 2018), 并且, 植物的木材密度也会影响生态系统生物量的蓄积(Falster *et al*., 2011); 而对于演替过程中的生态系统, 生物量与植物叶片氮含量的多样性具有显著正相关关系(Conti & Díaz, 2013; Zuo *et al*., 2016), 而与叶片碳含量和比叶面积成反比(Yang *et al*., 2019); 在草地生态系统中, 较高的比叶面积和叶片氮含量以及较低的叶片干物质含量有助于提高草地生态系统的生物量(Grigulis *et al*., 2013)。

从净初级生产力来看, 影响供给服务的植物功能性状指标主要包括: 植物叶片氮含量、最大高度、比叶面积、叶片干物质含量、叶片磷含量以及气孔导度等(图3)。在草地生态系统中, 叶片比叶面积和干物质含量多样性差异对生态系统净初级生产力变化具有很强的解释力(Klumpp & Soussana, 2009); 而在农业生态系统中, 植物的最大高度与生态系统净初级生产力具有较弱的负相关性(Lienin & Kleyer, 2012); 较高的叶片氮含量能促进光能的利用效率以提高生态系统的净初级生产力(Quétier *et al*., 2007); 在湿地生态系统中, 叶片厚度与生态系统净初级生产力具有很强的相关性(Fu *et al*., 2014); 而也有研究表明, 在控制实验中, 叶片韧性也影响着生态系统净初级生产力(La Pierre & Smith, 2015); 但种子质量增加会降低生态系统的地下部分的生产力(Zirbel *et al*., 2017)。

2.3　植物功能性状对调节服务的影响

调节服务是指从生态系统在维持能量流动和物质循环过程中对人类生存环境产生的调节效应(如: 洪水调蓄、气候调节、有害生物控制、净化水质等), 在生态系统尺度上, 通常使用土壤有机碳、水文调节、温度调节、土壤保持和生物控制作为调节服务的主要指标(Millennium Ecosystem Assessment Board, 2005; de Bello *et al*., 2010)。植物功能性状通过影响物质生产和根系代谢而影响土壤有机碳储存, 通过改变冠层结构影响水文和温度调节服务, 通过改变生态系统地表及地下结构而影响生态系统土壤保持功能, 通过改变栖息地条件以影响生物控制功能。

