干扰对树线生态过程的影响研究进展

王亚锋¹, 梁尔源^{2,3*}

1. 南京林业大学生物与环境学院, 南京 210037;

2. 中国科学院高寒生态重点实验室, 中国科学院青藏高原研究所, 北京 100101;

3. 中国科学院青藏高原地球科学卓越创新中心, 北京 100101

* 联系人, E-mail: liangey@itpcas.ac.cn

2018-12-19 收稿, 2019-02-07 修回, 2019-02-12 接受, 2019-04-04 网络版发表

国家自然科学基金(41661144040, 41771222)资助

摘要 作为重要的非气候因子之一, 干扰与树线之间的关系已成为干扰生态学研究的重要内容之一, 开展受干扰树线研究对于实施山区生态保护或修复具有重要意义. 当前, 关于干扰如何调控树线对气候变化的响应仍缺乏系统的研究. 为此, 本研究梳理了气候变化背景下多种干扰因子对树线生态过程的影响. 已有的树线研究中涉及的自然干扰主要包括: 火山喷发、冰川进退、野火、雪崩、生物活动、极端低温、强风等; 人为干扰包括: 森林砍伐、放牧、人为用火、开矿、农耕、药草采集、旅游等. 在多数情况下, 由于在强度、频率、持续时间上的差异, 不同干扰因子对树线生态过程具有不同的效应. 在干扰迹地上, 根据土壤生境状况, 树线变化将经历由多种环境因素驱动的原生或次生演替过程以及由气候驱动的林分变化两个主要阶段. 当前研究中缺少对常见干扰因子的连续观测资料, 且未能很好地区分干扰历史和气候变化对树线生态过程影响的相对贡献. 相关研究需同时关注干扰因子对树线的破坏性和增益性影响, 尤其加强后者研究可避免对树线干扰因子的片面认识. 今后亟待开展干扰状况下的树线模拟研究. 基于多种研究手段, 围绕关键生态过程, 针对树线人为干扰因子进行长期跟踪调查是值得尝试的研究思路. 值得提出的是, 青藏高原既拥有北半球最高海拔的天然树线, 也分布着不同类型的受干扰树线, 是开展天然树线与受干扰树线对比研究的理想区域.

关键词 树线, 干扰, 树轮生态学, 气候变化, 青藏高原

早在1807年, Humboldt^[1]就观察到树线在阿尔卑斯山、比利牛斯山、喜马拉雅山、安第斯山等不同山地均有分布, 由此认识到树线是一个全球性的植被界限, 可作为指示气候变化的重要生物性指标. 自1950年以来, 研究者围绕树线变化以及树线与气候因子的关系开展了大量的工作^[2-12]. 尤其是近20年来, 树线结构与格局变化及其对气候变化的响应已成为全球变化生态学关注的热点科学问题之一^[13-17]. 与之相应, 树线作为关键词的文献数量呈显著增加趋势(图1), 且大部分文献关注气候变化对树线生态过程的影响. 然而, 目前树

线与诸多非气候因子之间的关系尚不明晰^[18-23].

作为重要的非气候因子之一, 干扰与树线波动间的关系仍缺乏系统研究. 有综述研究指出, 在全球195个树线样点中, 仅有两个样点关注了干扰对树线位置变化的影响^[24,25]. 造成这一现状的重要原因是: 绝大多数野外调查只选取天然树线作为研究对象, 这样有助于厘清气候因子对树线的影响, 从而尽可能排除干扰因子的影响. 在Web of Science以及中国知网数据库中, 1950年以来树线相关研究论文共1002篇, 其中仅10.8%关注于干扰与树线(表1), 表明当前相关研究仍十分

引用格式: 王亚锋, 梁尔源. 干扰对树线生态过程的影响研究进展. 科学通报, 2019, 64: 1711-1721

Wang Y F, Liang E Y. Research advances in disturbance and ecological processes of the treeline ecotone (in Chinese). Chin Sci Bull, 2019, 64: 1711-1721, doi: 10.1360/N972018-01273

图1 (网络版彩色)2000~2018年与树线相关的文献数量变化。SCI检索词: treeline, tree-line, timberline, timber-line; 中文检索词: 树线, 林线
Figure 1 (Color online) Variations in the number of literatures associated with treeline from 2000 to 2018. SCI search term: Treeline, tree-line, timberline, timber-line; Chinese search term: Treeline, timberline

匮乏。

当前,陆地上80%的生态系统都已受到自然或人为的各种干扰^[26],森林和树线生态系统也不例外^[4,27-31]。尽管一些研究只关注干扰较少或几乎未受干扰的天然树线^[20,21,24],本文特将研究对象设定为受到明显干扰的

高山或高纬树线。通过综述国内外受干扰树线研究的相关进展,梳理多种干扰因子对树线生态过程的不同影响,总结干扰因子对树线的作用规律,并强调开展受干扰树线研究的重要意义。

1 干扰的定义及干扰因子类型

尽管不同学者对干扰的定义有所不同^[32-34],但多数学者认为,干扰是指发生在一定的时间尺度上,影响生态系统的结构与生态过程,使资源、物质可用性 or 自然环境发生变化的所有干涉行为或事件^[26]。值得提出的是,不同于扰动,干扰具有突发性、难以预知、连续性较差等特征,且干扰过后,生态系统无法很快恢复到原有的景观面貌^[32]。

基于不同的角度,干扰有不同的划分方法^[34]。按功能,干扰可分为内部干扰与外部干扰;按传播特征,干扰可分为局部干扰和跨界干扰;按性质,干扰可分为生物干扰和非生物干扰;按起因,干扰可分为自然干扰和人为干扰^[32]。尽管分类众多,但树线研究中讨论较多的却是自然和人为干扰^[9]。具体来说,自然干扰是指无人介入的、在自然状况下发生的干扰^[32],而人为干扰则是指人类活动对自然生态系统的所有行为^[35]。鉴于

表1 受干扰树线在树线研究中的比例^{a)}

Table 1 Percentage of disturbed treeline literatures in treeline studies^{a)}

Web of Science检索标题	文献篇数	中国知网检索主题	文献篇数	所占比例(%)
Treeline or tree-line	735	树线/林线	267	—
Treeline or tree-line & disturbance	9	树线/林线、干扰	15	2.40
Treeline or tree-line & volcanic eruption	0	树线/林线、火山	7	0.70
Treeline or tree-line & glacier	14	树线/林线、冰川	10	2.40
Treeline or tree-line & fire	14	树线/林线、火	0	1.40
Treeline or tree-line & avalanche	0	树线/林线、雪崩	0	0
Treeline or tree-line & herbivore	2	树线/林线、动物	8	1.00
Treeline or tree-line & insect	3	树线/林线、昆虫	0	0.30
Treeline or tree-line & pathogen	3	树线/林线、病原菌	0	0.30
Treeline or tree-line & wind	10	树线/林线、风	0	1.00
Treeline or tree-line & deforestation	1	树线/林线、砍伐	0	0.10
Treeline or tree-line & grazing	0	树线/林线、放牧	2	0.20
Treeline or tree-line & mining	0	树线/林线、开矿	0	0
Treeline or tree-line & land use	6	树线/林线、土地利用	3	0.90
Treeline or tree-line & agriculture	1	树线/林线、农耕	0	0.10
受干扰树线总计	—	—	—	10.80

a) 文献检索选自1950~2018年;所占比例是指与检索词相关的中英文论文总数在1002篇论文中的百分比

此, 本文综述了多种自然和人为干扰因子对树线生态过程的影响。

2 干扰对树线生态过程的影响

2.1 自然干扰对树线生态过程的影响

树线研究中提及的自然干扰因子主要包括: 火山喷发、冰川进退、野火、雪崩、野生动物活动、虫害、病原菌入侵、极端低温、强风等^[9,36-42]。这些干扰因子在强度、频率、持续时间上明显不同, 相应地, 它们对树线结构与格局的影响也存在显著差异。

作为最强烈的自然干扰因子之一, 火山喷发(volcanic eruption)对树线生态系统具有毁灭性的影响。在短时间内, 火山喷发可摧毁高山植被和树线, 毁灭林下生境条件, 进而引发所在山区的原生演替过程, 这也为研究原生演替的早期阶段提供了理想实验场所。研究发现, 1707年富士山火山喷发造成的机械干扰以及数年的异常气候降低了多个树种的树线位置^[40]。此后90余年, 富士山火山喷发区的植被处于自然恢复阶段。自1800年以来, 富士山受干扰的树线上升了157 m。干扰引发的原生演替过程与气候变暖是树线快速爬升的驱动力^[40]。在中国, 树线研究也有类似发现。例如, 1702年长白山发生了火山喷发事件, 之后的300年存在3个不同的树线变化格局: 1702~1890年期间, 火山喷发区地面生境及植被快速恢复; 1891~1996年期间, 树线缓慢爬升; 1997年以来, 树线迅速爬升^[42]。第一阶段主要是原生演替过程驱动, 之后两个阶段的树线爬升速率与同期的变暖速率关系密切^[42]。全球有550多座活火山, 每年有近60座火山喷发, 但有关火山喷发对树线影响的研究十分少见^[43]。迄今, 我们尚不清楚在东亚以外, 火山喷发事件是否显著影响了树线变化。

冰川进退(glacier fluctuation)与山地森林、树线动态关系密切^[44-46]。在气候冷期, 冰川向低海拔区前进, 生长于前进路径上的树木常受到伤害甚至被摧毁^[9]。反之, 在气候暖期, 冰川向更高海拔后退, 其覆盖的地表露出, 成为树线扩张的潜在区域^[47]。冰川后退时, 留下的裸地生境状况如何至今仍不清楚。根据高海拔区冰川与树轮波动研究, 冰川退缩后, 树木在裸露的冰川地表上定居期为3~50 a^[45]。很短的定居期意味着冰川退缩迹地的生境状况良好。基于美国高山景观照片, 研究揭示树线在冰川退却迹地上的爬升十分有限^[48]。针对阿尔卑斯勃朗峰山区的预测研究显示, 到2080年, 该地

区冰川面积将退缩20%, 森林增加9%, 在冰川退缩迹地上树线位置将大幅度爬升^[49]。然而, 目前冰川退缩迹地上土壤养分、植被演替等状况如何调控树线对变暖的响应仍有待进一步的研究。

闪电等自然因素引发的野火(wildfire)在塑造树线结构与格局变化方面发挥着重要作用^[50,51]。发生频率较高的低强度野火可以阻碍树线爬升, 导致树线呈突变型或破碎化外观^[1,9]。当发生高强度野火时, 火后次生演替过程、气候、树种的耐火特征(再萌芽、抗火树皮、耐高温闭果等)可能共同驱动了树线的动态变化^[41,52,53]。例如, 1988年严重的野火烧毁了美国黄石国家公园25万公顷以上的森林^[53], 之后的研究发现, 美洲云杉/银杉森林及其种子均被大火烧毁, 而受到竞争作用抑制的扭叶松(*pinus contorta*), 由于能产生耐高温的球果, 在火后迅速传播种子并定居, 占据了美洲云杉(*picea sitchensis*)和银杉(*Cathaya argyrophylla*)的原有分布区^[54]。中等或高强度的野火均能降低树线位置, 然而, 当适应野火的树种缺失时, 火后树线的生态恢复过程将十分缓慢^[55]。当火的强度较低时, 树线上的地被层受破坏较大, 但成年树受到的影响很小, 因此火后树木的更新过程或树线上的入侵过程可能加速。值得一提的是, 由于高山灌木群落火灾多发生在秋季, 这与啮齿类动物大量埋藏种子的时间相耦合, 因此啮齿类动物对土壤种子库种子数量的填充有利于火烧后高温促进树线上树木种子的大量萌发以及随后的扩张。这些情况说明野火对树线生态过程也能产生有利的影响^[56]。总体上, 国外已开展过很多野火干扰研究, 但国内仍鲜有相关报道^[57]。至今, 我们仍不了解火灾强度、树种特征和气候变化等因素在树线变化中各发挥了什么作用。

雪崩(snow avalanche)对热带以外地区的树线变化有显著影响^[34]。雪崩具有发生突然、运动快速、历时短暂、流程不长、破坏力大、难以预测等特点^[58,59]。在生长季前期或早期, 30°~50°的陡坡上深厚的积雪融化容易引发雪崩^[60]。通过掩埋、毁折或破坏生境等方式, 雪崩将当前树线抑制在气候树线位置以下^[61]。大的雪崩事件可抵消气候变暖对树线的有利影响, 导致树线位置不变或后退, 并改变群落结构, 偶发的小雪崩则可调控变暖背景下树线的爬升速率^[34,62]。1962年2月18日, 瑞士阿尔卑斯山海拔2800 m处发生了大雪崩, 导致下方100公顷的森林被摧毁, 树线急速下降^[34]。1964~1965年的科考发现, 在中国藏东南波密县古乡地区, 大雪崩及其气浪摧毁了成片的原始森林和树线, 直

接导致山坡岩土裸露^[62]。雪崩频发区可形成特定的雪崩通道(avalanche pathways),造成树线分布的不连续性和景观异质性,这对于火灾的蔓延可起到隔离作用^[34,63]。漏斗型地貌增加了雪崩的发生概率,而较高的森林覆盖率则减少了雪崩的发生^[57,63]。国内外围绕雪崩灾害与社会经济之间的关系已有不少报道^[64],但受雪崩干扰的树线如何响应气候变化至今仍不清楚。

野生动物活动(wildlife activities)、虫害(insect outbreaks)、病原菌入侵(pathogen invasion)等生物因素是影响树线结构与格局的重要自然干扰因子^[39,65,66]。研究指出,高密度的红鹿等有蹄动物的啃食行为限制了欧洲赤松(*Pinus sylvestris* L.)树苗的更新和高生长,导致变暖背景下欧洲赤松树线位置变化不显著^[66]。虫害爆发对树线波动也有类似的负效应。在瑞典高纬林区,1964~1965年螟蛾等昆虫爆发事件导致2009年的树线位置比1952年降低了120 m,而且,附近10多公里范围的树线均因昆虫干扰而后退^[39]。与之类似,从美国新墨西哥州中部到科罗拉多州中北部,1850~1880年期间的甲虫爆发(beetle outbreak)对云杉森林和树线的结构和格局产生了强烈影响^[67]。此外,病原菌入侵能够影响树线变化。在美国西部林区,真菌入侵是美国白皮松(*Pinus albicaulis* Engelm)更新和生长的限制因子之一,对树线爬升可产生抑制作用^[68]。在川西贡嘎山区,真菌感染引发的腐朽病促使树木枯死,对峨眉冷杉(*Abies fabri* Craib)树线的种群稳定产生了不利影响,但对树线位置的影响至今仍不清楚^[65]。以上树线研究主要集中于生物因素的负效应上,目前对生物因素的正效应关注甚少^[36]。例如,研究发现,大型有蹄动物对林下或树线上植被的踩踏或啃食可减少种间竞争,动物也可将种子携带到树线之上的区域,这对树线处树木幼苗的更新、定植或树线扩张可能产生有利影响^[36]。在气候变化背景下探讨生物干扰对树线生态过程的增益性影响是生态学研究需要回答的重要科学问题之一。