在土壤有机碳储存方面, 影响调节服务的主要

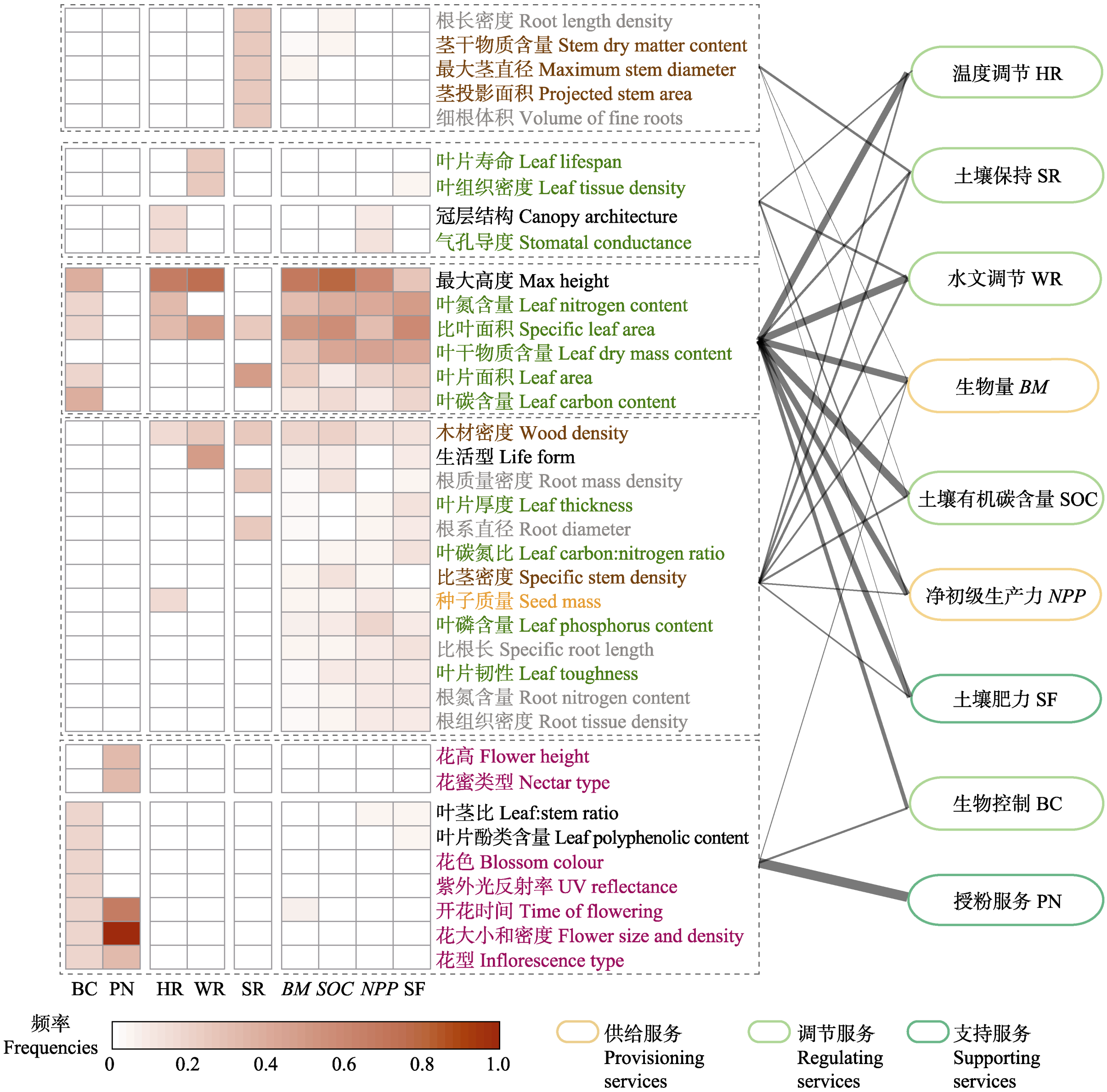

图3　植物功能性状与生态系统服务关系研究频率统计。字的颜色代表植物性状所在的部位。线条粗细代表研究中用到的植物功能性状与生态系统服务关系研究的频率。

Fig. 3　Frequencies of the research on the relationship between plant functional traits and ecosystem services. Colors of the word represent the location of trait. The thickness of the black lines represents the frequencies of different plant functional traits used to correlate with ecosystem services. BC, biocontrol; *BM*, biomass; HR, heat regulation; *NPP*, net primary production; PN, pollination; SF, soil fertility; *SOC*, soil organic carbon content; SR, soil retention; WR, water regulation.

植物功能性状指标有植物的最大高度、叶片氮含量、比叶面积、叶片干物质含量、木材密度以及叶片碳含量等(图3)。研究表明, 植物最大高度是冠层生长率的重要影响因子, 能通过促进冠层生长以增加土壤有机碳含量(Conti & Díaz, 2013; Lundholm *et al*., 2015); 在森林生态系统中, 植物群落叶片比叶质量的加权平均值与土壤有机碳储量呈正相关关系, 而降低的叶片比叶质量多样性会降低土壤有机碳储存量(Adair *et al*., 2018), 另外, 土壤有机碳含量与植物群落中的木材密度呈正相关关系, 而与比叶面积和叶片氮含量呈负相关关系(Lin *et al*., 2016); 在农业生态系统中, 高的叶片氮含量能够促进土壤有机碳储存(García-Palacios *et al*., 2018); 在草地生态系统中, 植物叶片比叶面积、叶片干物质含量多样性能够解释土壤碳储量48%的变化率(Klumpp & Soussana, 2009); 值得注意的是, 土壤有机碳含量还与比根长、根直径和根组织密度高度相关(Garcia *et al*., 2019)。

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在水文调节方面, 影响调节服务的主要植物功能性状指标有: 植株最大高度、比叶面积、生活型、木材密度、叶片寿命以及叶组织密度等(图3)。植物冠层密度以及细根百分率对生态系统水文调节服务都有重要影响(Wen *et al*., 2019); 生态系统雨水捕获能力主要受植物高度和冠层结构影响(Lundholm *et al*., 2015); 叶片比叶面积以及叶片厚度与群落蒸散量具有很强的正相关关系(Everwand *et al*., 2014); 而叶片的气孔导度作为影响植物群落蒸散的直接影响因素, 由于受植物水分保持和碳吸收权衡的影响, 其影响程度在不同季节之间变化剧烈(Everwand *et al*., 2014; Matheny *et al*., 2017)。

在温度调节方面, 影响调节服务的主要植物功能性状指标有: 植株最大高度、比叶面积、叶片氮含量、冠层结构以及叶片气孔导度等(图3)。在城市屋顶绿化中, 具有高气孔导度和冠层密度的植物群落在白天降温效应更为明显, 并且在晚上也同样具有较好的保温效果(Monteiroa *et al*., 2017); 植物比叶面积和高度也通过影响植被的冠层密度从而间接影响生态系统的温度调节功能(Lundholm *et al*., 2015), 而Lundholm等(2014)的研究结果表明, 植物高度与温度调节之间只具有微弱的正相关关系。

在土壤保持方面, 影响支持服务的主要植物功能性状指标有: 植物叶面积、根系直径、茎干物质含量以及茎投影面积等(图3)。在地上部分, 植物叶片形状和大小也会影响泥沙的拦截能力, 并且叶片圆度指数和大小与拦截的泥沙量成正比(Burylo *et al*., 2012a); 而在地下部分, 土壤侵蚀强度与植物根直径呈显著的正相关关系, 并且与比根长、根长密度以及根系外表面积也具有一定的相关性(Burylo *et al*., 2012b)。在半干旱草地的证据也表明, 根直径较小的群落对于生态系统土壤保持具有积极的作用(Zhu *et al*., 2015)。

在生物控制方面, 影响调节服务的主要植物功能性状指标包括: 植物开花时间、植物最大高度、比叶面积、叶片氮含量、花型、花期长度、花蜜类型以及花的颜色等(图3)。诸多研究表明: 植物功能性状多样性对生态系统生物控制具有积极的作用(Hatt *et al*., 2017; Santala *et al*., 2019); 花的颜色和紫外线反射率是吸引昆虫的重要性状, 与白色和紫色花朵相比, 黄色花朵能吸引更多的寄生害虫, 但花粉甲虫(*Meligethes* spp.)更容易被具有高的紫外线反射率的花所吸引, 并且花蜜的可用性同样影响着植物对昆虫的吸引力(Hatt *et al*., 2018); 晚期开花的植物可以避开虫害高峰期从而减轻害虫危害(Lundin *et al*., 2019); 除此之外, 比叶面积、叶片干物质含量等影响植物叶片适口性的植物功能性状与植食性昆虫的种类和数量具有很强的相关性(Storkey *et al*., 2013)。

2.4 植物功能性状对支持服务的影响

支持服务是指生态系统支撑供给、调节和文化服务形成和维持的服务(如: 土壤肥力与养分循环、土壤形成与保持、授粉等), 在陆地生态系统中, 支持服务可用土壤保持、土壤肥力和授粉等作为支持服务的主要指标(Millennium Ecosystem Assessment Board, 2005; de Bello *et al*., 2010)。植物功能性状通过影响生态系统物质分解过程以及植物根系代谢等途径进而影响生态系统土壤肥力, 通过给授粉媒介提供栖息地条件以保障授粉服务。

在土壤肥力方面, 影响支持服务的主要植物功能性状指标包括: 植物最大高度、比叶面积、叶片干物质含量以及叶片氮含量等(图3)。叶片碳氮含量多样性能够促进凋落物分解, 从而增加土壤肥力(Handa *et al*., 2014), 较低的叶片干物质含量也能促进凋落物分解(Quétier *et al*., 2007); 而在干旱区的研究表明, 植物群落比叶面积加权平均值是土壤碳氮含量最佳预测指标之一(Zuo *et al*., 2016)。在植物根系方面, 根的分布形态和最大根深对土壤肥力也具有较大影响, 一般来说, 侧向分根率较低的物种, 更有利于改善土壤肥力(Navarro-Cano *et al*., 2018)。

在作物授粉方面, 影响支持服务的主要植物功能性状指标有: 花力、开花时间、花型、花颜色、花蜜类型、花期长度、花的高度等(图3)。花的高度和花蜜浓度与昆虫的吸引力都有较强的相关性, 其中授粉媒介对植物的吸引力与花的高度以及花蜜浓度正相关, 而与花的反射光谱以及花形状多样性负相关(Fornoff *et al*., 2017); 也有研究表明, 花的面积和开花时期也会影响植物群落对传粉媒介的吸引力(Lundin *et al*., 2019); 而在景观尺度上, 配置多种生活型、多种花型和花期共存的植物对于维持生态系统授粉服务具有重要作用(Robleño *et al*., 2018)。