除上述情况以外,极端低温(extreme low temperature)、强风(strong wind)等自然干扰因子对树线变化也有显著影响^[69]。在阿尔卑斯山、比利牛斯山、落基山、长白山、武夷山等山区,极端寒冷的气候或强风造成树木无法正常生长,并导致旗状树冠、矮曲林或风倒木的形成^[70~73]。频繁的强风还能塑造“树篱”(hedge)型林分外貌^[74]。在中国,位于秦巴山脉以南的山顶苔藓矮曲林以及位于东北地区的偃松/岳桦矮曲林都与极端低温、强风有十分密切的关系^[75]。在强

风、极端低温的共同作用下,树线处树木往往具有多茎形态(multi-stemmed trees),这与弱风、相对温和环境下的单茎形态(single-stemmed trees)显著不同^[15]。通过识别树木生长形态或相邻地区林分对比,可以区分极端低温和强风对树线的不同影响。例如直立的旗状林分或倒伏木大多是强风干扰造成的,而树木的多茎形态或矮曲状态则可能是极端低温、强风共同导致。纬度相近的福建武夷山与台湾中部山地森林区提供了有趣的案例。武夷山1700 m的海拔处就形成了矮曲林^[72],而台湾中部高山树线的海拔在2800~3000 m之间^[76],这在一定程度上说明强风对武夷山矮曲林的形成更为重要。不过,清晰区分极端低温、强风对矮曲林树线的影响仍需要在不同林区开展大量的观测研究。针对加拿大高纬树线的研究发现,8 m/s的风速就能对伸出积雪之外的树木枝干造成机械损伤^[77]。在欧洲的巨人山区,平均风速可达12 m/s,强风导致树线上树木依赖克隆生殖,树冠形状不规则,种群呈聚集分布格局^[69]。在强风长期干扰下,位于赤道附近的安第斯山树线和位于北欧的斯堪的纳维亚山树线分别位于其气候树线50和100 m以下^[78,79]。当树木暴露在强风频发的环境中,即使20世纪显著的气候变暖也难以驱动树线爬升^[80]。由于地形因子(坡向、海拔、崎岖度等)的差异,同一山坡的迎风面与背风面、风向上/下方可能出现不同的树木生长和分布格局^[74]。如果有利的微样点和气候变暖能够缓解强风和低温胁迫,矮曲树将通过生长释放而导致树线的快速爬升^[81]。目前,在欧洲和北美,强风被视为控制景观或局地尺度上生态状况、树木生长、树线位置与树木空间格局的重要生态因子^[74]。相比而言,中国树线研究集中于对矮曲林微环境或地理格局的探讨^[75],较少关注极端低温、强风与树线生态过程之间的关系。

2.2 人为干扰对树线生态过程的影响

人类活动已经对森林和树线生态系统造成了强烈的干扰^[9]。人为干扰因子主要包括森林砍伐、放牧、人为火、开矿、农耕、药草采集、旅游等。受人类活动历史、森林管理政策、社会经济发展水平等因素的影响,以上人为干扰因子对树线处物种组成、林分结构、分布动态等具有不同的影响^[29,47,82]。

森林砍伐(deforestation)对树线生态系统有显著影响。在基于农业生产的历史时期以及工业化前期,为了满足居民生活或工业生产的需求,乱砍乱伐在世界范

围内普遍存在^[27]。林木皆伐可能导致树线地区林分密度降低、树种优势度下降,甚至会造成树线位置后退或生态系统退化^[83]。在欧洲阿尔卑斯山,因森林砍伐等人为干扰活动,一些地区树线位置降低了150~300 m^[84]。在加拿大魁北克地区,历史时期持续的森林砍伐导致不少地区树线远低于其气候界限^[85]。法国东部一项树线研究发现,在20世纪60年代伐木活动停止后,1978~1993年期间的树线位置快速爬升,种群密度显著增加^[86]。由此可见,针对砍伐区树线的生态恢复状况展开调查,对于评估森林管理政策具有重要意义。此外,适度择伐对森林更新和群落发展具有积极作用^[35],但迄今为止,在树线过渡带仍未见相关研究报道。

放牧(grazing)是世界很多高山区居民的重要生活方式^[59,87,88],因此受放牧干扰的树线在世界上十分常见^[9]。不同的放牧压力对树线具有不同的影响。当放牧压力较低时,放牧对森林或树线的影响不显著。出现过度放牧时,牲畜的反复践踏导致林下土壤板结或幼苗死亡,牲畜对叶片、枝条、树皮的啃噬会降低幼树的生长量和生物量,进而抑制树线的爬升^[80,89]。芬兰东北部树线研究指出,树木更新的阶段变化与驯鹿密度的时空变化相吻合^[86]。在川西林区,牛羊在冬季对树皮的啃食抑制了岷江冷杉(*Abies faxoniana* Rehd)树线处树木的更新和生长^[90]。如果树线处灌木群落与树木之间存在竞争作用,那么放牧可能阻碍灌木建植,从而有利于树线树木幼苗的定居和后续发展^[91]。鉴于以上背景,制定科学的林草管理政策,让牲畜数量维持在合理的放牧水平上,这对于受干扰树线生态系统的稳定与发展具有重要价值。围绕牲畜放牧压力与树线之间的关系,国外已开展过多项研究^[89,92,93]。然而,此类研究在国内仍十分匮乏。在中国高山林牧区,维持多大的放牧强度才能同时实现经济效益和生态效益的平衡是研究者亟待解决的重要科学问题。

人为火(man-caused fire)是影响树线变化的重要驱动因子之一^[94]。人为火具有很强的目的性,往往对景观尺度上的森林/树线有显著影响。通过抑制树线扩张、减小林分密度、破坏林下层灌丛群落,人为火有利于高山草甸面积的维持或扩大。当人为火被禁止时,树线快速爬升到当前的气候生态位,林分密度显著增加,林下层灌丛填充和入侵现象明显。在西班牙的比利牛斯山区和中国的横断山区,20世纪的树线位置分别爬升了67和70 m,人为火干扰的停止以及气候变暖被视为树线显著爬升的驱动力^[47,95]。在秘鲁安第斯山,频繁的

人为火可导致树线位置下降^[96],而发生频率较低的高强度人为火对树线的物种组成、林分结构和海拔位置也有显著影响^[94]。以上研究为我们理解人为火对树线波动的影响提供了理论依据,然而,受研究手段的限制,目前还不能准确区分人为火和气候对树线波动的相对贡献。

除上述人为干扰因子外,开矿(mining)、农耕(farming)、药草采集(medicinal plant collecting)、旅游(tourism)等对树线变化也有相当大的影响。通过砍伐或人为火清除树线森林后,进行矿山开采造成的山体塌陷或耕作活动在一些山区曾有报道^[97]。在西班牙比利牛斯山、意大利亚平宁山、瑞士阿尔卑斯山和挪威斯堪的纳维亚山,气候变暖、禁止开矿以及辍耕等因素共同促进了树线爬升^[98~101]。不过,在大多情况下,矿山开采集中于森林下限。由于树线附近气候严酷、土壤相对贫瘠,因此树线处的农业耕作活动远没有放牧等人为干扰常见。事实上,在欧洲和美国部分山区,开矿、农耕对树线的影响仅有少量报道^[97~101]。此外,药草采集、旅游在一些林区愈加常见^[26,102]。目前,中国山地森林区还缺乏以上方面的研究。

2.3 干扰对树线生态过程影响的小结

尽管不同的干扰因子与树线变化存在不同的关系,但各种干扰因子对树线的影响却遵从一定的规律。归结起来,有以下3点:

(1) 少数干扰因子(火山喷发等)可彻底摧毁森林及其依存的土壤生境^[51]。干扰过后,树线变化将经历长期的原生演替和气候驱动的林分正常变化两个主要阶段^[42]。然而,多数干扰因子不能彻底毁灭林下土壤生境^[52],因此对树线的影响取决于干扰的强度;高强度干扰之后,树线变化将经历短期的次生演替和气候驱动的林分正常变化两个主要阶段^[103]。

(2) 在某些情况下,一些自然和人为干扰因子对树线生态过程的影响具有相同的效应^[36]。例如,野火与人为火、野生动物活动与牲畜放牧的差异只在于起因的不同,但它们对树线生态系统的作用规律却基本相同。

(3) 自然干扰因子不可控制(火山喷发、冰川进退、雪崩等)或不易控制(野生动物活动等),而诸多人为干扰因子(森林砍伐、放牧、旅游等)则可以有效控制。人为干扰因子的可控性是森林干扰研究中的核心理论之一,也是制定森林保护与草牧业管理政策的重要依据^[26]。

3 研究展望

树线研究中, 加强对干扰因子的研究有重要的理论价值和现实意义. 从生态学理论的角度来看^[26,52], 极端低温、强风等干扰因子属于气候因子, 各种生物活动属于生物因子, 各种人为干扰活动都属于人为干扰因子; 其他干扰因子可通过影响生物、气候、土壤、地形因素, 直接或间接地驱动树线变化. 因此, 厘清干扰因子与树线生态过程的关系, 有助于深化人们对生态学理论的理解. 从应用价值来看, 火山喷发、雪崩、冰川进退等干扰因子仅存于特定的区域^[42,46,63], 对这些地区的森林开展长期监测, 能为当地森林保护、社会经济发展提供科学支持. 例如, 国外已在尝试开展关于雪崩频发区森林恢复方面的工作^[63]. 尤其需要强调的是, 加强对人为干扰因子的特征、影响范围、作用路径等方面的研究, 能够为山地开发与生态保护提供科学依据^[104].

近20余年来, 国内外学者围绕干扰与树线之间的关系已开展了大量工作^[36,42,53,57,105~107]. 干扰如何影响树线生态过程及树线对气候变化的响应是很多研究者关注的核心科学问题之一. 随着人们对生态环境保护的重视^[108], 干扰因子与树线之间的关系值得进一步的研究. 然而, 当前的树线研究仍存在以下5点不足:

(1) 缺少对常见干扰因子的连续观测, 而且对干扰因子的增益性影响认识不足. 火烧、放牧等干扰因子的发生频率很高^[4,22,32], 是树线干扰研究中最活跃的生态因子. 只有基于连续的野外观测, 研究者才能充分了解干扰因子的不同特征, 进而厘清干扰因子与树线波动之间的关系. 很多干扰因子都具有破坏性和增益性两个方面^[26]. 综述研究指出, 适度的干扰对森林的更新、分布以及生物多样性可能产生有利的结果^[32]. 尽

管如此, 目前的树线研究格外关注破坏性干扰对树线变化的不利影响^[34], 但对增益性干扰的有利影响重视不足^[109]. 只有全面认识干扰因子对树线的破坏性和增益性影响, 才能实现对高山森林的优化管理.

(2) 对干扰条件下的树线生态过程缺乏深入研究, 对树轮生态学方法不够重视. 在受干扰树线研究中, 研究者多侧重于对生态格局的揭示, 但对具体生态过程缺少连续监测或控制实验, 这导致研究中难以区分干扰、气候因素对树线的影响. 在研究手段方面, 树轮生态学具有恢复过去生态过程时间序列方面的学科优势, 在区分一些生态因子相对贡献方面发挥了重要作用^[50,110]. 然而, 目前的树线干扰研究较少使用树轮生态学方法^[47], 限制了人们对干扰、气候因子与树线波动关系的深入理解.

(3) 树木应对干扰的生存策略还有待进一步的研究. 为适应频繁的干扰, 树线上的树木或产生抗干扰的树皮、球果等, 或形成聚集分布格局, 或依靠根等营养器官进行克隆繁殖(sprout-regeneration)^[6,25,31]. 干扰状况下不同的生存策略(例如R或K策略)为理解树线波动对气候变化的非线性响应提供了新视角.

(4) 亟待开展在干扰和气候变化背景下的树线模拟研究. 在世界上很多山地森林区, 干扰因子的监测资料处于严重匮乏状态^[9]. 因此, 基于有限的野外资料, 开展树线模拟研究对于深入理解干扰条件下长期的树线生态过程变化具有重要意义^[68,111~113].

(5) 作为地球的第三极, 青藏高原既具有北半球最高海拔的天然树线^[1,20,21], 也具有多种类型的受干扰树线^[28,46,47,62,75], 是开展天然树线与受干扰树线对比研究的理想场所. 然而, 青藏高原当前的树线研究集中于气候因子的影响上, 不清楚干扰等非气候因子的影响.