3 研究展望

目前, 围绕植物功能性状与生态系统服务的关

系, 已经取得一系列研究进展, 这些研究表明: 植物功能性状途径深化了生态系统服务形成机制的认识。但是由于植物功能性状本身的多样性与复杂性以及生态系统服务复杂的时空尺度特征, 植物功能性状与生态系统服务关系的研究仍存在诸多亟待解决的问题, 以下四个方面的具体问题值得进一步深入探讨。

3.1 植物功能性状对生态系统多功能性的影响

生态系统多功能性是指生态系统往往同时能提供多种生态系统功能和服务(Hector & Bagchi, 2007)。一般来说, 随着生物多样性的增加, 生态系统多功能性往往比单个生态系统服务表现出更强的增长效应(van der Plas, 2019), 但也有研究表明, 这种增长效应很大程度上取决于生态系统功能多样性指标中所选取的生态系统功能或服务(Allan *et al*., 2015)。因此, 基于植物功能性状途径揭示生物多样性对生态系统多功能性或多种生态系统服务的影响(Lu *et al*., 2014), 对于进一步认识植物功能性状与生态系统服务的复杂关系至关重要。

3.2 植物功能性状相关性对植物功能性状与生态系统服务关系的影响

植物功能性状是不同植物在各种环境条件下的适应性表征, 不同植物功能性状之间存在着复杂的相互作用与功能联系, 且不同功能性状之间存在着显著的相关性(Wright *et al*., 2004; Bin *et al*., 2019), 但具有相关关系的不同植物功能性状之间对生态系统服务的解释能力存在巨大差异(Hu *et al*., 2019), 如: Pakeman等(2011)研究表明, 叶片氮含量与叶片干物质含量具有显著的负相关关系, 但叶片干物质含量对凋落物分解速率的解释能力远远高于叶片氮含量。因此, 研究植物功能性状之间的相关性, 明晰影响不同生态系统服务的主要植物功能性状及其影响路径, 是揭示植物功能性状相关性对生态系统服务影响机制的重要任务。另外, 为阐明植物功能性状之间的复杂联系以及其在不同群落中的协同变化, He等(2020)提出了植物功能性状网络(Plant Trait Networks), 这为探究植物功能性状的相关性对生态系统多种功能之间关系的影响提供了重要的思路。

3.3 气候变化和人类活动对植物功能性状与生态系统服务关系的影响

气候变化和人类活动干扰是影响全球生态系统的两大关键因子(文志等, 2020)。植物功能性状和生态系统服务都会受到气候以及人类活动等因素的影响: 一方面, 气候变化和人类活动能够直接影响生态系统服务的形成与供给(Zheng *et al*., 2019); 另一方面, 气候变化和人类活动也能改变植物功能性状并影响生态系统的功能组成(Schröter *et al*., 2005; Tecco *et al*., 2010)。但是复杂的气候变化和人类活动导致植物功能性状与生态系统服务关系存在巨大的不确定性, 同时也增加了植物功能性状对生态系统服务影响机制的复杂性。因此, 在不同气候条件和人为干扰因素梯度下开展植物功能性状与生态系统服务关系研究, 对于降低植物功能性状与生态系统服务关系的不确定性至关重要。

3.4 植物功能性状与生态系统服务关系的时空尺度特征

生态系统过程和服务的研究依赖特定的空间和时间尺度(欧阳志云和郑华, 2009)。然而, 将植物功能性状与生态系统服务关系的研究推广到更大的空间尺度以及更长的时间尺度上面临着巨大的挑战。一方面, 生态系统尺度上的植物功能性状与生态系统服务的关系难以推广到区域尺度; 另一方面, 生态系统服务与植物功能性状不仅年际间存在变化, 并且可能在一年甚至一天之内也存在变化。因此, 将个体的植物功能性状与宏观的生态系统服务关联起来是进行其时空尺度推广的重要环节。He等(2019)认为: 生态系统性状能够将实地调查、涡流观测、遥感大数据以及生态模型进行相互关联和整合, 是将传统的植物功能性状关联到宏观尺度的有效途径, 同时也为揭示植物功能性状与生态系统服务关系的时空尺度特征提供了重要思路。另外, 还有必要建立多尺度、长时间的观测平台, 以建立植物功能性状与生态系统服务空间网格数据库(Kattge *et al*., 2011; Anderson-Teixeira *et al*., 2015), 进而为揭示植物功能性状影响生态系统服务的机制提供证据(Willemen, 2020)。

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