参考文献

- 1 Körner C. Alpine Treelines: Functional Ecology of the Global High Elevation Tree Limits. Basel: Springer, 2012
- 2 Daubenmire R F. Alpine timberlines in the Americas and their interpretation. *Butler Univ Bot Stud*, 1954, 11: 119–136
- 3 Troll C. The upper timberlines in different climatic zones. *Arc Alp Res*, 1973, 5: A3–A18
- 4 Tranquillini W. Physiological Ecology of the Alpine Timberline. New York: Springer, 1979
- 5 Kullman L. Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *J Ecol*, 2002, 90: 68–77
- 6 Körner C. Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems. Berlin: Springer, 2003
- 7 Cui H T, Liu H Y, Dai J H. Study on Mountain Ecology and Alpine Timberline (in Chinese). Beijing: Science Press, 2005 [崔海亭, 刘鸿雁, 戴君虎. 山地生态学与高山林线研究. 北京: 科学出版社, 2005]
- 8 Danby R K, Hik D S. Variability, contingency and rapid change in recent subarctic alpine tree line dynamics. *J Ecol*, 2007, 95: 352–363
- 9 Holtmeier F K. Mountain Timberlines: Ecology, Patchiness, and Dynamics. Dordrecht: Springer, 2009
- 10 Gou X, Zhang F, Deng Y, et al. Patterns and dynamics of tree-line response to climate change in the eastern Qilian Mountains, northwestern

- China. *Dendrochronologia*, 2012, 30: 121–126
- 11 Morueta-Holme N, Engemann K, Sandoval-Acuña P, et al. Strong upslope shifts in Chimborazo's vegetation over two centuries since Humboldt. *Proc Natl Acad Sci USA*, 2015, 112: 12741–12745
 - 12 Sigdel S R, Wang Y, Camarero J J, et al. Moisture-mediated responsiveness of treeline shifts to global warming in the Himalayas. *Glob Change Biol*, 2018, 24: 5549–5559
 - 13 Kullman L. 20th century climate warming and tree-limit rise in the Southern Scandes of Sweden. *AMBIO-A J Human Environ*, 2001, 30: 72–80
 - 14 Shiyatov S G, Terent'ev M M, Fomin V V. Spatiotemporal dynamics of forest-tundra communities in the Polar Urals. *Russ J Ecol*, 2005, 36: 69–75
 - 15 Devi N, Hagedorn F, Moiseev P, et al. Expanding forests and changing growth forms of Siberian larch at the Polar Urals treeline during the 20th century. *Glob Change Biol*, 2008, 14: 1581–1591
 - 16 Jump A S, Huang T J, Chou C H. Rapid altitudinal migration of mountain plants in Taiwan and its implications for high altitude biodiversity. *Ecography*, 2012, 35: 204–210
 - 17 Bryn A, Potthoff K. Elevational treeline and forest line dynamics in Norwegian mountain areas – A review. *Landscape Ecol*, 2018, 33: 1225–1245
 - 18 Wang Y F, Liang E Y. A review on progresses in treeline dynamics and climate change (in Chinese). *J Earth Environ*, 2012, 3: 855–861 [王亚锋, 梁尔源. 树线波动与气候变化研究进展. 地球环境学报, 2012, 3: 855–861]
 - 19 Wang Y F, Liu B. Impacts of climate and topography on treeline position across the Tibetan Plateau (in Chinese). *Chin J Ecol*, 2018, 37: 3508–3515 [王亚锋, 刘波. 气候和地形对青藏高原树线位置的影响. 生态学杂志, 2018, 37: 3508–3515]
 - 20 Liang E, Wang Y, Eckstein D, et al. Little change in the fir tree-line position on the southeastern Tibetan Plateau after 200 years of warming. *New Phytol*, 2011, 190: 760–769
 - 21 Liang E, Wang Y, Piao S, et al. Species interactions slow warming-induced upward shifts of treelines on the Tibetan Plateau. *Proc Natl Acad Sci USA*, 2016, 113: 4380–4385
 - 22 Liu H Y, Yin Y. Response of forest distribution to past climate change: An insight into future predictions. *Chin Sci Bull*, 2013, 58: 4426–4436
 - 23 Lyu L, Zhang Q B, Deng X, et al. Fine-scale distribution of treeline trees and the nurse plant facilitation on the eastern Tibetan Plateau. *Ecol Indic*, 2016, 66: 251–258
 - 24 Harsch M A, Hulme P E, McGlone M S, et al. Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecol Lett*, 2009, 12: 1040–1049
 - 25 Harsch M A, Bader M Y. Treeline form—A potential key to understanding treeline dynamics. *Glob Ecol Biogeogr*, 2011, 20: 582–596
 - 26 Zhu J J, Liu S R. Ecological Research on Forest Disturbance (in Chinese). Beijing: Chinese Forestry Press, 2007 [朱教君, 刘世荣. 森林干扰生态研究. 北京: 中国林业出版社, 2007]
 - 27 Fang J Y, Chen A P. Dynamic forest biomass carbon pools in China and their significance (in Chinese). *Acta Bot Sin*, 2001, 43: 967–973 [方精云, 陈安平. 中国森林植被碳库的动态变化及其意义. 植物学报, 2001, 9: 967–973]
 - 28 Fang J Q, Wu N, Luo P, et al. Impacts of disturbances on alpine timberline reformation (in Chinese). *Chin J Ecol*, 2005, 24: 1493–1498 [方近圻, 吴宁, 罗鹏, 等. 干扰对高山林线再形成过程的影响. 生态学杂志, 2005, 24: 1493–1498]
 - 29 Batllori E, Camarero J J, Gutiérrez E. Current regeneration patterns at the tree line in the Pyrenees indicate similar recruitment processes irrespective of the past disturbance regime. *J Biogeogr*, 2010, 37: 1938–1950
 - 30 Wang B, Chen T, Xu G, et al. Anthropogenic-management could mitigate declines in growth and survival of Qinghai spruce (*Picea crassifolia*) in the east Qilian Mountains, northeast Tibetan Plateau. *Agric For Meteorol*, 2018, 250–251: 118–126
 - 31 Xu C, Liu H, Zhou M, et al. Enhanced sprout-regeneration offsets warming-induced forest mortality through shortening the generation time in semiarid birch forest. *For Ecol Manage*, 2018, 409: 298–306
 - 32 Chen L D, Fu B J. Ecological significance, characteristics and types of disturbance (in Chinese). *Acta Ecol Sin*, 2000, 20: 581–586 [陈利顶, 傅伯杰. 干扰的类型、特征及其生态学意义. 生态学报, 2000, 20: 581–586]
 - 33 Sun R Y, Li Q F, Zhu C J, et al. Ecology (in Chinese). Beijing: Science Press, 2000 [孙濡永, 李庆芬, 朱翠娟, 等. 生态学. 北京: 科学出版社, 2000]
 - 34 Holtmeier F K, Broll G. Subalpine forest and treeline ecotone under the influence of disturbances: A review. *J Environ Protect*, 2018, 9: 815–845
 - 35 Zhu J J, Liu Z G. A review on disturbance ecology of forest (in Chinese). *Chin J Appl Ecol*, 2004, 15: 1703–1710 [朱教君, 刘足根. 森林干扰生态研究. 应用生态学报, 2004, 15: 1703–1710]
 - 36 Cairns D M, Moen J. Herbivory influences tree lines. *J Ecol*, 2004, 92: 1019–1024
 - 37 Schickhoff U. The upper timberline in the Himalayas, Hindu Kush and Karakorum: A review of geographical and ecological aspects. In: Broll G, Keplin B, eds. Mountain Ecosystems: Studies in Treeline Ecology. Berlin: Springer, 2005
 - 38 Schickhoff U, Bobrowski M, Böhner J, et al. Do Himalayan treelines respond to recent climate change? An evaluation of sensitivity indicators. *Earth Syst Dynam*, 2015, 6: 245–265

- 39 Van Bogaert R, Haneca K, Hoogesteger J, et al. A century of tree line changes in sub-Arctic Sweden shows local and regional variability and only a minor influence of 20th century climate warming. *J Biogeogr*, 2011, 38: 907–921
- 40 Sakio H, Masuzawa T. The advancing timberline on Mt. Fuji: Natural recovery or climate change? *J Plant Res*, 2012, 125: 539–546
- 41 Donato D C, Harvey B J, Turner M G. Regeneration of montane forests 24 years after the 1988 Yellowstone fires: A fire-catalyzed shift in lower treelines? *Ecosphere*, 2016, 7: e01410
- 42 Du H, Liu J, Li M H, et al. Warming-induced upward migration of the alpine treeline in the Changbai Mountains, northeast China. *Glob Change Biol*, 2018, 24: 1256–1266
- 43 Zhou S N, Liang Y, He H S, et al. Factors affecting vegetation succession after volcano eruptions (in Chinese). *Chin J Ecol*, 2016, 35: 234–242 [周胜男, 梁宇, 贺红士, 等. 火山喷发后植被演替的影响因子. 生态学杂志, 2016, 35: 234–242]
- 44 Xu P, Zhu H F, Shao X M, et al. Tree ring-dated fluctuation history of Midui glacier since the Little Ice Age in the southeastern Tibetan Plateau (in Chinese). *Sci China Earth Sci*, 2012, 55: 521–529 [徐鹏, 朱海峰, 邵雪梅, 等. 树轮揭示的藏东南米堆冰川小冰期以来的进退历史. 中国科学: 地球科学, 2012, 42: 380–389]
- 45 Liu W W, Xu P, Zhu H F, et al. A review on dendroglaciology study in southeast Tibetan Plateau (in Chinese). *Quat Sci*, 2015, 35: 1238–1244 [刘雯雯, 徐鹏, 朱海峰, 等. 藏东南地区树轮冰川学研究进展. 第四纪研究, 2015, 35: 1238–1244]
- 46 Zhu H, Shao X, Zhang H, et al. Trees record changes of the temperate glaciers on the Tibetan Plateau: Potential and uncertainty. *Glob Planet Change*, 2018, doi: 10.1016/j.gloplacha.2018.12.004
- 47 Baker B B, Moseley R K. Advancing treeline and retreating glaciers: Implications for conservation in Yunnan, P.R. China. *Arct Antarct Alp Res*, 2007, 39: 200–209
- 48 Donato D C. Limits to upward movement of subalpine forests in a warming climate. *Proc Natl Acad Sci USA*, 2013, 110: 7971–7972
- 49 Carlson B Z, Georges D, Rabatel A, et al. Accounting for tree line shift, glacier retreat and primary succession in mountain plant distribution models. *Divers Distrib*, 2014, 20: 1379–1391
- 50 Wang X C, Ji Y. Review of advances in dendrochronology (in Chinese). *Chin J Plant Ecol*, 2009, 33: 587–597 [王晓春, 及莹. 树木年轮火历史研究进展. 植物生态学, 2009, 33: 587–597]
- 51 Veraverbeke S, Rogers B M, Goulden M L, et al. Lightning as a major driver of recent large fire years in North American boreal forests. *Nat Clim Change*, 2017, 7: 529–534
- 52 Xue J H. Forest Ecology (in Chinese). Beijing: Chinese Forestry Press, 2006 [薛建辉. 森林生态学. 北京: 中国林业出版社, 2006]
- 53 Paula S, Pausas J G. Burning seeds: Germinative response to heat treatments in relation to resprouting ability. *J Ecol*, 2008, 96: 543–552
- 54 Turner M G, Romme W H, Gardner R H, et al. Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecol Monogr*, 1997, 67: 411–433
- 55 Stueve K M, Cerney D L, Rochefort R M, et al. Post-fire tree establishment patterns at the alpine treeline ecotone: Mount Rainier National Park, Washington, USA. *J Veg Sci*, 2009, 20: 107–120
- 56 Wang J, Yan Q L. Effects of disturbances on animal-mediated seed dispersal effectiveness of forest plants: A review (in Chinese). *Chin J Appl Ecol*, 2017, 28: 1716–1726 [王静, 闫巧玲. 干扰对动物传播森林植物种子有效性影响的研究进展. 应用生态学报, 2017, 28: 1716–1726]
- 57 Yao Q, Brown P M, Liu S, et al. Pacific-Atlantic Ocean influence on wildfires in northeast China (1774 to 2010). *Geophys Res Lett*, 2010, 44: 1025–1033
- 58 Hu R J, Ma H, Jiang F Q. Geographical environment in the area of Tianshan station for snow avalanche research, Yili, Xinjiang, China (in Chinese). *Arid Land Geogr*, 1997, 20: 25–33 [胡汝骥, 马虹, 姜逢清. 中国天山积雪雪崩站区的地理环境. 干旱区地理, 1997, 20: 25–33]
- 59 Butler D R, Malanson G P, Walsh S J, et al. The Changing Alpine Treeline: The Example of Glacier National Park, MT, USA. Amsterdam: Elsevier Science & Technology, 2009
- 60 Zhang F C, Li J, Wu L X, et al. GIS-based assessment on risk of snow avalanche to glacial lake: A case study in the Koshi River Basin, Himalayas (in Chinese). *Arid Zone Res*, 2016, 5: 1132–1139 [张福存, 李净, 吴立限, 等. 基于GIS的雪崩对冰湖风险性评估—以喜马拉雅山科西河流域为例. 干旱区研究, 2016, 5: 1132–1139]
- 61 Walsh S J, Butler D R, Allen T R, et al. Influence of snow patterns and snow avalanches on the alpine treeline ecotone. *J Veg Sci*, 1994, 5: 657–672
- 62 Deng Y X. Avalanches in the Guxiang region of Tibet and their impacts on physical geographical processes (in Chinese). *Acta Geogr Sin*, 1980, 35: 240–252 [邓养鑫. 西藏古乡地区的雪崩及其在高山自然地理过程中的作用. 地理学报, 1980, 35: 240–252]
- 63 Bebi P, Kulakowski D, Rixen C. Snow avalanche disturbances in forest ecosystems—State of research and implications for management. *For Ecol Manage*, 2009, 257: 1883–1892
- 64 Chou J Q. The Study of Snow Avalanche (in Chinese). Urumchi: Xinjiang Science and Technology Press, 2004 [仇家琪. 雪崩学. 乌鲁木齐: 新疆科学技术出版社, 2004]
- 65 Shen Z H, Fang J Y, Liu Z L, et al. Structure and dynamics of *Abies fabri* population near the alpine timberline in Hailuo Clough of Gongga

- Mountain (in Chinese). *Acta Bot Sin*, 2001, 43: 1288–1293 [沈泽昊, 方精云, 刘增力, 等. 贡嘎山海螺沟林线附近峨眉冷杉种群的结构与动态. *植物学报*, 2001, 43: 1288–1293]
- 66 Herrero A, Zamora R, Castro J, et al. Limits of pine forest distribution at the treeline: Herbivory matters. *Plant Ecol*, 2012, 213: 459–469
- 67 Baker W L, Veblen T T. Spruce beetles and fires in the nineteenth-century subalpine forests of western Colorado, USA. *Arctic Alpine Res*, 1990, 22: 65–80
- 68 Smith-McKenna E K, Malanson G P, Resler L M, et al. Cascading effects of feedbacks, disease, and climate change on alpine treeline dynamics. *Environ Model Software*, 2014, 62: 85–96
- 69 Kašpar J, Hošek J, Trembl V. How wind affects growth in treeline *Picea abies*. *Alp Bot*, 2017, 127: 109–120
- 70 Holmeier F K. What does the term “krummholz” really mean? Observations with special reference to the Alps and the Colorado front range. *Mt Res Dev*, 1981, 3-4: 253–260
- 71 Camarero J J, Gutiérrez E. Pace and pattern of recent treeline dynamics: Response of ecotones to climatic variability in the Spanish Pyrenees. *Clim Change*, 2004, 63: 181–200
- 72 Xiong D S. Wuyi Mountains (in Chinese). Guangzhou: World Publishing Corporation, 2014 [熊德胜. 武夷山脉. 广州: 世界图书出版公司, 2014]
- 73 Meng Y Y, Zhou L, Zhou W M, et al. Characteristics of plant species diversity in a windthrow area on Changbai Mountain after 26 years of natural recovery (in Chinese). *Acta Ecol Sin*, 2015, 35: 142–149 [孟莹莹, 周莉, 周旺明, 等. 长白山风倒区植被恢复 26 年后物种多样性变化特征. *生态学报*, 2015, 35: 142–149]
- 74 Holtmeier F K, Broll G. Wind as an ecological agent at treeline in North America, the Alps and the European subarctic. *Progr Geogr*, 2010, 31: 203–233
- 75 Yao Y H, Zhang B P, Zhao C. Geographical distribution of cripple tree forest and its importance for forest line in China (in Chinese). *Progr Geogr*, 2017, 36: 491–499 [姚永慧, 张百平, 赵超. 中国矮曲林的分布特征及生态意义. *地理科学进展*, 2017, 36: 491–499]
- 76 Greenwood S, Chen J C, Chen C T, et al. Strong topographic sheltering effects lead to spatially complex treeline advance and increased forest density in a subtropical mountain region. *Glob Change Biol*, 2014, 20: 3756–3766
- 77 Scott P A, Hansell R I, Erickson W R. Influences of wind and snow on northern tree-line environments at Churchill, Manitoba, Canada. *Arctic*, 1993, 46: 316–323
- 78 Kullman L, Öberg L. Post-Little Ice Age tree line rise and climate warming in the Swedish Scandes: A landscape ecological perspective. *J Ecol*, 2009, 97: 415–429
- 79 Wagemann J, Thies B, Rollenbeck R, et al. Regionalization of wind-speed data to analyse tree-line wind conditions in the eastern Andes of southern Ecuador. *Erdkunde*, 2015, 69: 3–19
- 80 Kullman L. Wind-conditioned 20th century decline of birch treeline vegetation in the Swedish Scandes. *Arctic*, 2005, 58: 286–294
- 81 McIntire E J, Poyer F I, Fajardo A. Wind exposure and light exposure, more than elevation-related temperature, limit tree line seedling abundance on three continents. *J Ecol*, 2016, 104: 1379–1390
- 82 Ameztegui A, Coll L, Brotons L. Land-use changes as major drivers of mountain pine (*Pinus uncinata* Ram.) expansion in the Pyrenees. *Glob Ecol Biogeogr*, 2010, 19: 632–641
- 83 Yan J Z, Zhang Y L, Bai W Q, et al. Forest succession based land use changes: Deforestation, regeneration and ecological degradation (in Chinese). *Sci Chin Ser D: Earth Sci*, 2005, 11: 1060–1073 [阎建忠, 张懿铨, 摆万奇, 等. 基于植被演替的土地覆被变化研究: 大渡河上游的森林采伐、更新和退化. *中国科学院院刊: 地球科学*, 2005, 11: 1060–1073]
- 84 Holtmeier F K, Broll G. Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. *Glob Ecol Biogeogr*, 2005, 14: 395–410
- 85 Payette S, Gagnon R. Late Holocene deforestation and tree regeneration in the forest-tundra of Québec. *Nature*, 1985, 313: 570–572
- 86 Carlson B Z, Renaud J, Biron P E, et al. Long-term modeling of the forest-grassland ecotone in the French Alps: Implications for land management and conservation. *Ecol Appl*, 2014, 24: 1213–1225
- 87 Yi S L. Agropastoral transhumance in the eastern Tibet Plateau and its impacts on the alpine treeline patterns (in Chinese). Doctor Dissertation. Beijing: Chinese Academy of Science, 2008 [易绍良. 青藏高原东部混农季节性放牧及其对高山林线格局的影响. 博士学位论文. 北京: 中国科学院研究生院, 2008]
- 88 Mische G, Mische S, Böhner J, et al. How old is the human footprint in the world's largest alpine ecosystem? A review of multiproxy records from the Tibetan Plateau from the ecologists' viewpoint. *Quat Sci Rev*, 2014, 86: 190–209
- 89 Speed J D M, Austrheim G, Hester A J, et al. Browsing interacts with climate to determine tree-ring increment. *Funct Ecol*, 2011, 25: 1018–1023
- 90 Cheng W, Luo P, Wu N. Ecological characteristics of mingjiang fir (*Abies faxoniana* Rehd. et Wild) population near timberline on upper Min River (in Chinese). *Chin Appl Environ Biol*, 2005, 11: 300–303 [程伟, 罗鹏, 吴宁. 岷江上游林线附近岷江冷杉种群 (*Abies faxoniana* Rehd. et Wild) 的生态学特点. *应用与环境生物学报*, 2005, 11: 300–303]

- 91 Vacchiano G, Garbarino M, Lingua E, et al. Forest dynamics and disturbance regimes in the Italian Apennines. *For Ecol Manage*, 2017, 388: 57–66
- 92 Aakala T, Hari P, Dengel S, et al. A prominent stepwise advance of the tree line in north-east Finland. *J Ecol*, 2014, 102: 1582–1591
- 93 Speed J D M, Austrheim G, Hester A J, et al. Experimental evidence for herbivore limitation of the treeline. *Ecology*, 2010, 91: 3414–3420
- 94 Bush M B, Alfonso-Reynolds A M, Urrego D H, et al. Fire and climate: Contrasting pressures on tropical Andean timberline species. *J Biogeogr*, 2015, 42: 938–950
- 95 Peñuelas J, Boada M. A global change-induced biome shift in the Montseny mountains (NE Spain). *Glob Change Biol*, 2003, 9: 131–140
- 96 Sarmiento F O, Frolich L M. Andean cloud forest tree lines. *Mountain Res Dev*, 2002, 22: 278–287
- 97 Zier J L, Baker W L. A century of vegetation change in the San Juan Mountains, Colorado: An analysis using repeat photography. *For Ecol Manage*, 2006, 228: 251–262
- 98 Gehrig-Fasel J, Guisan A, Zimmermann N E. Tree line shifts in the Swiss Alps: Climate change or land abandonment? *J Vege Sci*, 2007, 18: 571–582
- 99 Penniston R, Lundberg A. Forest expansion as explained by climate change and changes in land use: A study from Bergen, Western Norway. *Phys Geogr*, 2014, 96: 579–589
- 100 Ameztegui A, Coll L, Brotons L, et al. Land-use legacies rather than climate change are driving the recent upward shift of the mountain tree line in the Pyrenees. *Glob Ecol Biogeogr*, 2016, 25: 263–273
- 101 Vitali A, Urbinati C, Weisberg P J, et al. Effects of natural and anthropogenic drivers on land-cover change and treeline dynamics in the Apennines (Italy). *J Vege Sci*, 2017, 29: 189–199
- 102 Li F, Wu Z F, Xu C, et al. The spatial distribution of *Ophiocordyceps sinensis* suitability in Sanjiangyuan region (in Chinese). *Acta Ecol Sin*, 2014, 34: 1318–1325 [李芬, 吴志丰, 徐翠, 等. 三江源区冬虫夏草资源适宜性空间分布. *生态学报*, 2014, 34: 1318–1325]
- 103 Smith E A, O’Loughlin D, Buck J R, et al. The influences of conifer succession, physiographic conditions and herbivory on *quaking aspen* regeneration after fire. *For Ecol Manage*, 2011, 262: 325–330
- 104 Wang X H, He J, Rao S, et al. Design of implementation path of ecological engineering for ecological protection and restoration of multi ecological elements (in Chinese). *Environ Protect*, 2018, 46: 17–20 [王夏晖, 何军, 饶胜, 等. 山水林田湖草生态保护修复思路与实践. *环境保护*, 2018, 46: 17–20]
- 105 Turner M G, Whitby T G, Tinker D B, et al. Twenty-four years after the Yellowstone Fires: Are postfire lodgepole pine stands converging in structure and function? *Ecology*, 2016, 97: 1260–1273
- 106 Herrero A, Almaraz P, Zamora R, et al. From the individual to the landscape and back: Time-varying effects of climate and herbivory on tree sapling growth at distribution limits. *J Ecol*, 2016, 104: 430–442
- 107 Cullen L E, Stewart G H, Duncan R P, et al. Disturbance and climate warming influences on New Zealand *Nothofagus* tree-line population dynamics. *J Ecol*, 2001, 89: 1061–1071
- 108 Zhao Q G, Huang G Q, Ma Y Q. The ecological environment conditions and construction of an ecological civilization in China. *Acta Ecol Sin*, 2014, 36: 6328–6335 [赵其国, 黄国勤, 马艳芹. 中国生态环境状况与生态文明建设. *生态学报*, 2014, 36: 6328–6335]
- 109 Johansson M U, Granström A. Fuel, fire and cattle in African highlands: Traditional management maintains a mosaic heathland landscape. *J Appl Ecol*, 2014, 51: 1396–1405
- 110 Fang K Y, Gou X H, Chen F H, et al. The advance of dendroecology (in Chinese). *J Glaciol Geocryol*, 2008, 30: 825–834 [方克艳, 勾晓华, 陈发虎, 等. 树轮生态学研究进展. *冰川冻土*, 2008, 30: 825–834]
- 111 Bugmann H K M, Solomon A M. Explaining forest composition and biomass across multiple biogeographical regions. *Ecol Appl*, 2000, 10: 95–114
- 112 Schwörer C, Henne P D, Tinner W. A model-data comparison of Holocene timberline changes in the Swiss Alps reveals past and future drivers of mountain forest dynamics. *Glob Change Biol*, 2014, 20: 1512–1526
- 113 Liang Y, Duveneck M J, Gustafson E J, et al. How disturbance, competition, and dispersal interact to prevent tree range boundaries from keeping pace with climate change. *Glob Change Biol*, 2017, 24: e335–e351

Summary for “干扰对树线生态过程的影响研究进展”

Research advances in disturbance and ecological processes of the treeline ecotone

Yafeng Wang¹ & Eryuan Liang^{2,3*}

¹ College of Biology and the Environment, Nanjing Forestry University, Nanjing 210037, China;

² Key Laboratory of Alpine Ecology, Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing 100101, China;

³ CAS Center for Excellence in Tibetan Plateau Earth Sciences, Beijing 100101, China

*Corresponding author, E-mail: Liangey@itpcas.ac.cn

The treeline ecotone refers to the transition from the timberline to treeless alpine vegetation. As either the upper-elevation or northernmost limit of erect trees, treeline will be sensitive to environmental change. An increasing number studies have focused on influence of climatic change on treeline dynamics. Treeline shift rate is also considered to be a fingerprint of influence of global change on terrestrial ecosystems. However, less is known about how disturbance, as an important non-climatic factor, mediates the response of treelines to climate change. Such studies can provide useful information to guide implementation of key ecological protection and rehabilitation measures in these comparatively cold biomes. Herein, we review research progress relating to impacts of different disturbances on ecological processes on the treeline ecotone. Based on the Web of Science and CNKI database, only a modest 10.8% of 1002 treeline-related publications from 1950 to 2018 focused on disturbance. Disturbances include natural and human-caused categories according to their causes. Natural disturbances mainly include volcanic eruptions, glacier fluctuations, wildfire, snow avalanche, biological activities, extreme low temperature, and strong wind. Human-caused disturbances mainly include deforestation, grazing, human-caused fire, mining, farming, medicinal plant collecting and tourism. In most cases, due to differences in intensity, frequency and time duration, different disturbances could have different effects on the ecological processes of the treeline ecotone. Under some circumstances, the impacts of natural and human-caused disturbances on treelines may not differ significantly. For example, natural wildfires and human-caused fires, as well as wildlife activities and livestock grazing, may contribute similar forcing in driving treeline dynamics. In disturbed areas, based on soil habitat regimes, treeline changes would follow two main stages, i.e., primary succession or secondary succession processes driven by multiple environmental factors and climate-driven stand changes. Observational data for the common disturbance influences (e.g. fire and grazing) were rare in recent studies, failing to distinguish relative effects of disturbances and climate change on ecological processes in the treeline ecotone. Additionally, attention should be paid to both the negative and positive effects of disturbances at the treeline ecotone. In particular, more studies are necessary to better understand positive effects of disturbances driving treeline shifts and ecological strategies of trees at disturbed treelines. To adapt to frequent disturbances, treeline trees might counteract disturbance through bark and cone characteristics, by clumped distributions, or by clonal reproduction (e.g. sprout-regeneration). Ecological strategies of trees under different disturbance regimes provide a new perspective for explaining non-linear responses of treeline shift to climate change. Humans cannot control most natural disturbances (e.g. volcanic eruption, glacier fluctuations, wildfire and snow avalanche), whereas we can control human-caused disturbances (e.g. grazing, deforestation and tourism). In this context, human-caused disturbance is a key issue for forest management policies. Further work should consider incorporating disturbance factors into treeline modelling. In most forest regions, monitoring data for common disturbance factors are very scarce. In order to have a better understanding of treeline ecological processes, it is necessary to model changes of disturbed treelines in response to disturbance regimes. Based on multiple approaches, researchers should focus on key ecological processes and perform long-term tracking surveys at the disturbed treelines. It should be noted that the Tibetan Plateau not only hosts the Northern Hemisphere's highest natural treelines but also diverse disturbed treelines. The Tibetan Plateau could be an ideal location to investigate different contributions of disturbance and climatic change in driving treeline dynamics. In particular, it would be interesting to investigate how fire or grazing shapes treeline structure, and how interactions between disturbances and climatic change drive treeline shift on the Tibetan Plateau.

treeline, disturbance, dendroecology, climate change, Tibetan Plateau

doi: [10.1360/N972018-01273](https://doi.org/10.1360/N972018-01273)